BEHAVIOUR AND SOCIAL ORGANIZATION OF THE AFRICAN JACANA *ACTOPHILORNIS AFRICANUS*

by

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ABSTRACT

The behaviour, nesting, food resources and mating system of the African Jacana *Actophilornis africanus* were studied at Muzi Swamp, northern KwaZulu-Natal and at Darvill Sewerage Works, KwaZulu-Natal.

African Jacanas show highly polyandrous behaviour associated with a marked reversed sexual size dimorphism. A high clutch loss was recorded because of predation and weather conditions.

Contact behaviour was recorded, which is unusual in Charadriiformes. Vocalization and visual displays were distinctive and closely related to territorial and sexual behaviour. Unlike the Wattled Jacana *Jacana jacana*, the African Jacana practises male guarding behaviour.

Rich food concentration in the African Jacana habitat was shown by field tests and this may be a reason for this species evolving in a floating environment. The presence of simultaneous polyandry in the African Jacana was analyzed mathematically and by computer modelling in order to determine possible advantages of polyandry.

PREFACE

The experimental work described in this thesis was carried out in the Department of Zoology & Entomology, University of Natal, Pietermaritzburg, from September 1990 to January 1997 under the supervision of Professor Gordon L. Maclean.

These studies represent original work by the author and have not been submitted in any form to another university. Where use was made of the work of others it has been duly acknowledged in the text.

ACKNOWLEDGEMENT

I want to thank Prof. Gordon Maclean for his supervision, comments and analysis, and my friend Dr Dave Gaynor, who helped me both in finding a study area in northern of KwaZulu-Natal and in discussing the computer model I adopt in this thesis.

I owe a great debt to Prof. S. T. Emlen from Cornell University for reading and giving me some useful comments on the first and second chapters. I am grateful to Prof. S. Piper for reading the last two chapters.

I also wish to thank my close friend, John Mazibuko, for his friendship and for helping me in checking African Jacana nests. Also, his brother, Themba Mazibuko, who revealed the secret of catching jacanas using bulbs of waterlilies.

Most of all, I want to express my gratitude to my wife, Liliana, who helped me with time-budget sampling and being so patient during all the writing up of my thesis. I wish also to extend my gratitude to Prof. Roger Gravil for supporting and encouraging me throughout my study.

I thank Dr W. Tarboton too for sending me information about his own work on jacanas in the Transvaal. I would like to thank Dr R. Miller for identifying some species of insects, Mrs J. Browning for identifying some species of aquatic plants, and the National Botanical Institute for providing me with information on the distribution of some plant species.

I would like to thank Fundación Banco del Sur's award of the César Milstein Scholarship (Argentina), University of Natal Research Fund (South Africa) through Prof. G. L. Maclean for financial support and Natal Parks Board for allowing me to catch and ring African Jacanas at Muzi Swamp.

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INTRODUCTION

The African Jacana *Actophilornis africanus* is one of only eight species in the world that comprise the distinctive family Jacanidae. Two similar species of jacanids occur in the New World: the American Jacana *Jacana spinosa* is restricted to Central America while the Wattled Jacana *Jacana jacana* is found throughout tropical and subtropical South America. The latter species shows wide subspecific variation expressed mainly in plumage colouration. In Africa, the African Jacana and the Lesser Jacana *Microparra capensis* occupy almost the same niche but the latter is less abundant (Urban *et al.* 1984); the Madagascar Jacana *Actophilornis albinucha* is the most similar in appearance to the African Jacana, except for the reversed colouration pattern of the neck and head. In Southeast Asia live three species of jacanids: the Pheasanttailed Jacana *Hydrophasianus chirurgus* (the only migrant among jacanids), the Bronzewinged Jacana *Metopidius indicus* (confined to the extreme south) and the Combcrested Jacana *Irediparra gallinacea* (southern Malaya to northern Australia).

Jacanids inhabit shallow water bodies with dense floating aquatic vegetation like *Nymphaea, Pistia, Hyacinth, Ludwigia and Potamogeton*. This environment has imposed on these birds some unusual anatomical and behavioural changes such as the development of very elongated toes allowing the bird to walk on floating vegetation and the bent radius (Fry 1983) which is supposed to assist in chick-carrying behaviour (Fry 1983, Tarboton 1992), a unique behaviour pattern in which the male jacana holds his offspring under his wings in order to transport and protect them. The African Jacana shows a marked difference in sexual size: females are about 15 % bigger than males but unlike many other polyandrous waders there is no difference in plumage colouration. The mating system is mainly polyandrous, one of the most uncommon systems of reproduction in vertebrates, in which the female may mate with up to seven males (Tarboton 1992). The sexual roles are partially reversed: females are dominant over males and patrol a superterritory containing the male's subterritories. Incubation and rearing of chicks are performed by males while females spend most of the time mating, foraging and defending their territories.

The African Jacana shares the same environment with the Lesser Jacana but the latter is exclusively monogamous (Urban *et al.* 1984; Tarboton & Fry 1986), which poses an interesting question about the different evolutionary pressures to which these species have been subjected to.

Nests are made at the surface of the water and are highly exposed to the environment. Newly hatched chicks can swim and dive in case of danger. A peculiar behaviour of African Jacana is **Chick-Carrying** which is performed by males to protect the chicks from cold weather and as a way to move the brood to a secure place in case of danger.

Little is known about the origin of jacanids, but according to Sibley *et al.* (1988) the family Jacanidae is closely related to the Rostratulidae. Jacanas are considered to have evolved from waders which became adapted to living on floating vegetation (Tarboton 1992).

The best field study to date on the African Jacana was made by Tarboton over eight years of observation on the floodplain of the Nyl River, Transvaal, South Africa. However, there are still some important biological aspects not fully covered by him: one is an assessment of the possible causes of low hatching success and, secondly, the possible causes leading to simultaneous polyandry and the likelihood of extra-pair reproductive success that arises from that.

The main objective of this study is to derive an integrative mathematical model to explain the occurrence of polyandry in the African Jacana by determining the major variables involved, since this is the most important aspect of social organization from an ecological and evolutionary point of view. As a consequence of that, I expected also to contribute to an explanation of the evolution of the other two major mating systems, monogamy and polygyny.

Plan of the thesis

Chapter 1 outlines a field study of the principal causes of low hatching success in the African Jacana, focusing particularly on the structure and dynamics of the nest and the availability of flying-food resources in different areas inhabited by the African Jacana. This is the first time that nest resistance and sinking processes have been studied. Data were limited based to a single breeding season because no permit was granted by Natal Parks Board to continue this field study on the subsequent year. However, this study opens a new perspective for any intended long-term study of polyandry in jacanids or for any research in which the species builds floating nests.

In Chapter 2 behaviour and social communication are explored in order to investigate other behaviour patterns adapted to the environment.

Chapter 3 is concerned with the advantages arising from extra-pair success as a result of simultaneous polyandry.

Chapter 4 is a mathematical model which explores the main selective pressures leading to polyandry and attempts to explain the difference in mating systems between the Lesser Jacana and the African Jacana.

Chapter 5 is a mathematical model which explores the main selective pressures leading to polyandry and attempts to explain the difference in mating systems between the Lesser Jacana and the African Jacana. A computer disk containing the programmes which rendered some of the figures included in this chapter is enclosed on the cover of this thesis.

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CHAPTER 1

CHARACTERISTICS OF THE NEST OF THE AFRICAN JACANA AND FOOD RESOURCES RELATIVE TO BREEDING SUCCESS

ABSTRACT

Nests of the African Jacana *Actophilornis africanus* were checked regularly over a period of five months at Muzi Swamp, KwaZulu-Natal, South Africa and their features and success determined. Three tests were done to explain the choice of nest site in the African Jacana. This study shows that nest maintenance is one of the main problems for successful breeding in this species. African Jacanas built basically two types of nest at Muzi Swamp: (a) inshore nests made of *Ludwigia stolonifera* with a low sinking rate and high resistance to the weight of the bird's body (these were the most successful nests recorded during the 1991-1992 breeding season) and (b) offshore nests made of *Potamogeton pectinatus* and anchored on *Nymphaea lotus* over relatively deep water (these had a high sinking rate with low resistance compared with inshore nests). The breeding success in offshore nests was extremely low. Causes of clutch loss included predation, weather, hippopotamuses, cattle and warthogs. The habitat of the African Jacana at Muzi Swamp was checked for the food richness on floating vegetation. The results show that a large volume of insects was available, particularly in the offshore areas. Furthermore, bulbs of waterlilies *Nymphaea lotus* are a possible food resource especially during drought.

INTRODUCTION

The African Jacana *Actophilornis africanus* is a common freshwater wader peculiar to Africa. It has a polyandrous mating system (Vernon 1973) and reversed sexual size dimorphism (RSSD) (Tarboton 1992). The male African Jacana is solely responsible for incubating the eggs and rearing the chicks. The primary cause of clutch losses in jacanas has been ascribed to predation (Osborne 1982; Tarboton 1992,1995), and flooding (Tarboton 1992) as a secondary cause. However, problems arising from the type of nest have not been taken into account up to now. The "easy breeding hypothesis" of Maxson & Oring (1980) explains the occurrence of polyandry in conditions of low hatching success and high availability of resources. The purposes of this study are to describe the important features of African Jacana nests, particularly in relation to breeding success to explain why African Jacanas choose specific areas for nesting and to measure the abundance of flying-food resources in order to know whether the "easy breeding hypothesis" of Maxson & Oring (1980) is consistent with the breeding system in the African Jacana.

MATERIALS AND METHODS

The study was conducted at Muzi Swamp (27° 37' S; 32° 24' E) on 42 ha on the southeast side of the swamp where human interference was minimal.

I found three important aquatic-plant communities at Muzi Swamp which determined the location, structure and dynamics of the nest: the first community corresponded to the fringing vegetation comprised of *Ludwigia stolonifera*, an aquatic herb with thick, erect and creeping stems which root at the nodes. The parts of the stems that touch the water produce white spongy pneumatophores (see Fig.15 B in Cook *et al.* 1974). *Ludwigia stolonifera* consists of an emergent foundation giving strong support to the nest. During the study the most successful nests occurred in this plant community. *Ludwigia* is widely distributed throughout southern Africa (Launert *et al.* 1978).

In the second community the dominant species was the waterlily *Nymphaea lotus* consisting of a layer of floating leaves mixed with submerged species like *Najas pectinata* and *Ceratophyllum demersum*. Waterlilies were used mainly as a foundation for the nest.

The third aquatic-plant community consisted of the submerged *Potamogeton pectinatus.* Although African Jacanas did not nest on that substratum they constructed offshore nests mainly with *Potamogeton pectinatus.*

Other species of aquatic plants of less importance found at Muzi Swamp were *Nymphaea caerulea*, *Potamogeton crispus, P. thunbergii* and *Chara zeilanica*.

The breeding season of the African Jacana at Muzi Swamp started at the end of September 1991 and finished at the end of February 1992. At Muzi, 23 African Jacanas were captured and ringed with combinations of four rings (one metal and three coloured plastic) two being placed on each tibiotarsus. For example, *OB/*R* means ***O***range and ***B***lue rings on the left tibiotarsus and metal ring (*) and ***R***ed ring on the right tibiotarsus.

Observations were made at close range from the shore or from a rubber boat using 16×40 Zenith binoculars. On at least every second day the shore of the study site was checked for new nests and the condition of every nest was recorded over a period of five months.

The jacanas were trapped using a walk-in trap made of 25-mm-diameter chicken-mesh with three entrances. The trap was placed over the nest for catching incubating males and on the shoreline of the swamp using tubers of *Nymphaea lotus* cut in half as bait for non-incubating birds.

Once trapped, the jacanas were ringed with coloured plastic rings for identification purposes. Eggs were marked with adhesive transfer letters, measured and weighed and the order of laying noted whenever possible. Details of the nest were also recorded: distance from the water's edge, general dimensions, resistance of the nest to sinking, depth of the water over which the nest was floating, daily sinking rate, nest shift during incubation, nest replacement and any other change observed.

Nest resistance (the greatest weight a nest can support until it is completely submerged) for most of the nests recorded at Muzi Swamp was measured whenever possible in order to characterize the type of nest. The nest resistance was estimated by using a raingauge fixed by its base to a plastic disc of 13,9 cm diameter (Fig.1.1A). The eggs were first removed, the device placed on the nest and water poured into the raingauge until the water level of the lake reached the upper surface of the plastic disc. The resistance of the nest is equal to the weight of the device plus the weight of the water measured in the raingauge. The sinking rate of the nest was determined by using a marked plastic straw fixed vertically 8 cm from the clutch. Nests were checked daily and their success determined.

In order to determine the nesting-site preference of the African Jacana at Muzi Swamp 300 leaves of waterlilies *Nymphaea lotus* were measured on 25 March 1992 at three sites of different depths: 60 cm, 80 cm and 130 cm depth. The leaves were taken along a line of constant distance from the shore. The density of waterlily leaves was also estimated at the same three sites using a string 10 m long and counting the number of leaves touching the transect line.

The third test was done on 11 March 1992. It consisted of building 40 false nests very similar to real African Jacana nests: 10 nests at a depth of exactly 25 cm on *Ludwigia* vegetation and 10 at depths of 62 cm, 82 cm and 136 cm on waterlily leaves. The nests were built only of *Potamogeton pectinatus* and the resistance of each one was fixed at 400 g by adding nest material

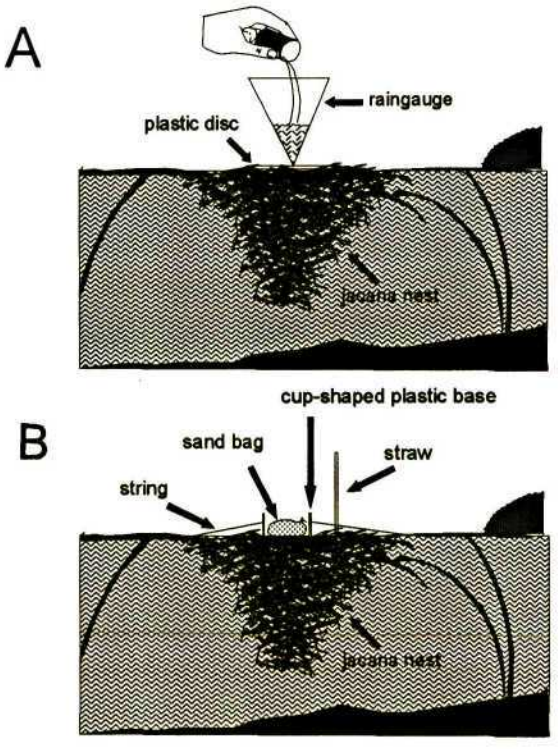


Fig. 1.1A Procedure to measure nest resistance in the African Jacana.
1.1B Device to test nest sinking at different depths.

and checking the resistance (with the same raingauge used before) until it reached 400 g. The weight of the bird and its clutch were simulated with the cup-shaped plastic base of a 2-l soda bottle 6 cm tall and 10 cm in diameter containing a plastic bag with sand weighing 138 g, corresponding to the weight of a typical male African Jacana (Fig. 1.1B). The rest (the plastic base and a little wire to fix the weight) weighed 40 g, representing the weight of a clutch of four eggs. The plastic cup was fastened on the nest so as not to be displaced by wind or other factors. Beside the plastic cup a vertical marked straw was fixed to determine the sinking rate. The straw was marked at water level before starting the experiment. The nests were left for 48 hours and then the straws were marked again following the same procedure.

Jacanas are omnivorous feeders as was particularly noted in the Wattled Jacana *Jacana jacana* by Beltzer & Paporello (1984). My observation was that flying aquatic insects were the main food source of the African Jacana at Muzi Swamp, although it also ate aquatic larvae, fishes (small *Tilapia* sp.) and aquatic beetles.

Arthropod abundance was sampled every second month by means of cylindrical sticky traps at five different locations for 48 hours each. For every sample site a can 13,5 cm high and 10,5 cm diameter was used. It was painted green and wrapped in cellophane paper measuring 12,5 cm x 32,5 cm, giving about 400 cm^2 of sample area. The outer surface of the cellophane was painted with permanently wet Fly-Tac glue used for fruitflies and yellowtraps on citrus. The can was placed in a cage 30 cm high and 26 cm diameter made of 2,5-cm mesh "chicken wire" to prevent captured insects from being picked off the trap by birds. The can and the cage rested on a polystyrene board measuring 30 cm x 30 cm x 2,5 cm to keep the trap afloat, and was anchored to the floating vegetation by string. At each trapping session, the traps were placed along the same trapline for 48 hours to include sites on shoreline, fringing vegetation, waterlilies and emergent aquatic plants offshore. Once the sampling was completed, the cellophane of the can was removed and stuck on to another bigger piece of cellophane to enclose the insects between the two layers with no sticky surface exposed. The trapped insects were examined under a dissecting microscope to identify the species and count the individuals. Using this technique the species and numbers of individual insects from a set of samples each of 400 cm^2 taken during the peak breeding season of African Jacanas at Muzi Swamp were identified and counted. The approximate volume of each insect was measured by the method shown in Fig. 1.2.

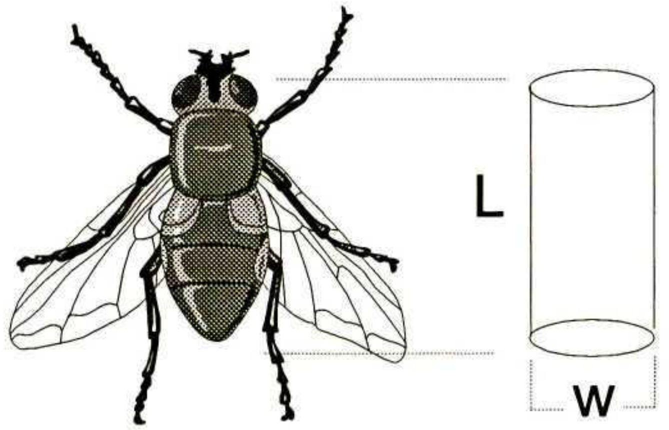
Wing dimensions and very small arthropods like Collembolla were disregarded because of their size. Identification was done as far as possible but when it was not possible to differentiate between species in the same family the insects were categorized as "very small", "small" and "large" according to the relation in size between them. Then insects were removed with an organic solvent and the dry weight/400 cm^2 determined.

Monthly sampling was done during my stay from October 1991 to April 1992 (and I returned from 29-30 May 1992) of the amount of waterlily bulbs on 5 km of shoreline at Muzi Swamp. The bulbs were classified into three categories: *empty, open* and *complete*. They were considered empty when only the external husk was found, *open* when the bulb still contained material inside with signs that it had been opened and *complete* when it had not been opened at all. The inside contains fresh starch which is a potential food supply for jacanas. Complete bulbs were marked with coloured-headed pins.

RESULTS

African Jacana nests

The nest of the African Jacana is complex compared with that of other Charadriiformes. It comprises two floating pads. The first one, the primary pad, is around 0,5 m in diameter and anchored under water among leaves and stems of aquatic vegetation. That supports a smaller one,



$$V = 0,785 \,.\, L.\, W^2$$

Fig. 1.2 The approximate volume of each insect was measured by considering the insect as occupying the volume of a cylinder. V = volume; L = length; W = width.

the secondary pad (on which eggs are laid), about 15 cm in diameter and emerging through the water surface.

According to the distance from the water's edge at Muzi Swamp, African Jacana nests can be classified as *inshore nests*, *offshore nests* and *other types*.

Inshore nests were significantly different from offshore ones in dimensions and resistance (Fig. 1.3). Edge vegetation consisted almost exclusively of *Ludwigia stolonifera* which made up most of the nest. Such nests were commonly found in very shallow water, close to the shoreline where *Ludwigia* grows. The inshore nests were the most successful at Muzi Swamp (72,7% hatching success). Of the inshore nests checked, 62,5% were built between 16 November and 15 December.

Offshore nests were placed in relatively deep water and constructed mainly of emergent plants like *Potamogeton pectinatus*, *Ceratophyllum demersum* and *Najas pectinata*. Compared with inshore nests they were relatively weak in structure as they had bigger primary pads (Fig. 1.3). Of the offshore nests checked at Muzi Swamp, 90,9% were found mainly during the last period of the breeding season from 16 December to 15 February, coinciding with low precipitation and low water level (Figs 1.4 and 1.5). This kind of nest was subjected to continual sinking and the jacanas compensated for this by adding material to the nest. When a nest sank uncontrollably the birds made another close to the first and moved the eggs to it.

I found four *other types* of nests at Muzi composed of reeds. The clutches found in this type were completely successful. Three more atypical nests were found at Muzi, built at the edge of three different small islands and composed of semiaquatic grass. Curiously each nest was at the north side of the island and failed.

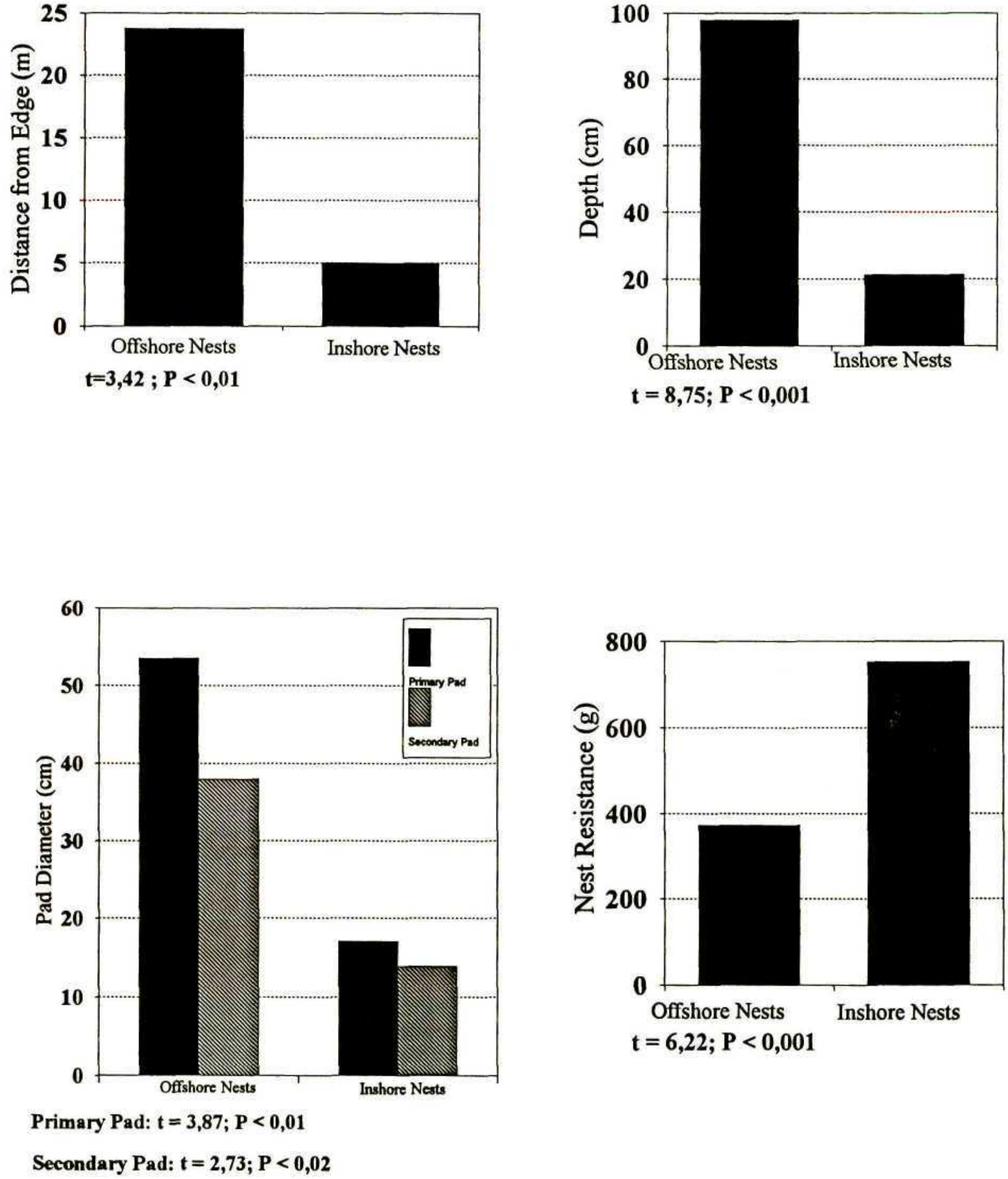


Fig. 1.3 A comparison between offshore and inshore nests of the African Jacana at Muzi Swamp

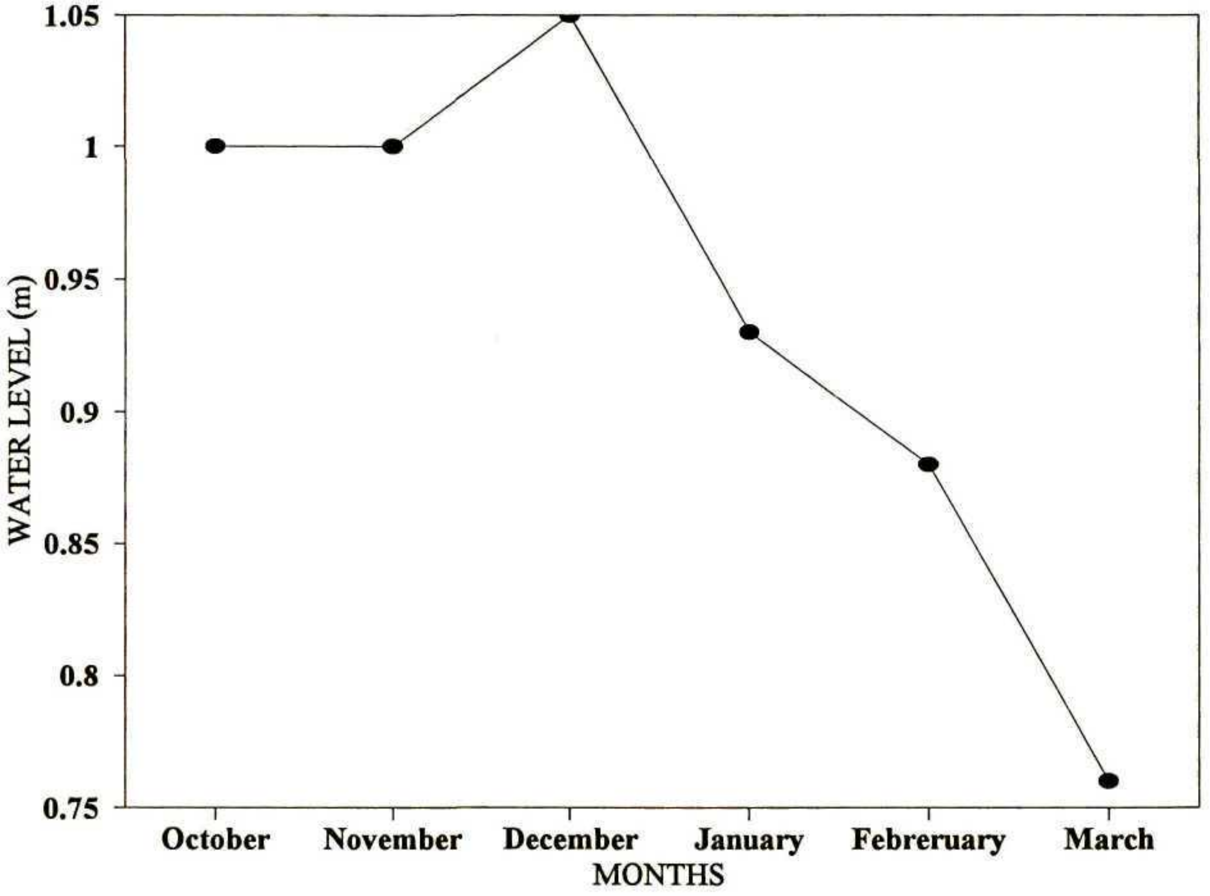


Fig. 1.4 Mean monthly water level at Muzi Swamp, KwaZulu-Natal from October 1991 to March 1992.

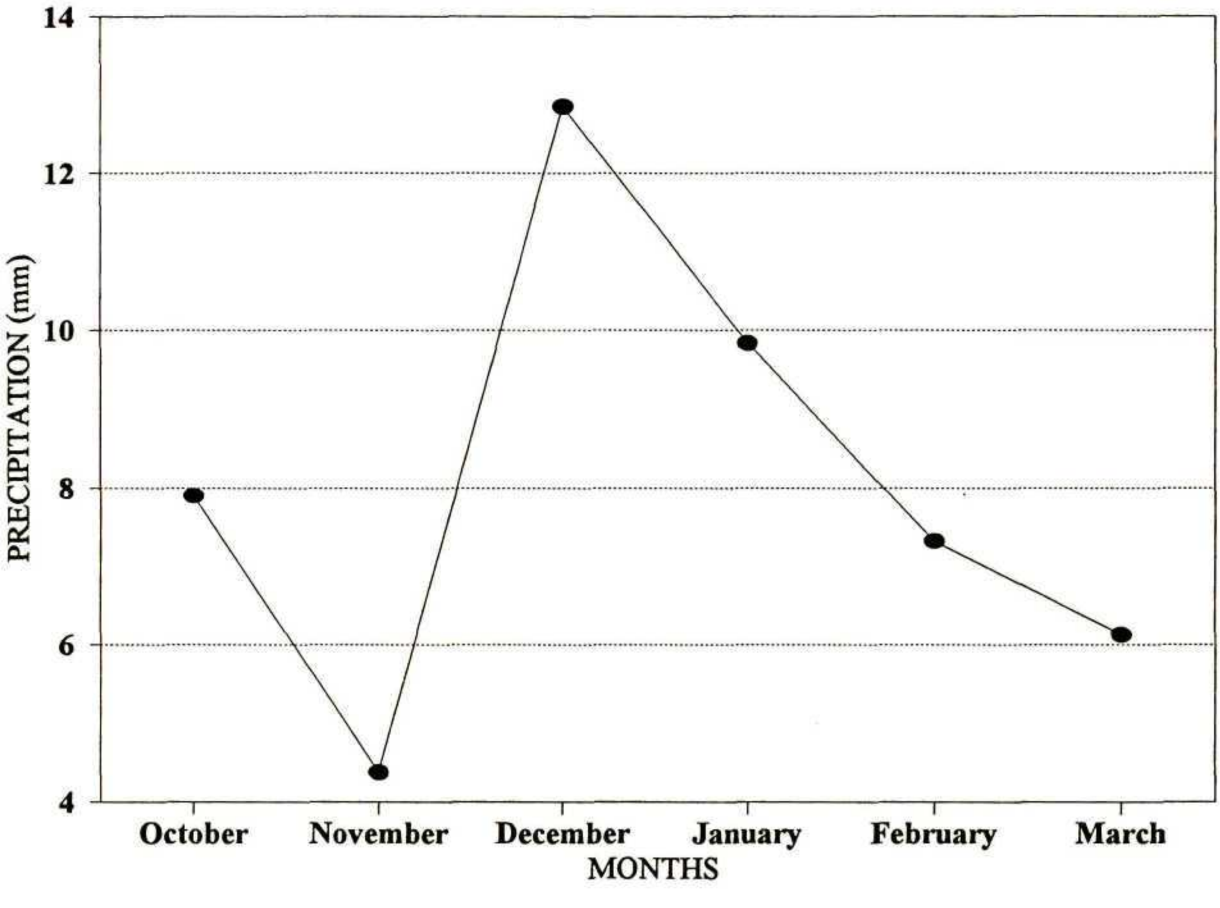


Fig. 1.5 Mean monthly rainfall at Muzi Swamp, KwaZulu-Natal from October 1991 to March 1992

Hatching success

Seventy-eight eggs were measured at Muzi Swamp: $\bar{x} = 31,56$ mm x 23,16 mm, mass 8,9 g (27,7-34,4 mm x 20,47-24,9 mm; mass 5-12 g). Only 22 (28%) of the eggs in the study area hatched. Clutch losses from weather effects on offshore nests were significantly higher than on inshore ones ($\chi^2_1 = 4$; $P < 0,05$); hatching success was also significantly higher in inshore nests ($\chi^2_2 = 9,3$; $P < 0,01$). One of the females studied (*B*/GG*) laid 27 eggs over 116 days (119% of her weight) which is one clutch every 17 days on average. All newly laid eggs at Muzi Swamp had clearer colouration than those laid one or more days earlier. This was very useful in determining the last egg laid on the day when a clutch was found with more than one egg.

Nest disturbance

At Muzi the disturbance of nests was complex and diverse (Fig. 1.6). Major causes of clutch loss at Muzi were predation, weather effects and cattle.

<u>Predation:</u>

Nile Monitors *Varanus niloticus* were among the main predators responsible for the disappearance of African Jacana eggs. I also saw jacana eggs being collected by local children and eaten *in situ*. Black Crakes *Amaurornis flavirostris*, Goliath Herons *Ardea goliath* and Common Moorhens *Gallinula chloropus* may be regarded as potential predators too.

<u>Environmental effects:</u>

Sometimes heavy rain, wind and waves contributed to the loss of the clutch. Rain hastens nest sinking and may displace the eggs to one side when it strikes hard. Wind creates waves which cause egg displacement and increase nest sinking.

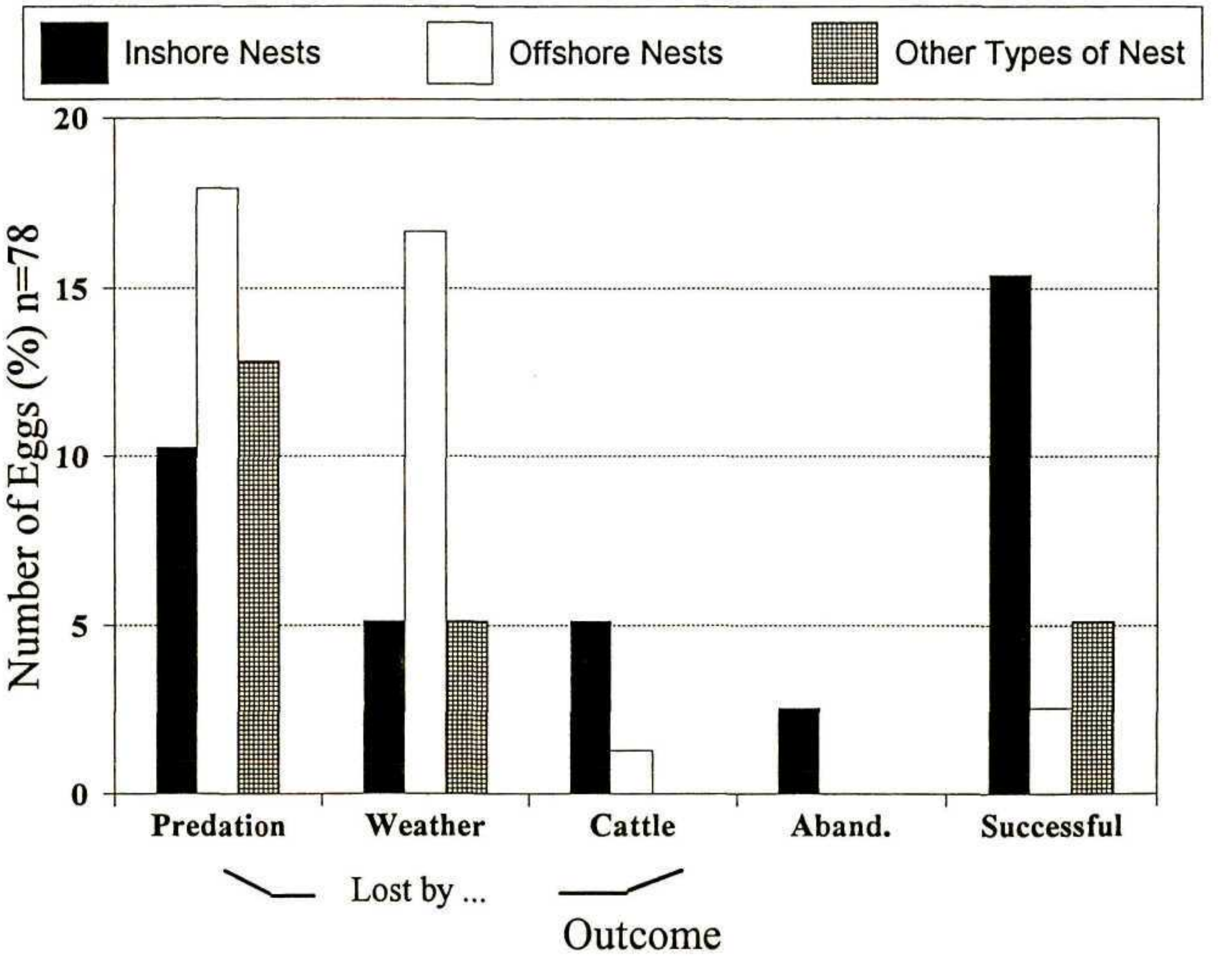


Fig. 1.6 Outcome of 78 eggs recorded at Muzi Swamp (Aband. = abandoned).

Other possible effects:

Hippopotami *Hippopotamus amphibius* leave the swamp at night to feed on the surrounding vegetation, dragging everything in their wake and making waves which dislodge jacana eggs. An estimated population of at least 50 hippopotami occurs at Muzi Swamp.

Warthogs *Phacochoerus aethiopicus* are diurnal. They drink and dig on the shoreline apparently in search of tubers of waterlilies. Cattle passed along the shoreline twice a day, grazing and drinking.

Local people are allowed by the Natal Parks Boards to fish at Muzi Swamp. They leave their boats in little bays where African Jacanas breed. The effect of local fishery activity was similar to, but less serious than, that of hippos.

Pack-hunting of catfishes *Clarias gariepinus* is a very common scene at Muzi Swamp. Many catfishes swim together, side by side, forming a compact mass about 1-2 m in diameter, moving slowly through the shallow water and removing everything in their path. This phenomenon could be related to social hunting behaviour described by Bruton (1980) and might be a possible reason for clutch loss considering that on average pack-hunting of catfishes was recorded every other day.

Choice of nest site

The water of Muzi Swamp started to recede about the middle of December 1991 (Fig. 1.4). The breeding period of five months could be divided into a "wet stage" from September 1991 to the middle of December 1991 and a "dry stage" from December 1991 to February 1992 (Fig. 1.5). During the dry stage 54,54 % of the eggs laid were lost as compared with only 21,42 % during the wet stage of the breeding season. During the dry stage breeding success was nil because of increased egg loss as a result of predation and bad weather. Furthermore, the first attempts at nesting by African Jacanas during the first part of the breeding season at Muzi Swamp were mostly inshore and after failure they shifted to offshore nests (Fig. 1.7).

Tarboton (1995) found that, in years when the water level in the Deelkraal Dam (floodplain of the Nyl River) was high, the population of African Jacanas living there preferred to nest on *Ludwigia* (= inshore nests) and experienced a higher breeding success.

Of 23 nests checked at Muzi Swamp, a significant correlation was found between nest resistance and water depth (r_{23} = -0,75; r = 57%; $P < 0,001$; Fig. 1.8) and between distance from shore and water depth (r_{23} = +0,6; $P < 0,0026$). Another question is why the African Jacana's nesting was so uncommon on the *Nymphaea* substratum at a depth of 30-60 cm.

Three tests were done at Muzi Swamp during March 1992 in order to determine why African Jacanas tend to choose a nesting site in the middle of the area covered by *Nymphaea lotus* and not close to the border (close to *Ludwigia* or to *Potamogeton* areas) especially when they shift from an inshore site to an offshore site.

The difference in leaf diameter between the three samples taken was significant (ANOVA: F = 941; P < 0,001). The diameter of the waterlily leaves increases according to distance from the shore.

Although there was no significant difference between the three sites ($\chi^2_2 = 2,3$), the highest density of leaves was recorded in the second sample, at a depth of 80 cm and 20 m from shore with 7,88 leaves per m^2. The other samples showed 5,35 leaves per metre at a depth of 64 cm and 10 m from the shore (close to the *Ludwigia* area) and 2,82 leaves per m^2 at a depth of 130 cm and 30 m from the shore (close to the *Potamogeton* area).

The results of the experiments using artificial nests showed that the sinking rates were significantly different (K-W ANOVA: H = 20,2; $P < 0,001$) and the lowest incidence of sinking

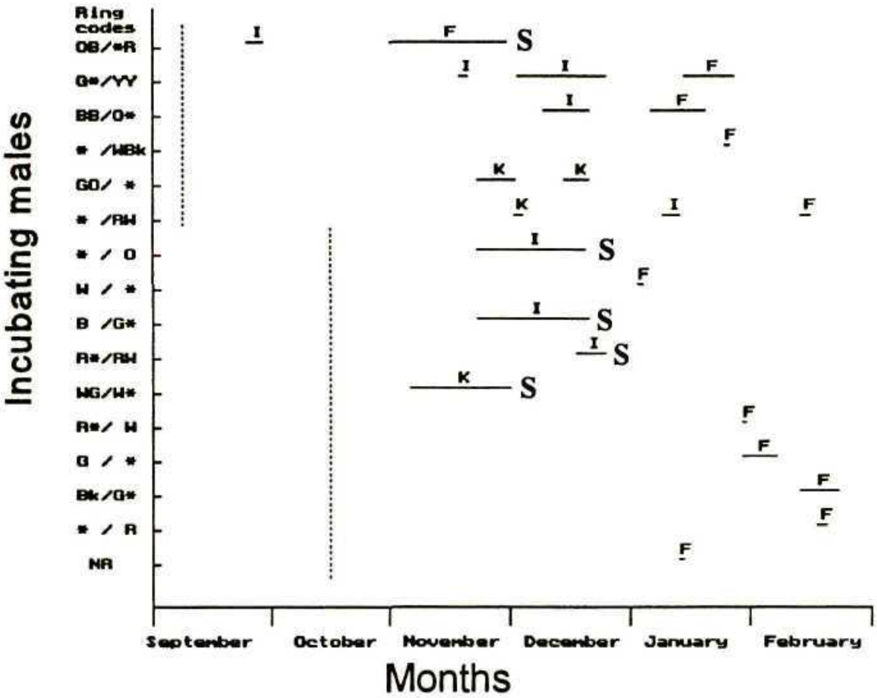


Fig. 1.7 Nest replacement of marked African Jacanas during the breeding season 1991-1992 at Muzi Swamp. The length of each line is the duration of each clutch. S = nest successful in producing at least one young. I = inshore nest. F = offshore nest. K = nest of other type. Thedotted lines denote when the site began to be monitored.

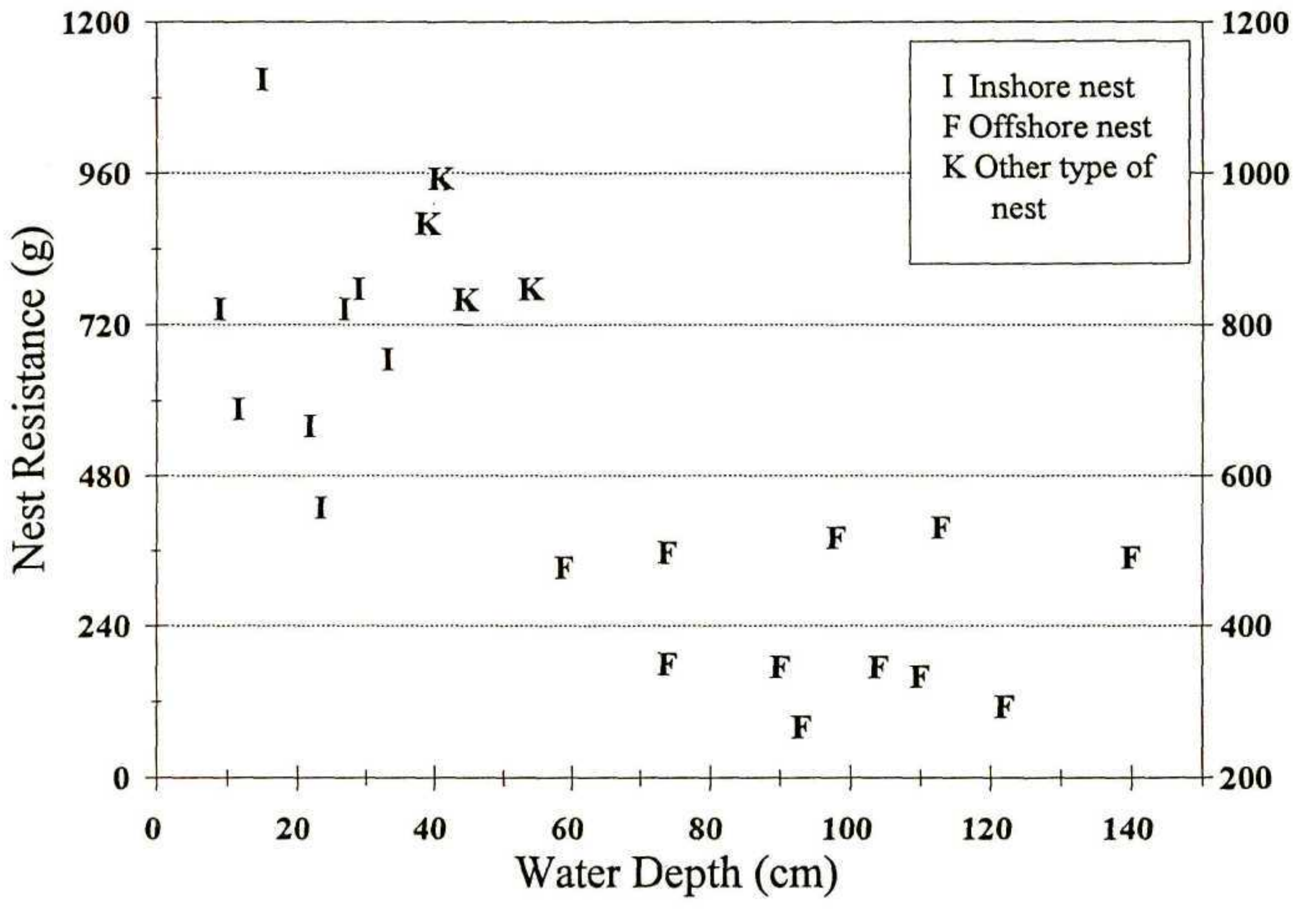


Fig. 1.8 Nest resitance and water depth of 23 African Jacana nests checked at Muzi Swamp (r = -0,75; r = 57%; P < 0,001).

was recorded inshore on *Ludwigia* vegetation, while the second-lowest was on waterlily leaves of medium size.

These tests suggest that the African Jacana prefers to nest on medium-sized waterlilies because the density of such leaves is highest, providing good support for the nest. It is not good to nest on waterlilies close to the *Ludwigia* area because of the small diameter and relatively low density of their leaves.

Tarboton (1992) found a negative correlation between reproductive success and water depth for the population of African Jacanas at Deelkraal Dam (Nyl River). The effect of rain, wind and waves is greatest beyond the area of waterlilies (for example, at 35-40 m from the shore) and would be least at the shoreline.

The "hippo" factor would affect the jacana territory evenly because hippos move anywhere leaving a wake of around 1 m wide. If the average territory is 0,4 ha as it was at Muzi Swamp for male jacanas, the area affected by a hippo would be only 1-2% of it.

Only one out of 23 nests (4%) monitored at Muzi was destroyed by hippos. At Muzi Swamp cattle and warthogs ventured into the shallow water especially during the driest month of the study period (February). An offshore nest would not be disturbed by mammals approaching from the shore but an inshore nest could be. For instance, one inshore nest was trodden on by cattle.

Fig. 1.9 shows a hypothetical function of reproductive success related to nest location based on environmental effects and predation at Muzi Swamp. Predation may be considered inversely related to distance from the shore and to reproductive success. The breeding success, considering only environmental effects from the shoreline to 40 m offshore, would be close to an exponential relationship (*a, b*). The point *h* in each figure denotes the appropriate distance from the shore

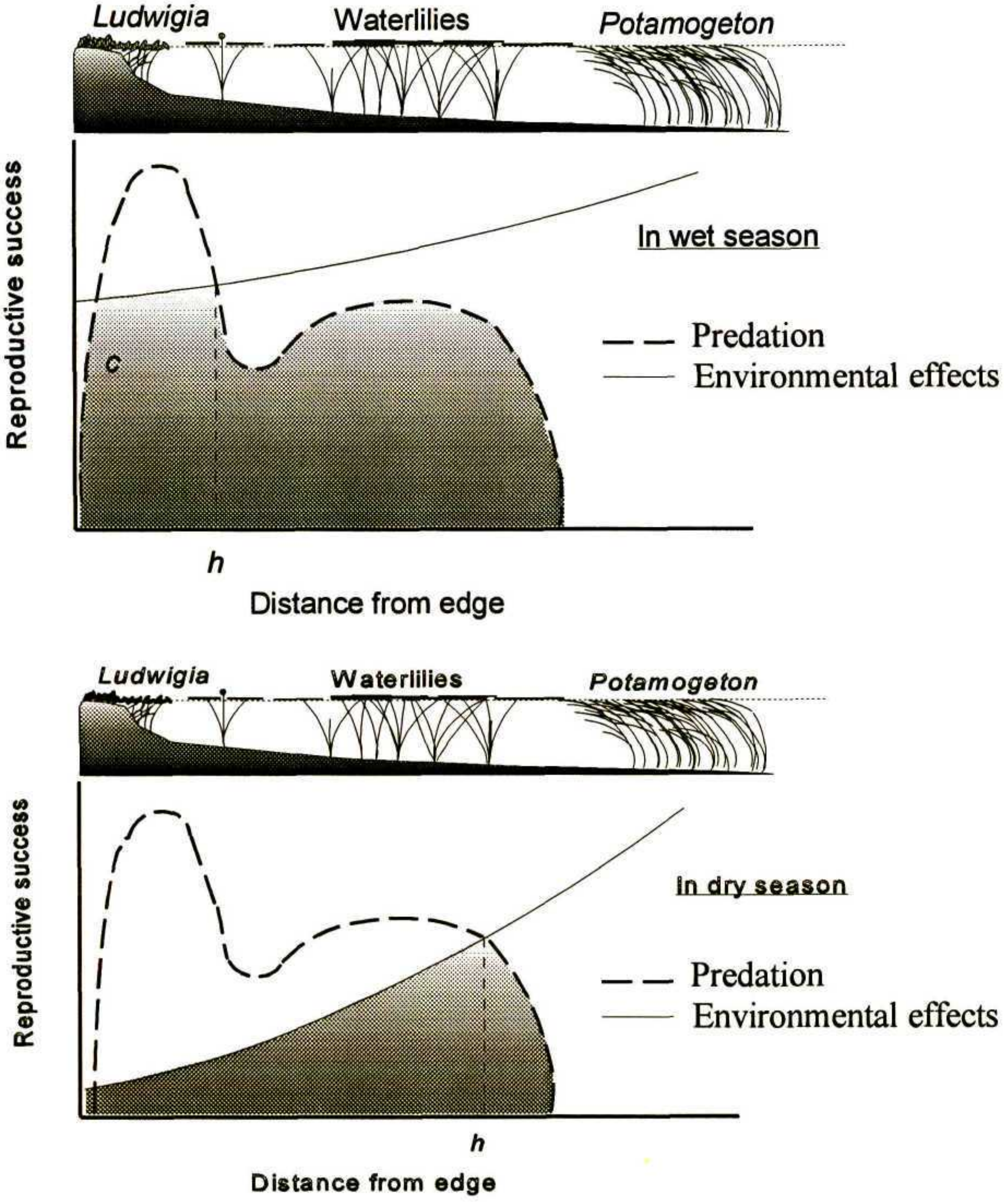


Fig. 1.9 Hypothetical curves of reproductive success related to nest location in the African Jacana based on environmental effects (*a, b*) and predation (*c, d*). The point h in each case is the point of greatest likely success of a nest. See text for further explanation.

where a jacana should nest for maximum breeding success. In other words, jacanas have to nest where predation and weather effects are minimal and substrata support is the greatest.

Nest resistance and nest sinking

Special attention was paid to three nests whose sinking level, relative to nest resistance and quantity of nest material brought, was recorded daily. The following are the results of the three particular cases given below:

Nest 1 was an offshore nest 27 m from the shoreline, floating over 74 cm of water. The owner (*BB/O**) started to incubate on 5 January. The most interesting feature of this case was that the jacana shifted the nest three times (30 cm N; 70 cm SW; 25 cm E) losing his clutch during the last move (Fig. 1.10). Another important feature was that the shifting occurred when the nest resistance was getting close to the minimum of 215 g (body weight of 175 g plus 40 g of clutch weight) (Fig. 1.10). Over 15 days he collected around 3,4 kg (wet weight) of nest material.

Nest 2 was an offshore nest 20 m from the shoreline over 74 cm of water. Incubation started on 13 January by the male jacana *G*/YY*. The clutch survived nine days until it was swept away by heavy rain. In this case a correlation was found between nest resistance and nest sinking (Pearson's $r = 0{,}73$; $P < 0{,}05$). Compared with nest 1, nest 2 showed high resistance ($P < 0{,}001$) despite being situated offshore. Nest shifting occurred on the second day of incubation and the male moved only the secondary pad. This shift coincided with the lowest nest resistance recorded.

Nest 3 was an inshore one made by male **/RW* 5,4 m from the shoreline over 9 cm of water and found on 4 January. It was monitored regularly only for three days until it was preyed on by a Nile Monitor. The nest showed high resistance and little nest material was used.

On one occasion an offshore nest found in the KwaZulu area of Muzi Swamp was placed on top of a piece of polystyrene which gave it high nest resistance. The jacana did not bring any

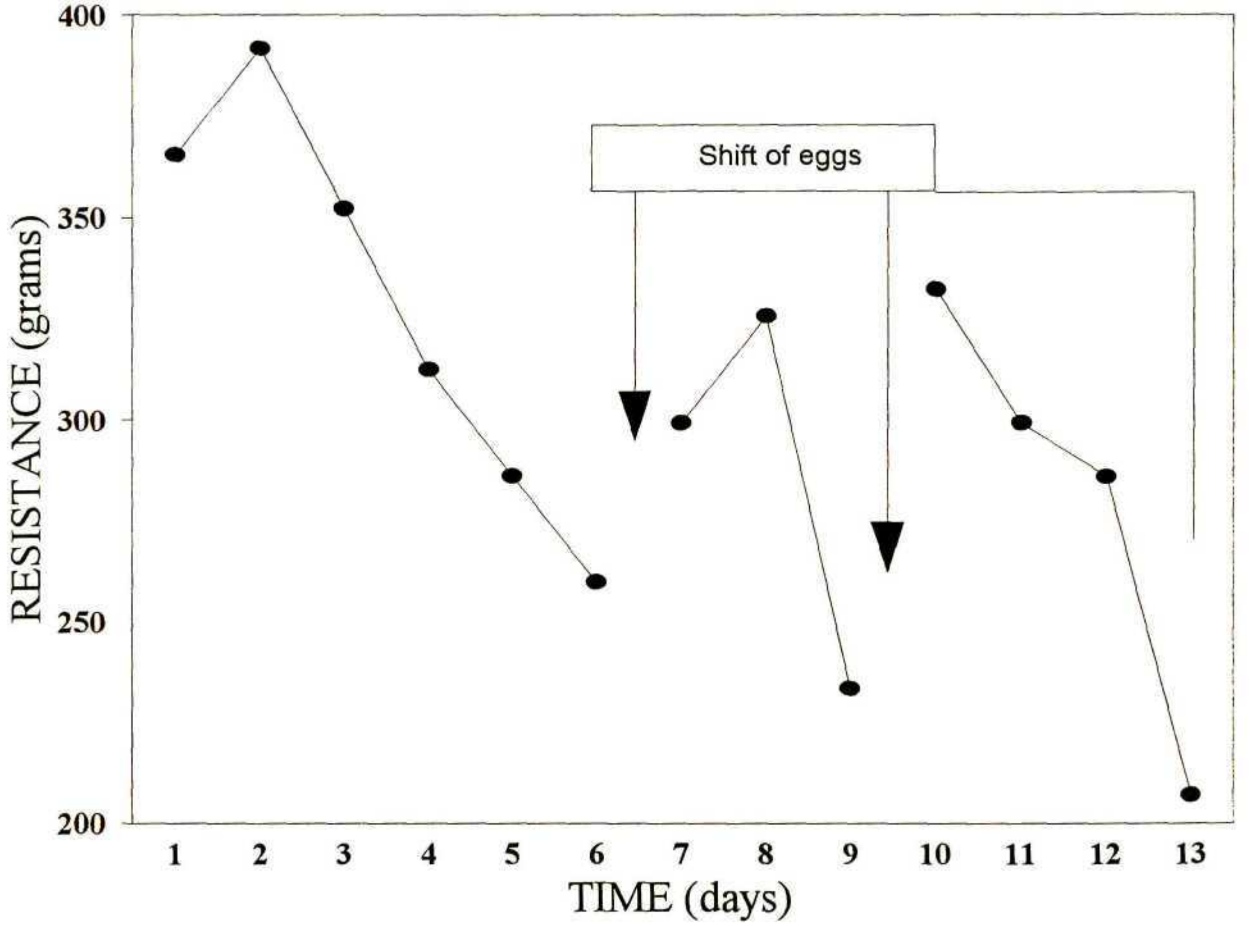


Fig. 1.10 Nest resistance of a nest of male jacana BB/O* during 14 days before the clutch was lost.

material to the nest but continued incubation. This seems to indicate that adding nest material to the nest is stimulated by nest sinking.

From these examples it is possible to assess the situation for African Jacanas, especially when they establish a nest in deep water. The main problem is that the nest sinks because of its weight, losing its ability to support the bird and its clutch. The only immediate solution is to bring more material to the nest, leaving the clutch exposed. This may have grave consequences, especially during heavy rain. When the amount of material brought to the nest does not compensate for the loss of resistance, the jacana will be forced to build another nest close to the first and then move the eggs.

I witnessed a typical scene on 23 November 1991 during a brief but heavy shower. Male (*OB/*R*) had to leave the nest and take material from the surroundings while his clutch was getting wet. The rain started to strike hard on the nest and all he could do was add material, but he finally lost one egg.

An important thing to note is that the mass of the jacanas differs between sexes because of sexual dimorphism, so a higher sinking effect might be expected in incubating females than in males.

Food-sampling analysis

Species composition

Twelve families of arthropods were found living over the water (Table 1.1). Diptera were the most important order and the majority of them were represented by the Families Ephidriidae and Chironomidae.

Table 1.1. Eleven families of insects and one species of fresh-water shrimp found living on the water of Muzi Swamp, KwaZulu-Natal, South Africa.

INSECTS

Order	Family	Number of Species
Diptera	Ephidriidae	4
	Chironomidae	3
	Psychodidae	1
	Cecidomyiidae	1
	Stratiomidae	1
Hymenoptera	Eulopidae	2
	Formicidae	1
Trichoptera	Hydroptilidae	1
Lepidoptera	Hepialidae	1
Odonata	Coenagrionidae	1
Coleoptera	Curculionidae	1

CRUSTACEA

Division Caridea

Family Atyidae

Genus *Caridina*

Abundance

The most abundant species were chironomids in the *Potamogeton* area and the second in importance were ephidriids on waterlilies (Fig. 1.11 A, C, D, G).

Organic mass available

Although chironomids were most abundant in deep water because of their small size, they were not as numerous as the ephidriids (Fig. 1.11 B, D, F, G). The result of these tests is that a high concentration of food was found on waterlily and *Potamogeton* regions (Fig. 1.12, 1.13) made up especially of ephidriids measuring 4,5 mm x 1,5 mm. According to Beltzer & Paporello de Amsler (1984) insects of 3 -10 mm constituted 93% of the food of the Wattled Jacana *Jacana jacana*. Ephidriids fall into this size category.

At Muzi Swamp from September 1991 to April 1992 I recorded that bulbs of *Nymphaea lotus* were eaten by African Jacanas. The availability of this food was possible mainly because of the presence of hippopotamuses after the water started to recede from January 1992 because of the drought. I have seen plenty of waterlilies floating and loose in the wake left by hippos.

At first it was not clear whether other birds first started to open the bulbs thus exposing the starch for jacanas, but soon I witnessed a female jacana starting to open a bulb. After that I used the bulbs cut in half as bait to catch non-incubating males to ring them. The method of feeding is to concentrate pecking at only one point, thus enlarging the hole through which then the bird eats only the starchy part of the bulb.

An analysis of the contents of the bulbs made by the Department of Agricultural Development showed that more than 8 % consists of protein (see Table 1.2).

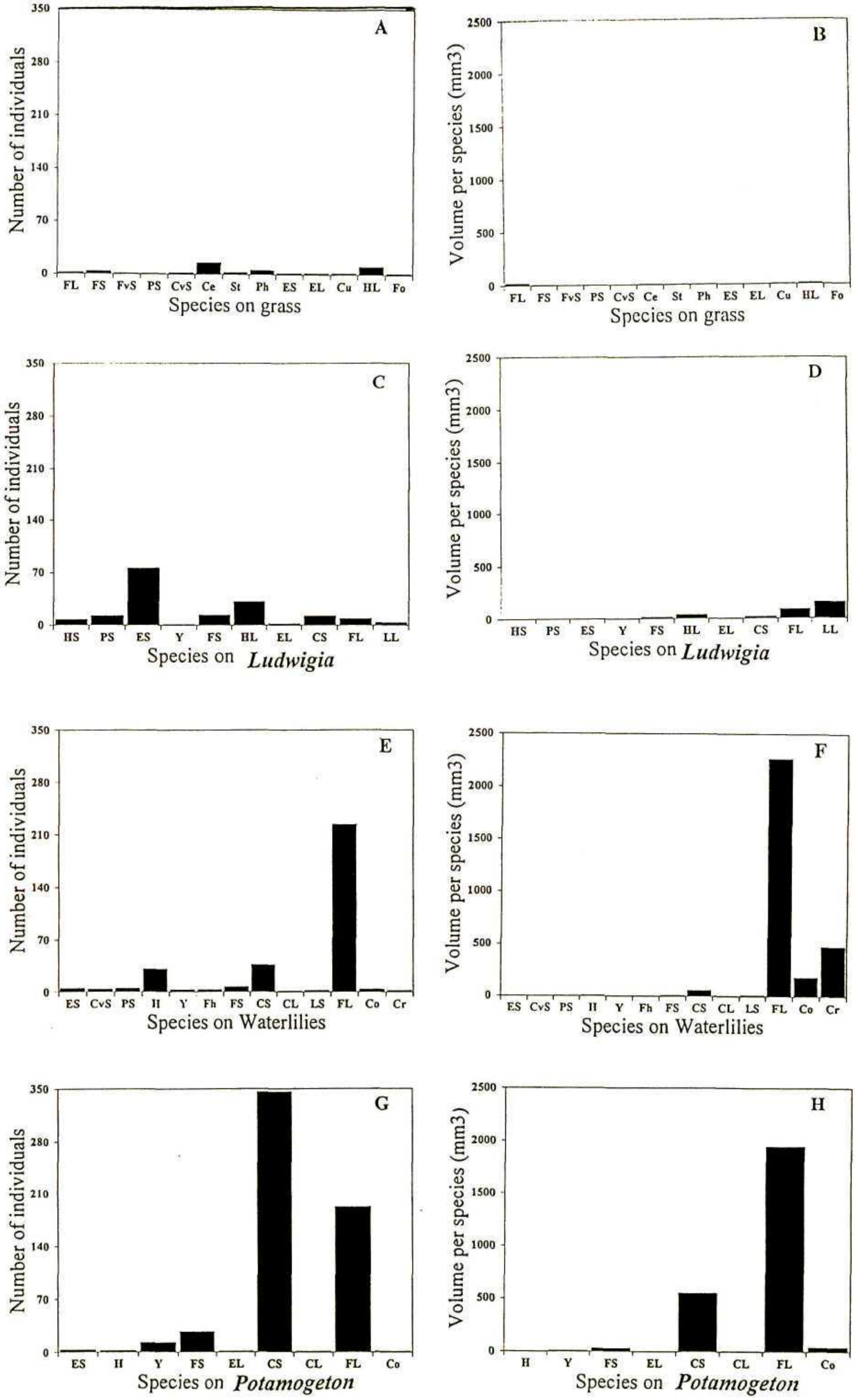


Figure 1 . 11 : Number of individuals and approximate volume (mm3) per species on 400 cm2-surface sample in four different locations (grass, Ludwigia, Nymphaea lotus, Potamogeton) at Muzi Swamp. FL = Large ephidriid;FS = Small ephid FvS = Very Small ephidriid; CvS=Very Small chironomid; CS = Small chironomid; CL = Large chironomid; Ce = Cecidomyiidae; Ph = Phoridae; St = Stratiomyidae; PS=Small Psychodiidae; EL = Large eulopids; ES = Small eulopid; Cu = curculionid; HL = Large Hydroptilidae; LL = Large Lepidoptera; Fo = Ant; Co = Damselfly; Cr = Shrimp

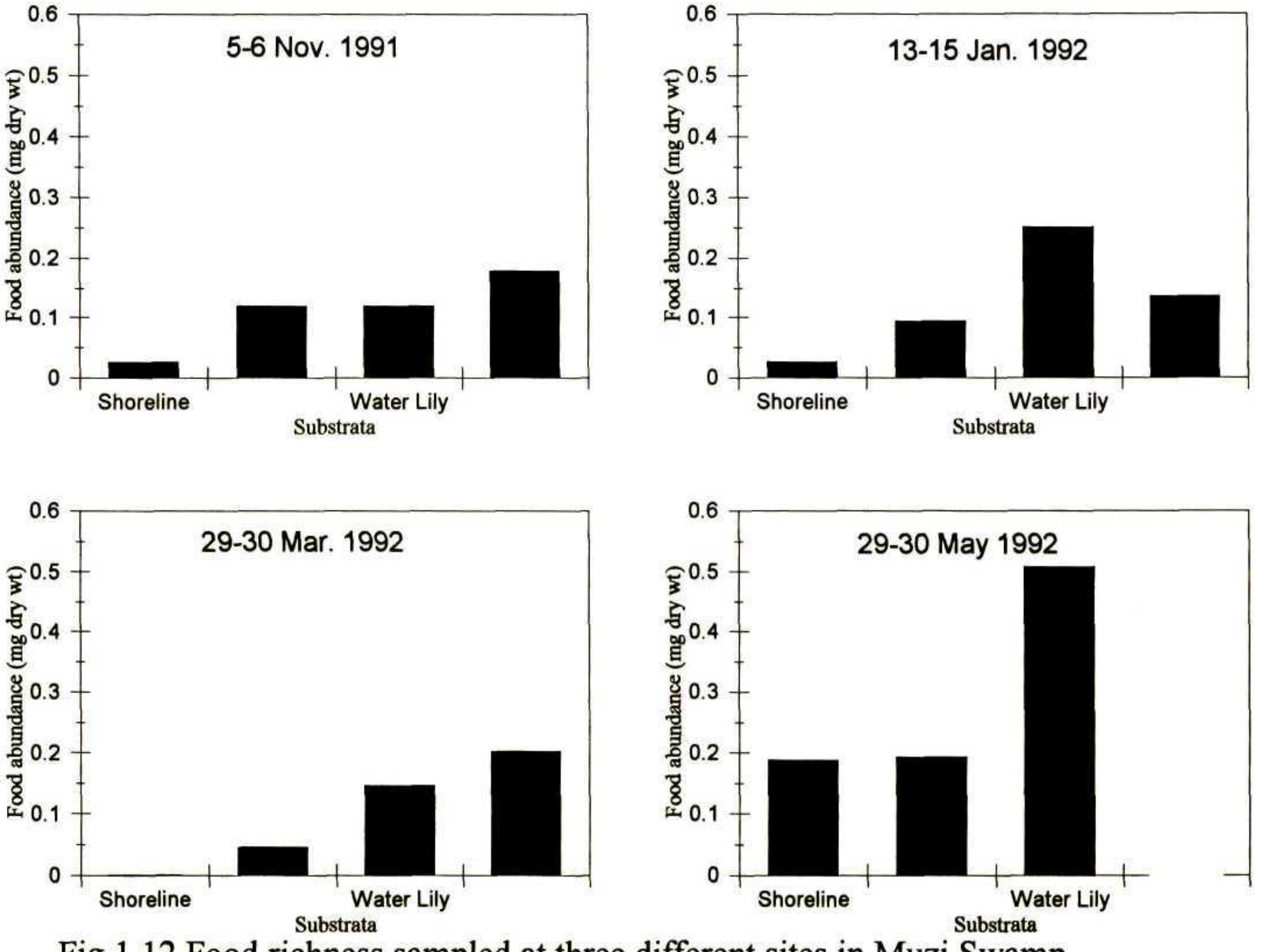


Fig.1.12 Food richness sampled at three different sites in Muzi Swamp.

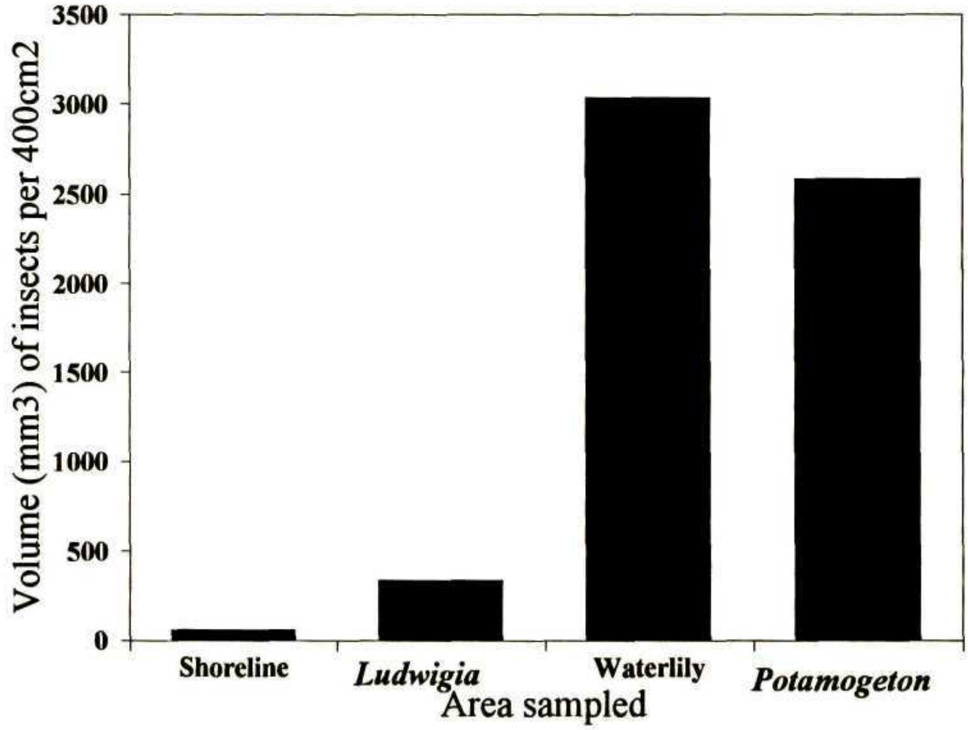


Fig. 1.13 Volume of insects found at three different sampling sites in Muzi Swam

Table 1.2 Analysis of starch of waterlily *Nymphaea lotus* bulbs performed by Cedara Feed Laboratory, Department of Agricultural Development, KwaZulu-Natal.

Components	Amount
Fat	0,71%
Fibre	2,53%
Ash	2,36%
Protein	8,23%
Nitrogen	1,32%
Calcium	0,11%
Magnesium	0,15%
Potassium	0,72%
Sodium	0,08%
Phosphorus	0,25%
Zinc	22 ppm
Cu	4 ppm
Manganese	21 ppm

I found that the proportion of *empty* and *open* bulbs did not change significantly during the study period, but the proportion of *complete* waterlily bulbs ($\chi^2_7 = 30,3$; $P < 0.05$) increased, especially during the driest months (May 1992) (Table 1.3). This is probably a consequence of increasing exposure when the water of the swamp receded and of more hippo activity. Although no marked bulbs were found during the months of observation, I believe that the activity of hippos provides the jacanas with this alternative source of food; this activity is especially important at times of high water level when the bulbs are otherwise submerged.

DISCUSSION

These data support the hypothesis that African Jacanas choose the areas of strongest nest support available in the male's territory (on fringing vegetation in the first place and secondarily on waterlilies at water depth of around 90 cm) because these two typical areas provide the highest nest resistance and lowest sinking rate compared with other sites.

Nesting in deep water requires great effort to keep the resistance and sinking rates of the nest within acceptable limits to be successful. However, why does the African Jacana move to an offshore area while there is still available fringing vegetation after losing a clutch? If incubating on fringing vegetation always gives high breeding success why not persist in building a nest on the fringing area instead of moving to an offshore area? A possible explanation would be the presence of the main predator, the Nile Monitor *Varanus niloticus*: as long as monitors are not aware of the presence of a clutch then it has a high chance of success, but once the clutch is found by the reptile the risk would be greater than nesting on an offshore area if it intensifies its searching patterns in the area where the clutch was found. Nothing is known about the foraging patterns of the Nile Monitor, but individual males of the sympatric Rock Monitor (*V. albigularis*) in Namibia can find specific locations 3-4 km apart (Phillips 1995). Because the Nile Monitor has

Table 1.3 Number of *empty, open* and *complete* waterlily *Nymphaea lotus* bulbs per km walk found on the shoreline of Muzi Swamp between October 1991 and May 1992.

MONTH	*EMPTY*	*OPEN*	*COMPLETE*
October	104	11,5	3
November	97	9,5	1
December	98,5	17,5	2
January	94,5	6,5	2
February	105	16	5
March	93	12	9
April	91	15	11
May	103,5	8	15
Significance (χ^2 test) $P < 0,05$	Not significant	Not significant	Significant

a much smaller home range, J. A. Phillips (pers. comm.) suggests that it has a much greater chance of remembering specific locations. Also, because monitor lizards are long-lived and expand their home ranges as they mature, this would also increase the likelihood that an individual lizard would memorize its surroundings. Maybe, a study of foraging behaviour in monitors would bring to light some new information to explain the apparently poor breeding strategy in the African Jacana.

The environment in which jacanas nest is subject to various influences such as changes of water level (Tarboton 1992, 1995), wave action, wind, predation (Tarboton 1992, 1995), variation in temperature at the water surface and in substrata support. Waves generated by wind or movements of hippopotamuses may dump eggs and hasten nest sinking, resulting in greater energy expenditure in male jacanas, as well as forcing them to spend more time away from the nest and hence heightening the risk of the clutch being preyed on or swept away by rain or other causes.

During the last three months of the study period there was an increase in visits by warthogs and cattle to the shore area and predation by monitors also increased (as was also noted by Tarboton (1992)).

The problem is that as the drought increases the pond or lake becomes the only body of water available for many mammals and as the waterline recedes the fringing vegetation becomes more exposed, providing inadequate cover to hide nests, so the only option would be to nest in a completely exposed area over deep water where mammals and predators cannot reach. However, other problems then arise like sinking and loss of resistance of the nest.

The shifting of eggs during incubation was reported by Jenni & Betts (1978) in the American Jacana and in the African Jacana by Urban *et al.* (1986). In the latter this was done when nest resistance was extremely low. Moving eggs to another place is a good strategy, but it increases the likelihood of egg loss.

Nest-site selection by African Jacanas consists largely of a compromise between the level of predation and the extent of weather effects. African Jacanas will nest where the effects of the combination of these factors are least, yielding the highest chance of success in breeding.

Jenni & Betts (1978) suggested anti-predator adaptations and also phylogenetic inertia as the possible causes of failing to construct a more substantial nest.

Although Tarboton did not sample the food abundance available to African Jacanas at Deelkraal Dam he stated that the "easy breeding hypothesis" of Maxson & Oring (1980) fits into the breeding system of the African Jacana (Tarboton 1995). The amount of food estimated at Muzi Swamp is more than that found by Maxson and Oring (1980) in the habitat of the Painted Snipe. This suggests that the breeding organization of the African Jacana definitely follows the "easy breeding hypothesis" proposed by Maxson and Oring (1980) in which high food availability select for polyandry.

Up to now, there has been no information that waterlily bulbs are eaten by the African Jacana. Osborne & Bourne (1977) and Beltzer & Paporello de Amsler (1984) found that in the Wattled Jacana plant food consisted only of seeds.

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CHAPTER 2

REVERSED SEXUAL SIZE DIMORPHISM (RSSD) IN THE AFRICAN JACANA *ACTOPHILORNIS AFRICANUS*: A NEW HYPOTHESIS

ABSTRACT

Reversed sexual size dimorphism is well known in the African Jacana and current theories propose mainly that this evolved as a consequence of the female's practice of laying multiple clutches in order to offset high clutch loss. In this paper I argue that it might be right to regard the male's small size as also advantageous because he undertakes all incubation duties alone on a floating which is therefore less likely to sink.

In the African Jacana *Actophilornis africanus* the parental roles of the sexes are reversed and polyandrous behaviour has been recorded for most species of jacanas except for the Lesser Jacana *Microparra capensis*. Females are dominant and may initiate courtship, while incubation, nest maintenance and rearing the offspring are the duties of the males

Reversed sexual size dimorphism (RSSD) is well expressed in the African Jacana.. Females are bigger than males, weighing 68% more than males in the Transvaal (Tarboton 1991) but only 49,9% (n = 23) at Muzi Swamp.

Ross (1979) proposed that "large females have been selected for their greater capacity to lay multiple clutches to replace high egg losses" and the size of males is selected for the purpose of optimal foraging. Tarboton (1991), however, stated that "female size (expressed as log-mass) had no apparent effect on the number of clutches they laid (Spearman's r = -0,09; P = 0,84)".

Jehl & Murray (1986) explain RSSD in polyandrous birds as a result of interfemale competition. Interfemale aggressiveness is reported for the American Jacana *Jacana spinosa* (Jenni 1974) but it seems that this is not particularly the case for the African Jacana (Tarboton 1991; pers. obs.).

RSSD was also seen by Tarboton (1991) & Ross (1979) as a consequence of the energetic requirements for laying multiple clutches. However, although the Painted Snipe *Rostratula benghalensis* is also polyandrous (Komeda 1983), the female is only about 8% bigger than the male. It nests on the ground or in the fringing vegetation and the female lays multiple clutches of four eggs. Another example is the North American Spotted Sandpiper *Actitis macularia* whose egg-volume:female-mass ratio is the greatest of any waders (Table 2.1). Where is the saving in laying multiple clutches in these species ?

Mueller & Meyer (1985) suggest that in birds of prey RSSD allows a reduction in food competition. Mendelsohn (1986) on the other hand proposes that selection favours smaller birds because they are more successful hunters.

Neither Jehl & Murray's (1986) hypothesis nor Tarboton's (1991) is able to explain satisfactorily the occurrence of RSSD in jacanids. However, part of the RSSD of the African Jacana and other shorebirds could be explained through female interest: males tend to be more active during courtship, trying to gain access to the female and the female selects her mates. Females have physical control over copulation (Knowlton & Greenwell 1985) and may also prefer to mate with particular males (O'Donald 1983). Therefore the sexual difference in size in polyandrous birds could favour the choice of mate by the female in four ways:

(a) avoiding rape attempts from rejected males;

Table 2.1 Female mass (g), egg dimensions (mm) and ratio between egg volume and female mass in 16 species of polyandrous birds.

Species	Female mass (g)	Mean L x B (mm)	Egg volume index	Egg volume/female mass	Reference
Actitis macularia	38,42	33 x 23	174,57	4,54	*a*
Aenigmatolimnas marginalis	61	29,6 x 21,2	133,03	2,18	*b*
Charadrius morinellus	117	41 x 29	344,8	2,94	*a*
Phalaropus fulicaria	57,5	30 x 22	145,2	2,52	*a*
Phalaropus lobatus	37,4	30 x 21	132,3	3,52	*a*
Rostratula benghalensis	134	36 x 26	243,3	1,81	*a*
Tringa erythropus	181	47 x 32	481,28	2,65	*a*
Actophilornis albinucha	239	36,8 x 25,2	233,7	0,97	*c*
Actophilornis africana	232	32,6 x 23,1	174	0,75	*d*
Hydrophasianus chirurgus	231	37,4 x 27,6	284,9	1,23	*e*
Irediparra gallinacea	130	30,2 x 21,6	140,9	1,08	*d*
Jacana jacana jacana	143	30 x 23	158,7	1,11	*f*
Jacana jacana spinosa	145	30 x 23	158,7	1,09	*g*
Microparra capensis	41	24,7 x 17,9	79,1	1,93	*h*
Metopidius indica	210	36,4 x 25,1	229,36	1,09	*b*

a Cramp & Simmons (1983); *b* Urban *et al.*(1986); *c* Rand 1936; *d* Tarboton (1991); *e* Johnsgard (1981); *f* Osborne & Bourne (1977); *g* Jenn & Collier (1972); *h* Ali & Ripley (1969)

(b) avoiding injury from extended or multiple copulations;

(c) ability to chase undesirable males;

(d) saving gametes, spending them only on preferred mates.

RSSD would allow a female African Jacana to become dominant and hence to exploit several male territories for foraging, thereby extending her food supply. This is important because females are unable to move quickly over deep water where the food concentration is high (refer to Chapter 1) and where she might feed faster. Because of their size females are restricted to wading in shallow water or walking on ground close to the shoreline (Tarboton 1991; pers. obs.). Another factor is that females would exert more pressure on the floating nest, making it sink more than males do during incubation. It would therefore be advantageous if incubation were confined to the smaller males. Over a deep-water area the heaviest male jacana would have little chance of completing incubation without facing problems of nest sinking and loss of nest resistance (refer to Chapter 1). The heaviest males would be successful in breeding only on fringing vegetation.

This leads me to believe that female African Jacanas are larger than males because during phylogeny smaller males had more chance to be successful in breeding on deep water than larger ones because of the weak structure of the nest. I propose here that males, and not females, have been more affected by selection pressures because they are responsible for incubation on floating vegetation. The lightest males may have the greatest chance of successfully completing incubation. The effect of nesting on floating vegetation might be expressed in the difference in body size between polyandrous jacanids and other polyandrous waders.

The polyandrous mating system would permit females to be freed from parental duties, allowing them more foraging time. I should stress that female African Jacanas may have a large territory in which they can meet their energy requirements without being chased by males. The area of a single male territory would be insufficient for the female's requirements, and because of her dominant behaviour towards males, facilitated by her size, she can use all the territories of her males.

I suggest that a reduction of body size and egg size is a way to maximize the chance of breeding successfully. I propose that RSSD in the Jacanidae is reinforced by their need to nest over deep water.

An indirect effect of male preference by females would be expected if light males were selected primarily for their potential to complete incubation. Females would prefer to mate with smaller males than those close to female size. Females may benefit from such preference by increasing their breeding success.

Eggs might have become smaller proportionally because the size of the male would determine the brood-patch area; on the other hand a reduction in size could improve incubation on account of the reduced weight on the nest, minimizing the problem of sinking and resistance.

I suggest that the combination "big female : small male : small eggs" is the only possible response to the environment in which the African Jacana lives. A question that arises therefore is why the Lesser Jacana *Microparra capensis* is monogamous ? This small species of jacana shares the same habitat as the African Jacana and reaches an incubation attentiveness of up to 80% (Tarboton & Fry 1986). It seems that under the same kind of ecological pressure the solution is different. Little is still known about the Lesser Jacana. There is no information available on reproductive success and on the duration of the incubation period. The answer to this question may lie in the size of the bird and its eggs. The Lesser Jacana weighs around 70% of the weight of a male African Jacana and eggs are about 40% smaller than those of the African Jacana. This could mean that the sinking problem created by body weight is reduced, thereby affecting the nest less and reducing the chance of predation because the clutch is more constantly attended and the incubation period may be shortened. For the Lesser Jacana monogamy might be the best choice, as polyandry is for the African Jacana. Against this background a lower rate of clutch loss might be expected in the Lesser Jacana.

Selective forces:

Something that should be investigated in jacanids is that in spite of the high RSSD there is no sexual difference in plumage. Even though the sexes are alike in plumage, the sexual difference in size is the most marked among jacanids. It seems that size is likely to be the character selected for during courtship. If so, a non-assortative mating system would be advantageous to fix the sexual size dimorphism. The interesting thing is that an absence of any difference in plumage in polyandrous waders occurs only among jacanids.

Intrasexual selection might lead to big males and big females as a consequence of intermale competition and interfemale competition respectively (Jehl & Murray 1986) (Fig. 2.1).

Natural selection might oppose intrasexual selection selecting the smallest males and females because more food is available over deep water. Besides that, small males might be selected for because of the greater chance of breeding successfully.

The selective forces would therefore be asymmetrical in a jacanid population and the outcome would favour big females and small males. The only selective force which could lead to RSSD should be through a size-disassortative mating system and this should be tested.

The conflict between the male's interest and the female's interest:

The male's interest is to assure his paternity and to prevent another male's sperm competing successfully with his (Parker 1984). There are several possible ways to achieve this: for instance

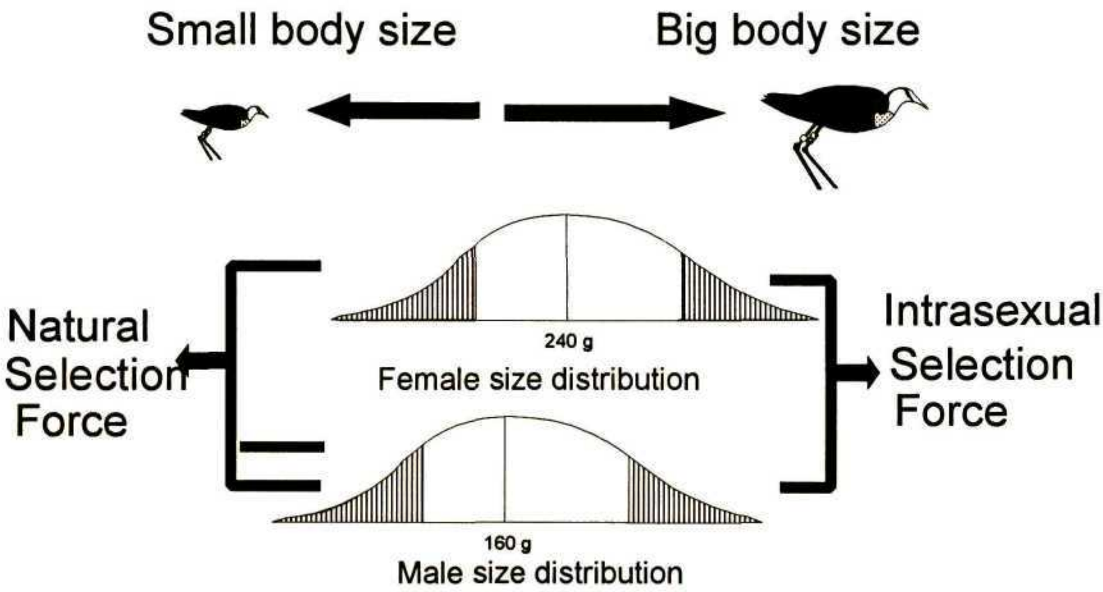

Fig. 2.1 Possible selective forces that fix body size in the African Jacana.

prolonged copulation, postcopulatory guarding, take-over avoidance, and multiple copulations (Parker 1984).

The frequency of copulation would be a good index of male and female interest. The frequency of copulation would depend on:

(a) the number of partners (*n*) that a female can have.

(b) the male rank (*r*) in the hierarchy of the males mated with one female.

In this case *r* represents the male's interest, while *n* denotes the female's interest. The likelihood of a given incubating male's egg containing his genes is in direct relation to his rank because by competing successfully with other males he will be better able to gain the female's attention and ensure a greater likelihood of paternity at least until he has a full clutch of eggs to incubate.

Females should not select big males because (a) it could increase intrasexual competition, reducing *n* and finally reducing female fitness and (b) big males would not have as much breeding success as small males because of the sinking factor of the nest on floating vegetation.

It seems that everything favours small males, but high intermale competition could increase selection for body size and therefore a male's access to a female; but it would be a contradiction if she selects only small males. The dominant male should be small for the female but bigger than the other males and the only solution to this problem is that the female could probably select small, aggressive males capable of dominating over all other males regardless of their size.

A very similar case to that of the African Jacana was reported by Petrie (1983). He suggests that female Moorhens *Gallinula chloropus* exhibit high interfemale competition for small, fat males because this type of male is apparently the most effective at incubating eggs: he spends less time foraging. Only the heaviest females tend to succeed in fights, the outcome of which is RSSD.

Females should compete for males when they are scarce. Petrie (1985) states that competition between females for males is likely to occur when there is great variability in male quality. He lists some of the "good qualities", but what should be "good quality" in the male African Jacana? This should include (a) providing good care in incubation and maintenance of the nest and (b) exhibiting highly territorial behaviour which ensures the defence of the territory as a valuable resource especially during parental care.

There should be some variation in male quality if it is purely heritable (Petrie 1985) and in jacanas male body size is directly related to the ability to defend a territory, so points (a) and (b) are in conflict: it may be more likely for the female to find a "big" male capable of defending his territory properly or a "small" male able to perform his breeding successfully rather than a "tiny aggressive" one which can perform both tasks equally well. The variation is therefore maintained despite the difficulty of finding small, highly territorial males.

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CHAPTER 3

VOCAL AND VISUAL COMMUNICATION IN THE AFRICAN JACANA

ABSTRACT

Social communication in the African Jacana is rich in vocal and visual behaviour patterns. This richness could be a reflection of the complex social system imposed by polyandry. Calls and visual displays were recorded in the African Jacana, revealing very defined patterns. The most important call types in the African Jacana are characterized by low-amplitude contact calls while highly variable and louder calls play a role in different contexts.

INTRODUCTION

<u>VOCALIZATIONS</u>

Vocalization in jacanids has been best investigated in the American Jacana *Jacana spinosa* by Jenni *et al.* (1972) who found a highly flexible vocal repertoire in this species. It seems that the complexity in the vocalization might denote the presence of a highly complex social structure.

With regard to the African Jacana little has been done to understand vocalizations. This species has a well defined repertoire as elaborate as that of the American Jacana (Jenni & Betts 1972), but the vocalizations studied in the African Jacana cannot be directly compared with those of the American Jacana at present because Jenni & Betts (1972) did not record the context in which the vocalizations were performed. Some vocalizations have multiple functions, such as the typical *guang-guang* call heard during the breeding season; it is a sexual soliciting call by the female and is also used by males when defending their broods.

One particular feature of bird calls is that they usually elicit an immediate effect on the behaviour of other conspecifics (Catchpole 1979), which is useful in determining their possible functions in the social organization.

VISUAL DISPLAYS

The only information about displays in the African Jacana is from Tarboton (1992) on courtship behaviour. This chapter reveals for the first time many displays that have never been described before.

MATERIAL AND METHODS

The contexts in which the calls were performed were recorded in order to analyze the possible functions of each type of vocalization. Each item was recorded by means of a simple code:

1. Whether the bird was accompanied by a conspecific.

2. What the jacana was doing: flying away, arriving, short flights, incubating, displaying, meeting another, in precopulatory behaviour, in postcopulatory behaviour, copulating, in possible danger, doing nothing at the moment of the call.

3. How other members of the group react:

(a). utter the same call.

(b). utter a different call.

(c). escape, alert, follow, etc.

4. The vocalization uttered.

5. The time.

Example

Guang ♂4; 1S (♀ appr) 15:43

This means that Male 4 performed sexual soliciting behaviour while he was uttering the *guang* vocalization. The response of the female was to approach at 15:43 hours.

This kind of recording method allowed me to generate two types of information: the first relates the calls to the contexts and the second shows the effect of each call on conspecifics. For purposes of analysis, the contexts considered above were confined to only four groups related to: territory, sex, sudden alarm and chasing.

RESULTS

I distinguished eight types of vocalizations in the African Jacana as follows:

(a) *Peep* call: A whistling sound performed by chicks, reaching nearly 4 kHz when they demanded the father's presence (Fig. 3.1A).

(b) *Harsh call*: This is a very variable call, but basically consisted of four harmonics extending from 2,5 kHz to 4,0 kHz and the duration averaged 0,21s (n = 14) (Fig. 3.1B). This vocalization functions mainly as a territorial signal (Fig. 3.2A) and was always recorded during chasing behaviour (Fig. 3.2B). Sometimes the *harsh* call was effective as a sexual call, especially when it was uttered by the female. The *harsh* call elicits the same call in neighbouring jacanas (Fig. 3.3A) and is also capable of driving them off. This supports the idea that the call is strongly related to territorial signalling behaviour.

(c) *Screech* call: This call is very high-pitched, reaching 5 kHz with up to four harmonics. The duration averaged 0,23 s (n = 21), (Fig. 3.4A) and was performed as a warning signal. Sometimes this call was performed in a group and was accompanied by an upright posture. Both the *harsh* and *screech* vocalizations were recorded during disturbances (in cases of alarm) (Fig. 3.2C), but with the difference that the *harsh* call was recorded particularly when the bird was

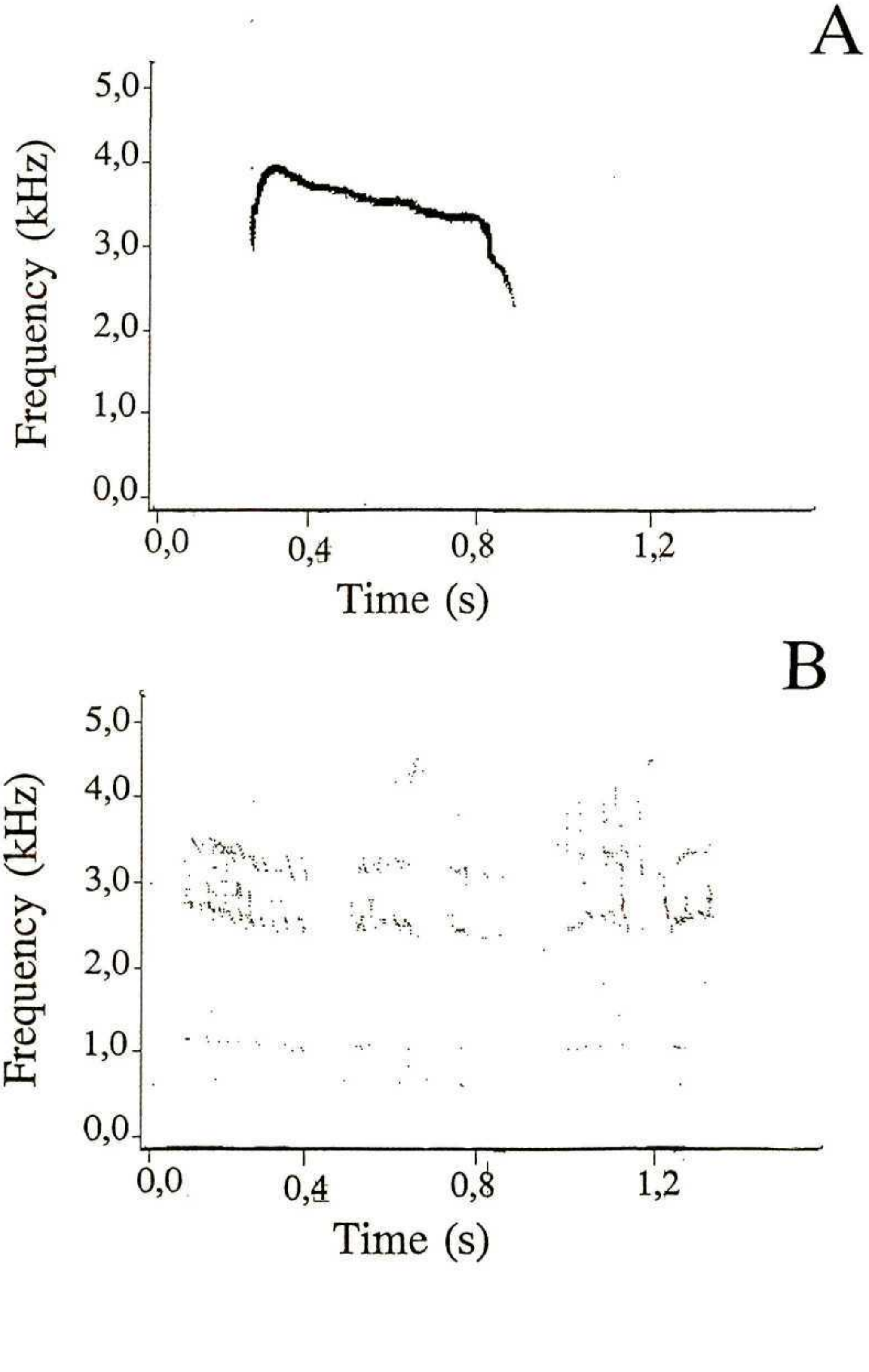

Fig. 3.1 *Peep* call (A) and *Harsh* call (B) in the African Jacana.

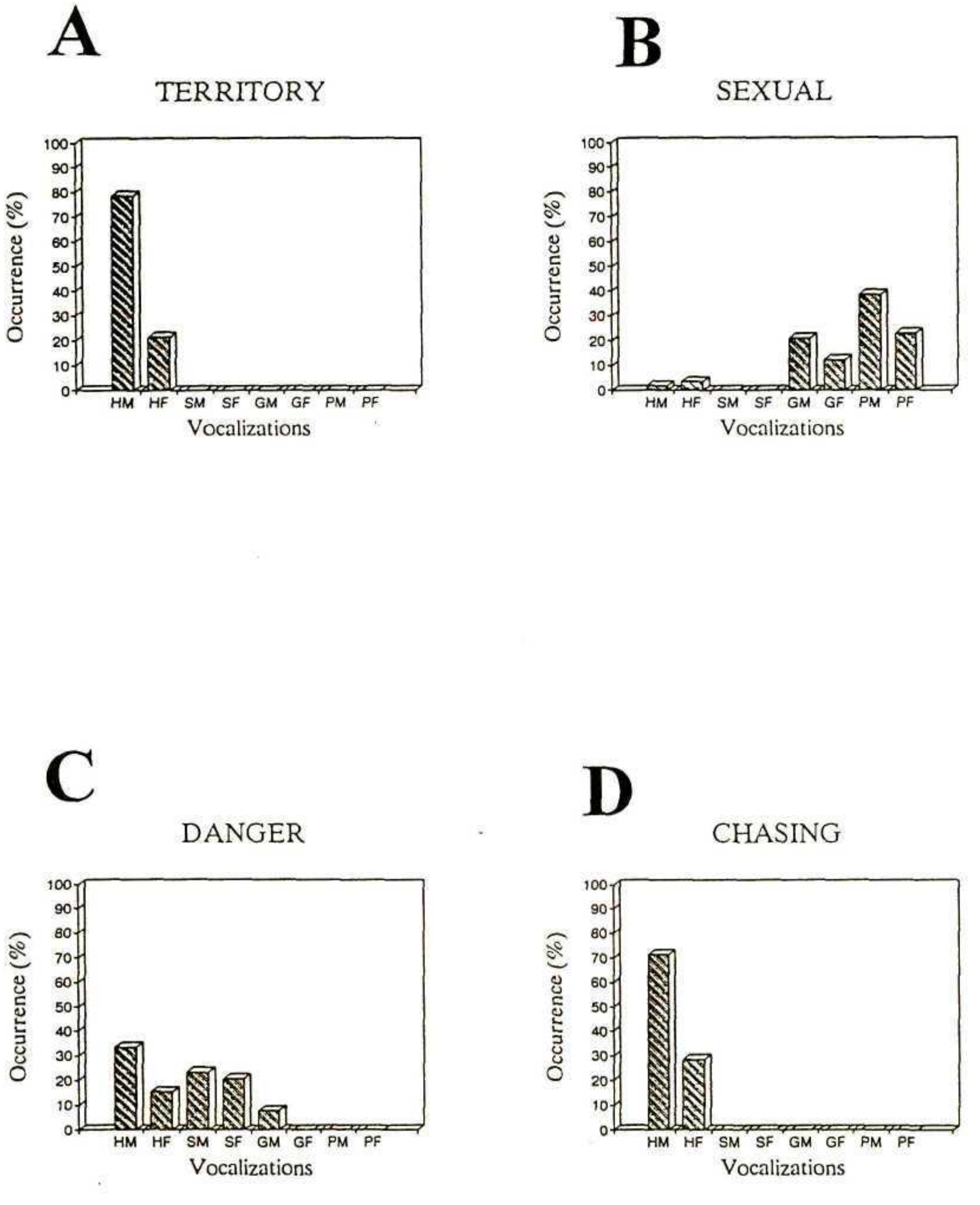

Fig. 3.2 Occurrence (%) of the different calls in the African Jacana according to the context recorded. H = *Harsh* call; S = *Screech* call; G = *Guang* call; P = *Purring* call. M and F stands for male and female.

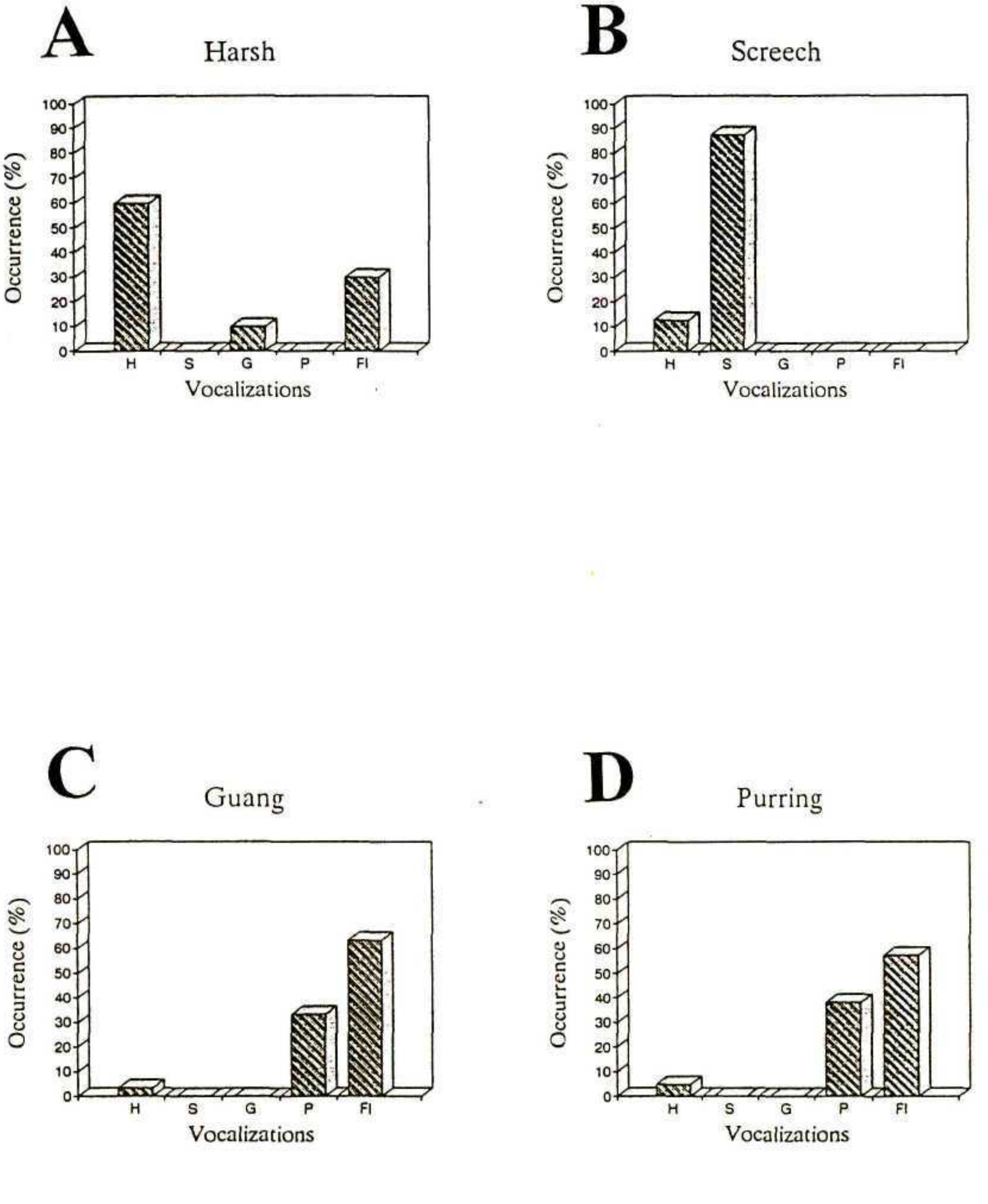

Fig. 3.3 Occurrence (%) of the different calls in the African Jacana as a result of hearing Harsh call, Screech call, Guang call and Purring call from conspecifics. H = *Harsh* call; S = *Screech* call; G = *Guang* call; P = *Purring* call. M and F stands for male and female.

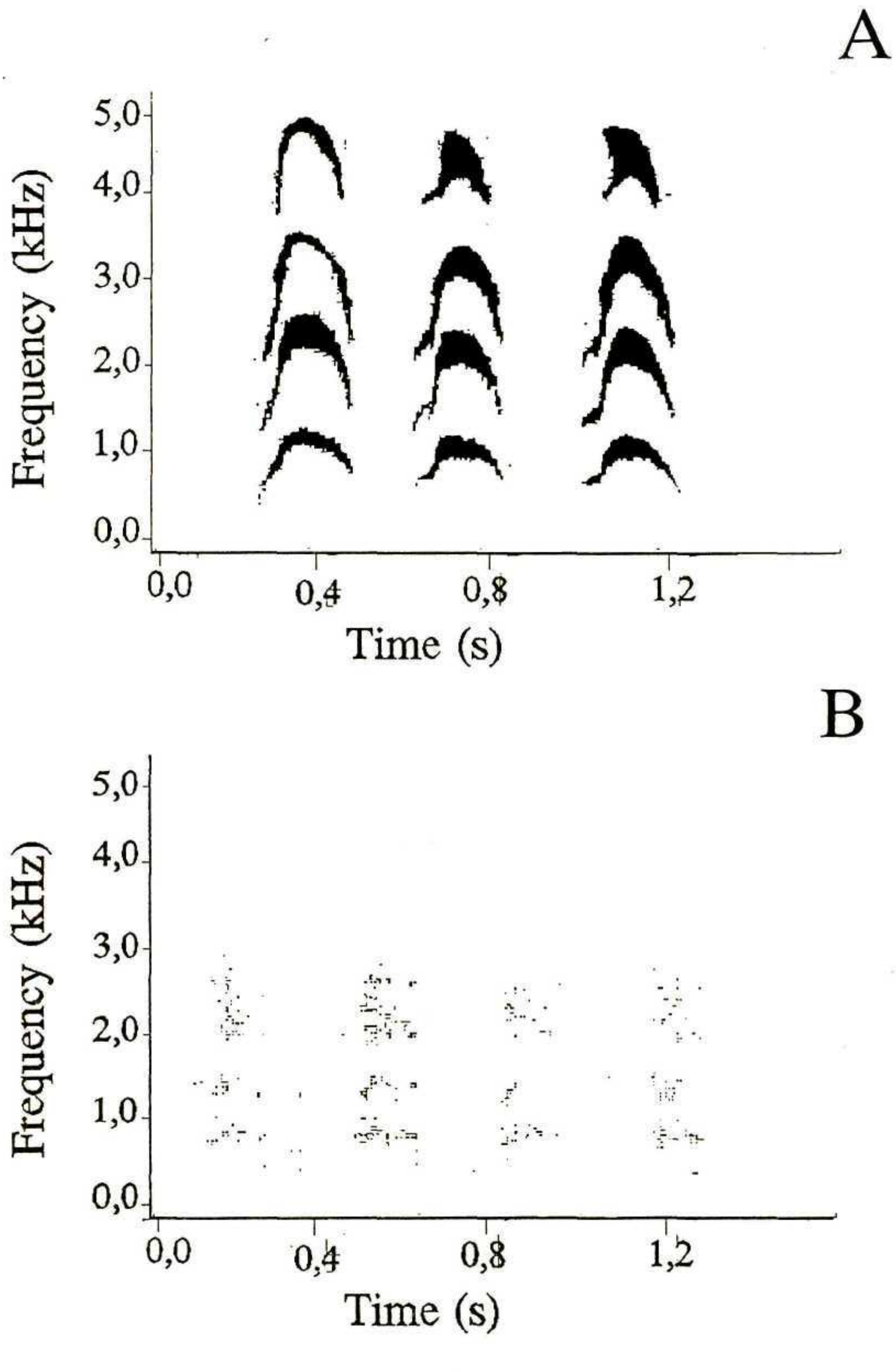

Fig. 3.4 *Screech* call (A) and *Purring* call (B) in the African Jacana

accompanied and the *screech* usually when it was alone. The *screech* elicited the same type of call from conspecifics (Fig. 3.3B), but did not cause any movement such as flight.

(d) *Purring* call : This was low-pitched, similar to a cat's purring. It lasted about 0,13 s (n = 24) and consisted of three harmonics from 0,5-3,0 kHz (Fig. 3.4B). This particular call was associated with both pre-copulatory and post-copulatory behaviour. Sometimes this call was used by the male during sexual soliciting (Fig. 3.2B). *Purring* elicited the *guang* call, random movements and more *purring* as a response from other jacanas within earshot (Fig. 3.3C, 3.3D).

(e) *Chick-calling* call: This was a flute-like sound performed by the male to summon the chicks (Fig. 3.5A).

(f) *Harsh Trilled* call: Consisted of three to four harmonics extending from 1,0-4,5 kHz of 0,8 s duration (Fig. 3.5B). In this type of harsh vocalization it is easy to distinguish the notes and the lowest harmonic. This particular call served the same purpose as harsh vocalization, especially during distraction displays in males.

(g) *Fear* call: This was a very long call that lasts 1,8 s but varied in frequency from 3,0-7,0 kHz, starting with three harmonics and ending with two (Fig. 3.6A). I recorded this only when the birds were in extreme danger.

(h) *Guang* call: This call occurred mainly during sexual soliciting (Fig. 3.2B). The call typically comprised two or three harmonics. The average duration was about 0,09 s (n = 29) (Fig. 3.6B).

A possible interpretation of the different vocalizations

To understand how each vocalization evolved in the African Jacana I found some salient features which could contribute to interpreting the whole pattern.

There are two possible ways of analyzing the vocal patterns: direct comparison and functional analysis.

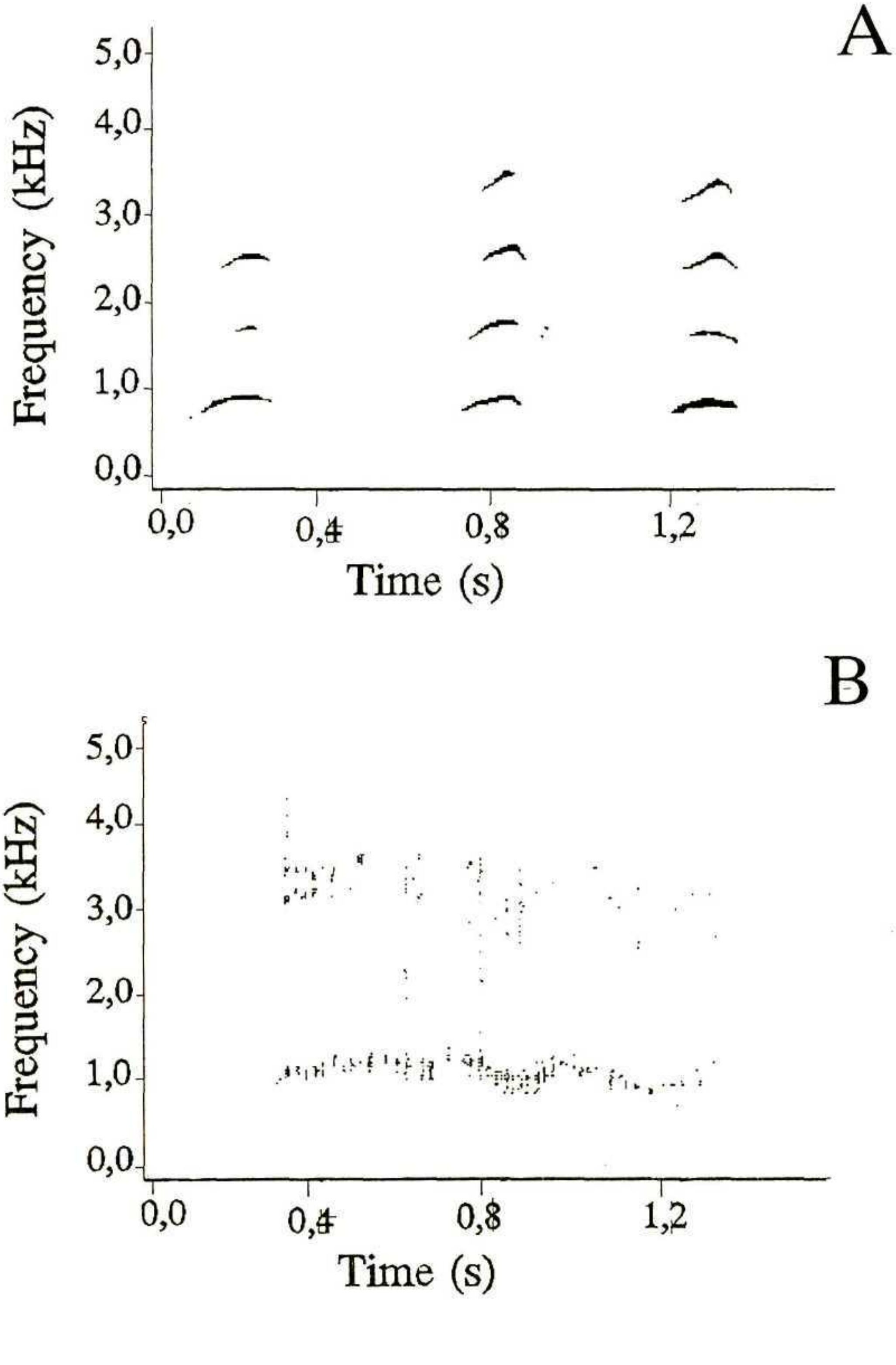

Fig. 3.5 *Chick-calling* call (A) and *Harsh-Trilled* call (B) of the African Jacana.

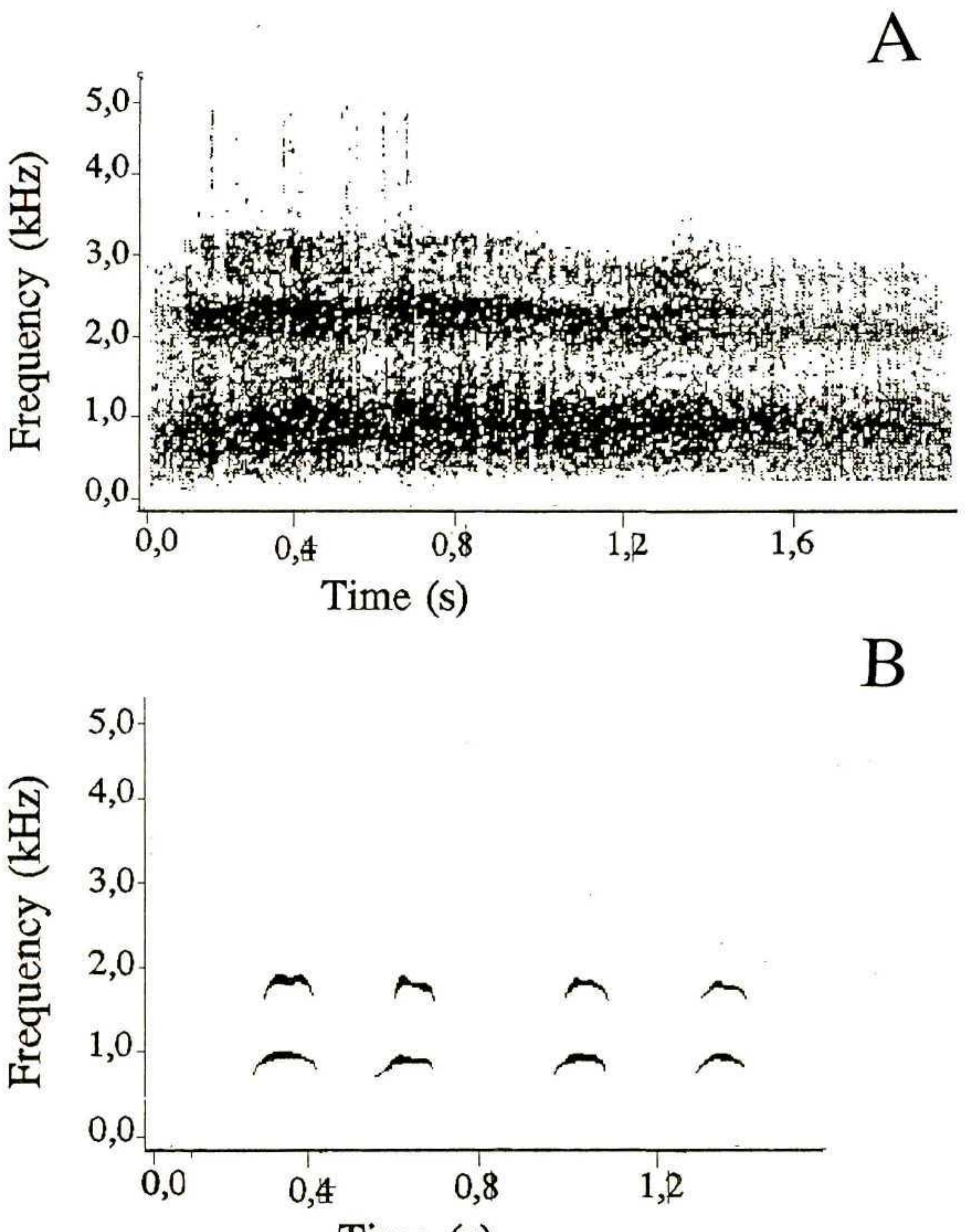

Fig. 3.6 *Fear* call (A) and *Guang* call (B) in the African Jacana.

Direct-Comparison Analysis

Using the *peep* call as a basis, any type of vocalization may be derived from two or three modified harmonics which are similar to it. The *harsh* vocalization can be considered as a highly modified form of the *guang* call. This is very easy to distinguish when uttered during distraction displays where two kinds of transformation may occur, both deriving from the *guang* call's typical form: one is the fusion of the extremes of harmonics (vertical fusion) and the other is the almost total merging of the notes (horizontal fusion) to form a distinctive harsh note which still remains just identifiable by the harmonics (Fig 3.7). If the vertical fusion is incomplete the outcome is a *harsh-trilled* call.

Another modification that may occur is a change in the duration of the interval between notes but without important alteration in the note itself, as happens in the *guang* call and *chick-calling* call.

An important transformation occurs in the duration of the *screech* call and *fear* call, showing a rise in frequency and expansion into a broad harmonic.

These three types of changes in vocal pattern are accompanied by the three typical functions of vocal communication:

(a) Alert, detecting disturbance and/or danger in the environment.

Vocal Pattern: broad notes of long duration.

(b) Appeasement display, to attract or keep a partner close by.

Vocal Pattern: change mainly in interval and breadth of the note.

(c) Territorial display, to advertise and expel other conspecifics from the territory.

Vocal Pattern: extensive transformation by reduction of interval (lateral fusion), decrease of individual note duration, reduction of the height of each harmonic and vertical fusion.

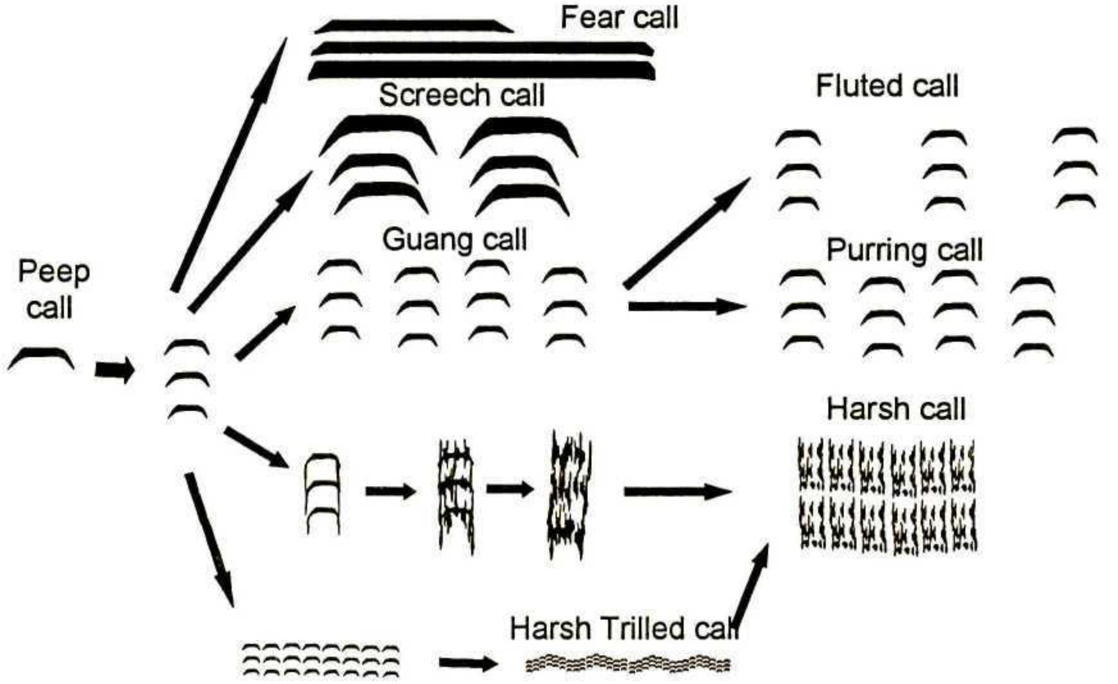

Fig. 3.7 Possible phylogeny of African Jacana call patterns when compared sonagraphically.

Functional Analysis

The functions of African Jacana calls are easily understood because they are performed in specific contexts or accompanied by fixed behaviour patterns (Catchpole 1979). In the African Jacana the vocalizations were classified as: alarm, contact and territorial calls.

Alarm calls

It is assumed that these calls convey a minimum of directional information, so that it is difficult to locate the source of the call. One of the characteristics of passerine alarm calls when a hawk flies over is a high pure whistle or squeak. The unbroken vocalization makes binaural comparison impossible because the frequency is too high for phase differences and too low for intensity differences to be appreciable enough to locate the bird (Wollemann & Olaszy 1976).

The *fear* call was a distress signal recorded only when the bird was trapped by myself or cornered by other jacanas during a fight. This type of call is very similar to that shown by Marler (1959) for passerines as an alarm call under conditions of possible danger. But it differs in that, in the jacana's case, the first harmonic is at a very low frequency which I think does help in its location, because this vocalization occurs only in situations of extreme danger such as when the bird is trapped. I suggest that its purpose is to intimidate or distract the enemy's attention in an attempt to escape (Catchpole 1979). Not all jacanas trapped for ringing uttered this particular call: only females did and certain males. During fights on the water this particular vocalization was also recorded.

The *Screech* call resembles the high-intensity alarm call of the Blackheaded Gull and the mobbing call of some passerines (Marler 1955). *Screech* calls are short, start and end abruptly, cover a wide range of frequencies and are often repeated. This is what Catchpole (1979) calls directional information. This was recorded when an African Fish Eagle *Haliaeetus vocifer* flew over, in the presence of crocodiles or the sudden appearance of people on the shore. I could also elicit this vocalization in a group of jacanas simply by clapping. I even recorded *screech* calls after copulation if there was any disturbance in the environment. Interestingly, when jacanas were in a group they all uttered a synchronized *Screech*, thereby revealing the precise location of each particular bird. As a typical alarm call it alerts conspecifics to the presence of possible danger in the environment. The difference between the *fear* call and the *screech* call is equivalent to the distinction between distress and alarm calls, the one warning of impending trouble, the other confirming that one is in trouble (Grier 1984).

Contact Calls

The *guang* call is the typical sexual soliciting call common to both sexes. The main feature is the separation between notes which gives it directionality: for example, in the *chick-calling* call it helps particularly in locating it. Both the *chick-calling* and *guang* calls carry over long distances while the *purring* call is a short-distance call because it is uttered only when the interacting birds are adjacent or it alternates with the *guang* call when one bird is watching another approaching. The harmonics are extremely fragmented and difficult to distinguish.

Territorial calls

There are two basic types of territorial calls: the *harsh* vocalization and the *harsh-trilled* call. I could not find any difference in context between them, except that both were performed during territorial displays. The *harsh* call is the most common utterance when males are keeping possible intruders out of the territory. This call seems to impart more specific information than I expected as it has great variability, probably conveying information about the motivational state of the bird. More studies are needed in this respect.

Analysis of the vocal-response data and vocal-context data

The *harsh* call shares the same context with the *screech* call because both are present in territorial encounters (Fig. 3.2A), in a group and during a disturbance (Fig. 3.3A). However, *screech* calls were recorded only during disturbances. The occurrence of the *harsh* call during "chasing" and "territorial" behaviour shows clearly the characteristics used for locating the bird. *Harsh* calls were likely to elicit either the same response or to provoke flight in nearby males as soon as they noticed that the territory was already occupied. The *screech* call elicited the same type of vocalization but not immediate flight. It appeared to serve as a communal alarm system.

Guang calls elicited *purring* calls but never the same calls nor flight in the mate, which explains the function of contact calling. A similar response was found to *purring.* This means that *guang* calls and *purring* calls are both sexual signals.

VISUAL DISPLAYS

Varying postures among African Jacanas during territorial encounters and attempts to monopolize the female's attention were recorded.

Aggressive threat displays

(a) *Upright* posture: the bird extends the neck with the nape feathers upright and utters the *harsh* vocalization. It has been recorded in the presence of passing crocodiles, monitors and when allospecific birds like Blacksmith Plovers *Vanellus armatus* were on the copulation platform of the jacanas. If the high-intensity *upright* posture was assumed, the jacana faced the intruder whereas from a low-intensity position it merely gave a sidelong glance (Fig. 3.8A).

(b) *Neck-retracted* posture: this was recorded in females during visits to the territories of incubating males (Fig. 3.8B). The neck is completely retracted and the bird tends to walk slowly. In two cases this posture was seen while the bird was pattering on the water in a very similar way to that of males when they perform distraction displays (see below).

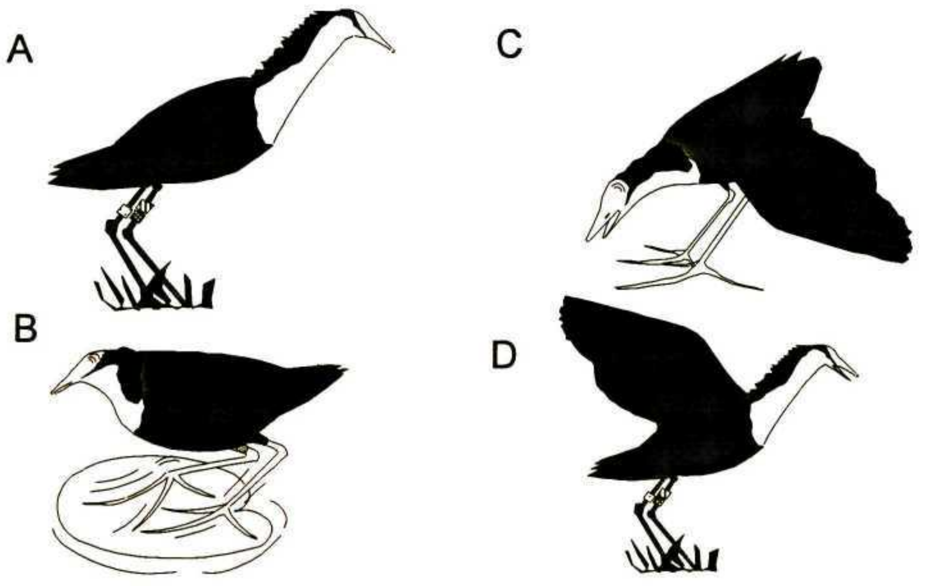

Fig. 3.8 Aggressive threat displays of the African Jacana. A = *Upright*;

B = *Neck Retracted*; C = *Wing Down*; D = *Spread Wing*.

© *Wing-Down* posture: assumed chiefly by males towards females in sexual encounters and towards other males during territorial confrontations (Fig. 3.8C). The posture is always accompanied by a strong *guang-guang* call which is somewhat different from the sexual soliciting call. The most characteristic feature of this display is drooped or half-spread wings. At high intensity one or both wings are completely spread.

(d) *Spread-Wing* posture: this is the most common display recorded during the study period. I consider this display as typically territorial and I have only seen it performed by males. The salient feature is raised wings while the jacana utters *harsh* calls (Fig. 3.8D).

Distraction displays

The survival of chicks after hatching depends particularly on some distraction displays performed by male jacanas and the cryptic behaviour of the chicks. One form of "distraction" was for the male to display himself well away from the chicks (around 60-80 m) when the observer was at some distance (about 20 m). But when I was close to the offspring the male pattered the water surface with his feet as he slowly submerged or performed *spread-wing* displays.

The response to predators of the male jacanas when they are caring for chicks is more uniform than when they are incubating. Some jacanas with eggs close to hatching performed distraction displays close to the nest and yet others even when they were only starting to build it.

Chick-carrying behaviour.

Chicks within a few days of hatching nestle under the father's wings. This behaviour is both for brooding and to conceal the chicks from predators. *Chick-carrying* behaviour is initiated when the father utters a low-pitched *chick-calling* call. When the chicks come closer to the father he opens his wings slightly, allowing them to huddle underneath. Then he walks slowly with the chicks clamped under each wing taking his young away from the danger. If he is followed he will drop the chicks which immediately submerge in the water, keeping only the bill above the surface. The male jacana may then distance himself by flight from the chicks before performing distraction displays. If the chicks are still in danger they may shift their position by swimming. The *harsh* vocalization warns the chicks to remain submerged and motionless. While this is advantageous for disturbances of short duration, it can prove fatal for a prolonged period. For example, two chicks died of cold due to prolonged submersion due to my presence for three hours trying to take videos.

Contact behaviour

First at Darvill Sewerage Works and then at Muzi Swamp I recorded peculiar behaviour among African Jacanas during courtship. The female kept completely motionless while the male walked around her, ruffling her feathers and pecking gently at her back to the point of putting his head under her wings and tail. This behaviour was recorded during pre- and post-copulatory activity and especially when copulation was unsuccessful.

Sexual behaviour.

Tarboton (1992) described a distinctive courtship sequence in two steps, which according to my observations correspond to the pre-copulatory displays and copulation, but I would add a post-copulatory stage, making three (Fig. 3.9).

<u>Pre-copulatory displays</u>

Sexual soliciting behaviour

The first part of the pre-copulatory stage is the sexual soliciting call (*guang* call). However, a *harsh* call and a *purring* call were recorded especially when the partner was close to the

a) SEXUAL SOLICITING

b) PRE-COPULATORY DISPLAYS

Head-down Posture and/or Contact Behaviour

c) COPULATION

Copulation and "Neck-pecking" Behaviour

d) POST-COPULATORY DISPLAYS:

Head-down Posture and/or Contact Behaviour

e) Head-up Posture

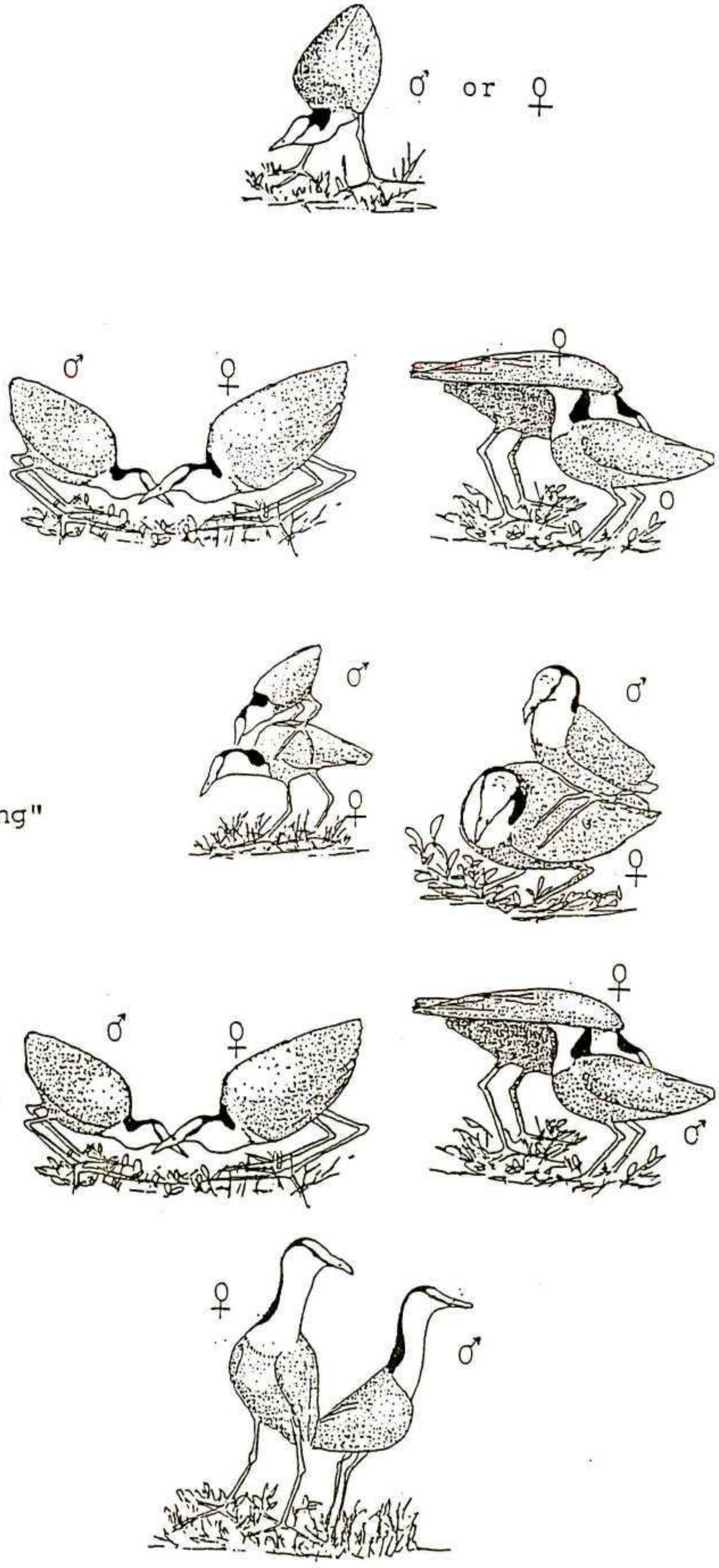

Fig. 3.9 Courtship behaviour sequences of the African Jacana.

copulatory site. During the display the jacana bent the body with the neck slightly curved upwards. Very often ground-pecking behaviour was observed. Sexual soliciting was performed by both sexes (average duration of 46,63 s for the female and 54,32 s for the male, counting from the first heard *guang* note to the arrival of the solicited partner), always in one or two designated areas of the male's territory. At the Darvill Sewerage Works males solicited a sexual encounter in 63% of the recorded cases, mainly using the *guang* call: females solicited in only 36% of the cases, uttering the same type of call. These percentages are close to what Tarboton (1992) found at Deelkraal Dam, Transvaal: 72% for males and 28% for females.

Head-down Postures.

When two birds met each other, a *head-down* posture was adopted for approximately 41,14 s (n = 14). It did not differ much in appearance from sexual soliciting behaviour except in the utterance of the *purring* call. Either the male or the female greeted the partner by presenting the sky-blue frontal shield and the black band on the neck. In each case the female remained motionless while the male walked around her, both sexes maintaining the same posture. Males interrupted the stereotyped display 3,4 times on average (n = 13), briefly to survey the surroundings. Furthermore, short withdrawals by males have been recorded, averaging 1,38 (n = 13) per courtship sequence. This typical *head-down* display was performed immediately before and after copulation. Head-pecking occurred at the start of copulation. The pecks were aimed at the black side of the neck of the female. A maximum of 16 copulations in a day experienced by a female was recorded at Darvill. The duration of copulation averaged 35,52 s (n = 12).

Post-copulatory displays

Immediately after copulation the *head-down* posture continued with contact behaviour and then an *upright* display was performed. This is the same type of *upright* posture recorded during the *screech* call but is less prominent. The neck is stretched strongly upwards but the nape feathers are not raised. The *alarm upright* posture was usually performed first by the male followed by the female.

Pair-bond formation

Courtship behaviour was always performed in a fixed area of the territory at Darvill Sewerage Works and at Muzi Swamp. One of the copulatory sites belonged to the female, from where she called the male. The other belonged to the male from where he could call her for sexual encounters.

When a male finds a new female, the pair bond does not become established immediately but takes some time. I could distinguish four states of relationships according to the female's response:

State 1: The female does not respond to the male's sexual call and he may even be chased or attacked by her.

State 2: The female responds to the male's call but she does not permit the male to mount. He pulls at nest material while the female appears completely indifferent.

State 3: The female responds to the male's call and allows him to mount, but copulation is not achieved successfully. Contact behaviour is observed.

State 4: Copulation is successfully achieved.

Territorial behaviour

The African Jacanas studied at Darvill showed conspicuous territorial behaviour. Male territories averaged 0,342 ha (n = 4). Female territory included the four male territories. The main characteristics of the territories were the existence of sludge and some vegetation which partially covered the ponds on which copulation was performed. The roosting areas were characterized by the presence of water and aquatic grass around the margin. Occasionally the male territories were visited by other transient male jacanas which were immediately repelled by the owners. Males advertised their territories by means of a *harsh* vocalization, especially around midday.

At Muzi Swamp male territories averaged 0,40 ha (n = 12). The territory size varied according to the stage of breeding. All successful parents of at least one offspring expanded their territories and then abandoned the place. In one case a male's territory shrank when the owner (*G*/YY*) lost his clutch and a new male (*BB/*R*) settled on one side of his territory, competing for access to the same female. *BB/R** started to displace *OB/*R*'s territory on the opposite frontier when his offspring were about 24 days old and another male (**/WBk*) took over the original *OB/*R*'s location where the female laid one egg which was robbed the following day. Nine days later **/WBk* left.

The Alarm Display

Two main observations support the idea that the *upright* posture that accompanies the *screech* call is elicited more by an impulse to escape than to be aggressive.

(a) The posture occurred mainly when a sudden disturbance happened, such as the sudden appearance of an eagle, crocodile or any threatening intruder. The interval between the appearance of the intruding figure and the reaction was sometimes so short that there was no time to escape. However, as a general rule aggression took more time to manifest itself than the drive to escape.

(b) The *upright* posture was always present as part of the post-copulatory display, which means that, once the sexual act was complete, the sexual drive decreased, as did aggression; the fear drive became dominant as the birds separated, prompting a strong tendency to escape. Fear arises because during copulation the birds cannot pay enough attention to their surroundings. The male almost always performed the *upright* posture first and then the female joined him. This suggests that the male is less aggressive than the female and that is why he adopted the *upright* posture first.

DISCUSSION

The African Jacana presents a well defined set of call patterns, easy to distinguish through sonagraphic analysis. The major call types are low-amplitude contact calls for communicating with mate or offspring (*guang-guang* call, *purring* call, *chick-calling* call) and highly variable and louder calls given in many different contexts (*harsh* call, *screech* call, *harsh-trilled* call).

A polyandrous mating system might have promoted the evolution of a highly variable vocalization system in which determining territorial boundaries, assessing female sexual receptiveness and conveying information about possible threats could be essential for survival. One indication of this is that the territorial vocalizations (*harsh* and *harsh-trilled* calls) are extremely variable and uttered mainly by males which are forced to share the female superterritory. Living side by side may have prompted the development of mechanisms to avoid serious attacks between males, thereby smoothing social interactions and that could be the reason for the variation in the expression of territorial calls.

Many questions arise when visual displays are related to vocal communication and contact behaviour. One of these is the presence of a colourful fleshy shield on the crown. The parts of the male's anatomy that is rubbed on to the female's body during contact behaviour are actually the crown and bill. Is the shield so highly sensitive that this sensation could be part of sexual reward during courtship behaviour ?. Both sexes present the shield with no apparent variation. Is this a legacy of a formerly monogamous mating system involving mutual ruffling of feathers ? Does the *head-down* posture has something to do with the presentation of the shield?

More investigation about the origin and evolution of visual displays is needed but this would be achievable only when similar studies are done on the other species of jacanids and rallids with fleshy shields. A typical example of a comparative study would be between the Madagascar Jacana *Actophilornis albinucha* and the African Jacana. The colour pattern on the neck and head is reversed between these two closely related species, which is the only difference in plumage colouration between them. Could this single difference in colour pattern lead to a difference in visual displays?

Tarboton (1992) was the first to notice that male African Jacanas prod at females with the bill during courtship, but he did not give it special attention, nor did he note that a male may tuck his head under the female's wings.

Contact behaviour is well known, especially in Psittaciformes and in some Passeriformes but not in Charadriiformes according to the available literature. The origin of this ritualized behaviour might be explained in terms of classical ethology. Many cases have been reported in which behaviour typical of chicks is incorporated into the ritualized behaviour of adults. For example, food exchange in young parrots is one of the sources of ritualization considered by Dewsbury (1978). *Head-tossing* in gulls is an example of an infantile movement that becomes ritualized to an appeasement display in adults (Tinbergen 1959). In *head-tossing* the head is lifted upwards and the bill may be open wide or shut. The posture is accompanied by a chick-like call. Tinbergen (1959) suggested that this display in Laridae is derived from food-soliciting behaviour in young gulls. *Head-tossing* is performed by both sexes as a pre-copulatory display; in other words, the infantile soliciting pattern reappears later in the ontogeny of gulls as a part of sexual soliciting behaviour. Another example is the courtship feeding of lovebirds *Agapornis* (Dewsbury 1978) in which food-transfer behaviour by females to chicks is performed by males to females during courtship. However, food is not exchanged in the more recent species of lovebirds, though it is in more primitive species.

The reason why many courtship-feeding displays occur in animals is because infantile movements reduce aggression (Lorenz 1963). Infantile behaviour is very commonly used in appeasement to reduce the aggression in the partner by stimulating a parental response (Manning 1979). Contact behaviour may occur during courtship because of the temporary invasion of individual space in order to copulate.

Ritualized behaviour may evolve from movement patterns already established in an organism (Grier 1984; Dewsbury 1978; Drickamer & Vessey 1992). Contact behaviour in the African Jacana as part of courtship may have evolved from *Chick-carrying*. Considering the ancestral Jacana to be monogamous because of the presence of a bent radius in both sexes (Fry 1983), it is possible that the female African Jacana would still be able to perform *Chick-carrying*, at least in a ritualized form. It is quite likely that *Chick-carrying* behaviour, a set of behaviour patterns established during the downy stage in the African Jacana, serves as a ritualized appeasement display in adults.

Chick-carrying and contact behaviour differ in orientation. In the former, the chicks enter the father's wings from the front while most of the contact behaviour is performed from the back (though it could occur from the front and sides as well). This change in orientation could easily have happened as a result of ritualization. It is not necessary that the whole structure of primary *Chick-carrying* behaviour becomes ritualized: only some of the features of the pattern need be modified according to the context.

This is a possible explanation of the evolution of contact behaviour in a species belonging to an order in which it is extremely rare. This behaviour is well documented by Miller 1951;

Pitman 1960; Hopcraft 1968. *Chick-carrying* was also reported by Mathew (1964) for the Bronzewinged Jacana *Metopidius indicus*.

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CHAPTER 4

THE ADVANTAGE OF POLYANDRY IN THE AFRICAN JACANA *ACTOPHILORNIS AFRICANUS*

ABSTRACT

In a group of polyandrous African Jacanas the female does not always allocate a clutch to the male with which she was copulating the most, but rather to a male which recently lost a clutch. This raises the problem of paternity for the male which receives the new clutch. The advantage of polyandry to the female is to improve her reproductive success through increasing the number of partners, while the advantage of polyandry to the male is the possibility that other males may incubate his eggs because of the potentially greater competitive advantage of his sperm. The origin of polyandry according to Lenington (1984) is discussed here.

INTRODUCTION

Polyandry occurs when females establish pair bonds with more than one male during a breeding season and has been recorded for most species of jacanas. In African Jacanas *Actophilornis africanus* the polyandrous state is variable. African Jacanas in the Transvaal, South Africa, have been recorded as monogamous during droughts but polyandrous in wet seasons (Tarboton 1995). Tarboton (1995) suggested that this was related to the rate of clutch loss and the response of dominant males which do not allow lower-ranked males access to the female: during drought the clutch loss increased because of an increase in predation and presence of mammals on the breeding area of jacanas. As soon as a dominant male African Jacana loses his clutch, he solicits for another one to the female. When clutch loss is very high the female spends most of her time with a single male.

MATERIALS AND METHODS

The study was conducted on 42 ha of the Muzi Swamp, Northern Natal, South Africa (27° 37'S; 32° 24'E) on the southeast side of the swamp where human interference was least. The breeding season of the African Jacana at Muzi Swamp started at the end of September 1991 and finished at the end of February 1992. Observations were made at close range from the shore or from a rubber boat using 16×40 Zenith binoculars.

The jacanas were trapped using a 'walk-in' trap made of 25-mm-diameter chicken-mesh with three entrances. The trap was placed over the nest for catching incubating males and on the shoreline of the swamp using tubers of *Nymphaea lotus* cut in half as bait for non-incubating birds. Once trapped, the jacanas were ringed with coloured plastic rings for identification purposes. At Muzi, 23 African Jacanas were captured and ringed with combinations of four rings (one metal and three coloured plastic)two being placed on each tibiotarsus. For example, *OB/*R* means Orange and Blue rings on the left tibiotarsus and metal ring (*) and Red ring on the right tibiotarsus. The study focused on a female and her four male partners (the largest number of males of any female in the population, within a breeding season).

RESULTS

At Muzi Swamp, copulation was recorded on the third laying day with a minimum interlaying period of 5 days. The frequency of copulations of four males paired with the same female was recorded (Table 4.1). In many cases the female did not follow the allocation of a clutch according to the frequency of copulation with her mates. Sometimes, a male which had few

Table 4.1 : Copulatory activity of four male African Jacanas at Muzi Swamp, KwaZulu-Natal

	Clutches							
	1st	2nd	3rd	4th	5th	6th	7th	8th
Interval[1]		31	18	11	6	27	8	10
Ratio[2]	5	6	6	3	5	4	3	5
Male *OB/*R*	0,93[3]	0,36[4]	0,0	0,0	0,0	0,0	0,0	0,0
Male *G*/YY*	0,06	0,64	0,95	0,84	1,0	0,13	1,0	0,0
Male *BB/O**	0,0	0,0	0,04	0,15	0,0	0,87	0,0	0,17
Male **/WBk*	0,0	0,0	0,0	0,0	0,0	0,0	0,0	0.83

Notes:

[1] the time elapsed between clutches, expressed in days.

[2] the female frequency of copulation, expressed as number of copulations per day (from 6:00 to 18:00).

[3] The male that received the clutch is denoted by a cell with double frame.

[4] The male that received a clutch and is successful is denoted by a cell with thick frame.

observed copulations with the female might receive a clutch despite the female having experienced more copulations with other male.

The chance that one egg drawn from each clutch belongs to its incubating male is expressed in Figure 4.1 using the equation [5]. Males OB/*R and G*/YY showed a possibility of sharing paternity with other male partner of the female. When male (*OB/*R*) received a clutch (first clutch) his female switched to a second male (*G*/YY*), but the former male lost his clutch and she then started to copulate with both. However, the first male was the one to receive the next clutch. This shows that when a dominant male receives a clutch while the female is maintaining a relationship with a subordinate male, there might be an increase of extra paternity for the latter.

DISCUSSION

The origin of polyandry

Lenington (1984) attempted to explain the emancipation of the female from parental duties by means of three possible models:

(a) Simple Predation Model;

(b) Replacement Clutch Model;

© Energetic Model.

The "Simple Predation Model" indicates that it is advantageous for females to lay multiple clutches in response to high predation rates and high availability of food. Lenington (1984) predicted that the benefits of uniparental care would be greater only under low predation. She supported this model by the fact that she did not find a significant difference between the success rates of hatching for monogamous species and for polyandrous species.

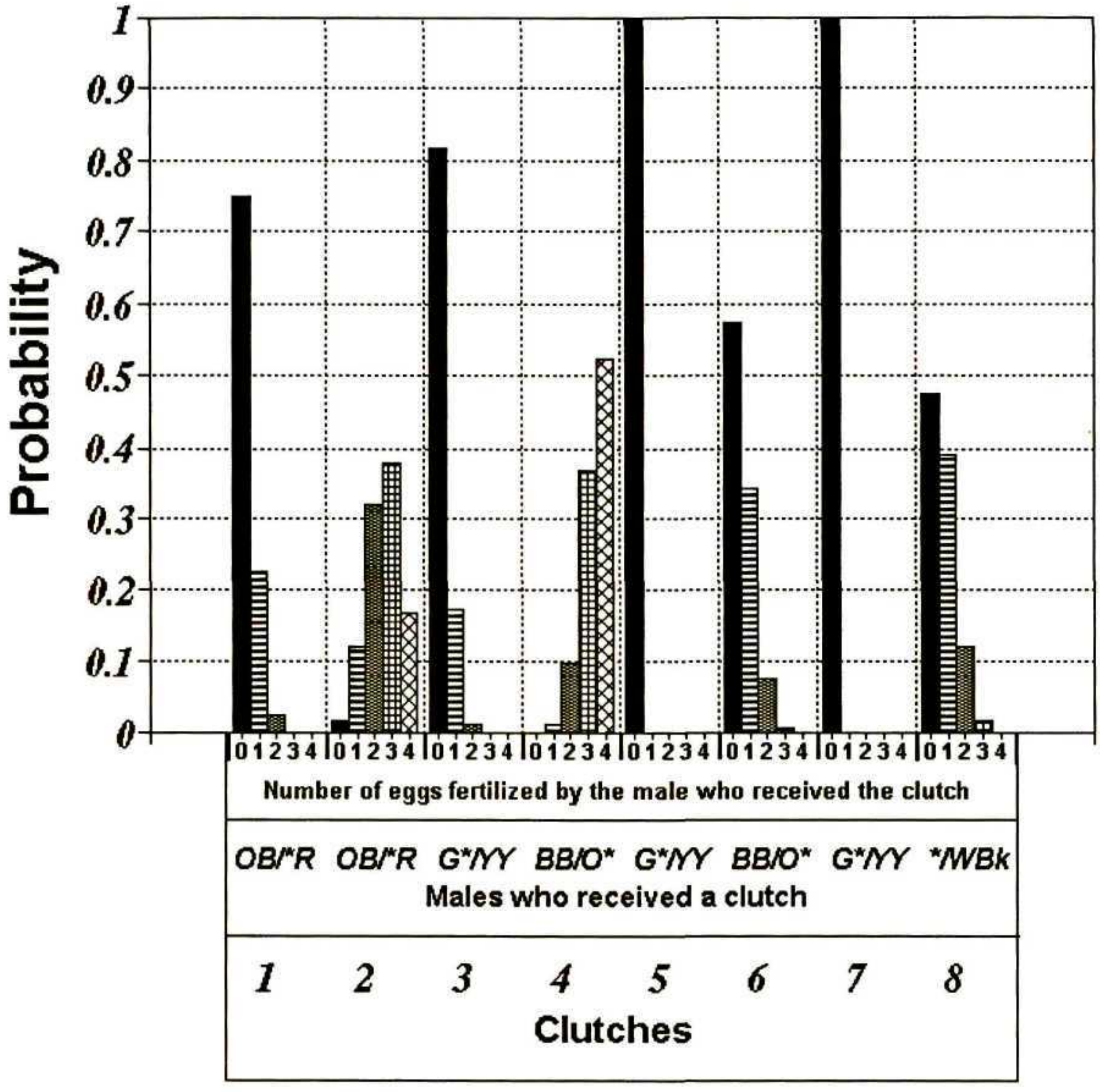

Figure 4.1: The probabilities that an incubating male fertilized 1, 2, 3 or all eggs from its clutch at Muzi Swamp.

The notations she used are as follows:

p = the probability that a nest will be destroyed

q = the probability that a nest will not be destroyed

X = the expected number of chicks raised to maturity if the nest is not destroyed and both parents participate in parental care.

aX = the expected number of chicks raised to maturity if the nest is not destroyed and only one parent tends the brood, $0 < a < 1$. Thus, a is the relative fitness of uniparental as compared with biparental pairs.

$1 - a$ = the cost of uniparental care.

Lenington (1984) compared two mating systems: (a) a typical biparental system in which the female re-nests once if the initial clutch is destroyed, and (b) a mating system consisting of rapid multiple-clutches. In a biparental system the reproductive success would be expected to be $qX(1 + p)$ and for a rapid multiple-clutch system it is $2qaX$. If a rapid multiple-clutch system should evolve it would be:

$$2qaX > qX(1+p) \quad [1]$$

This is to say that:

$$a > \frac{(1+p)}{2} \quad [2]$$

This means that for a given value of a the inequality is more likely to be satisfied only if predation is low (Fig. 4.2).

Lenington's (1984) conclusion about this inequality is that a rapid multiple-clutch system could evolve only under conditions of low predation and would be the pathway to polyandry.

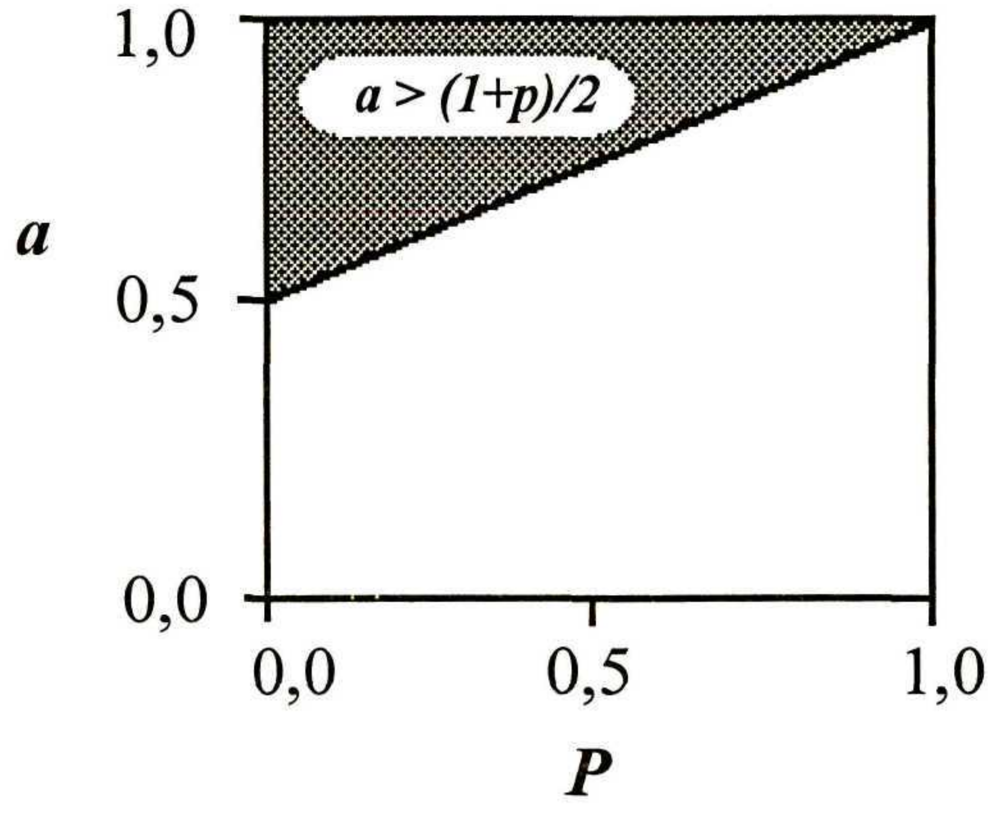

Figure 4.2: The condition for a rapid multiple-clutch system to evolve. For a given value of *a* the inequality is more likely to be satisfied only if predation is low.

I do not agree with this conclusion because Lenington(1984) considered a rapid multiple-clutch system a step on the way to polyandry, for which so far there is no evidence. The "stepping-stone" model sustained by Jenni (1974), Pitelka *et al.* (1974) and Pienkowski & Greenwood (1979) was rejected particularly by Erckmann (1983) using the following arguments:

(1) lack of evidence that selection for large female size occurs in double-clutching waders;

(2) no systematic relationships between double-clutching and polyandrous species;

(3) some polyandrous species share incubation at one nest which was not reported in double-clutching systems.

According to Lenington (1984), in a monogamous system the expected reproductive success would be $qX(1+p)$. In a polyandrous system the reproductive success for each clutch laid for a particular male plus a replacement clutch would be $qaX(1+p)$, but for n males per female it would be $nqaX(1+p)$. For a polyandrous system to evolve from monogamy, the following inequality must be satisfied: $nqaX(1+p)>qX(1+p)$ [3]

Such that: $na>1$ [4]

For a given value of a, the inequality is likely to be satisfied **with an increase in the number of partners** for a given female (Fig. 4.3).

In Lenington's (1984) "Replacement Clutch Model" the female spends more time in feeding than in incubation because of a low food supply. However, laying multiple clutches requires a high energy input which is unlikely to be met in such a situation. Lenington (1984) predicts by mathematical deduction that, if the probability of predation is high and the likelihood that an incubating female replaces the clutch immediately is low (because of poor food supply), the

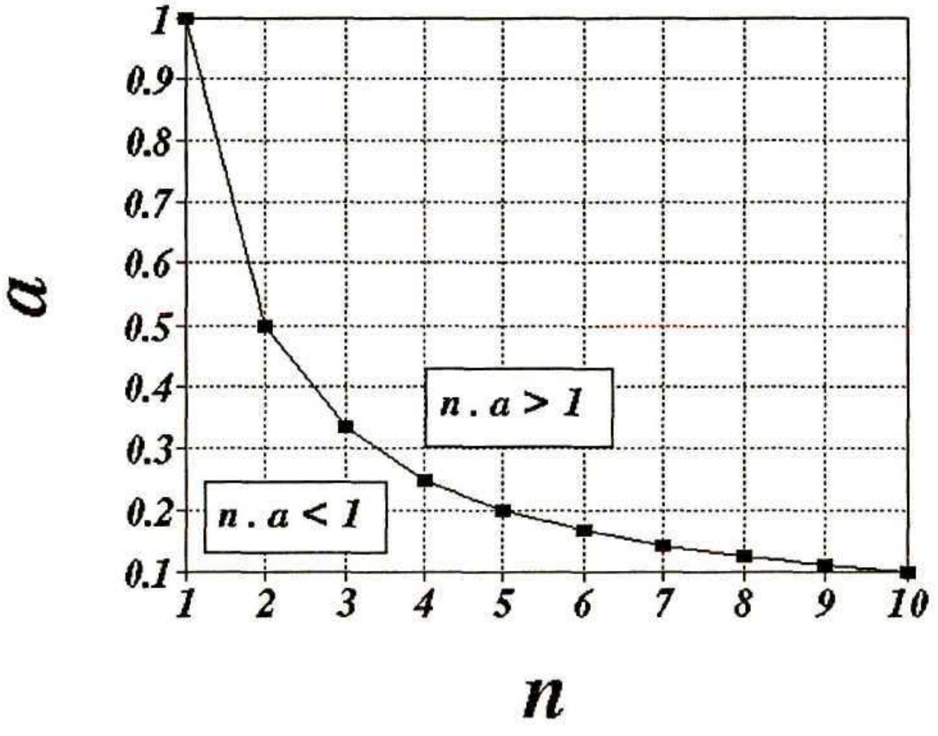

Figure 4.3: Polyandry could evolve from monogamy if the combined parental effort of all male is greater than 1. For a given value of ***a***, the inequality is likely to be satisfied with an increased in the number of partners for a given female.

female should delegate incubation duties to the male. However, Lenington (1984) found that in monogamous shorebirds incubating females tend to desert late in the breeding season (when food becomes more limited); yet they would adapt more successfully if female desertion took take place early in the breeding season.

In the "Energetic Model" desertion by the female is not related to predation but to the resource richness. Females would desert in years of low food supply. Besides that, females might abandon parental duties if there is a high probability that males remate with the same female in subsequent years.

Equation [4] shows that the female's interest is to increase the number of partners, thereby increasing the spread of her genetic information. In that way polyandry benefits females. However, little is known about the male's interest in polyandry. Valle (1994) indicates that polyandry is in the male's interest "if males gain a benefit by inseminating the female before she deserts, thus siring at least part of the subsequent brood she lays for another male". Ligon (1993) stated as well that certain compensation for males might be required to turn the system to polyandry. Valle's hypothesis would be feasible as long as the viability of sperm stored in the female cloaca is such as that it can compete against later sperm from other males.

There are two aspects to take into account: (a) the average period of sperm viability and (b) how the sperm is stored in the female cloaca.

It is known that viable sperm can be stored for about 10 days in any bird (Birkhead & Møller, 1992). No work has been done on the duration of the sperm stored in the female cloaca of African Jacanas. Birkhead & Møller(1992) found a strong correlation between the duration of sperm storage and the spread of laying.

This possibly leads one to expect cross-paternity between males because the storage time exceeds the minimum inter-laying period.

Sperm distribution in the storage tubules is important in terms of how sperm of one male would compete against sperm of other males. Birkhead *et al.* (1990) found that if insemination in Zebra Finches *Poephila guttata* takes place less than 4 h apart then paternity is proportional to the number of sperm from each male (Martin *et al.* 1974); otherwise, it was found that the last male to inseminate the female before egg laying fertilizes the majority of eggs (Birkhead 1990).

It is not possible to know the actual storage system in the African Jacana. For the African Jacana it will be assumed that the sperm from different males mixes proportionally in the female's cloaca. Another assumption of the model is that each egg in a clutch is fertilized *independently* since each one becomes receptive to fertilization at a different time at intervals of 24 hours. A third assumption in the model is that extra-pair copulations can result in extra-pair paternity (Birkhead *et al.* 1989).

Simultaneous polyandry has an advantage which has not been mentioned before and that is the possibility of maximizing the conservation of a wide range of unique traits which might disappear given a high rate of clutch loss. In monogamous species of birds with biparental care, in which the female replaces the clutch every time it is lost, the parental traits of neither mate will remain if one of the pair dies or if all clutches are lost during the breeding season. If in a polygynous mating system each female lays a replacement clutch, the result would be the same as in a monogamous one. The only advantage would be to increase the likelihood of producing descendants of the male. In the event of the death of the incubating bird (the female) all the genetic information is lost concerning both female and clutch and in this respect it would not differ much from a monogamous species.

In simultaneous polyandry each male shares the chance of rearing the young of other males. This is an important point in the sense that, no matter if one male bird dies or loses all his clutches, his genetic information will remain in eggs fertilized by him, but incubated by the other males.

What follows is a mathematical attempt theoretically to describe why simultaneous polyandry with clutch replacement is the best choice for a greater representation of the genetic traits of each male member in a group sharing the same female. Let

n = the number of partners a female can have;

N = the number of clutches the female is able to lay during one breeding season;

4 = clutch size;

f = the frequency of copulations of a particular male over the total number of copulations that the female experiences during an inter-clutch period.

I assume that sperm from different males mixes in the female's cloaca as was stated before and the chance to be fertilized by each of her males is proportional to the frequency of copulations (f). Considering the number of clutches the female lays per breeding season and the number of males with which she mates, the frequencies of copulation $f_{i,j}$ for each male I during the period leading up to clutch j can be expressed as in Table 4.2A:

To use these frequencies in the probability calculations it is necessary to convert them to probabilities $p_{i,j}$ that an egg in clutch j was fertilized by male I. If one assumes that the probability is proportional to the frequency of copulation, then the conversion can be expressed as in Table 4.2B. The probability that the male which received the clutch fertilizes 1, 2, 3 or all eggs is given by he following equation:

$$P = {}_4C_m \cdot (1 - p_{n,N})^{4-m} \cdot p_{n,N}^{m} \qquad [5]$$

where:

m = the number of eggs fertilized by the male who received the clutch.

n = male number

Table 4.2: A. frequency of copulations. B. Probability of paternity.

A

Males	Clutches laid				
	1st	*2nd*	*3rd*	....	*Nth*
1	$f_{1,1}$	$f_{1,2}$	$f_{1,3}$	....	$f_{1,N}$
2	$f_{2,1}$	$f_{2,2}$	$f_{2,3}$	....	$f_{2,N}$
:	:	:	:	....	:
n	$f_{n,1}$	$f_{n,2}$	$f_{n,3}$	....	$f_{n,N}$

Where:

$$1 = \sum_{i=1}^{n} f_{i,1}; 1 = \sum_{j=1}^{N} f_{i,N}$$

B

Males	Clutches laid				
	1st	*2nd*	*3rd*	....	*Nth*
1	$p_{1,1}$	$p_{1,2}$	$p_{1,3}$	....	$p_{1,N}$
2	$p_{2,1}$	$p_{2,2}$	$p_{2,3}$	......	$p_{2,N}$
:	:	:	:	....	:
n	$p_{n,1}$	$p_{n,2}$	$p_{n,3}$	....	$p_{n,N}$

N = clutch number

$$_4C_m = \frac{4!}{n!(4-n)!} \qquad [6]$$

Lenington(1984) did not find any difference between hatching success between monogamous and polyandrous waders, which means that the only explanation for female desertion is that a high food resources permits the female to produce as many clutches as necessary resulting in a similar breeding system success to monogamy. Davies (1992) found that in the Dunnock *Prunella modularis* the mating system is determined by the size of the female's territory. The larger a female's territory the more likely it is to be defended by more than a single male, thus leading to polyandry. Davies (1992) also found that the female's territory size depends upon the distribution of food: larger territories occurred in impoverished habitats. This indicates that territories of polyandrous Dunnock females have low food resources compared to polygynous ones. Female desertion is not feasible for the Dunnocks because of low food availability. This indicates once more that food richness is a fundamental condition in female desertion. Low food availability to Dunnocks is associated with the lack of female desertion, male cooperation, production of a single nest, female cooperation in feeding chicks and female involvement in nest building.

African Jacanas present the opposite picture with female desertion, no male cooperation, and production of as many clutches as there are male partners available; even with clutch replacement for each male and no female participation in nest building and chick rearing food availability must be very high. This means that neither the "Energetic Model" nor the "Replacement Clutch Model" presented by Lenington (1984) is feasible because they involve female desertion in the presence of low food resources. Non-limiting food resources was also found for the Wattled Jacana *Jacana jacana* by Osborne & Bourne (1977) and for the Spotted Sandpiper *Actitis macularia* by Maxson & Oring (1980). Erckmann (1983) and Maxson & Oring (1980) indicated that scarcity of food selects for biparental care rather than desertion.

The crucial point of this analysis is that when simultaneous polyandry and male hierarchy occur, then the chance of distributing genes throughout the population is increased. As a consequence of this, an amalgam of favourable and unfavourable mutations in the population could be expected, but with greater survival of the favourable ones because of faster extinction of the unfavourable traits as a result of high environmental stress. This chain of consequences from incubating the eggs of others would enhance the appropriate fitness required for a highly adverse environment, which a strictly monogamous mating system would not achieve. Research on sperm viability and distribution is needed in order to explain the system of sperm competition in the African Jacana. A paternity study using DNA finger printing would also help to elucidate this.

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CHAPTER 5

A MODEL TO ANALYSE THE OCCURRENCE OF POLYANDRY IN THE AFRICAN JACANA

ABSTRACT

A mathematical computer model was developed for the analysis of the conditions leading to polyandry in the African Jacana and related waders. The purpose of the model was to find out the environmental conditions which favour the main mating systems with particular attention to polyandry.

The model is focused on the interaction between ecological conditions (predation, weather conditions, food availability), phylogenetic traits (number of clutches laid, clutch size, parental care, egg size) and the availability of gametes. The model proposes a new scenario for weighting the contribution to the reproductive success in each mating system by using the availability of gametes as a framework.

The model predicts that polyandry is likely to occur in the African Jacana when the environment provides rich resources and when the loss of clutches is high. Polyandry is indeed the mating strategy for the population of African Jacanas living in the NE and E of South Africa as predicted by the model. Furthermore, the model suggests monogamy for the Lesser Jacana, which offers a better reproductive success for this species.

INTRODUCTION

The African Jacana *Actophilornis africanus* is a waterbird restricted to warm and wet regions of Africa. During the past decade, it has been studied extensively by Warwick Tarboton at the Deelkraal Dam, Nyl River, Transvaal. His study and mine show that African Jacanas are polyandrous (one female having several mates during a breeding season). Females are dominant over and bigger than males and do not participate in incubation and brooding duties meaning that sexual roles are reversed (see Chapter 2). Females produce replacement clutches for each of their mates as many are lost during the breeding season. A similar mating system is found in the Wattled Jacana *Jacana jacana*, American Jacana *Jacana spinosa*, Bronze-winged Jacana *Metopidius indica*, Pheasant-tailed Jacana *Hidrophasianus chirurgus* and Comb-crested Jacana *Irediparra gallinacea*. However, monogamy is the mating system recorded for the Lesser Jacana *Microparra capensis* (Tarboton & Fry 1986).

During the past decades attempts has been made to explain the adaptive significance of polyandry, since it seems a very costly mating system for females in terms of egg production and for males in terms of low genetic investment.

My object is to develop a mathematical model to understand the possible conditions leading to polyandry in the African Jacana and monogamy in the Lesser Jacana in view of their peculiar features, and to establish whether this prediction is in accordance with what actually happens in the field. Additionally, it should yield some new insights into reasons for the evolution of other mating systems, such as polygyny. This model is therefore intended to be used for the analysis of mating systems of other bird groups as well.

I shall base the derivation of the model largely on my own study of the African Jacana at Muzi Swamp, northern KwaZulu-Natal, South Africa. The studies of Erckmann (1983), Lenington (1984) and Tarboton (1991, 1992a, 1992b, 1995) have also been major influences in shaping my model.

The main contributions of this model are to develop a new perspective in the understanding of the problem of mating systems in waders and to unify the current theories on the mating systems of other birds.

GENERAL CONCEPTS

Before developing the model mathematically, certain general concepts about measuring reproductive success, avian system structure, variable selection and the value of modelling must be examined.

Differences between avian and mammalian mating systems

Before starting to determine the variables of the model, I will explain the main context in which avian mating systems are structured. There is an important difference between the determinants of mammalian and avian mating systems. While terrestrial mammals (except bats) mostly move in two dimensions and very slowly compared with birds, the main determinant is female distribution (Clutton-Brock 1991). In birds those determinants operate in a three-dimensional world and move so fast that location in time is seldom a main factor. However, the problem is that their eggs are exposed to the environment, involving high risks of predation during the incubation period (which does not happen in eutherian mammals because development occurs *in utero*). In mammals polygyny is widespread (Krebs & Davies 1993), while monogamy and polyandry are relatively poorly represented. This is because of the special characteristics of mammals, such as internal development and long lactation period, which entail a high mother-offspring dependence (Krebs & Davies 1993).

To date no male mammal capable of providing milk for the offspring has been discovered (Daly 1979). The males of all known species offer only foraged food and protection. Monogamy in mammals seems much more a "reduced-to-a-unit" polygynous mating system, whereas in some male birds, such as the African Jacana, brood patches for incubation are present in males, while male pigeons can even produce crop milk. The fact that monogamous male birds can incubate the clutch implies that they can cooperate at a much earlier stage in the development of the offspring than mammals. This suggests why monogamy in birds is the most widespread mating system. The same holds good for polyandrous behaviour. It is well known that the African Wild Dog *Lycaon pictus* and some human societies practice polyandry (Borgerhoff Mulder 1991). However, the care of the offspring is performed by the mother, which is not comparable to avian polyandry at all and, in any case, these societies have been classified as exhibiting cooperative polyandry. Rather it resembles promiscuous behaviour practised to attain optimum survival prospects. Thus, mating systems with a "true" monogamous pair bond are possible in birds because females are not embryo-dependent as mammal are. However, an additional hazard is the risk of clutch loss during incubation. Polyandrous behaviour such as occurs in the avian system (completely reversed sexual size dimorphism, paternal care, etc.) is not present in mammals because the eggs develop *in utero*.

Monogamy or polyandry with a single male ?

Many authors regard it as monogamy even when the female does not participate in incubation or brooding duties. Tarboton (1992a, 1995) mentioned that the African Jacana can be monogamous, polyandrous or even polygynous. However, my opinion is that the words "monogamy" and "polygyny" are misused when it comes to a highly polyandrous species like the African Jacana. In order to avoid any possible misunderstanding during the validation of the model these terms must be examined: the African Jacana's pattern of male parental care is **inflexible**, and females do not help males in incubation (Tarboton 1992a). My opinion is that the African Jacana is completely polyandrous even when a female can acquire only one male or even when a male can have access to more than one female. The fact that the female does not cooperate in nest building, incubation and brooding does not qualify her for those non-polyandrous mating systems such as monogamy and polygyny. To be more specific, African Jacanas perform *resource-defence polyandry*, a type of polyandry in which females control access to males indirectly, by monopolizing critical resources (Tarboton 1995). Tarboton (1995) stated that "there are two factors which appear to dictate the extent to which monogamy or polyandry is developed, namely the rate of clutch loss and the rate at which a female recycles clutches. In a rapid clutch loss situation (as occurred in the dry year) the aggressive behaviour of the dominant male leads to his obtaining most of the clutches laid by one female. Under these conditions breeding by subordinate males is suppressed and the opportunities for polyandry are minimal." This suggests that what Tarboton considers as "monogamy" is the consequence of the behaviour of a polyandrous female being solicited continuously by a dominant male because of the high clutch-loss rate.

Reproductive success per season or per attempt ?

Davies (1992) suggested that short-term estimates of breeding success, like the number of offspring produced per breeding attempt, are not good indicators of an individual's reproductive success; only long-term advantages could determine the mating system. Breeding success must be measured as the reproductive output per season and not per breeding attempt (Davies 1992).

This is important because any mating-system strategy suggested by this model is meant to be assessed over a long-time scale. If the model suggests that under particular ecological and phylogenetic conditions monogamy must be practised it does not mean that monogamy is the only mating system which will evolve in that situation, but that it is likely to be the best under those conditions.

Considering the right variables

Many authors have tried to understand polyandrous behaviour in terms of a few isolated variables. The most common factor considered was clutch replacement resulting from high predation rates (Jenni 1974; Emlen & Oring 1977; Maxson & Oring 1980; Tarboton 1995), though Lenington (1984), using a mathematical model, denied that this could lead to the evolution of polyandry. Nevertheless, Lenington (1984) suggested that food availability might be a possible explanation for the evolution of polyandry. Some other theories attempt to explain "female desertion-male incubation" as an inherent trait in waders. For example, Pienkowski & Greenwood (1979) and Ridley (1980) say that monogamous male waders shoulder most of the burden of incubation and, further, that polyandry could have evolved from monogamy through double-clutching (Graul 1974). Erckmann (1983) made a critical evaluation of most of the hypotheses mentioned above, and found that no hypothesis is convincing enough to give a complete explanation for the evolution of polyandry in Charadriiformes. Moreover, he proposes that certain conditions like reduced clutch size, the capacity to lay multiple clutches and the tendency of monogamous male waders to share more in parental care probably combine to select for polyandry. He also suggests that field data and theoretical models fail to correspond because some of the latter can be applied only under particular circumstances. Therefore, there has been a tendency to assume that a single *key factor* bears the main responsibility for the variability in the system. Perhaps, the best example of considering a key factor is employed by Hixon (1987) when using territory area as the main determinant of mating systems. However, I hereby propose that there is no single *key factor* involved in the control of the mating system. What prevails is rather the interaction between many variables of different types and origins. Besides that, some of these variables are quite dynamic, such as food concentration and other environmental effects such as predation and weather conditions. Far from a single factor determining the mating system, the model will actually show a cumulative contribution of each separate factor which promotes the evolution of a particular mating system.

There are two main problems in modelling . One is to establish the critical set of variables in the system and the other is the tendency to confer a capital value on each variable (the *key-factor* tendency). Alternatively, one might contemplate the whole package of variables, though this raises the problem of how to assess to what extent any particular variable could affect the whole system. Is any variable critical or does it merely share equal importance with the rest? What is the contribution of each variable to the system ? To determine how the outcome will be expressed, for instance, with all variables taken into account, one might investigate how the ultimate decision to adopt any particular mating system is reached.

Many of the most interesting and important questions in the biology of such systems in birds, especially among waders, concern aspects of individual life history, such as reproductivity, parental care, predation, etc.

Mathematical modelling can test a hypothesis and determine its applicability. Mathematical models allow one to test hypotheses about the operation of a system based on one's understanding of its components. Development and analysis of mathematical models provide information about the necessity of various conditions for a system and often also result in the formulation of new hypotheses or predictions.

Additionally, by systematically changing the value of variables and parameters of the model, it is possible to determine the relative contribution of specific variables to the overall performance and outcome of the system. Generally, variables that have large effects on the performance or outcome of a mathematical model can be presumed to have similar effects on real-life systems as well.

Theories on polyandry

Several theories have been proposed to explain polyandry since the classic paper on the American Jacana *Jacana spinosa* by Jenni (1974). Krebs & Davies (1984, 1994) use the ESS (Evolutionary Stable Strategy) model to explain polyandry.

P_0, P_1, and P_2 are the probabilities of survival of eggs under no parental care, uniparental care and biparental care, respectively;

p, the chance of remating again of a deserting male;

W, the number of eggs laid by a deserting female;

w, the number of eggs laid by a female who cares for the clutch;

It is assumed that $P_0 < P_1 < P_2$ and $W > w$.

The ESS model states that female desertion (withdrawal from parental care) is feasible only if :

$$WP_1 > wP_2 \qquad [1]$$

otherwise, the female will care, and also that :

$$P_1 > P_0(1+p) \qquad [2]$$

Krebs & Davies (1994) say that expression [1] is favoured only if the non-parental female is able to lay more than a parental one, and only if two parents are not much better than one in caring. Female African Jacanas are able to produce as many clutches as are solicited by males.

Biparental care would not be appropriate, first because of the weight exerted by the female on the nest would increase the sinking rate of the floating nest more than the male does and secondly, the female would not spend enough time foraging in order to produce enough eggs to offset the high clutch loss. So, the ESS model can explain, though superficially, the existence of polyandry in African Jacanas.

Erckmann (1983) explained polyandry in terms of environmental conditions: he drew attention particularly to food availability, the capacity of females to lay multiple clutches and the male capacity to assist in incubation. He did not think that high variation in food availability could select for polyandry, though a high rate of clutch loss could do so if a long breeding season permitted the multiple replacement of clutches.

Lenington (1984) indicates that low food supply selects for monogamy while high food resources for polygyny, but she says that, "Although polyandry is also hypothesized to occur under conditions of food abundance, it is probably the outcome of a process that first selects for male uniparental care".

Jehl & Murray (1986) built a model to explain the relationship between sexual size dimorphism and mating systems based on:

1 - "the ratio of breeding males to total males";

2 - "the ratio of breeding males to breeding females";

3 - "whether territorial and courtship displays occur mainly on the ground or in the air".

The polyandrous behaviour of jacanids fits into Jehl & Murray's (1986) model because as they explain "when males outnumber females sufficiently that males successful in establishing territories or dominance are often unsuccessful in obtaining mates, a male can increase his probability of breeding not by intensifying his aggression for the opportunities to obtain one of the few females but by forgoing aggression and accepting polyandrous relationships. Under these conditions, selection can favour females who contest for territories or dominant positions, leading to selection for reverse sexual size dimorphism".

Emlen & Oring (1977) state that "males should assume the bulk of parental care when there is a great fluctuation in the environmental suitability for breeding or when there is a very low success rate of reproductive attempts caused for example predation rate". Their theory indicates that the determination of a mating system is given by the degree of monopolization of mates and this in turn is established by an environment suitable for polygamy (high food resources) and ability to monopolize mates on that environment.

Jenni (1974) remarked on the importance of considering food abundance, suitable breeding habitat and predation pressure.

SELECTION OF VARIABLES

I consider the problem of finding the critical variables in a completely different context. Figure 5.1 shows a representation of life and its continuity. An organism can be viewed as an "information pool" made up of energy. For its existence it takes energy from the environment or from another "information pool". Two information pools can be combined to give rise to more of them. In this simplified framework there are two basic different components: the **information** stationary or being transferred, and **energy** coming in or going out. Contributions made so far to the explanation of the existence of any mating system are directly or indirectly in terms of energy such as using the variables of food resources (Erckmann 1983), sex ratio (Jehl & Murray 1986), capacity to lay multiple clutches (Erckmann 1983), and male incubation readiness (Lenington 1984). However, no attempt has ever been made to explain mating systems using the **amount** of information transferred.

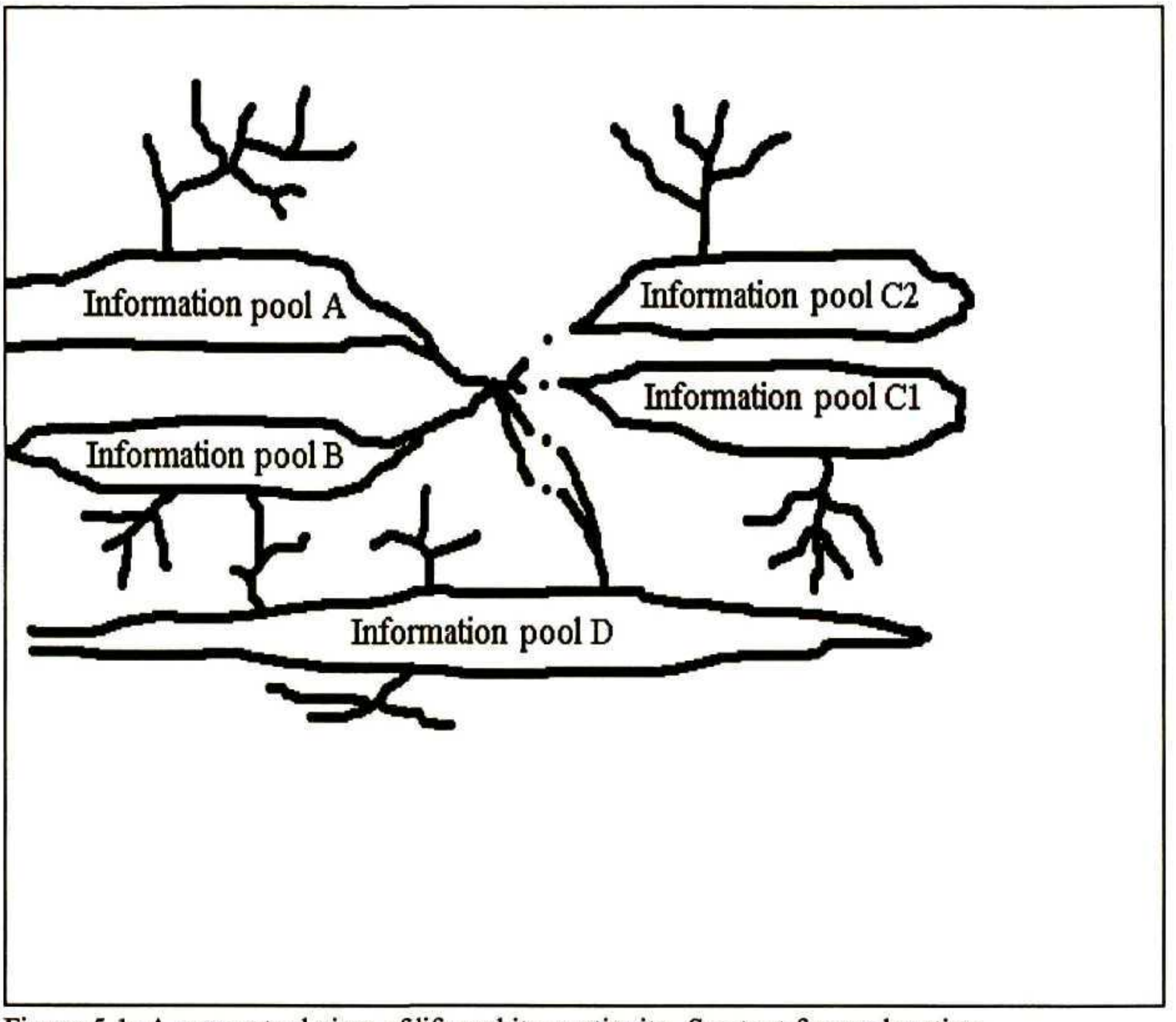


Figure 5.1: A conceptual view of life and its continuity. See text for explanation.

Mating systems are processes of transferring information from one generation to the next. It is a process that allows continuity of information. Its transfer plays an important role in the determination of mating systems. Since information passes to the gametes the number of them involved in fertilization will be used in the model as a measure of information transferred .

In the model of "information pools" the information itself is energy which can be transferred to other "information pools". For that transference, energy is required, so egg production is measured as the function of clutch size, number of clutches and number of partners (which determines indirectly the number of clutches that can be laid).

Since the energy required for information transfer may be limited, insufficient or transferable to other information pools, operational variables will be considered in the model such as cost of laying (which affects in turn the initial egg production), uniparental care, body condition and hatching success (these are highly sensitive to predation and weather).

Variability of egg production

Clutch Size

This is very stable in waders, being four eggs in the northern hemisphere and generally fewer in the southern (Maclean 1972). Erckmann (1983) indicates that the fixed clutch size of these birds could have prompted polyandry in those species which experience high clutch loss, for their only means of increasing productivity is to lay a larger number of clutches.

Clutch replacement

The number of clutches incubated by a particular male, that a female can replace, is highly variable and dependent on the species and environment in question. Thus, waders that breed in the Arctic show low clutch replacement compared with tropical species (Erckmann 1983).

Number of partners

This applies only to polygamous mating systems. In the African Jacana normally it is four to six, while Tarboton (1992a) reported as many as seven males per female.

Operational variables

Index of maximum uniparental care

In monogamous birds incubation attendance is around 99% , while in polygamous birds the sole caring member alone gives as much as 80% (Lofaldii 1985). In the American Jacana males incubate for about 45% of the day (Jenni & Betts, 1978). In the Bronze-winged Jacana 54% (Mathew 1964). Hoffmann (1950) recorded that the Pheasant-tailed Jacana a percentage of incubation of 13% during the height of the day and 60-70% during morning and evening. Lesser Jacanas incubate 82% (Tarboton & Fry 1986). In the African Jacana Postage (1984) recorded 50% and Tarboton (1992b) about 53%. Tarboton (1992b) found that during cool days the nest attendance increased to 70,9% and during a hot sunny day dropped to 43,5%. These figures for the African Jacana are very low compared with uniparental-care waders such as the Painted Snipe *Rostratula benghalensis* 80,4% (Komeda 1983), Sanderling *Calidris alba* 81% (Pienkowski & Green 1976), Pectoral Sandpiper *Calidris melanotos* 85% (Norton 1972), Great Snipe *Gallinago media* 90,3% (Lofaldii 1985) and Dotterel *Charadrius morinellus* 90% (Kalas 1986).

I define the value of maximum uniparental care as the greatest amount of time that the incubating partner devotes to the nest. In monogamous species it would be around 48% considering that the incubating attendance is almost 99%. The Lesser Jacana would have a similar figure of 41% and the African Jacana 70% since this is the highest value recorded for incubating males by Tarboton (1992b).

I assume that a biparental system of sharing the duty of incubation is better than if it were done by only one partner, since no incubation time need be lost through feeding.

The Cost of Egg Laying

The cost of egg laying to a given female can be calculated as a function of the mass of an egg to mass of the female's body. This does not take into account the relative effort of acquiring enough food to produce an egg (effort is likely to vary from species to species and habitat to habitat).

For instance, an African Jacana lays an egg of about 10 g and her body mass is around 260 g , so that, the cost of laying one egg is about 1/26 which means that for every gram of the body 0,038 g goes into the production of one egg.

Index of Body Condition:

An index of body condition for a given wader on a scale of 0-1, can be calculated relative to its theoretical food supply. Other variables are not taken into account in the calculation of this index. Figure 5.2 shows two hypothetical curves of food requirement levels for the Lesser Jacana and the African Jacana. Because of its small body size the Lesser Jacana requires less food to reach the optimum body condition.

The study in chapter 1 shows a high concentration of flying insects over the deeper waters compared to what was found by Maxson & Oring (1980) in the study of the Spotted Sandpiper could be regarded as highly abundant. Flying insects were considered in order to make a comparison with the environment of the Spotted Sandpiper, but only as an index not as an absolute value which could only have been assessed from stomach for samples which no collecting

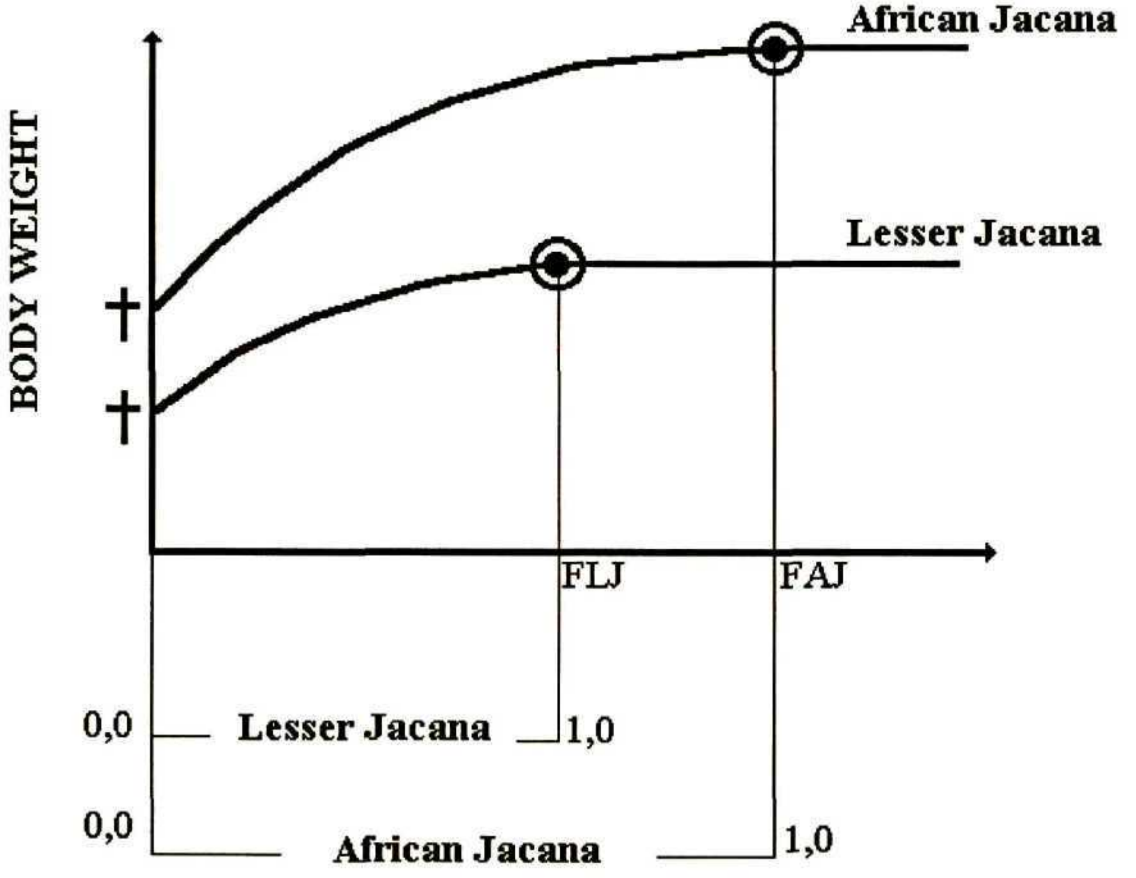


Figure 5.2 : Food requirement levels for the Lesser Jacana and the African Jacana. See text for explanation.

permits were granted. The objective of this study is to assess whether the environment of the African Jacana is comparable with that of Spotted Sandpiper in terms of food abundance.

My study and Tarboton 's (1995) opinion indicate that the breeding system observed in the African Jacana population is consistent with the predictions of the "easy breeding hypothesis" of Maxson & Oring (1980) in which both food abundance and clutch loss were high.

Hatching Success

This is highly dependent on predation and weather. I do not adopt breeding success as a measure because that includes brooding and indeed the entire fate of the chick up to attaining adulthood. For the sake of simplicity, the variables affecting incubation alone are much easier to establish and more readily accessible in the literature.

Tarboton (1992a) recorded an overall 75% of clutch loss in the African Jacana. Clutch survival (□=25%) was low in years of poor rainfall (11%) and higher in wet years (33%) Tarboton (1995). The surface area of floating vegetation used by the jacanas was less in a dry year as the breeding season progressed while in the wet year it was more extensive. Lastly, predators had a much greater impact on clutches in the dry year (0/16) than in the wet year (14/39) (Tarboton 1995).

Tarboton (1992a) found a significant proportion of clutches hatched during high water (32,7%) than during low water (11,1%) and suspected predation as the main cause of clutch loss. Moreover, he concluded that shallow water probably made nests more accessible to predators. In addition, there was the increased risk of their being trampled by cattle and other herbivores entering the water to drink and graze while greater water depth might reduce accessibility to predators. However, some clutches failed as a result of being flooded by rising water levels (Tarboton 1992a). During years of heavy rainfall jacanas find more concealment for their nests, whereas during droughts nests become more exposed to predation and adverse weather conditions.

Variables of gametic resources

These are related to the fact that the number of gametes available for fertilization during the female's lifetime is extremely small compared to the number of gametes that a male can offer during fertilization.

THE MODEL

For my model I make the following eight assumptions:

(1) Every gamete or haploid genome contains different genetic information because of recombination during Meiosis II, so each gamete is **unique** in terms of the information it contains (A. J. F. K. Craig, pers. comm.; J. Cummins, pers. comm.). Recently J. Cummins (Pers. comm.) stated that, given that each gamete is unique, an individual which produces large numbers of gametes invariably has a greater range of genotypes and phenotypes on which selection can act.

(2) The larger the number of gametes present, the greater the diversity in the set of gametes released. If it is accepted that each gamete is unique, then diversity should increase with measuring numbers of them. The diversity might be limited because of the maximum possible number of chiasmata. Besides that, there is the problem of viability of gametes. According to Cohen (1969, 1975, 1977) most of the spermatozoa are not viable. The spermatozoa go through a process of gamete selection until only the "perfect ones" reach the ova. He attributes the low viability in gametes to inexact chiasma formation.

(3) Whereas spermatogenesis is an ongoing process after puberty in males, the female ovary is invested with a limited number of primary oocytes even before birth, which will last only for her reproductive lifetime and will become exhausted at her menopausal stage (Austin & Short, 1987).

(4) Even though the number of oocytes in birds runs into millions, only a few will reach ovulation (Sturkie 1965).

(5) In birds, the number of available female gametes is thousands of times smaller than the number of available male gametes because:

(I) only one functional gamete is produced during the completion of Meiosis II in females (¼);

(ii) only the left ovary is functional (½);

(iii) in males meiosis is continuous whereas in females it happens only once for every primordium generated;

(6) Gametic availability (and therefore the variability) in the female decreases every time an ovum is released during ovulation because no new primordium will be generated and because of the process of atresia.

(7) The availability of gametes in the male is the same or similar during each copulation because gamete production is a continuous process.

(8) The total number of genes contained in a population is called the gene pool; all these genes are in chromosomes incorporated in gametes acting as a vehicle to convey them. If an individual is a mutant, its trait will not usually be transmitted, although a possibility exists that one of the chromosomes in the gamete does harbour the mutant gene and could be passed on. Therefore, for an analysis of mating-systems analysis it is more convenient to consider not the gene pool and individual genes, but rather the *gamete pool* and, in particular, viable gametes.

The number of gametes that a female can expose during her lifetime is termed the *female-gametic contribution* (in the African Jacana it could be around 200 if the female lays eight clutches per breeding season and can survive at least five years). The same feature in the male, is the *male-gametic contribution* (there are no data on spermatozoon numbers in the African Jacana but as a yardstick in the Domestic Fowl *Gallus domesticus* it is about 2,8 x 10^9 spermatozoa per ejaculate (Cohen 1969), the relationship between the two contributions is the *gametic ratio*.

I do not know whether the proportion of non-viable gametes comprises 90 or 99,99% as Cohen suggested (1969) for humans, but I would suggest a much more conservative figure of 30%. In fact the real figure does not influence the model as long as it is recognized that only VIABLE gametes are considered. Cohen (1969) coined the expression *gamete redundancy* as "the final number of sperms offered to each egg". Cohen (1977) expressed gamete redundancy as:

$$R=\frac{S}{E} \quad [3],$$

where R = Gamete redundancy, S = Number of gametes offered and E = Number of eggs fertilized. Cohen's idea is that only a very small part of the ejaculate contains viable sperm; the rest are non-viable because of imperfections acquired particularly during crossing over in meiosis. He found a very high correlation (r = 0,81) between sperm redundancy and chiasma frequency. While Parker (1984) claims that the number of spermatozoa is driven primarily by sperm competition, Cohen suggests that a high number of spermatozoa is necessary in order to produce more viable gametes to reach the female gamete. A number of questions are still not properly answered by the sperm-competition theory and why it is that so many oocytes (about 6 000 000) have to be produced in order to use only at most 40 of them in humans. Most of the rest are not fertilized (360) and the remainder undergo atresia.

Another aspect about which very little information is available in the literature is the relation between genetic information and number of spermatozoa. The latter is driven primarily by sperm competition (Parker 1984).

The uniqueness of each gamete is relative because the number of crossings over and therefore the number of recombinations per gamete is limited. "Groups" of gametes will be similar in terms of the information that they contain, like different gamete types. The gamete concept was used by Cohen (1969) to explain sperm number by saying that "there is more variety available to future generations if enormous numbers of gametes are produced". The diversity of information is also implicit in the following statement of Cohen (1969): "A very important implication of the theory concerns the rate of evolution. The implication is that genetic variation of the gametes, and in some cases of the zygote, may be a much broader spectrum than that of the adults. Note that this may be true whether or not chiasmata produce mutation as well as gene assortment, simply because of the enormous disparity of numbers in so many cases."

Cohen (1977) defined *true redundancy* (r) as the ratio of all spermatozoa (S) to all viable spermatozoa (n); therefore r^{-1} is the proportion of viable spermatozoa.

For the purpose of my mating model,

$$N = r^{-1} . S \qquad [4]$$

where N is the number of acceptable gametes (viable and with no errors), similar to the n value of Cohen. Then,

$$I = \frac{C}{N} \qquad [5]$$

where I is the proportion of viable gametes which form zygotes and therefore the amount of genetic information passed to the next generation. This is crucial for the model of mating systems. I shall use the amount of transferred information as the framework for my model of mating systems. Birds maximize the information from one generation to the other by maximizing the reproductive output. Females not only select males but once they have done so they must produce as many offspring as they can at least in the longer term (e.g.: a breeding season). Male reproductive success depends on the number of spermatozoa potentially able to fertilize the egg (Parker 1984) or the amount of information put back to the system.

Eggs are subjected to environmental effects such as predation, food availability, and temperature, as well as to endogenous factors like clutch size, cost of single-parent care and energy drainage produced by laying eggs.

So, from the original clutch size of four eggs in waders, the final number of eggs to hatch successfully is dependent on those variables mentioned above. This may be expressed as:

$$e = B \,.\, U \,.\, (F - E \,.\, C) \qquad [6]$$

where

(units are in brackets)

e is the percentage of eggs that are successful in hatching.

C is the clutch size [eggs].

U is the index of the cost of uniparental care [0,0-1,0].

E is the index of the cost of laying one egg [0,0-1,0].

F is the body-condition index [0,0-1,0].

B is the hatching-success index [0,0-1,0].

Figure 5.3 is a diagrammatic representation of the production of a clutch of eggs in an African Jacana: there are non-viable and viable spermatozoa, from which only four will be used

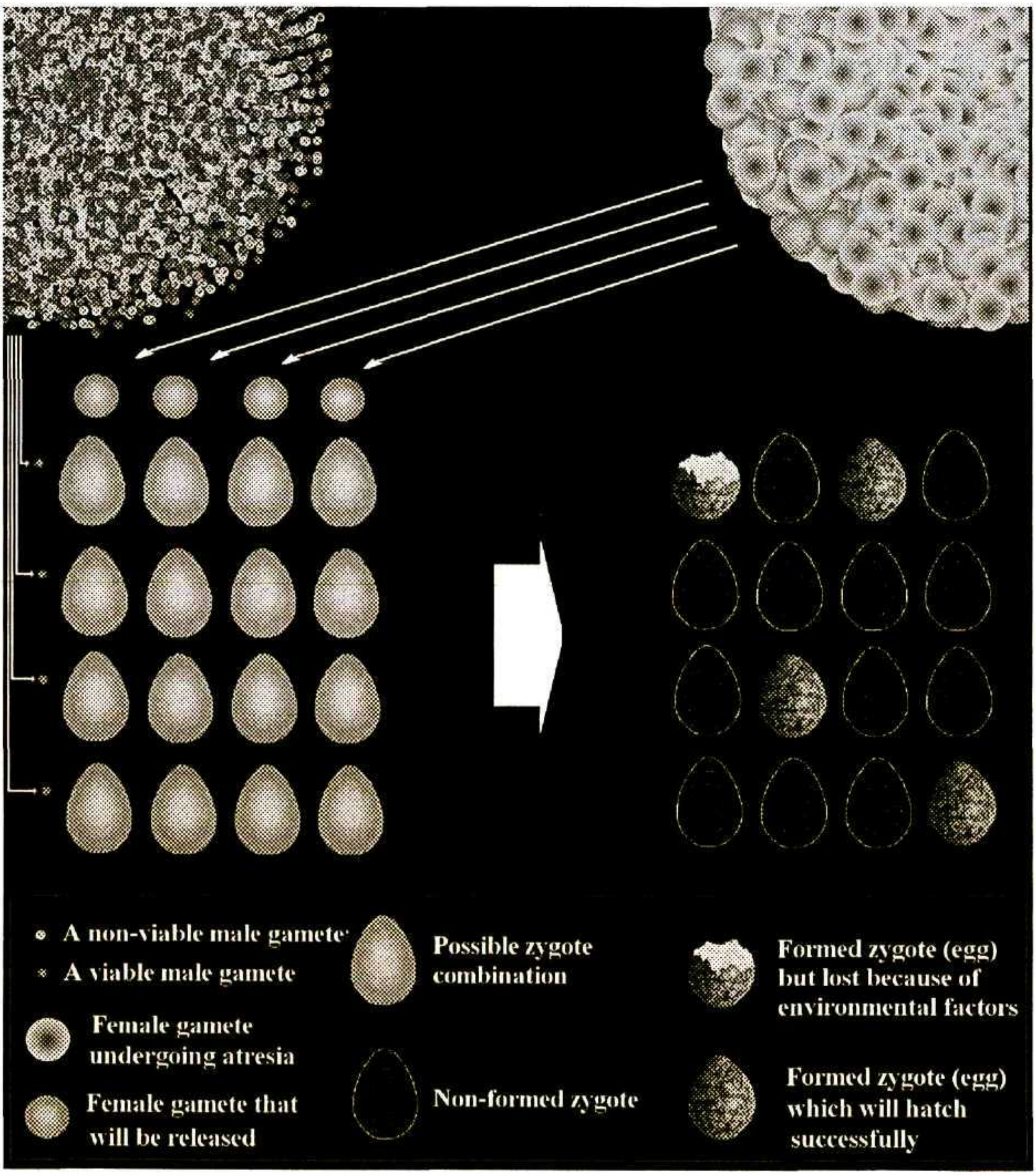


Figure 5.3 : Production of a clutch in the African Jacana. See text for explanation

during each fertilization. A similar feature occurs in the female. During fertilization 16 possible zygote combinations arise from which only four will occur in the eggs laid, and of these only some will hatch successfully. The three complete eggs in the figure represent the amount of information successfully transferred. A mathematical approach to this idea would be the following:

If $N_{♂x}$ is the total number of viable gametes available for fertilization of a particular male and only four of them fertilize eggs, then

$$\frac{C}{N_{♂x}} \quad [7]$$

would be the genetic information supplied by the male during copulation.

$$\frac{C}{N_{♀x}} \quad [8]$$

denotes the same for the female. Then $N_{♂x}$ x $N_{♀x}$ represents the number of zygotes that would be yielded if every male gamete successfully fertilized every available female gamete.

$$\frac{C^2}{N_{♂x} . N_{♀x}} \quad [9]$$

represents the proportion of all possible combinations of zygotes to the available gametes and

$$\frac{C}{\sqrt{N_{♂x} . N_{♀x}}} \quad [10]$$

the proportion that achieved fertilization.

Because the number of male gametes fertilizing ova is determined by the number of ova available to be fertilized and, further, because the sum of ova produced will be affected by variables like food resources and egg-laying cost, it is much better to work at the level of :

$$\frac{C.e}{\sqrt{N_{\male x}.N_{\female x}}} \quad [11]$$

This is true for the first copulation. For each subsequent copulation C female gametes will be used, which will deplete the $N_{\female x}$ at the end of the life cycle of the female. So, from $N_{\female x}$ four gametes will be subtracted every time a female jacana lays a clutch of eggs. This can be expressed as:

$N_{\female x}$ For the first clutch laid

$N_{\female x}-4$ For the second clutch laid in the female's life

$N_{\female x}-8$ For the third clutch laid in the female's life.

$N_{\female x}-4(m-1)$ For *m* clutches laid in the female's life

$N_{\female x}-C(m-1)$ For *m* clutches laid and C clutch size in the female's life.

Accordingly, to calculate the reproductivity of each kind of mating system in the population I established the following equations for monogamous waders. I consider C = 4 as I am dealing with waders that lay a clutch size of four.

In monogamy (M) is,

$$M=\frac{C.e}{\sqrt{N_{♂}.N_{♀}}}+\frac{C.e}{\sqrt{N_{♂}.(N_{♀}-4)}}+\frac{C.e}{\sqrt{N_{♂}.(N_{♀}-8)}}+\frac{C.e}{\sqrt{N_{♂}.(N_{♀}-12)}}+....+\frac{C.e}{\sqrt{N_{♂}.[N_{♀}-C(m-1)]}} \quad [12]$$

then:

$$M=\frac{C.e}{\sqrt{N_{♂}}}.\sum_{i=1}^{m}[\sqrt{N_{♀}-C(m-1)}]^{-1} \quad [13]$$

For polyandrous birds the productivity in polyandry (P_d) is:

$$P_d=\frac{C.e}{\sqrt{N_{♂_1}.N_{♀}}}+\frac{C.e}{\sqrt{N_{♂_1}.(N_{♀}-4)}}+\frac{C.e}{\sqrt{N_{♂_1}.(N_{♀}-8)}}+...+\frac{C.e}{\sqrt{N_{♂_1}.[N_{♀}-C(m_a-1)]}}+...$$

$$...+\frac{C.e}{\sqrt{N_{♂_2}.N_{♀}-C(m_{a+1}-1)}}+\frac{C.e}{\sqrt{N_{♂_2}.N_{♀}-C(m_{a+2}-1)}}+\frac{C.e}{\sqrt{N_{♂_2}.N_{♀}-C(m_{a+3}-1)}}+...+\frac{C.e}{\sqrt{N_{♂_x}.N_{♀}-C(m_{a+b}-1)}} \quad [14]$$

then,

$$P_d=\sum_{i=1}^{m}\frac{C.e}{\sqrt{N_{\sigma_1}[N_{\female}-C(m_a-1)]}}+\sum_{i=1}^{m}\frac{C.e}{\sqrt{N_{\sigma_2}[N_{\female}-C(m_{a+b}-1)]}}+\ldots+\sum_{i=1}^{m}\frac{C.e}{\sqrt{N_{\sigma_x}[N_{\female}-C(m_{a+b+..+x}-1]^{-1}}} \quad [15]$$

and finally,

$$P_d=C.e\sum_{j=1}^{x}\sum_{i=1}^{m}\sqrt{[N_{\sigma_x}(N_{\female}-C(m_{a+b+...+x}-1))]^{-1}} \quad [16]$$

For polygynous birds:

$$P_g=\frac{C.e}{\sqrt{N_{\male}.N_{\female_1}}}+\frac{C.e}{\sqrt{N_{\male}.N_{\female_2}}}+\ldots+\frac{C.e}{\sqrt{N_{\male}.N_{\female_x}}} \quad [17]$$

Then:

$$P_g=\frac{C.e}{\sqrt{N_{\male}.N_{\female_1}}}+\frac{C.e}{\sqrt{N_{\male}.(N_{\female_1}-4)}}+\frac{C.e}{\sqrt{N_{\male}.(N_{\female_1}-8)}}+\ldots+\frac{C.e}{\sqrt{N_{\male}.[N_{\female_1}-C(m_1-1)]}}+\ldots$$

$$\ldots+\frac{C.e}{\sqrt{N_{\male}.N_{\female_2}}}+\frac{C.e}{\sqrt{N_{\male}.(N_{\female_2}-4)}}+\ldots+\frac{C.e}{\sqrt{N_{\male}.N_{\female_3}}}+\frac{C.e}{\sqrt{N_{\male}.(N_{\female_3}-4)}}+\ldots+\frac{C.e}{\sqrt{N_{\male}.[N_{\female_x}-C(m_x-1)]}} \quad [18]$$

and finally:

$$P_g = \frac{C.e}{N_{\male}} \cdot \sum_{j=1}^{x} \sum_{i=1}^{m} \sqrt{[N_{\female_x} - C(m_x - 1)]^{-1}} \qquad [19]$$

Another major consideration is the values of P_g and P_d from the male and female point of view respectively, so that the relevant equations of every mating system are:

Monogamy from male and female points of view.

$$M = \frac{C.e}{\sqrt{N_{\male}}} \cdot \sum_{i=1}^{m} [\sqrt{N_{\female} - C(m-1)}]^{-1} \qquad [20]$$

Polyandry from the male point of view.

$$P_{d\male} = \frac{C.e}{N_{\male}} \cdot \sum_{i=1}^{m} \sqrt{[N_{\female} - C(m_{a+b+...+x} - 1)]^{-1}} \qquad [21]$$

Polyandry from the female point of view.

$$P_{d\female} = C.e \sum_{j=1}^{x} \sum_{i=1}^{m} \sqrt{[N_{\male_x}(N_{\female} - C(m_{a+b+...+x} - 1))]^{-1}} \qquad [22]$$

Polygyny from the female point of view.

$$P_{g\female} = \frac{C.e}{\sqrt{N_{\male}}} \sum_{i=1}^{m} \sqrt{[N_{\female_x} - C(m_x - 1)]^{-1}} \qquad [23]$$

Polygyny from the male point of view.

$$P_{g♂}=\frac{C.e}{\sqrt{N_{♂}}}.\sum_{j=1}^{x}\sum_{i=1}^{m}\sqrt{[N_{♀_x}-4(m_x-1)]^{-1}} \qquad [24]$$

So far, the model tell that the amount of information passing from one generation to the next under a particular mating system. However, it says nothing about which mating system is the best, particularly considering that what is beneficial for the male might not be necessarily so for the female. The values obtained from these equations must be compared in order to determine from which mating system male and female obtain the greatest mutual benefit. At this point the outcome of the model will depend on the assumptions regulating the selection of mating system, that is whether one or both partners will benefit from participating in a particular mating system.

One of the most important assumptions of this model and which will be tested is that, merely to exist, any mating system must benefit both male and female. This is contrary to Erckmann's (1983) conclusion that "females need not benefit by male emancipation for polygyny to evolve, nor must males benefit by female emancipation for polyandry to evolve". Erckmann's statement was recently rejected by Ligon (1993) on the basis that some benefit must reach the males in order to turn the system to polyandry, for example siring first and subsequent broods.

Polyandry is very rare, being found in only 1% of the 8500 species of birds (Jenni 1974). This is probably because there exist few situations in which polyandry would benefit males. If polyandry were to benefit the males more than it actually does, it would be a more common mating strategy.

VALIDATION OF THE MODEL

Introduction

African Jacanas and Lesser Jacanas in South Africa are confined to the northern and eastern areas (Maclean 1985) corresponding to the forest and bushveld vegetation where swamps and lagoons are abundant because of a relatively high precipitation rate.

In order to validate the model it has to be able to predict the following :

1- that the ecological conditions for promoting polyandry in the case of jacanids are high food resources and low clutch success as expected from the theories of Emlen & Oring (1977), Maxson & Oring (1980) and Tarboton (1995).

2- that, considering the environmental conditions in the region where the African Jacana occurs in South Africa, it should explain the practice of polyandry by this population of African Jacanas and monogamy for the Lesser Jacana showing continuity throughout at least the last 100 years.

The use of this model will reveal incidentally the following :

1 - whether a single partner or both members of the bond are advantaged in the execution of a particular mating system;

2 - a possible relationship between precipitation level and the ecological conditions given by the precipitation level.

Material and methods

The computer model

The mathematical model developed above was written into a computer language using Turbo Pascal 7 in order to facilitate the calculations and allow the exploration of the model.

The programme considers three different mating systems: monogamy, polyandry and polygyny and calculates the information transferred for each type and member of each mating system, then according to specific rules it selects those which satisfy those rules.

The use of this programme permits one to examine how each variable considered may affect the whole context and provide tentative explanations of many cases of choice of mating system.

The programme consists of:

1- the **initialization** step: where all variables are initialized. The computer model assumes that:

Number of clutches laid in monogamy = 1

Number of male partners in polyandry = 4

Number of female partners in polygyny = 4

Clutch size in monogamy, in polyandry and in polygyny = 4

The cost of laying one egg in monogamy and in polygyny = 4/100

The cost of laying one egg in polyandry is = 0.038

Maximum index of uniparental care = 0.7 (nest attendance is 70% of the day time)

Gene pool in monogamy, in polyandry and polygyny = 10^9 (is a number big enough to be handled by Turbo Pascal and enough for the purpose of this model).

Female gamete contribution in monogamy, polyandry and polygyny = 100 (I assume that 100 ovules are produced during the lifetime in polyandry)

Gametic ratio in monogamy, polyandry and polygyny = 1E-6 (In this value 0,000 001, it is implicit the male-gamete contribution, which is 100 000 000. Probably this number is small but it is big enough for the model and to be handled by the compiler)

In the following a polyandrous female has four males and lays two clutches to each of her males, and the females in a polygynous system each lays a single clutch.

The male-gamete contribution for each mating system is obtained as:

Male-gamete contribution = Female-gamete contribution / Gamete ratio

2- the **calculation** step: where the amount of information transferred is calculated for each case of mating system following the equations [20], [21], [22], [23] and [24].

3- the **decision** rules: where the programme compares those information values and, following a logical operation (AND, OR), obtains the mating system that satisfies the set of rules.

4- the **presentation** step: the programme shows the result on a contour diagram portraying the range of body condition and hatching success. This step was modified according to the need of visualizing different variables.

The programme starts by reading the value of each variable, then calculates the information transference for each mating system and for each member and then compares those values: between them following a set of rules that *both female and male are advantaged by the mating system being performed.* The highest value of information transference obtained following that rule will be portrayed on the screen as a coloured dot corresponding to the mating system. For example, a red dot means that monogamy was selected, a green dot corresponds to polyandry and a magenta dot to polygyny, while a white dot means that the conditions do not satisfy the set rule. The whole procedure can run in different ways in order to explore the model: one of these ways is to run the model on a range of 0 to 1 for hatching success and 0 to 1 for body conditions producing a contour diagram as was done in Figure 5.7. Another possibility is to make it run as well on a range 0 to 1 of uniparental care rendering a 3D image as was done in Figure 5.9. Yet another way to view the model was to provide the system with specific values of body conditions and hatching success obtained from another source such as precipitation and plotting the dots on a graph (Fig 5.11 and 5.12) or on a map where the source value was taken (Figure 5.14).

For the second part of the prediction the model is tested using precipitation values corresponding to 94 years from 1900 to 1994 covering the northern and eastern of South Africa (Fig. 5.4). The data set comprises 934 stations on a total of 36 491 records. Data on precipitation were provided by the Computing Centre for Water Research, University of Natal, Pietermaritzburg. Precipitation was taken as the main variable determining the environmental conditions of the area in order to feed the model because:

1- it determines the availability of food (presence of plants and insects on/in water and air)

2- it determines the availability of water bodies and hence the presence of aquatic plants, such as waterlilies, thus establishing the right conditions for breeding.

3- excess of rain can lead to flooding, wiping out floating nests or causing sinking problems in the nest. Tarboton (1992a) recorded 8% of clutch loss because of rising waters.

4- lack of rain can have an even more dramatic effect leading to:

a - nest exposure to predation;

b - nests become more accessible;

c - decrease of food resources;

d - waterlilies as a breeding substrate become scarce;

e - reduction of space for establishing territories.

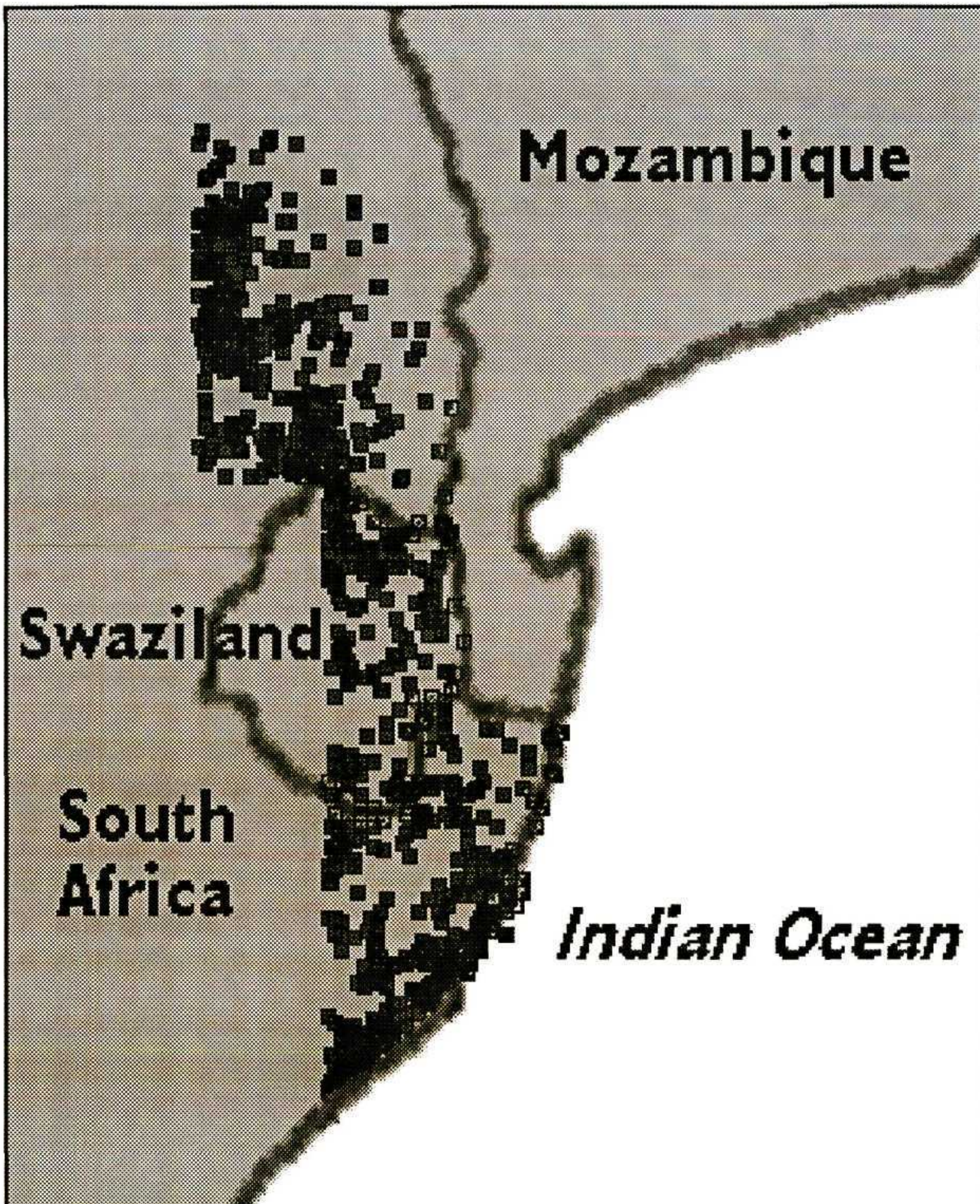


Figure 5.4 : Area of South Africa where data on precipitaion of 934 stations were used for the validation of the model.

The precipitation level of those areas was taken in order to obtain data on food availability and hatching success for the validation of the model. This was then converted into body-condition levels and hatching-success values.

Hatching success can be considered as an inverted quadratic function of the precipitation (Fig. 5.5):

$$H=-(\frac{P}{P_x}-0,5)^2+H_x \qquad [25]$$

where Hx is the maximum hatching success attainable under the best environmental conditions. Px is the maximum precipitation level under which all clutches are destroyed by flooding or weather conditions.

The relation between food availability and precipitation could be interpreted as a direct function. Three different functions were used since it is not possible to find the exact type of relationship (Fig. 5.6):

$$F=\sqrt{(\frac{P}{P_{op}})} \qquad [26] \qquad\qquad F=\frac{P}{P_{op}} \qquad [27] \qquad\qquad F=(\frac{P}{P_{op}})^2 \qquad [28]$$

where P is the precipitation level, P_{op} is the optimum precipitation level which yields the highest hatching success.

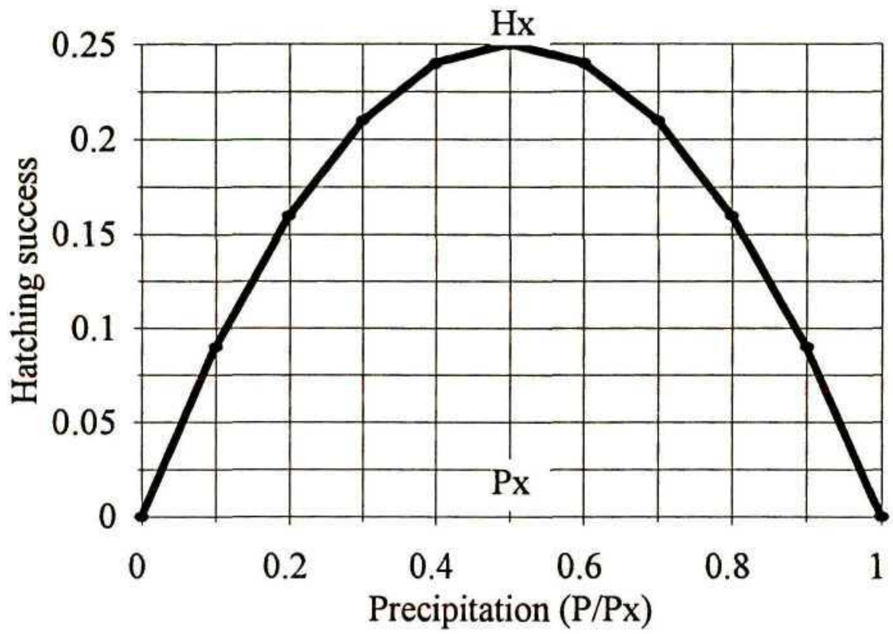


Figure 5.5 A possible relationship between maximum hatching success and precipitation levels. P = Precipitation level; Px = maximum precipitation level; Hx = maximum hatching success attainable under the best environmental conditi

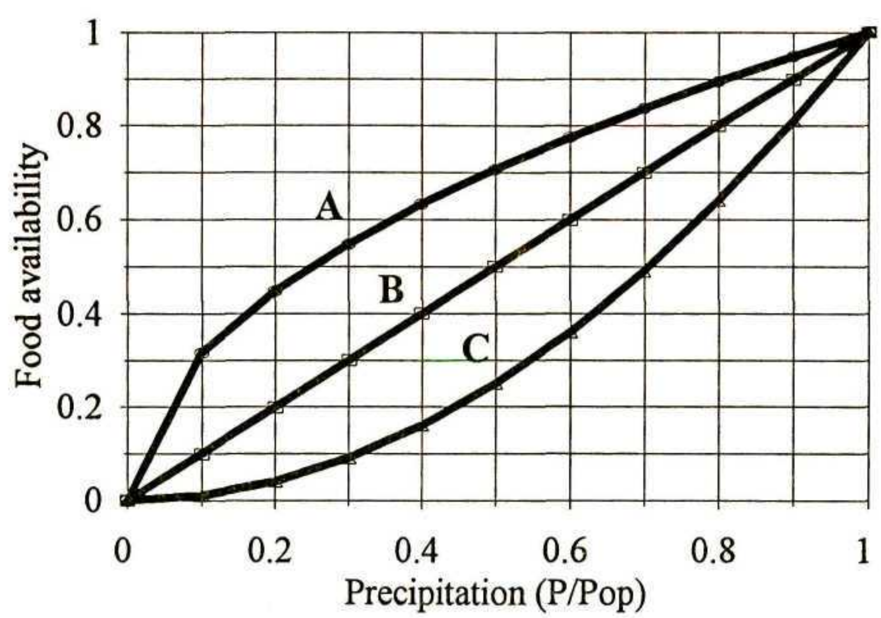


Figure 5.6 Three possible relationships between food conditions and precipitation levels. P = precipitation level; Po = Optimum precipitation level that yields the highest hatching success .

TEST

The environmental conditions for polyandry

Selecting the rules

According to Erckmann (1983) it is not necessary that both partners benefit to participate in a specific mating system while Ligon (1992) disagrees by saying that in polyandry the male must have some benefit too. Both these and more assumptions will be tested using the model by setting the rules as follows:

Rule 1: ***Both female and male benefit from participation in the mating system.***

Fig. 5.7A shows that the mating systems are not easily defined on the high hatching success-high food resources area of the contour diagram and polyandry appears as a narrow option in the area of high food resources and low hatching success. Monogamy seems possible only in the area where hatching success is high and food availability limited.

High hatching success-high food resources area, mating systems are not defined at all representing probably as the area of high cross interest between sexes. Polygyny does not appear on the diagram.

Rule 2: ***Only one partner benefits from the mating system (the female in polyandry, the male in polygyny and either partner in monogamy).***

Fig. 5.7B shows that polygyny arises where food supply and clutch survival are relatively high. The mating systems are defined and polyandry is not only expected as in the previous case but in the high hatching success-high food resources area of the diagram.

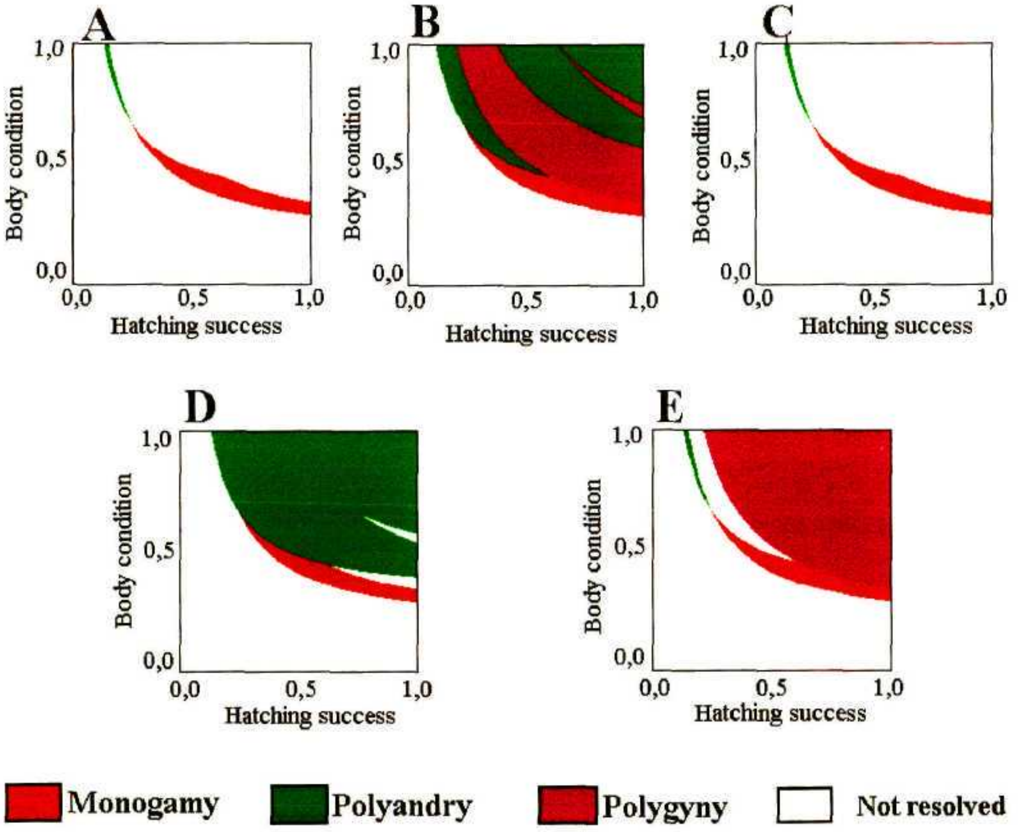


Figure 5.7: Model rendered under a range of body condition, hatching success and the following assumptions:

A: both female and male are advantaged by the mating system being performed.

B: only the male in polygyny and the female in polyandry are advantaged.

C: only females in polygyny and males in polyandry are advantaged.

D: only females are advantaged.

E: only males are advantaged.

Rule 3:*Only females benefit in polygyny and males in polyandry.*

Fig. 5.7C This is a similar image as in the first case. Polygyny is not resolved.

Rule 4: *Only females benefit.*

Fig. 5.7D shows that polyandry covers much of the high hatching success-high food resources area of the contour diagram and is very well defined. Interestingly, polygyny is not resolved at all. This shows that if female interest were the only requirement for mating choice, then polyandry would be a more common mating system.

Rule 5:*Only males benefit.*

Fig.5.7E shows that polygyny is broadly defined and in the area of high food resources and high hatching success. Polyandry is restricted as in the first case.

Conclusion

The best option would be to use rule 5 in which the model allows small opportunity for polyandry in the area of high food availability and high clutch loss as was foreseen by many authors, in particular by Tarboton 1995. Polygyny is quite widespread. The real situation would be an intermediate state between rule 1 and rule 5 because the female plays an important role. For example, Figure 5.8 shows the amount of information transferred in a polyandrous mating system, revealing that in polyandry the female gains the most, thus playing an important role in mating choice. Another thing is that, besides the enormous difference in values between males and the female, there is still a possibility for males to benefit by polyandry under conditions of high food supply and high clutch loss. For that reason, I assume the first rule to be the most representative because that both females and males play an important role in mating-system strategy.

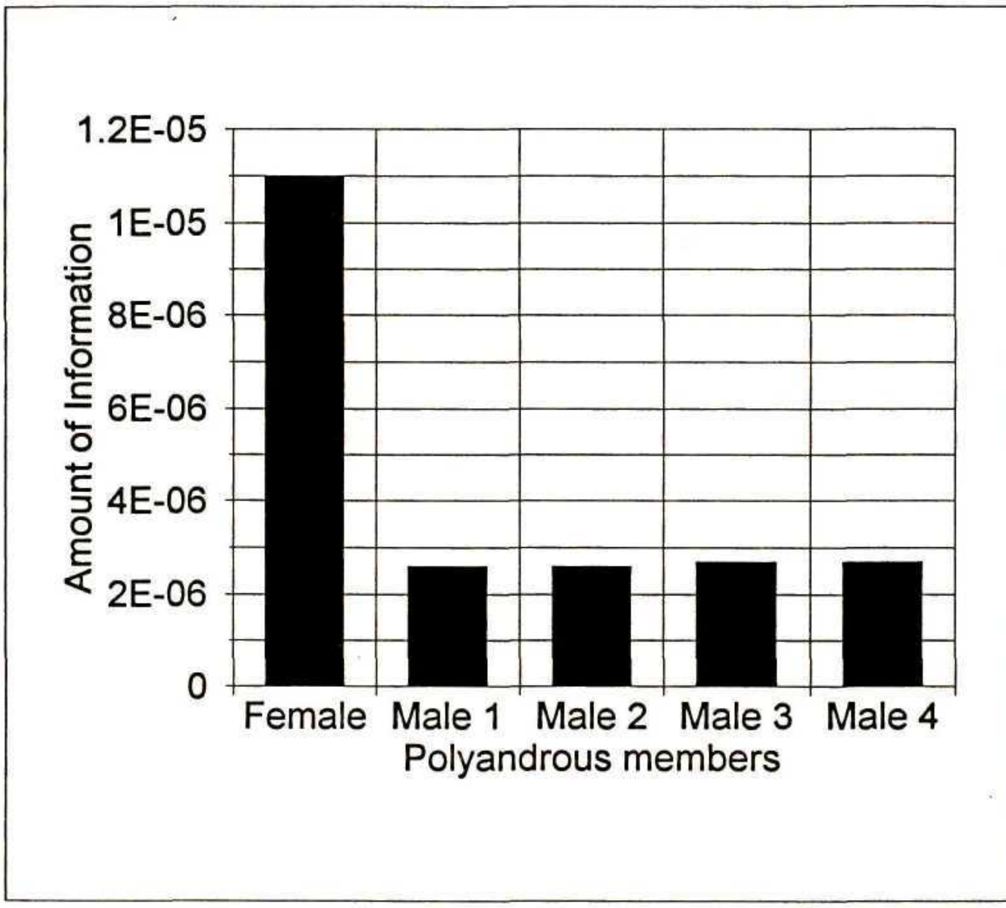


Figure 5.8: Amount of information transferred in a polyandrous mating system. The female gains the most.

If polyandry is regarded as the mating system with the most developed clutch replacement, because the female spends most of her time foraging, it occurs where there is high food concentration associated with high clutch failure. In fact, I found this to be the most suitable model for the African Jacana and other monogamous and polyandrous waders. When food supply is low and hatching success is high, only monogamy will prevail as the female cannot replace the clutch so easily.

Fig. 5.9A is Figure 5.7A plotted along a range of uniparental care. In this way it is possible to see that polyandry is manifested in areas of good body condition and low hatching success. This is consistent with the information available on the African Jacana and some other polyandrous waders and raises some questions about the evolution of monogamy in the Lesser Jacana.

Confirmation of this prediction

Food abundance

I found food concentration in the African Jacana's environment rather more than double that of the Spotted Sandpiper *Actitis macularia* (see Chapter 1), whose environment is regarded by Maxson & Oring (1980) as having "excellent and relatively predictable food resources". There is no separate study of food richness in the habitat of the Lesser Jacana because it shares the same habitat as the African Jacana, competes for the same type of food (arthropods), but overlaps only slightly with the territories of the African Jacana. Polyandrous waders like phalaropes *Phalaropus* and Eurasian Dotterels *Eudromias morinellus* living at high altitudes experience relatively better feeding conditions than monogamous Arctic waders (Erckmann 1983).

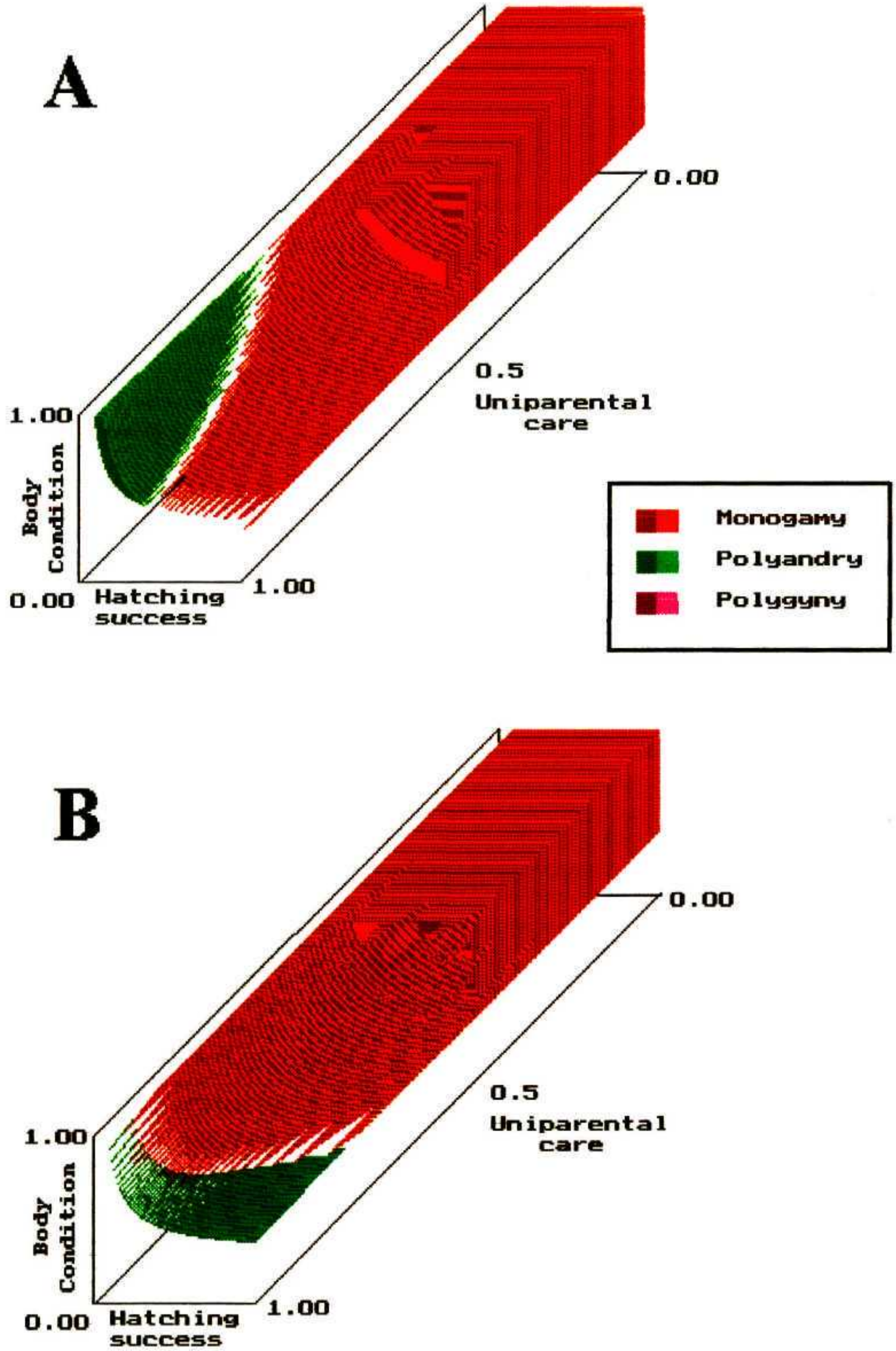


Figure 5.9 A: Outcome of the model rendered on a range of body conditions, hatching success and maximum uniparental care. Polyandry is manifested in areas of high body conditions (high food resources) and low egg hatching. Polygyny is not rendered.

B: Model generated with single clutch replacement for polyandry, monogamy and polygyny.

Hatching success

Hatching success in the African Jacana is extremely low, around 15% to 25%, mainly because of problems of nest sinking, weather, predation, disturbances, etc. In the Spotted Sandpiper the hatching success is higher, around 44.2% (Lenington 1984), probably because it does not have nest-sinking problems and suffers less predation (MacArthur 1972).

Uniparental care

Nest attendance in male African Jacanas is about 60-70 % (Tarboton 1992, 1995) which is less than that of the Spotted Sandpiper whose nest attendance is between 68.2% and 80.2% (Maxson & Oring (1980)). The greater value of "uniparental care" of the Spotted Sandpiper is probably demanded by the low temperature in the environment. Tarboton (1992b) indicates that low nest attendance by male African Jacanas is possible because high ambient temperatures, allow longer absence from the nest. American Jacanas, Bronzewinged Jacanas *Metopidius indicus* and Pheasant-tailed Jacanas *Hydrophasianus chirurgus* show lower nest attentiveness than do polyandrous waders of colder regions like the Red Phalarope *Phalaropus fulicarius*, Northern Phalarope *P. lobatus* and Eurasian Dotterels (Erckmann (1983).

Fig. 5.10 is a sketch of Figure 5.9A integrating the information on food concentration, hatching success and uniparental care and plots the mating systems of the African Jacana, Spotted Sandpiper, and Lesser Jacana.

The model predicts both polyandry and monogamy for the Spotted Sandpiper, but only the latter if one mate is unable to maintain a high degree of uniparental care. Monogamy is well recorded in Spotted Sandpipers by Maxson & Oring (1980). On the other hand, the African Jacana is restricted to polyandry because of the extraordinarily high food concentration and extremely low hatching success.

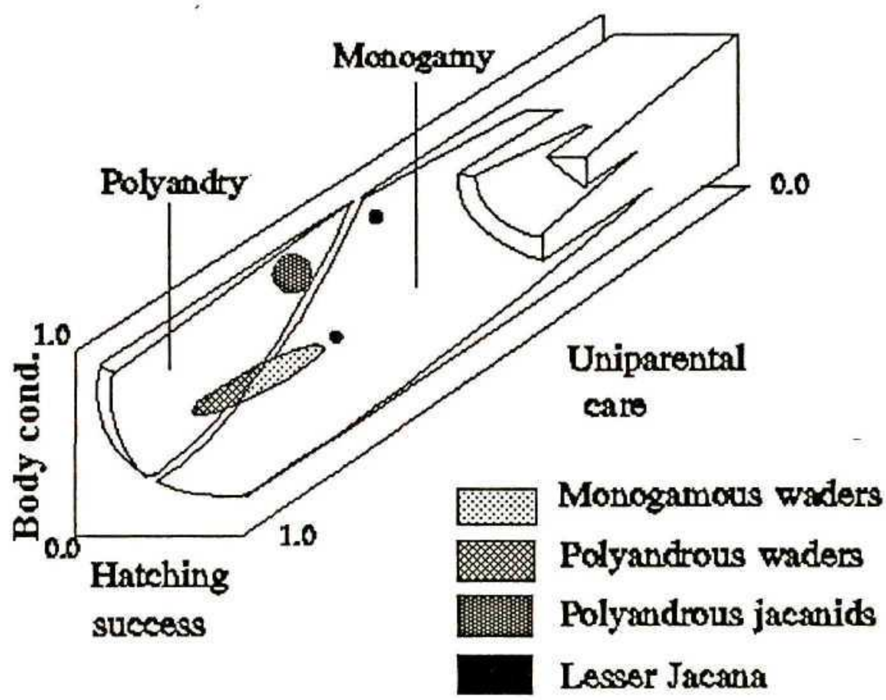


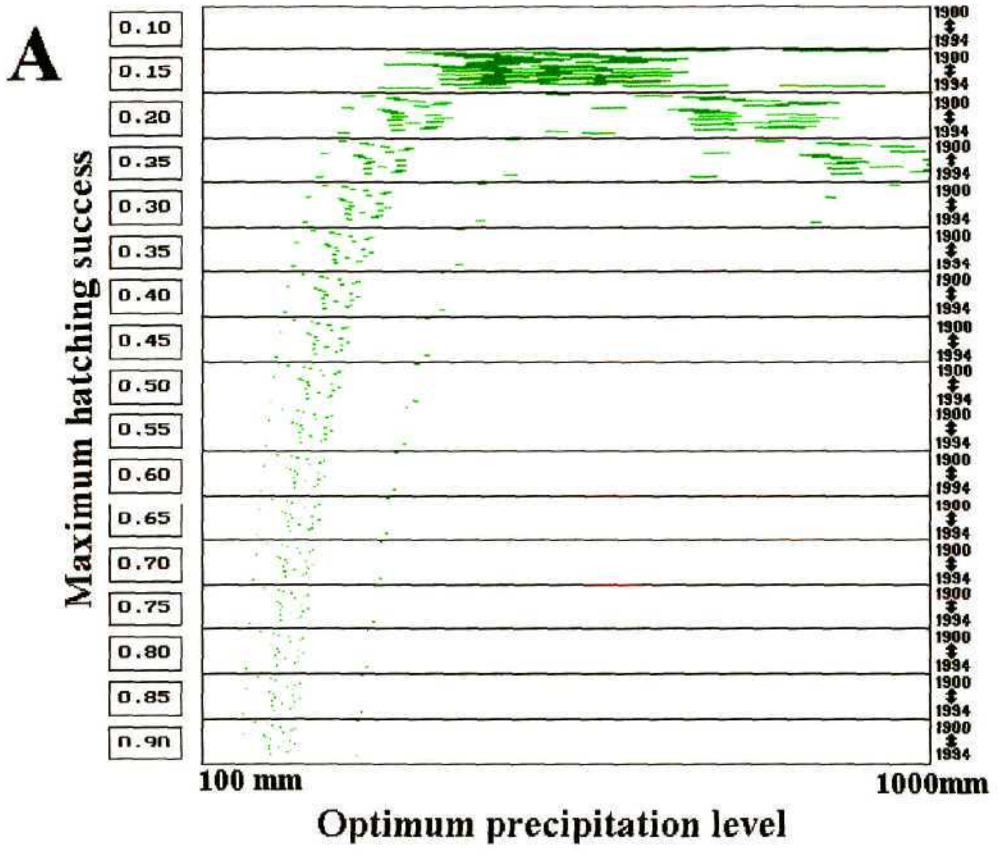
Figure 5. 10: Plan of figure 5.9A showing the area most likely to evolve polyandry and monogamy in waders.

The model suggests two possible explanations for the occurrence of monogamy in the Lesser Jacana. Either this species performs monogamy because food abundance is lower and hatching success higher than those of the African Jacana, or it shares similar food abundance and hatching success with the African Jacana, exhibiting monogamy because one mate alone is not able to match the uniparental care achieved by the African Jacana. This possibility requires further study.

Erckmann (1983) and Ligon (1993) present a convincing explanation about the evolution of polyandry in waders. They indicate that the almost invariable 4-egg clutch size (phylogenetic inertia) imposes a limit on reproductive success. The only way to increase productivity is to produce multiple clutches, which could also account for the emergence of polyandry. The model here is fully consonant with this idea. It works as long as the clutch size considered is four; otherwise a very different scenario arises.

2 - Polyandry in the population of African Jacanas in South Africa

So far the model has predicted that polyandry may occur as a consequence of high clutch loss and high food availability and that males play an important role in promoting the mating system. I produced three versions. An analysis of equations [26] , [27] and [28]. The result predicts a strong likelihood of polyandry around the mean precipitation value for the area concerned (536 mm/year) and corresponding to a maximum hatching success of 15% to 20%, which are in fact the values observed in the field study (Fig. 5.11A, Fig.5.11B, Fig.5.12A). Polyandry covers almost the same area of the three graphs. If monogamy is expected under conditions of low food resources and high hatching success then equation [28] represents more the relationship between food resources and precipitation levels.



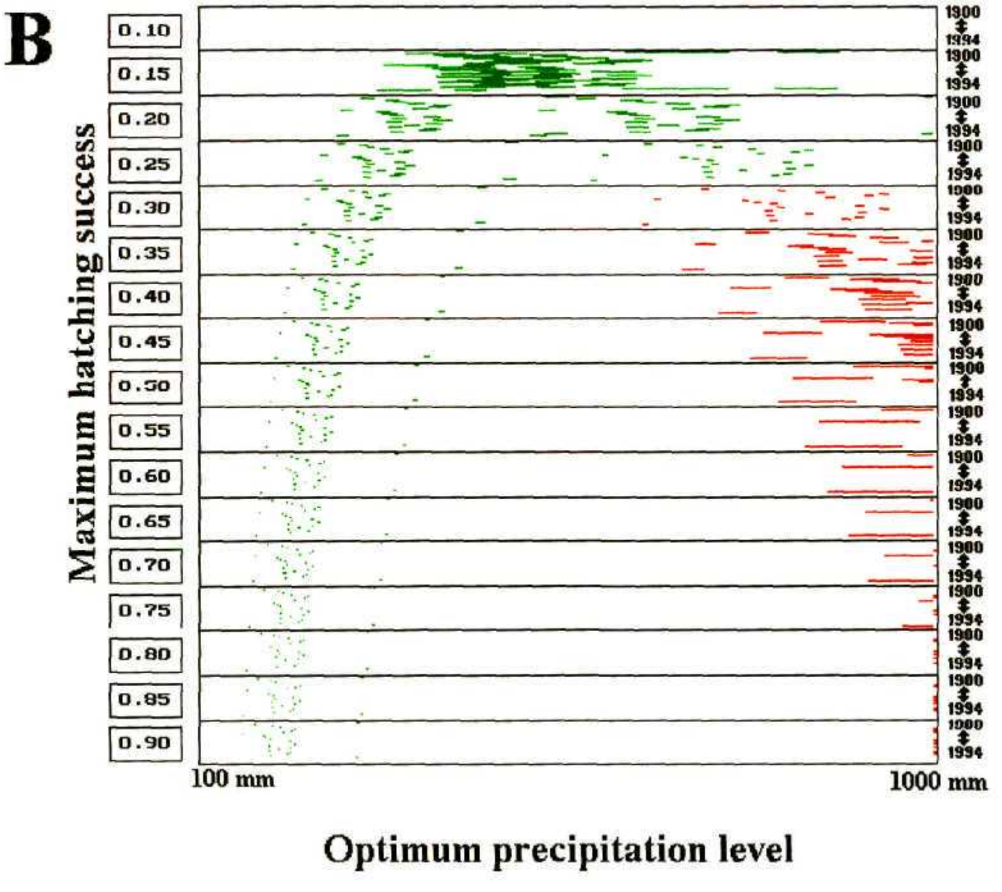


Figure 5.11: The model operated on a range of optimum precipitation on bands of 94 years repeated on a scale of maximum hatching success using: $F = \sqrt{\frac{P}{P_{op}}}$ (A) and $F = \frac{P}{P_{op}}$ (B)

Green colour denotes polyandry and red monogamy.

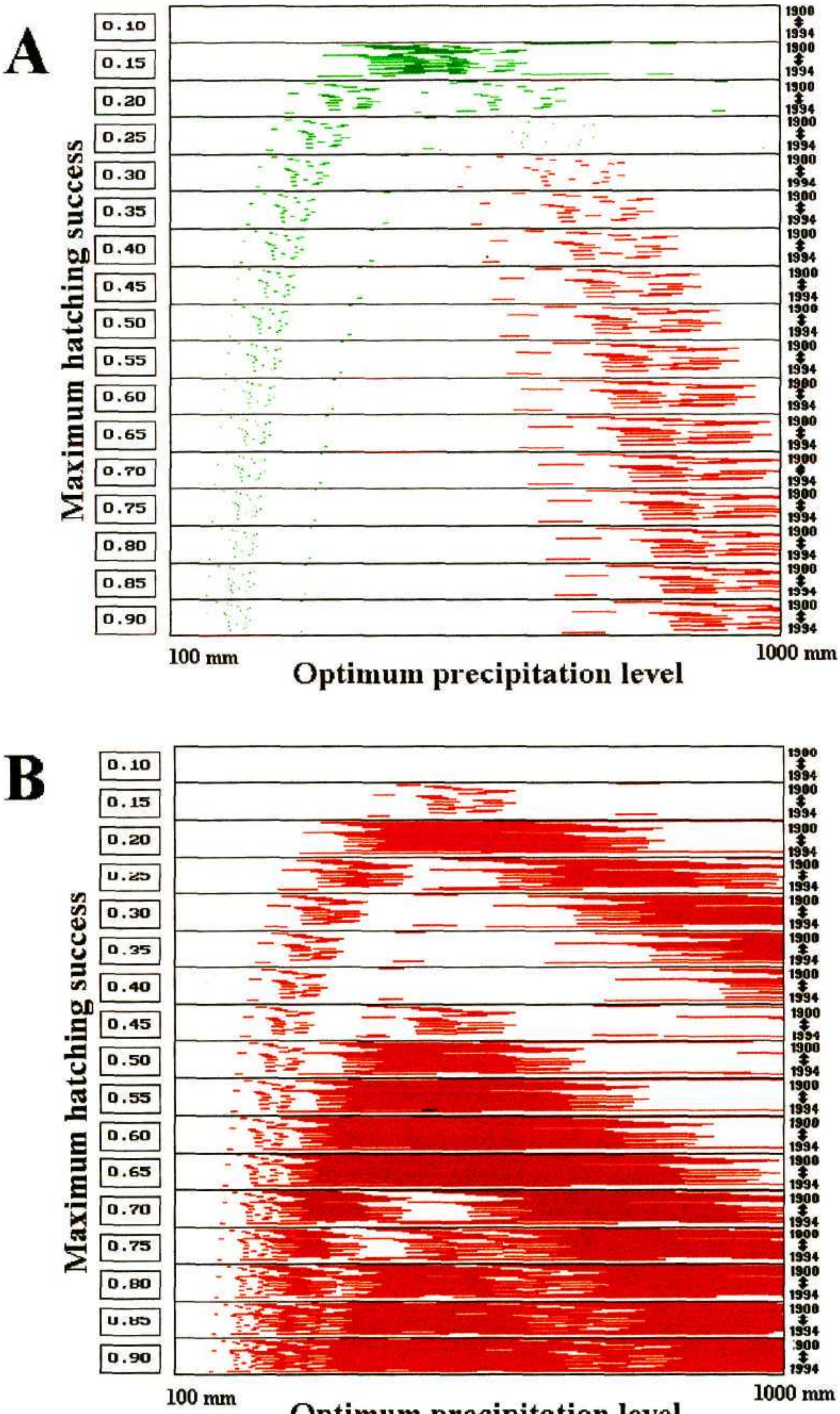


Figure 5.12: The model rendered on a range of optimum precipitation and bands of 94 years on a scale of maximum hatching success using

$F = (\frac{P}{P_{op}})^2$ (A) and for the Lesser Jacana: $F = \sqrt{\frac{P}{P_{op}}}$ (B)

Green colour denotes polyandry and red monogamy.

A similar type of graph was done by setting uniparental care at 41% corresponding to the Lesser Jacana and Figure 5.12B shows that only monogamy is expected under the same environmental conditions as those of the African Jacana.

Another variation of the programme plotted years vs highest hatching success (Fig.5.13), and shows that at about 14% of maximum hatching success, the conditions for polyandry between 1900 and 1994 was almost uninterrupted.

The programme then run with precipitation levels of each station and the result plotted on a series of maps along a range of hatching success, using uniparental care of 70% for the African Jacana and 41% for each parent of the Lesser Jacana (based on the 82% of parental effort found by Tarboton & Fry (1986)).

Fig. 5.14 is quite revealing: under about 70% uniparental care and around 15% of hatching success, the stations shows conditions for polyandry. Based on this picture I suggest that what possibly gives continuity to polyandry is the capacity of African Jacanas to move from one area to another. The prediction of 41% of uniparental care (82% of biparental care (Tarboton 1986)) for the Lesser Jacana is for monogamy with a higher hatching success.

The region of study shows values of high precipitation levels (Fig. 5.15C) which, when the equations [25] and [28] are used reveals a region of high food production but a very risky place for breeding.

DISCUSSION

The model presented above is an example of investigating a problem where there is much guesswork but few data available. Starfield & Bleloch (1991) state that, though this type of model is speculative, it "improves our understanding and enables us to find or use data we had not realized were relevant. That in turn leads us to a better model". This model depends greatly on

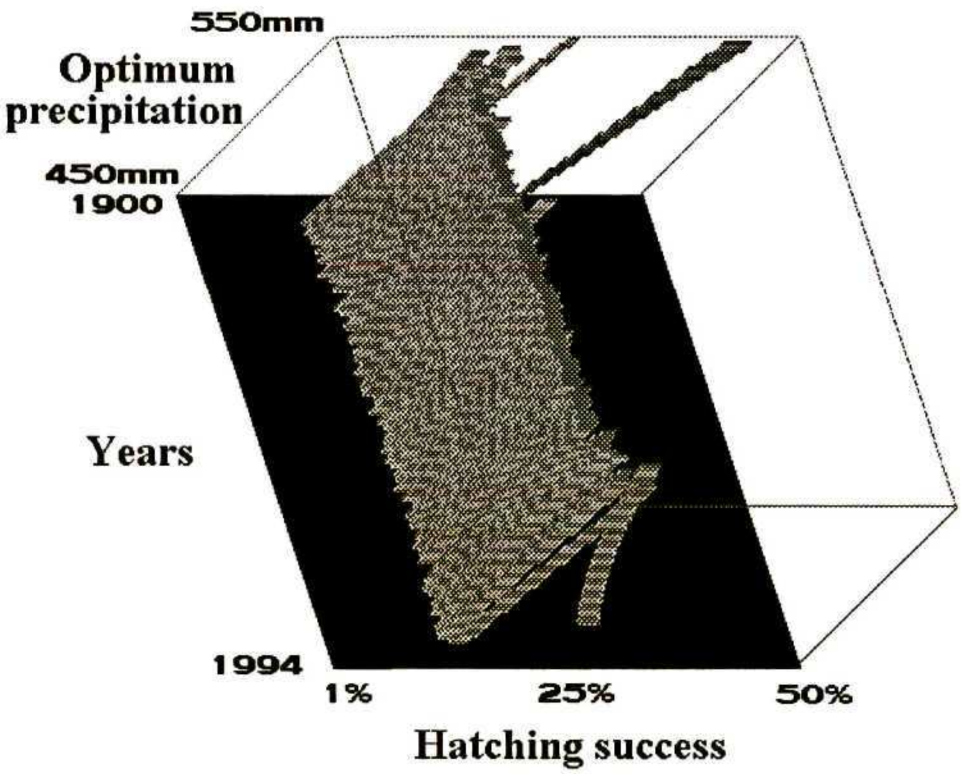


Figure 5.13: The model rendered on ranges of years, hatching succes and optimum precipitation.

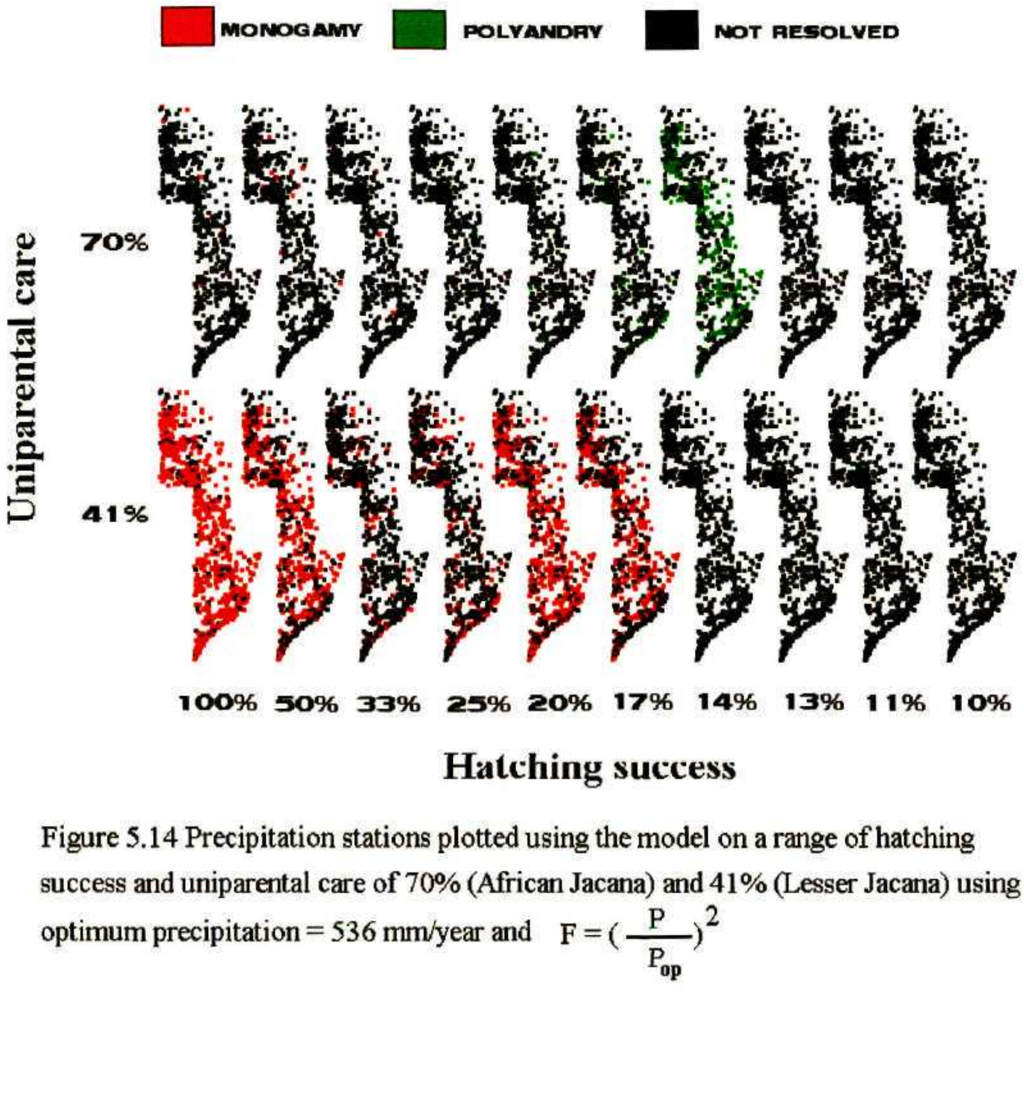


Figure 5.14 Precipitation stations plotted using the model on a range of hatching success and uniparental care of 70% (African Jacana) and 41% (Lesser Jacana) using optimum precipitation = 536 mm/year and $F = (\frac{P}{P_{op}})^2$

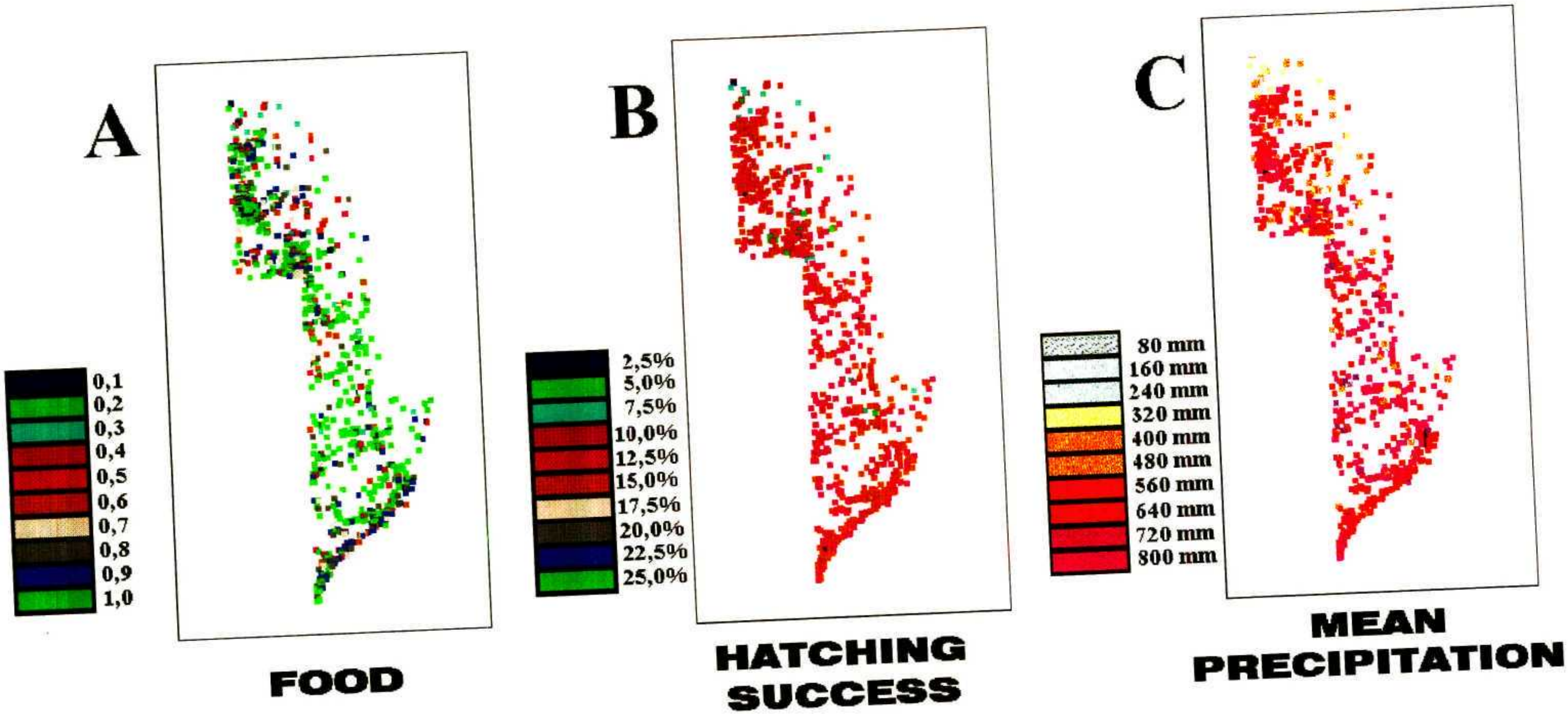


Figure 5.15: Food resources (A) and hatching success (B) given mean precipitation levels (C)

the weight attached to each variable, so the accuracy of the outcome depends on a continuous tuning process. When tuning one needs to know the direction indicated in the whole process. When there are not many data available in the literature or from field studies, one is reduced to a process of compromise between "going to what the field data show" first and then "going to what our logic dictates" second.

The tuning process is always around the field data (the only data from the real world), and what one expects from the model is what one sees in the field, which depends enormously on one's assumptions. The first assumption of this model is that the evolution of a particular mating system must be of some benefit to both sexes. It is possible to build the model with or without this particular assumption and explore the consequences. The predictions of the model were closer to the field data when I accepted the simultaneous-benefit assumption. Thus, the field data (from the real system) act as a feedback which tunes the whole virtual system (the model). Another important assumption is that mating systems may succeed according to the highest information-transfer rate, so the whole is based on equations which express the reproductive process. The validity of the model will also depend on the structure of the algorithms involved in the simulation. Formulae here employed or pieces of such equations are also grouped assumptions which, whether true or not, will depend on a confrontation of the model with data from the real world during the tuning process.

Much is known about the African Jacana and the Spotted Sandpiper but very little about the Lesser Jacana. Lamentably, there are no data on hatching success in the Lesser Jacana, but the model predicts a higher value of this for this species. This is understandable since a biparental system in Lesser Jacana gives more protection to the nest in terms of more vigilance provided by and a more continuous incubation. All this gives an scenario for a higher hatching success. The great value of the model is that the more accurately it predicts mating systems of very well known birds, the more confidence one can place on the predictions about poorly known species of birds, such as the Lesser Jacana.

The model presented here is at an early stage of development, but it is able to predict the variation in mating systems of most polyandrous waders.

There are certain aspects that could have affected the validation of the whole model, such as the fact that temperature was not taken into account. The conditions that facilitate incubation in the Jacanids are set by high ambient temperature (Tarboton 1992b). However, it was not included in the system because the temperatures in the area selected (northern and eastern) are not so variable or at least allow incubation during late spring and summer. This exclusion of temperature in the model helps in using it for other waders in which temperature is not a restriction, as in the cases of monogamous birds.

The model here presented is not biased by a particular variable, since each one considered plays an important role for the determination of a mating system. I believe that this model could be adjusted to many other bird groups and even the gametic availability approach could be used to explain mating system not only in birds but in insects, mammals, fishes and reptiles.

The approach taken to gamete availability is a new one, which needs much development in terms of adjustment to other groups of animals, which will depend particularly on the area of study of gametes. However, the idea of gamete availability is a "tool" in the model upon which other variables will act.

Sex ratio was not included since there is no real proof in the literature that it could be a determinant of a mating system. Besides that, I suspect that no matter if there is a surplus of males in the population, if the breeding conditions are tough, then there would not be the possibility for capitalizing on mates. However, this theory can still explain matters accurately enough without including sex ratio in the system.

The model was not intended to explain polygynandry, promiscuity, lek and other types of mating systems, since these do not happen in jacanids and related waders. Nevertheless, it would be very revealing to extend this model to those types of mating systems through the study of a group of birds that exhibit such reproductive strategies.

The cooperative polyandrous behaviour of the Dunnock *Prunella modularis* which is differently structured from that of the African Jacana. If the model is set to no clutch replacement in polyandry, it will reveal that polyandry appears on the opposite area to that of the case the African Jacana, that is, in conditions of restricted food supply and high hatching success. Davies (1992) gives very clear information about the breeding conditions for the Dunnock. He found that it does better in cooperative polyandry than in monogamy. Cooperative polyandry is likely to occur in harsh environments where one male and one female have difficulty in raising their young (Davies 1991; Faaborg 1980). What is interesting to see in Figure 5.9B is that the less uniparental care is provided, the earlier polyandry is expressed in the model. That is to say, the more mates as helpers the female can get (expressed as a reduction of uniparental care) the more likely is polyandry to occur.

I believe that the model can accommodate all the other mating systems but will depend on the assumptions and the integration of some new variables.

The model takes hatching success and not breeding success as a measure of the harshness of the environment because it is easier to get that information from the literature, hence easier to compare between species. That includes post-hatching parental care which will require the information about the entire fate of the chick up to attaining adulthood. In this way the model overestimates breeding success. If the difference between hatching success and survival of the young is high then, this could affect the reliability of the model. This is so because success in breeding happens only when the information transferred to the zygote can be then passed to the next generation. Otherwise, no matter if the system produces a high number of zygotes and then only few of them are able to deliver the information contained, the real success in information transference will arise not from the survival of zygotes but by the survival of those with prospects of reaching maturity and transferring the information through reproduction . For the African Jacana, in spite of the fact that hatching success is low (25%), survival of the young is higher at about 80% (Tarboton 1995). This is not considered as an important effect on the model. However, this aspect must be taken into account when the model is intended to be used for a completely different group of animals. In case of mammals, this would not be a problem since the information of survival of the young is always available.

The allocation of values for uniparental care, body condition and hatching success poses a particular problem: it is possible to distinguish between an acquired value and a real one. For example, for the body condition which is intimately linked with food resources the actual amount of food available in the environment is not a good indicator of body condition. This is because there are cases in which the food may be scarce but if the species under study learns how to obtain high amount of food or high quality of it then body conditions in this case are not equivalent to food resources but will need adjustment to a higher level. What is important is the intake of food. A typical case is chimpanzees. For them termites are unavailable until they learn how to get them. So, the learning process plays an important role in the food acquiring system. Another thing would be food storage.

Another aspect would be measuring hatching success: no matter how intense the predation level in the surroundings, if the animal has developed a system to avoid predation, then the level of predation that reaches the animal is lower than is expected. For example, an open nest like that of jacanids has a higher risk of being robbed than the closed nest of a passerine. One may say that there is an acquired hatching success and a real one. Another way of increasing hatching success (acquired) is by getting helpers. This is the case in the cooperative polyandry in which the female raises her reproductive success by getting males to help her in incubation and brooding duties (Davies 1992).

A similar effect happens with the designation of values to uniparental care particularly in jacanids. On cool days the nest attendance in the African Jacana is 70,9% while on hot days it is around 43,5% (Tarboton 1992b). The latter figure is similar to that for a monogamous species and this is possibly due to the high environmental temperature (Tarboton 1992b). So 43,5 % is an acquired value since it would not be feasible on a day of normal temperature.

The problem now is which to take for the model: the real value or the acquired one ? This must be according to the effect on the system. In the case of body condition and hatching success it should be the acquired value whereas in uniparental care it must be the real value because food searching and predator avoidance are controlled by the animal but it cannot continue foraging and neglecting the eggs on a cool day. It is not a continuous process like food searching and risk avoidance.

This aspect of real *vs* acquired values becomes very important when considering the possibility of applying this model to mammals whose body condition is highly determined by the process of learning to obtain food and shelter. Hatching success has to be measured in terms of litter survivals and this could be biased towards strong offspring defence.

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EPILOGUE

This study makes a twofold contribution. On the one hand, it opens a new perspective on the integrative study between the different species of jacanids in the world. It examines aspects of the life history of the African Jacana that have never been addressed before in any species of jacanids, such as nest sinking and resistance and the possible phylogenetic consequences of body size and high food resource in floating environments.

On the other hand, it promotes the use of computer modelling as an alternative means of integrating and testing existing theories and to derive more understanding from short-term studies where little information can be obtained because of constraints like number of breeding seasons required and scarce funds.

In future investigations of jacanids more attention should be paid to the type of nest material as well as to the physical conditions under which they are built. For example, in the Wattled Jacana nest sinking is rare (Emlen 1994 pers. comm.), probably because this species of jacanid uses buoyant plants (emergent aquatic plants with unanchored roots) and its body size is smaller than that of the African Jacana. In Lake Kariba, Zimbabwe, there is a massive quantity of exotic buoyant plants like *Salvinia, Hyacinth* and *Pistia* competing with the indigenous species. It would be instructive to compare the breeding success of African Jacanas in those lakes invaded by foreign species of buoyant plants with that of those jacanas in African lakes in which the dominant aquatic plant community is composed of indigenous species. Would the introduction of foreign species of aquatic plants enhance the breeding success of African Jacanas? In this case one should be mindful of the different levels and type of predators between South America and Africa.

There are still many questions waiting to be answered, such as why in the African Jacana a hierarchical social system arose while in the Wattled Jacana it did not.

Another revealing study would be to see whether all the world's six species of jacanids enjoy the same high food concentration in their habitats. This would show that there is adequate compensation for the high rate of clutch loss in a floating environment.

I tried to raise the possibility that, just as the female's larger size aids foraging and laying, the male's comparative smallness is similarly advantageous in minimizing nest sinking. This is another possible explanation for the evolution of the reversed sexual size dimorphism, but that would be fully verifiable only in a long-term study of about 10 or 15 years in a natural environment, as the sample size required would be great and the breeding success of this species is poor.

The real cause for the existence of polyandry, since it is such a "difficult" mating system, is hard to envisage and there is still much debate about whether real selection pressure for its evolution exists.

Data on environmental variables, which could possibly affect the mating system of a species, have been studied by many researchers but it is still very difficult to compare such data because of the lack of standardization and the different conditions under which each field study has taken place. Sometimes the only possible way to achieve some understanding of the problem is by modelling the whole system. This thesis pursues this goal.

My final conclusion is that the polyandrous behaviour of the African Jacana evolved from the need to compensate for high clutch loss in a floating environment. Moreover, the primary attraction for opting for such an unstable habitat is the abundant food resources, which compensate for the high clutch loss, as long as the female's hyper-productive laying capacity is maintained, which is possible only in a polyandrous mating system under which she is free of any incubation and other parental duties.