

Breeding behaviour of the African frog, *Chiromantis xerampelina*: multiple spawning and polyandry

MICHAEL D. JENNIONS*, PATRICIA R. Y. BACKWELL† & NEVILLE I. PASSMORE

Department of Zoology, University of the Witwatersrand, Wits 2050, Johannesburg, South Africa

(Received 22 May 1991; initial acceptance 2 August 1991; final acceptance 28 April 1992; MS. number: 3779)

Abstract. Breeding was observed in the foam-nest frog, *Chiromantis xerampelina*, in Hoedspruit, South Africa. The population had a 3-week breeding season with a male-biased operational sex ratio and asynchronous and unpredictable female arrival. Nests were built above water and at 14 out of 15 nests, from one to seven unpaired males ('peripheral males') gathered around the amplexing pair during nest construction. Those peripheral males closest to the pair competed with each other, and with the amplexing male, to position their cloacae against the female's cloaca during oviposition. It is suggested that multiple spawning was occurring. Of 30 males, 25 (83%) were observed as peripheral males, and 17 (56.7%) were observed both in amplexus and as peripheral males. Male mating success and participation at nests was unrelated to size or weight. Chorus participation was the best predictor of mating success and presence at nests. Nests were built in two to four sessions with females descending to the water between sessions. On 55% of 20 occasions amplexing males dismounted between sessions, but they had only an 11% probability of re-amplexing when the female returned to the nest. Of 15 females, 10 (66%) mated polyandrously with two or more males on one night.

Anurans are an ideal group for studies of mating behaviour and variation in mating patterns. Individuals are easily marked, handled and observed (Arak 1983). Many authors have suggested that the external mode of fertilization in frogs allows unambiguous quantification of the reproductive success of individuals (e.g. Howard 1988). External fertilization, however, is no guarantee of unambiguous paternity. In several fish species, group spawnings occur and paternity is divided amongst the males present. Workers assume either that fertilizations are shared equally among males (van den Berghe et al. 1989), or that fertilization success is related to proximity to the female (Gross 1985). Of course, estimates of reproductive success are most accurate when fertilization rates are calculated using paternity test data (Westneat et al. 1987).

Group spawning and the potential for sperm competition has not been demonstrated in anurans (Halliday & Verrell 1984). The dominant reproductive tactic in anurans is stationary calling. The

most frequently documented alternative tactics are: 'satellite behaviour', where non-calling males attempt to intercept females attracted to calling males (e.g. Perrill et al. 1978); 'dispossession', where unpaired males attempt to displace amplexing males (e.g. Telford & Van Sickle 1989); and 'active searching' by silent males that clasp any individual they encounter (e.g. Fairchild 1984).

Alternative reproductive tactics are usually a consequence of male-male competition for a limited number of females. Competition may limit the number of males that can employ the dominant mating tactic, thereby forcing some males to adopt alternative tactics with lower reproductive success (Kodric-Brown 1986). Generally, alternative reproductive tactics yield lower pay-offs than the dominant tactic, although tactics with equal pay-off (e.g. Gerhardt et al. 1987) and higher pay-off (e.g. van den Berghe 1988) have been reported. Tactics may be reversible or fixed, and opportunistic, conditional or part of a mixed evolutionarily stable strategy (Austad 1984). In most anurans, alternative tactics appear to be conditionally employed by smaller males (e.g. Howard 1978; Loman & Madsen 1986; Arak 1988; Krupa 1989).

*Present address: Wild CRU, Department of Zoology, South Parks Road, Oxford OX1 3PS, U.K.

†Present address: Smithsonian Tropical Research Institute, P.O. Box 2072, Balboa, Republic of Panama.

Fixed tactics have not been recorded in anurans, but when there is considerable variation in size, and tactics are size-based, males may be limited to a single tactic for an entire breeding season (Howard 1978).

In this paper, we present evidence for the occurrence of an 'opportunistic' reproductive tactic rarely recorded in anurans. We suggest that multiple spawning, and potential sperm competition, are common features of the mating pattern of *Chiromantis xerampelina*. We also document multiple mating by females.

STUDY SPECIES AND METHODS

Chiromantis xerampelina is a large (snout-vent length = 50–80 mm), prolonged breeding, African frog that lays eggs in foam nests built over water. Tadpoles develop inside the nest and drop into the water 4–6 days after nest building and spawning, which occur at the same time. Communal nest building involving 'helping' by unpaired males has been reported in all three species of *Chiromantis* (Coe 1967, 1974; Taylor 1971).

We observed marked, breeding frogs in December 1990, in the Hoedspruit district, Transvaal, South Africa (24°27'S, 30°52'E). The main study pond was approximately 500 m², with a maximum depth of 1.2 m. The closest breeding site was 800 m away. We also studied an unmarked population in December 1989, at Mkuze Game Reserve, Zululand (27°39'S, 32°10'E). The results of this pilot study are summarized separately as they reveal variation in breeding behaviour between populations.

Thirty-two males were collected individually by hand, measured, weighed, marked and released at the point of capture within 15 min. Snout-vent length (SVL) of all males was measured to the nearest 0.1 mm. The males were then hydrated and weighed to the nearest 0.1 g. Nine males were reweighed 3–19 days (mean = 14 days) after their initial capture. All males were individually marked by heat branding on the dorsum. We also measured 34 females collected at the main study pond and two neighbouring ponds.

Observations were made on 21 nights over a 22-night period during the breeding season. Only two nests were constructed in the 3 weeks prior to the study and no males were present at the pond on termination of the study. We censused the population each night. We located 12 sites where males

were consistently present (mean site size = 1.9 m², range = 0.4–4.9 m²); of these, seven corresponded to partially submerged trees, four to patches of emergent grass and one to a reedbed. The identity of males, the site they were in, and their behaviour were all noted. We tried to census the pond hourly, but this was not always possible if we were making observations of nesting. All males present at nests were identified.

We located females that were either unpaired in the water, or already in amplexus out of the water, and observed them throughout nest construction. Early each evening we checked the pond for nests not observed the previous night. This allowed for accurate correction of undercounts of female presence. We video recorded the construction of six nests. These recordings were used to determine the duration of the first 10 periods between activity bouts in each nesting session.

In our description of nesting, we refer to unpaired males on the lateral aspect of the branch with their legs in the foam, or that were immediately alongside another male whose legs were in the foam, as a 'peripheral male'. Any individual touching the foam nest is described as being 'on the nest'. Males are described as 'mated' if they were in amplexus during oviposition.

RESULTS

Demography and Male Behaviour

The breeding season lasted 22 nights (5–26 December) during which 32 males were marked and 26 females were present. If the two nests found before the study commenced are included, the overall sex ratio was 1:1.1. From seven to 28 males (mean = 19.6) and zero to six females (mean = 1.2) were present each night. The operational sex ratio ranged from 0 to 0.29 (mean = 1:1.4), with no correlation between the number of males and females present per night ($r_s = 0.26$, $N = 21$, $P > 0.2$). With one exception, absent males were not found at neighbouring ponds and are unlikely to have been engaged in reproductive activities elsewhere. On average, individual males were present on 13.7 nights ($SD = 4.5$, range = 2–20). The total number of 'frog-nights' was 408 (see Ryan 1985). Two males are excluded from all subsequent analyses as they were present for only a single night.

There was pronounced sexual size dimorphism with a female/male size ratio of 1:20. Mean female

size was 76.1 mm (SD = 3.2 mm, range = 67.8–81.3 mm, $N = 34$). The average male size was 63.2 mm (SD = 3.3 mm, range = 55.1–68.9 mm, $N = 30$) with a mean mass of 13.2 g (SD = 2.6 g, $N = 26$). Male SVL and mass were positively correlated ($r_s = 0.88$, $N = 26$, $P < 0.0001$). Male weight change as a percentage of initial body weight was insignificant (mean = -0.003% per day, $N = 9$; mean interval between weighings = 14 days).

Males called from elevated sites over water and defended neither active calling spaces nor territories. There were no agonistic interactions between unpaired calling males. Males continued to produce advertisement calls, even when positioned on top of one another. All males were observed to call but calling was sporadic. There was considerable variation in call rate between individuals (personal observations). We did not observe satellite males (sensu Perrill et al. 1978).

Individual males showed strong preferences for certain sites within the pond. The maximum number of nights a male was observed at a single site (one of the 12 delimited) was expressed as a percentage of the total number of nights the male was present at the pond. Mean 'site fidelity' was 65.3% (range = 29–95%, $N = 30$). Although males showed this high level of fidelity they were not invariably stationary. Ninety per cent of males ($N = 27$ of 30) moved between sites on at least one of the nights they were present.

Nesting Behaviour

Of 26 females that oviposited at the pond, 18 were observed in amplexus (69%) and initial pair formation was observed for 11 females (42%). Nests were built in two to four sessions. A nesting session consisted of egg-laying/churning bouts and intervals of relative immobility. On average, bouts lasted about 1–6 s. The intervals between bouts lasted 101.6 s (SD = 103.2, $N = 149$). Females left the nest between sessions and descended to the pond where they took up water. The sessions lasted 74.3 min (SD = 24.0, $N = 16$), whilst the period between sessions averaged 52.2 min (SD = 8.2 min, $N = 12$). Nest building occurred between 2000 and 0630 hours. One nest took over 7 h to construct. The following description of nesting and mating behaviour is based on detailed observations at 14 nests.

Females approached males from the water and then proceeded to climb the vegetation towards a

group of males. Females did not move between sites and any potential for female choice was at a local level (e.g. one of the 12 sites where males were present). There was a noticeable increase in male movement but no apparent change in calling behaviour (cf. Coe 1974) and the males did not descend to meet the female. Although females approached sites where males were calling, they did not appear to select a male. Initiation of amplexus did not involve a female making physical contact with a male, but occurred when a male jumped onto her. On at least two occasions the male jumped from 30–40 cm above the female. The amplexing male was not necessarily one that the female had been facing, nor one she had been moving towards. Males clasped the females in axillary amplexus above the forearm. Sexual size dimorphism resulted in the separation of the pair's cloacae by 2–3 cm.

At 93% of nests, single males were also present in the pair's vicinity in the period between amplexus and the start of foam production. Some of these males moved up to 12 m to reach and then follow the amplexing pair. The mated pairs moved 0.3–2 m from the initial point of amplexus before assuming a position on the side of a branch. Unpaired males then positioned themselves on either side of the pair. They clung directly to the branch, but lower down than the female, so that their cloacae were approximately in line with that of the female (Fig. 1).

Nest construction began when the female released an oviducal secretion and churned it into a white foam with movements that fully extended her hind legs. Egg laying began approximately 15 min after the start of foam production. Bouts of oviposition always occurred in conjunction with female churning. Between bouts males remained motionless, whilst females occasionally moved their hind legs (but rarely extended them fully). When oviposition and churning occurred the amplexing male scraped his feet down the female's dorsum. His feet moved between his and her cloacae. We suggest this action serves to distribute semen over the extruded eggs.

Peripheral males also responded to the female's churning motions. An 'active' peripheral male would swing his lower body away from the branch, then, with a jabbing motion, position his cloaca adjacent to that of the female (see Fig. 1). Cloacal proximity was maintained for 1–3 s. During this period peripheral males jostled each other and the amplexing male as they attempted to maintain cloacal proximity with the female. Peripheral males

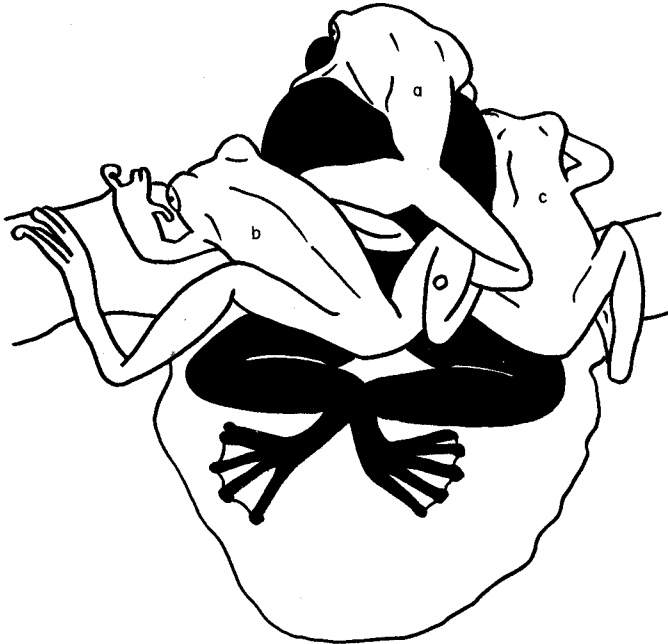


Figure 1. A nest with two peripheral males. The 'active' peripheral male b to the left of the amplexing pair is clearly positioning his cloaca against that of the female. Note the space between the amplexing male's a cloaca and the female's cloaca. Male c is 'inactive' to the right hand side of the mated pair.

competed to slide their lower bodies underneath the amplexing male whilst the latter attempted to continue making leg movements down the female's dorsum. After the female halted churning activity the peripheral males and the pair returned to their motionless pre-oviposition state. Attempts to maintain cloacal proximity were displayed primarily by the two males immediately adjacent to the amplexing pair, and less commonly by peripheral males further from the pair. Males further from the pair tended not to move during oviposition. We describe them as 'inactive' peripheral males.

Of the 23 nests built at the study site, two were communally built (one involved three females, the other two females). The behaviour of both sexes at these nests was identical to that at nests involving a single female. The number of males present at a nest varied. Between and during nesting sessions new males usually arrived and joined in as peripheral males. The mean number of peripheral males per session was 3.5 ($SD=1.7$, $N=33$ sessions), with a trend towards increased numbers of peripheral males in later sessions. The average number of males participating in a given nest was 5.5 ($SD=2.8$, $N=15$ nests) and the mean number of males per female at a nest was 4.9 ($SD=2.6$, $N=15$ nests).

Female departure at the end of a session was observed 20 times; in 11 cases (55%) the amplexing male dismounted leaving the female to descend to the water on her own. On the other nine (45%) occasions the male remained in amplexus. Unpaired females amplexed whilst returning to the nest for the start of the next session. The formerly amplexing male was successful in amplexing in only one of nine observed female returns (11.1%). While the female was absent, peripheral males remained within about 1 m of the nest, some remaining on the nest itself.

We observed amplexus displacement attempts on 14 occasions. They occurred either before nesting had started, or at the start of a subsequent nesting session. Seven (50%) of these 14 attempts were successful. There was no significant advantage to large male size, either as attacker or defender (sign test, NS).

The combination of amplexing males dismounting between sessions and successful amplexus displacement meant that females were not necessarily in amplexus with the same male in each nesting session. Of those females observed for two or more nesting sessions, 66% ($N=10$ of 15) amplexed with more than one male. Two females amplexed with at

least three males. Thus, a minimum of 66% of egg clutches were fertilized by more than one male owing to multiple matings.

Male Reproductive Success

The fertilization success of peripheral and amplexing males is unknown so data on variation in reproductive success are unavailable. Of the 30 males present at the pond for more than one night, 28 (93.3%) participated in at least one nest, 26 (86.7%) were seen as peripheral males, 18 (60.0%) amplexed at least once and 17 (56.7%) were observed as both peripheral and amplexing males. Males were observed to participate in an average of 2.5 nests ($SD=1.8$, $N=30$ males), and amplexed with an average of 1.2 females ($SD=1.2$, $N=30$ males; Fig. 2). The above data underestimate male reproductive behaviour, however, because only 69% of the gravid females known to be present at the pond were observed. When the data are extrapolated to include all 26 females present, the mean number of nests participated in is 3.8 and the mean number of females amplexed per male is 1.8.

Mating success and nest participation were analysed at four scales of interaction: nesting sessions; nests; nights; and breeding season (see Morris 1989). The first two scales are most likely to reveal female choice or direct male-male competition. There was no significant size difference between mated and peripheral males during nesting sessions (sign test, $N=32$ sessions, NS). Neither were mated males larger than the average peripheral males at the nests significantly more often than expected by chance (sign test, $N=15$ nests, NS). There was no significant pattern of mated males being larger than the median male size for that night ($\chi^2=1.24$, $N=29$ males, NS; see Ryan 1985). Nor were nesting males larger than non-nesting males on a significant number of nights (sign test, $N=12$ nights, NS). There was also no significant size difference between males that did or did not mate during the breeding season (Mann-Whitney $U=1.18$, $N=30$ males, $P=0.24$). The only significant correlate with the number of nests a male participated in was the number of nights he was present at the pond ($r_s=0.45$, $N=30$, $P<0.01$). Nights present was an even stronger predictor of mating success (number of females amplexed; $r_s=0.6$, $N=30$, $P<0.001$). There was no significant correlation between size and number of nights present but there was a significant correlation between

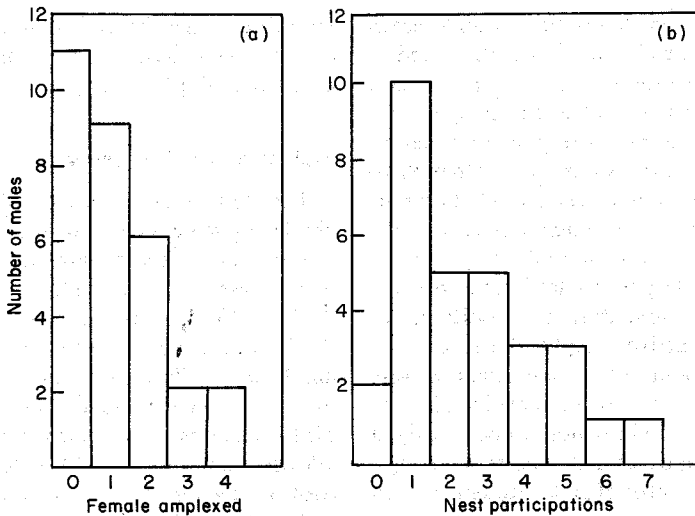


Figure 2. Male reproductive activity. (a) The number of females amplexed and (b) the number of nests participated in. Note that this represents only observed reproductive activity and does not include the eight females (30.8%) that built nests unobserved.

Table I. Variation in mating patterns between populations

	Study pond	
	Mkuze	Hoedspruit
Nights of observation	25	21
Males per night	28.4*	19.6
Females per night	1.36	1.20
Mean operational sex ratio	1:15*	1:14
Nests with peripheral males	92% (<i>N</i> = 22)	93% (<i>N</i> = 14)
Displacement attempts	No	Yes (<i>N</i> = 14)
Amplexing males dismounting	Every time a session ended	55% of observed departures
Female size	76.2 mm (<i>N</i> = 22)	76.1 mm (<i>N</i> = 34)
Male size	58.7 mm (<i>N</i> = 58)	63.2 mm (<i>N</i> = 30)
Size ratio	1.30	1.20

*Calculated for 9 nights.

nights present and site fidelity ($r_s = 0.49$, $N = 30$, $P = 0.008$).

Variation Between Populations

We also observed breeding at a second pond, in Mkuze Game Reserve, Zululand, which had approximately 50% more oviposition/call sites. Similarities and differences between the two populations are listed in Table I. Male spacing and territoriality were absent and calling behaviour

appeared similar to that at Hoedspruit. There were, however, several important differences between the Mkuze and Hoedspruit populations.

(1) Amplexus displacement attempts were never observed at Mkuze. Fourteen attempts were noted at Hoedspruit.

(2) All amplexing males dismounted between nesting sessions at Mkuze ($N = 24$ nests). Only 55% of males dismounted at Hoedspruit.

(3) Males were more mobile at Mkuze than at Hoedspruit. Mkuze males called from 3–4 m up a

large tree overhanging the water and regularly dropped into the water, swam towards the trunk and re climbed the tree.

(4) Mean female size at Mkuze was within 0.1 mm of that at Hoedspruit (t -test: $t=0.06$, $P=0.95$) whilst males at Mkuze were significantly smaller than males at Hoedspruit (t -test: $t=5.52$, $P<0.001$). At Mkuze females were 30% larger than males (t -test: $t=18.85$, $P<0.001$). At Hoedspruit females were 20% larger than males (t -test: $t=16.76$, $P<0.001$).

DISCUSSION

Overall Breeding Patterns

Chiromantis xerampelina may be considered a prolonged breeding frog (sensu Wells 1977). Male and female presence was not synchronized by rainfall, female arrival was unpredictable and the operational sex ratio was always strongly male biased. As in most other studies conducted over the major part of the breeding season, we found that chorus attendance is the best predictor of male mating success (e.g. Greer & Wells 1980; Woodward 1982; Jacobson 1985; Ryan 1985; Gerhardt et al. 1987). The percentage of nights that individual males were present in the chorus was high relative to that found in many other anuran species (e.g. Green 1990; Salvador & Carrascal 1990). Although the sample size is small, the stability in male body weight is interesting because it contrasts with the results of several other studies (see review in Halliday 1987; Given 1988).

At all scales of analysis, from nest sessions to the breeding season, we found no evidence for non-random mating with regard to body size. Mated males were no larger or heavier than unmated males. There was also no size-assortative mating (unpublished data). This suggests that there is neither female choice of large males, nor a large-male advantage in male-male competition. The distribution of matings among males was far more equitable than that recorded in other anurans. At least 60% of males successfully amplexed a female.

Peripheral Males

The most unusual aspect of the *C. xerampelina* mating pattern is the presence of peripheral males. Coe (1967) suggested that unpaired males helped in nest construction in *C. rufescens*. Our observations

on *C. xerampelina* do not support this suggestion. Our data provide strong evidence that peripheral males are fertile males exhibiting an alternative reproductive tactic. (1) Fifty-seven per cent of amplexing males also acted as peripheral males. These males were almost certainly fertile because all investigated nests had very high fertilization rates (more than 98%, personal observations). One male mated without peripheral males being present during nest construction and this nest produced tadpoles. This male was also observed as a peripheral male. (2) Peripheral males only competed with the amplexing male for cloacal proximity to the female during oviposition. (3) Peripheral and amplexing males were not observed helping to aerate the foam.

We suggest that the most plausible explanation for the presence of these males is that they were competing with amplexing males for fertilizations. We suggest that those peripheral males that actively compete to place their cloacae against the female's cloaca during oviposition are ejaculating. If so, their actions should lead to sperm competition. Our evidence is comparable to that for group spawning in several fish species where similar circumstantial evidence has led to the acceptance of a sperm competition hypothesis (Dominey 1980; Taborsky et al. 1987). It is more difficult to interpret the behaviour of inactive peripheral males. They may simply be waiting for an opportunity to get closer to the pair, or they may also be releasing sperm into the foam.

If the active peripheral males are pursuing an alternative reproductive tactic it is a fairly sophisticated one. For it to have evolved the following adaptive changes in behaviour were required: (1) the ability to release sperm without being in amplexus; (2) the ability to recognize the cue for oviposition without being in amplexus; and (3) the capacity to locate females from a distance. Most anuran species show little ability to recognize females at a distance (Wells 1977; Robertson 1986). In addition, peripheral males must (4) have the ability to juxtapose cloacae with the female from a variety of positions and to maintain cloacal proximity whilst other males are jostling.

Several workers who have examined group spawning in fish have shown that males obtaining 'sneak' fertilizations are a subset of the total male population. They are usually smaller and/or younger than dominant males and, in the short term, are largely limited to this sneaking tactic (e.g. Dominey 1980; Gross 1985; Taborsky et al. 1987;

van den Berghe & Warner 1989). The small size of 'sneakers' may be the result of (1) direct selection for small body size because it decreases conspicuousness (Gross 1985); (2) 'sneakers' being younger than dominant males (van den Berghe et al. 1989); (3) genotypic differences between males (Gross 1985; Ryan & Causey 1989); or (4) a response to an active female preference for larger males (Ryan & Causey 1989).

In contrast to the above studies we did not find that peripheral males were smaller than amplexing males. Size and age are related in anurans because of indeterminate growth, suggesting that peripheral males are no younger than amplexing males (but see Halliday & Verrell 1988). Individuals of all sizes were found in amplexus and acting as peripheral males. The alternative reproductive tactic of peripheral males does not appear to be a 'best-of-a-bad-job' tactic resulting from phenotypic constraints, but rather a reversible (*sensu* Austad 1984), 'opportunistic' tactic (Davies 1982). At present it is impossible to determine the relative fitness of the tactics because fertilization rates are unknown. Hence, the possibility of a mixed evolutionarily stable strategy occurring remains open. Explanations (1)–(3) do not account for the peripheral male tactic in *C. xerampelina*. The data do not support a hypothesis that the tactic is a response to female mate choice because the tactic was exhibited by almost all males; and there was no apparent female choice, although it may have existed in the past.

In *C. xerampelina* we also documented the alternative reproductive tactic of amplexus displacement. Our data are unusual in that we do not report a large-male mating advantage (*cf.* Telford & Van Sickle 1989). However, we did not measure the forearm length of males and it is possible that this influenced displacement success (Lee 1986). The rate of successful displacement (50%) is also the highest recorded in an anuran species (Telford & Van Sickle 1989). It is unclear why amplexus displacement was absent from the Mkuze population. Theory predicts that the intensity of male-male competition will correlate with the frequency of alternative mating tactics (Krupa 1989). However, two measures of the intensity of male-male competition, namely the operational sex ratio and male density, were almost identical at Mkuze and Hoedspruit. Intraspecific variation in this particular tactic has also been noted in *Rana temporaria* (Elmberg 1991).

Polyandry

Polyandrous behaviour whereby more than one male fertilizes eggs in a single clutch has been documented in only one other anuran, *Afrixalus delicatus* (Backwell & Passmore 1990). Here we report that 66% of females were polyandrous. The main cause of polyandry was the dismounting of amplexing males between nesting sessions. Males had only an 11% probability of reamplexing. Polyandry is often described as an adaptive female strategy (see Halliday & Arnold 1987), but we cannot construct a plausible adaptive explanation at present. Increasing the genetic diversity of progeny, or ensuring fertilization, is especially implausible if one accepts that multiple spawning is occurring. Further research is necessary to account for the proximate and ultimate mechanisms that result in males dismounting.

Sperm Competition in Anurans?

Sperm competition as a result of group spawning has been reported in many fish species with external fertilization. However, sperm competition has not yet been demonstrated in an anuran (Halliday & Verrell 1984). Our observations suggest that it probably occurs in *C. xerampelina*. If so, it is also likely to occur in the two congeners. Peripheral males that gather around the spawning pair have also been noted in the foam-nesters *Polypedates dennysi* (Pope 1931, cited in Duellman & Trueb 1986), *Rhacophorus schlegelli* and *R. arboreus* (Fukuyama 1991). Pyburn (1970) documented the presence of unpaired males at leaf nests of *Pachymedusa dacnicolor* and *Agalychnis callidryas*, but he also noted that these males were attempting to displace the amplexing male. Thus, the functional significance of the presence of these males remains obscure. Interestingly though, in both species females descend to the water and build nests in sessions.

At present, speculation about the evolution and significance of the peripheral male tactic is constrained by the absence of data on the relative fertilization success of amplexing and peripheral males. Preliminary electrophoretic work shows that there is almost no protein polymorphism in the study population (Jennions, Grant & Passmore, unpublished data), but we are investigating other techniques that may allow us to demonstrate conclusively mixed paternity arising from sperm competition.

ACKNOWLEDGMENTS

We thank the Natal Parks Board for permission to work at Mkuze. For field assistance we thank P. Bishop, M. de Fontaine, V. Egan, J. and H. Theron and J. Tooley. An anonymous reviewer, P. Bishop, M. Dyson, A. Green, P. Henzi, A. Monadjem, J. G. M. Robertson and A. Turner read drafts of this work and made helpful comments. This work was financially supported by the FRD and the CBRG of the University of the Witwatersrand. Animal Ethics Clearance Number 90-157-3.

REFERENCES

- Arak, A. 1983. Male-male competition and mate choice in anuran amphibians. In: *Mate Choice* (Ed. by P. Bateson), pp. 181-210. Cambridge: Cambridge University Press.
- Arak, A. 1988. Callers and satellites in the natterjack toad: evolutionarily stable decision rules. *Anim. Behav.*, **36**, 416-432.
- Austad, S. N. 1984. A classification of alternative reproductive behaviors and a method for field-testing ESS models. *Am. Zool.*, **24**, 309-319.
- Backwell, P. R. Y. & Passmore, N. I. 1990. Polyandry in the leaf-folding frog, *Afrixalus delicatus*. *Herpetologica*, **46**, 7-10.
- van den Berghe, E. P. & Warner, R. R. 1989. The effects of mating systems on male mate choice in a coral reef fish. *Behav. Ecol. Sociobiol.*, **24**, 409-415.
- van den Berghe, E. P., Wernerus, F. & Warner, R. R. 1989. Female choice and the mating cost of peripheral males. *Anim. Behav.*, **38**, 875-884.
- Coe, M. J. 1967. Co-operation of three males in nest construction by *Chiromantis rufescens*. *Nature, Lond.*, **214**, 112-113.
- Coe, M. J. 1974. Observations on the ecology and breeding biology of the genus *Chiromantis*. *J. Zool. Lond.*, **172**, 13-34.
- Davies, N. B. 1982. Alternative strategies and competition for scarce resources. In: *Current Problems in Sociobiology* (Ed. by King's College Sociobiology Group), pp. 363-380. Cambridge: Cambridge University Press.
- Dominey, W. J. 1980. Female mimicry in male blue sunfish: a genetic polymorphism? *Nature, Lond.*, **284**, 546-548.
- Duellman, W. E. & Trueb, L. 1986. *Biology of Amphibians*. New York: McGraw-Hill.
- Elmberg, J. 1991. Factors affecting male yearly mating success in the common frog, *Rana temporaria*. *Behav. Ecol. Sociobiol.*, **28**, 125-131.
- Fairchild, L. 1984. Male reproductive tactics in an explosive breeding toad population. *Am. Zool.*, **24**, 407-418.
- Fukuyama, K. 1991. Spawning behaviour and male mating tactics of a foam-nesting treefrog, *Rhacophorus schlegelii*. *Anim. Behav.*, **42**, 193-199.
- Gerhardt, H. C., Daniels, R. E., Perrill, S. A. & Schramm, S. 1987. Mating behaviour and male mating success in the green treefrog. *Anim. Behav.*, **35**, 1490-1503.
- Given, M. F. 1988. Growth rate and the cost of calling activity in male carpenter frogs, *Rana virgatipes*. *Behav. Ecol. Sociobiol.*, **22**, 153-160.
- Green, A. J. 1990. Determinants of chorus participation and the effects of size, weight and competition on advertisement calling in the tungara frog, *Physalaemus pustulosus*. *Anim. Behav.*, **39**, 620-638.
- Greer, B. J. & Wells, K. D. 1980. Territorial and reproductive behaviour of the tropical American frog, *Centrolenella fleischmanni*. *Herpetologica*, **36**, 318-326.
- Gross, M. R. 1985. Disruptive selection for alternative life history in salmon. *Nature, Lond.*, **313**, 47-48.
- Halliday, T. R. 1987. Physiological constraints on sexual selection. In: *Sexual Selection: Testing the Alternatives* (Ed. by J. W. Bradbury & M. B. Andersson), pp. 247-264. Chichester: John Wiley.
- Halliday, T. R. & Arnold, S. J. 1987. Multiple mating by females: a perspective from quantitative genetics. *Anim. Behav.*, **35**, 939-940.
- Halliday, T. R. & Verrell, P. A. 1984. Sperm competition in amphibians. In: *Sperm Competition and the Evolution of Animal Mating Systems* (Ed. by R. L. Smith), pp. 487-508. New York: Academic Press.
- Halliday, T. R. & Verrell, P. A. 1988. Body size and age in amphibians and reptiles. *J. Herpetol.*, **22**, 253-265.
- Howard, R. D. 1978. The evolution of mating strategies in bullfrogs, *Rana catesbeiana*. *Evolution*, **32**, 850-871.
- Howard, R. D. 1988. Reproductive success in two species of anurans. In: *Reproductive Success: Studies of Individual Variation in Contrasting Breeding Systems* (Ed. by T. H. Clutton-Brock), pp. 99-113. Chicago: University of Chicago Press.
- Jacobson, S. K. 1985. Reproductive behavior and male mating success in two species of glass frogs (Centrolenidae). *Herpetologica*, **41**, 396-404.
- Kodric-Brown, A. 1986. Satellites and sneakers: opportunistic male breeding tactics in the pupfish *Cyprinodon pecosensis*. *Behav. Ecol. Sociobiol.*, **19**, 425-432.
- Krupa, J. J. 1989. Alternative mating tactics in the Great Plains toad. *Anim. Behav.*, **37**, 1035-1043.
- Lee, J. C. 1986. Is the large male mating advantage an epiphenomenon? *Oecologia (Berl.)*, **69**, 207-212.
- Loman, J. & Madsen, T. 1986. Reproductive tactics of large and small male toads *Bufo bufo*. *Oikos*, **46**, 57-61.
- Morris, M. R. 1989. Female choice of large males in the treefrog *Hyla chrysoscelis*: the importance of identifying the scale of choice. *Behav. Ecol. Sociobiol.*, **25**, 275-281.
- Perrill, S. A., Gerhardt, H. C. & Daniel, R. 1978. Sexual parasitism in the green treefrog (*Hyla cinerea*). *Science*, **200**, 1179-1180.
- Pyburn, W. F. 1970. Breeding biology of the leaf-frogs *Phyllomedusa callidryas* and *Phyllomedusa dacnicolor* in Mexico. *Copeia*, **1970**, 209-218.
- Robertson, J. G. M. 1986. Female choice, male strategies and the role of vocalizations in the Australian frog *Uperolia rugosa*. *Anim. Behav.*, **34**, 773-784.
- Ryan, M. J. 1985. *The Tungara Frog*. Chicago: Chicago University Press.

- Ryan, M. J. & Causey, B. A. 1989. 'Alternative' mating behaviour in the swordtails *Xiphophorus nigrensis* and *Xiphophorus pygmaeus*. *Behav. Ecol. Sociobiol.*, **24**, 341-348.
- Salvador, A. & Carrascal, L. M. 1990. Reproductive phenology and temporal patterns of mate access in Mediterranean anurans. *J. Herpetol.*, **24**, 438-441.
- Taborsky, M., Hudde, B. & Wirtz, P. 1987. Reproductive behaviour and ecology of *Symphodus (Crenilabrus) ocellatus*, a European wrasse with four types of male behaviour. *Behaviour*, **102**, 82-117.
- Taylor, P. 1971. Observations on the breeding habits of *Chiromantis xerampelina*. *J. Herpetol. Assoc. Afr.*, **8**, 7.
- Telford, S. R. & Van Sickle, J. 1989. Sexual selection in an African toad (*Bufo gutturalis*): the roles of morphology, amplexus displacement and chorus participation. *Behaviour*, **110**, 62-75.
- Wells, K. D. 1977. The social behaviour of anuran amphibians. *Anim. Behav.*, **25**, 666-693.
- Westneat, D. F., Frederick, P. C. & Wiley, R. H. 1987. The use of genetic markers to estimate the frequency of successful alternative reproductive tactics. *Behav. Ecol. Sociobiol.*, **21**, 35-45.
- Woodward, B. K. 1982. Mating persistence and mating success in Woodhouse's toad (*Bufo woodhousei*). *Ecology*, **63**, 583-585.