

# VOCALIZATIONS AND BREEDING BEHAVIOUR OF *PTYCHADENA TAENIOSCELIS* (ANURA: RANIDAE)

N. I. PASSMORE

*Department of Zoology, University of the Witwatersrand, Johannesburg*

## ABSTRACT

Four distinct types of call are produced by male *Ptychadena taenioscelis* Laurent in breeding aggregations. The most common of these is the mating call. A male/male interaction or 'chorus call' is also produced regularly and its production is dependent on the presence of two or more individuals. A call with a territorial function and the release calls uttered by amplexant males are also described. The responses of calling males to the arrival of females and further males are discussed. Mention is made of the ovipositional behaviour of this species.

## INTRODUCTION

The predominantly tropical genus *Ptychadena* is represented in South Africa by six species. All of these occur in the southern part of the Mozambique plain. The genus has received some attention in the light of the subtraction of four of the component species in this region (Poynton 1964; Poynton & Bass 1970; Van Dijk 1971). *Ptychadena taenioscelis* Laurent is encountered less frequently than the other members of the genus because it is distributed in a discontinuous pattern, occurring only in a small number of fairly isolated localities towards the southern limit of its range, where the present work was conducted.

Although the genus as a whole seems to be particularly worthy of study (Poynton 1970; Stewart 1967) comparatively little appears to be known regarding the biology of this or other species (Wager 1965, Stewart 1967). This lack of knowledge can probably be ascribed in part to taxonomic difficulties that have existed in this genus (Poynton 1970). The identification of component forms from preserved material is difficult because of poorly defined species characters and a good deal of variation (Poynton 1970). Although very real difficulties may be encountered in dealing with such material, many of these can be resolved by careful investigation in the field. This paper describes the species-specific vocalizations of *P. taenioscelis* together with aspects of its breeding behaviour observed in summer-breeding aggregations.

## METHODS

All call recordings were made in the field. The operator at all times endeavoured to cause minimal disturbance of the animals during the recording operation. Field recordings were made during December 1973 and December 1974 at three localities in the KwaMbonambi district,

Zululand. The calls were recorded with a UHER 4200 portable tape recorder at a tape speed of 19 cm/sec, using a 5 m microphone extension cable.

The recorded calls were analysed on a sound spectrograph (Kay model 7029A spectrum analyser) within the frequency range 80 Hz–8 kHz using a wide band filter (300 Hz).

## RESULTS

### *Mating call and calling site* (Figure 1A)

The mating call is the most common vocalization and it provides a convenient and positive means of identification in the field. Table 1 summarizes the mating call data obtained.

TABLE 1

	<i>N</i>	<i>Range</i>	<i>Mean</i>
Call duration (seconds)	43	0,19 – 0,33	0,26
Call pulse rate (pulses/second)	44	112 – 194	139
Pulses/call	44	26 – 46	34

The dominant harmonic lies within the range 2,1 kHz–4,1 kHz and generally covers a frequency range of approximately 1 kHz. This call is a rapidly trilled low-pitched noise of short duration which is unmistakable in the field and its confusion with the mating calls of other local species of *Ptychadena* is unlikely.

The calling site is exposed and the animals do not attempt to conceal themselves while calling. Exposed calling sites appear to be chosen in preference to concealed or partially concealed sites, even when the latter are freely available. Breeding aggregations are formed only along the edges of vleis and flooded grassland. Artificial dams and streams in the study area are not used for breeding purposes. Calling individuals establish themselves near the edge of the water and are commonly encountered sitting in the wet marginal mud, often in cattle hoof impressions. The feet are generally submerged and the water may reach the level of the armpits.

A marked clustering tendency is exhibited by calling males, and a number of regional concentrations or aggregates is generally present, distributed over the whole or part of the area available for breeding. These aggregates are composed of from three to eight calling males, with each individual separated from its neighbours by distances ranging from 0,4 to 1,5 m. Each aggregate forms a separate calling unit. Temporarily isolated callers have been observed to

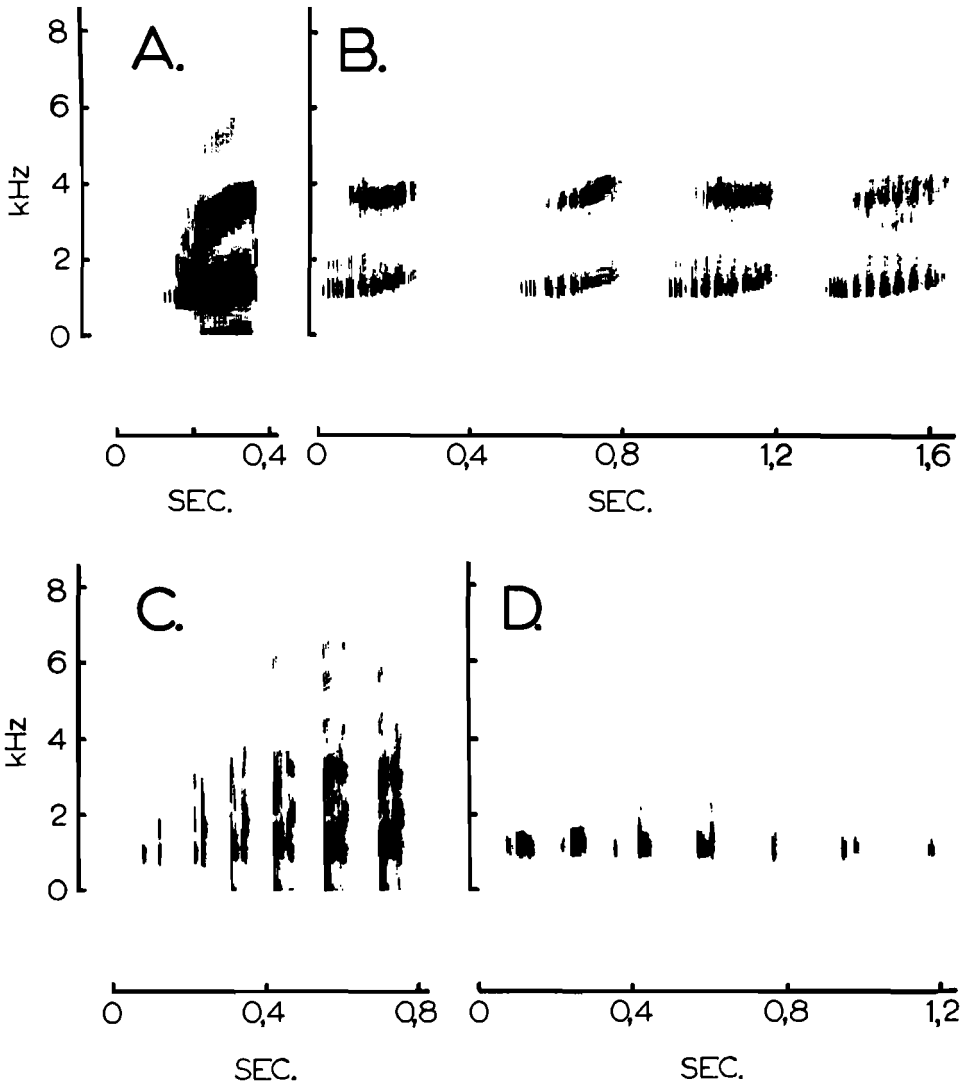


FIGURE 1  
Sonograms of four *Ptychadena taenioscelis* vocalizations.

- A: A single mating call.
  - B: Four chorus calls.
  - C: A single warning/territorial call.
  - D: A single release call.
- (80-8 000 Hz, wide band filter.)

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approach and finally form part of an aggregate, rather than to remain solitary for extended periods.

Mating calls are produced in successive bouts of varying length, separated by short intervals. At the beginning of a calling bout, the calls uttered by two adjacent males often alternate with one another in a regular fashion for a short while. As the bout progresses, this regular alternation of calls breaks down, giving way to a less organized situation, often with three or more participating males, where there is considerable temporal overlap between the calls produced. Where the calls are uttered in a regular alternating sequence, the interval between successive calls is distinct and the calls do not run together as a continuum.

#### 'Chorus call' (Figure 1B)

The 'chorus call' is spectrally very similar to the mating call, but is distinguished by a definite, clearly audible 'rasping or growling' quality. The chorus calls of 31 individuals were analysed. The duration of the chorus call is slightly greater than that of the mating call. It differs from the mating call principally in the complex alteration of the pulse rate. Rather than consisting of a train of similar and equidistant pulses, the pulse train is here broken up to 7–10 successive groups of about five pulses each. Each of these groups is separated from the next by a short interval. These intervals are responsible for the 'growling' auditory impression conveyed by the call.

Chorus calls are produced after a pair of adjacent individuals have been uttering mating calls for some time (see chorus structure). The mating call is simply replaced by the chorus call, after one or two intermediate-type calls. There is no interruption in the calling during this alteration, one call simply running into the other. The chorus calls are produced in a regular alternating sequence, in much the same manner as the initial mating calls of a calling bout.

The production of the chorus call is dependent on the presence of more than one individual and this call is absent from the repertoire of vocalizations of solitary callers. Adjacent males that had previously been producing mating calls generally chorus together, but this is occasionally disrupted by other nearby individuals. After 10–20 chorus calls have been produced by each member of a pair, calling ceases abruptly and the callers revert, usually after a short pause, to the mating call.

#### Warning/territorial call (Figure 1C)

This call is produced in two different situations. Under normal calling conditions it is uttered in the chorus situation by one or two males in an aggregate, usually within five seconds of the end of the chorus and occasionally terminating the chorus. It consists of a series of 5–7 widely separated 'cluck' noises. The warning/territorial calls of seven individuals were analysed.

The call functions in the maintenance of the spacing between callers. In situations where two or three males are very close together (5–20 cm), it is uttered regularly by all individuals involved, either together with, or in place of, the mating call. It results in the retreat of one or more of the individuals and its production continues until the callers are separated by distances in excess of about 30 cm. Thereafter it is replaced by the mating call.

### *Male release call (Figure 1D)*

This call is produced by amplexant or partially amplexant males and is uttered by one or both members of the pair until their separation. The duration of 'pseudo-amplexus' between males is generally not in excess of 30 sec. The call is a repetitive series of widely separated 'cluck' noises. It is aurally and spectrographically very similar to the warning/territorial call from which it differs principally in its length and in the time interval between successive syllables (Figure 1C, D).

### *Calling behaviour and chorus structure*

Calling intensity generally reaches peak level about an hour before last light and remains at this level for about two hours (eight observations). Sporadic single calls may be uttered at any time during the day (four observations) and chorus establishment may occur as early as three hours before dark, particularly on rainy or misty afternoons (two observations). Cessation of chorus occurs 3–4 hours after dark, following a gradual diminution of intensity over this period (11–15 and 18–20 December 1974). The sympatric *P. porosissima* and *P. oxyrhynchus* reach chorus peaks somewhat later.

During the daylight hours prior to chorus establishment, the males are involved in feeding. This activity ceases abruptly when the first series of mating calls is produced, usually by one, but sometimes by two males. Other males in the vicinity then approach these callers and mating and chorus calls are uttered by all the individuals concerned. This is the usual manner in which the chorus is established (four observations). The callers in this situation are separated by 0.4–1.5 m. With the arrival of further males, the chorus structure becomes more complex. Such males frequently disrupt the orderly spacing between calling individuals by alighting close to one of the active callers. The newly arrived male is thereupon mounted or partially mounted by one to six of the males in the vicinity. The 'huddle' of pseudo-amplexant males continues for up to 10 seconds, with release calls and an occasional strangled mating call issuing from it. These result in the separation of the males involved and their movement away from each other. Warning calls and mating calls are produced during this action. The 'huddle' of pseudo-amplexant males is re-formed in the event of any sudden movement of any of the participants and may re-occur up to five times before the desired spacing between individuals is established. Warning calls are uttered frequently during the retreat from the 'huddle' position and are finally replaced by mating and chorus calls following the establishment of a suitable spacing between individuals.

The appearance of females has been observed to result in the production of mating calls at an accelerated rate by the male(s) aware of their presence (three observations). In such situations, chorus calls are not produced and amplexus follows a cautious creeping approach by the male. The production of all calls ceases on mounting.

Call production by this species is not continuous but consists of a number of consecutive calling bouts separated by short intervals. The length of the calling bouts and the intervals between bouts are variable and depend on the intensity of the chorus. Intervals range from 45 seconds in a chorus at peak level to more than seven minutes either at the end or at the beginning of a calling session on a particular day. Calling bouts usually vary in length from one to two minutes and are initiated by a single male, which is later joined by other males as the bout

progresses. The same individual has been noted to repeatedly initiate the calling in successive bouts. This species is stimulated to call by nearby choruses of both *Ptychadena porosissima* and *P. oxyrhynchus*.

### Ovipositional behaviour

An amplexant pair was discovered at last light and observed intermittently for the following three hours. During this time the pair moved a distance of 8 m, eggs being produced over the entire distance. Usually two to three, but on occasion up to 10 single eggs are released at a time, in water ranging from 0,5 to 1 cm in depth. The eggs sink. The pectoral clasp of the male is typical, with the male continually squeezing the female with a pumping action of the forelimbs.

A series of complicated movements by both partners precedes the deposition of each group of eggs. The female moves her legs posteriorly from the normal sitting position, thus moving her body forward by about 2 cm (Figure 2). Simultaneously the back of the female is arched, lifting the cloacal region by just less than 1 cm. This results in a close juxtaposition of the cloacae of male and female. At this instant the male brings his feet from the normal position to one in which they touch each other in the midline just posterior to his cloaca, with their dorsal surfaces on the buttocks of the female. The hind feet of the male are at this stage pointing vertically down-

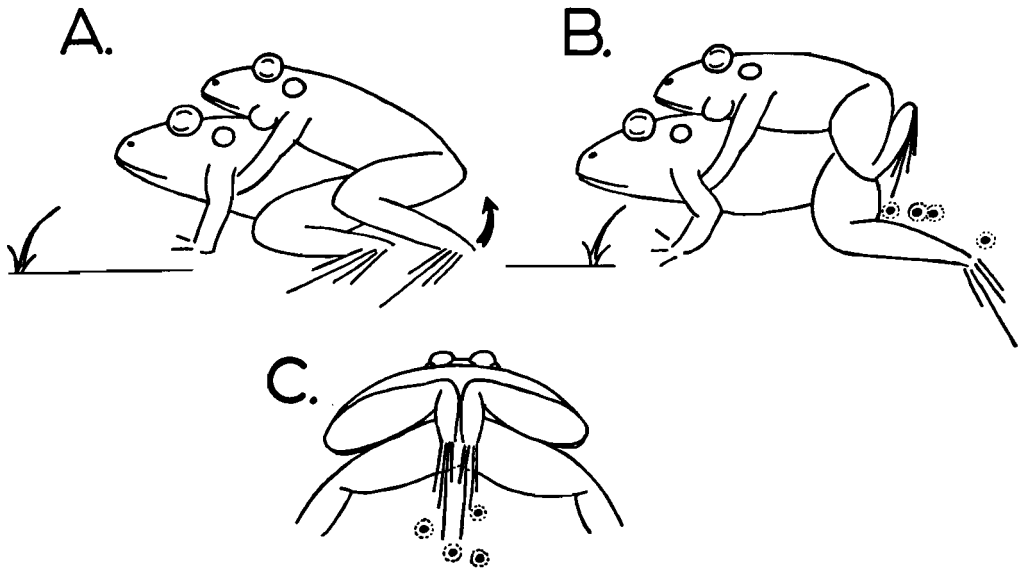


FIGURE 2  
Egg laying sequence (duration  $\pm 1,0$  sec.).

- A: Resting position.
- B: Female with legs extended and back arched, cloacae of male and female in close juxtaposition. Feet of male being applied to juxtaposed cloacae.
- C: Posterior view of amplexant pair at the moment of egg release.

ward, with the digits held close together and with the dorsal surface of both feet covering the juxtaposed cloacae. A group of eggs is then released by the female and seminal fluid is presumably funnelled over them by the hind feet of the male. The whole procedure is extremely rapid and lasts about one second. This egg-laying sequence is repeated four to six times, with intervals of two to five seconds between each. There follows a pause of up to three minutes before the egg-laying sequence is repeated. The eggs produced in this way sink very slowly and soon accumulate debris on the jelly capsule.

#### DISCUSSION

Most anurans possess a small organized vocabulary (Capranica 1965), the components of which are described in a review by Bogert (1960) and subsequently by Salthe & Mecham (1974). The mating call is the most common component of this vocabulary and studies on frog vocalization have been concerned mainly with this call (Pengilly 1971). The mating call has been found to be species-specific, each species differing distinctly from every other species in at least one, and often more, of the attributes of the call (Blair 1958). The mating call of *Ptychadena taenioscelis* is similarly highly characteristic and varies within fairly narrow limits in respect of each of the call parameters considered (Table 1). The vocabulary of most anurans consists of no more than four components (Salthe & Mecham 1974), and the mating call is the most frequently heard of these. It is therefore an easy matter to assign the label 'mating call' to the commonest call component. The fact that males, in response to the presence of a nearby female, produce this call at an accelerated rate and to the exclusion of all others is simple proof that this call functions at least in the close-range attraction of the female.

The position assumed by the male when calling, although highly variable between species, is generally consistent within species (Salthe & Mecham 1974). Call site differences in closely related sympatric species do play a role in reproductive isolation in a number of species (Salthe & Mecham 1974). The call site of *P. taenioscelis* is consistently exposed, and located along the edges of flooded grassland and vleis. The sympatric *Ptychadena porosissima* and *P. oxyrhynchus* in the study area call from rather different locations and breed in a wider variety of aquatic habitats.

The movement of nearby males towards the calling initiators and the subsequent formation of separate calling aggregates clearly demonstrates the importance of the mating call in establishing the distribution of the males over the available breeding territory. The aggregates or regional concentrations of males most probably facilitate the directed approach of female(s) towards the aggregate, with the subsequent location of a mate. A female, directed to an aggregate of males by their calls, would certainly locate one of the closely spaced males soon after her arrival. A random distribution of males over the breeding area might be less advantageous in this respect.

The application of the term 'warning/territorial call' to the vocabulary component uttered when males are inordinately close together is justified in that observable retreat of one or both of the individuals occurs as a result. Calls that function in the maintenance of spacing between individuals have been described in a number of species and are presently lumped together as territorial calls (Salthe & Mecham 1974). These authors mention the feasibility of separating

the above territorial calls into two categories, true territorial calls functioning at a distance and so-called aggression or aversion calls involved in close range interactions. The warning/territorial call here described for *P. taenioscelis* is, however, produced both as a close range interaction and as a 'true territorial call' operating at a distance (the latter referring to the production of this call near the end or terminating a calling bout and not involving two individuals in close proximity). It appears that this call is both a means of maintaining the distribution of males relative to one another and a means of establishing this distribution. It is apparently uttered in response to auditory rather than visual cues. In situations where closely spaced calling males were separated by a dense grass tussock and thereby effectively screened from one another, the call was believed to be aurally elicited. Outright aggression has not been observed in this species.

The call type here designated as the 'chorus call' is a commonly produced call in *P. taenioscelis* and in some of the other species of *Ptychadena* which have been investigated by the author. Although it is structurally significantly different from the other call types, its particular function has not become evident from fairly extensive observations of breeding aggregations. It is a male/male interaction call only produced when two or more individuals are calling and is not produced by solitary males like the mating call. Particular vocalizations may function in more than one capacity and the dividing line between different kinds of vocalization may be hazy (Salthe & Mecham 1974). The chorus call may indeed have a number of functions. It could be a territorial call which operates at a distance and influences the distribution of males relative to one another. The warning/territorial call functions in this way and it seems unlikely that two different calls serve exclusively the same function. Each calling bout could be described as 'initially organized' (Duellman 1967), in that only at the beginning of the bout are mating calls uttered in a regular antiphonic sequence. Later in the bout, and for the greater part of it, the calling is less organized with considerable overlap between the calls of all the participants. On the other hand, chorus calls are produced in a regular alternating sequence. When a female is near to an aggregate, a temporal separation between the calls of nearby males could enable the female to detect sonically the position of each male. Conversely, where no such temporal separation between the calls exists, the acoustical environment of the female is more complex with many of the calls overlapping each other. In such conditions, close range location of the male might be more difficult. Temporal separation of calls of conspecific males would simplify the acoustical environment of the female in much the same way as temporal separation of the calls of different species has been shown to do by Littlejohn & Martin (1969). If this interpretation is correct, the chorus call would be an accessory mating call functioning for close range attraction of the female, or this could be at least part of its function.

Release calls appear to be present in most families of anurans and although often present in both sexes, they are frequently better developed in males (Salthe & Mecham 1974). Release calls appear to be important in *P. taenioscelis* because males frequently attempt to grasp other males.

The ovipositional movements of this species are by no means unique and they seem to follow those described as characteristic for *Bufo*, *Gastrophryne carolinensis* and some species of *Rhacophorus* (Salthe & Mecham 1974). They are here described because information on this aspect of breeding biology in the genus appears to be lacking (Wager 1965; Stewart 1967).



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