© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

Notes on the Vocalisations of some Amphibians from the Serengeti National Park, Tanzania[1])

by

P. VAN DEN ELZEN, Bonn, and D. A. KREULEN, Haren

Received Sept. 1979

Anuran vocalisations are a convenient aid in the detection of individuals and breeding aggregations in the field. Amphibian mating calls also proved effective for the taxonomic differentiation of sibling species (Menzies & Zweifel 1974, Dubois 1975, van den Elzen 1976 a) and contributed to a better understanding of i. a. the *Bufo regularis* species complex (Keith 1968, Passmore 1972, Tandy & Keith 1972). Schiøtz (1964, 1967, 1975) was the first to publish a series of objective descriptions, as sonagrams, of the mating calls of African anurans. Recently Amiet (1973, 1974, 1976) and Amiet & Schiøtz (1972, 1974) described the mating calls of many species from Cameroon. Channing (1976 a, 1976 b), van den Elzen (1976 b, 1977, 1978), Passmore (1976, 1977) and Passmore & Carruthers (1975) presented data on australafrican amphibia. An assessment of the geographical variation of call structure or the study of parapatric and sympatric hybrid taxa remains to be made.

Wickler and Seibt (1974) already published sonagrams from the Serengeti, dealing with *Bufo regularis* and *Kassina senegalensis*. The present paper describes calls of 17 of the 22 amphibian species encountered (Kreulen, unpubl.) in the Serengeti. Sonagrams of mixed choruses are also presented. These add further data to those presented by van den Elzen and van den Elzen (1977) (vide also Hödl (1977)) demonstrating the use of different acoustical niches which, in addition to other parameters, may reduce interspecific interaction during courtship and may be essential for intraspecific communication.

Recording localities

Occasional recordings were made near Seronera and Kirawira, in the Serengeti National Park, Tanzania, during the period from 1970—1975. The park lies in the corner between the eastern shore of Lake Victoria and the Tanzania — Kenya border. Its gently un-

[1]) Serengeti Research Institute Publication no. 257

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

dulating topography is covered with various savanna vegetation types described by Herlocker (1975) and Schmidt (1975). Data on rainfall and climate have been published by Norton-Griffiths et al. (1975), and by Pennycuick & Norton-Griffiths (1976).

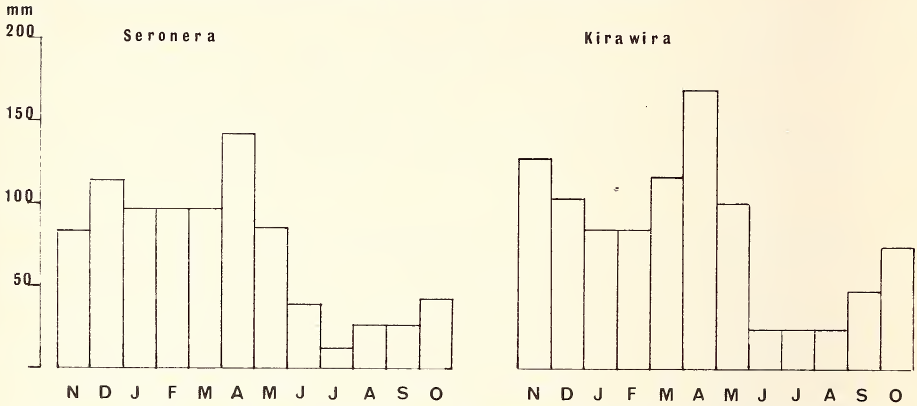

Fig. 1 Ten year (1962—1972) mean annual rainfall in the central region and the western corridor of the Serengeti National Park, Tanzania (after Norton-Griffiths et al. 1975).

Seronera lies in the centre of the Park, it is the Park's Headquarters and has a tourist lodge. The position is 34°49' East, 2°26' South and the altitude is 1510 m. The mean annual rainfall is ca. 800 mm, which is distributed according to a marked seasonal cycle (fig. 1). About 83 % of the total rain falls in the wet season from November — May, with peaks in December and April. The coefficient of variation of the year to year variability in total wet season rainfall is 25 % (S. D. as a % of the mean). Rain usually occurs as sporadic afternoon thunderstorms, so that many days during the wet season pass without any rain. The dry season ranges from June — October, July being the dryest month. Herlocker (1975) classified the vegetation at Seronera as semi-deciduous to deciduous thorn tree woodland with the genus *Acacia* dominant among the trees, *Pennisetum mezianum* and *Themeda triandra* being conspicuous among the grasses. Burning of the herbaceous cover is a regular phenomenon in this area during the dry season.

Kirawira lies 71 km. WNW of Seronera at 34°13' East, 2°09' South in the so-called western "corridor" of the Park. The altitude is 1195 m. There was formerly a guardpost here and a research station along the upper reaches of a tributary of the Ruwana river. The mean annual rainfall is ca. 1000 mm showing a seasonal distribution as at Seronera (Norton-Griffiths et al. 1975). The vegetation consists of semi-deciduous bushland (Herlocker 1975), i. e. evergreen thickets with emergent semi-deciduous thorn trees alternating with open grassland where *Chrysochloa orientalis* is one of the characteristic species.

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

Methods

All recordings were made with a Philips portable cassetterecorder (No. 2202) and its standard microphone. Recording was usually carried out in the evening between 19^{h}30 and 23^{h}00 when calling activity was highest. The ambient air temperature was not measured at the recording site but the corresponding (in time) minimum-maximum temperatures, recorded at the Research Institute, 5 km east of Seronera, are given when available. The calls were analysed using a Kay Electric 7030 A sonagraph. The sonagrams were produced in wide (filter band width 150 Hz) and the spectral characteristics were gained from these.

Results

1. Calling sites

As several different calling sites were visited a short description of each is given to illustrate, that different species gathered at a breeding site can have different microhabitat preferences.

At Galens Drift, Seronera, a temporary pool with a maximum depth of 75 cm is formed in the stream bed behind a concrete drift on the road between Seronera and the Serengeti Research Institute (Fig. 2). The edges were sparsely covered with partly submerged sedges, grasses, etc., the banks were lined with bushes and larger trees. Up to nine species of anurans were heard calling simultaneously from the waters of this pool. Of the 15 species breeding in this pool the calls of the following were recorded: *Xenopus borealis* Parker, 1936; *Cacosternum boettgeri* (Boulenger, 1882); *Phrynobatrachus acridoides* (Cope, 1867); *Phrynobatrachus natalensis* (Smith, 1849); *P. ukingensis mababiensis* Fitz Simons, 1932; *Ptychadena mascareniensis* (Duméril et Bibron, 1841); *Chiromantis petersii* Boulenger, 1882; *Hyperolius viridiflavus goetzei* Ahl, 1931; *Kassina senegalensis* (Duméril et Bibron, 1841); *Leptopelis bocagei* (Günther, 1864) and *Phrynomerus bifasciatus* (Smith, 1847).

The *Hyperolius* were clinging to sedges and other plants standing in the water and along the edge at varying heights above the surface. The *Cacosternum* sat in or just above the water amongst the vegetation. The *Phrynobatrachus natalensis* sat partly under water on plants or in the shallows near the edge. *Kassina* were seen on the ground between grass clumps near the edge of the pool or sometimes partly submerged between inundated vegetation. The *Phrynobatrachus ukingensis mababiensis* were sitting in bushes or tall grass up to 1 m above ground level near the pool's edge. One amplexed pair of *Phrynomerus* and two pairs of *Hyperolius* were floating in the

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

Fig. 2 Ephemeral pool in drainage line at Galens drift, Seronera. Overflowing on 24 April, 1971. Breeding habitat of 15 species of anurans.

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

water between the vegetation. The *Phrynobatrachus acridoides* were calling from a large patch of grasses and sedges standing in the water. *Ptychadena mascareniensis* sat partly submerged in between vegetation.

The same evening another breeding congregation was observed at the Lodge dam, Seronera. This is a shallow basin formed behind a dam with mudflats around it. The following species were observed calling: *Bufo regularis gutturalis* Power, 1927; *Cacosternum boettgeri; Phrynobatrachus natalensis; Ptychadena anchietae* (Bocage, 1867); *Chiromantis petersii; Hyperolius viridiflavus goetzei; Kassina senegalensis. Ptychadena mascareniensis* was also present but not calling. The *Bufo* were sitting on the wet mudflats or partly submerged in the water, usually partly under plant cover. Both *Ptychadena* sat, more or less exposed, on the mudflats between the plants, some partly submerged. The *Hyperolius* were amongst and on the vegetation above the water or the banks. The *Cacosternum* called from a sedge clump above water level.

On the 3rd December, 1970, *Bufo regularis gutturalis* and *Phrynobatrachus natalensis* were sitting along the edges of a small, temporary buffalo wallow in open woodland near Seronera. Some vegetation grows along the edges but it only contains water during short periods in the rainy season.

After heavy rain the previous day and earlier during the same day (115 mm), *Phrynomerus bifasciatus* started calling from flooded grassland near Seronera on 8 November, 1972. The frogs were sitting partly submerged or on damp ground between grass tussocks. *Bufo regularis gutturalis, Cacosternum boettgeri, Phrynobatrachus acridoides, Ptychadena anchietae, Kassina senegalensis* and *Leptopelis bocagei* were heard as well. *Cacosternum* called, sitting erect halfway above the water level, resting the anterior part of its body on a stem or a blade of grass; they usually sit well-concealed under overhanging vegetation. The *Ptychadena anchietae* were shrieking steadily on wet ground, more or less exposed. The *Kassina* were sitting on the ground, hiding between and under the grass clumps.

On the 5th March, 1975, several species *(Cacosternum boettgeri, Phrynobatrachus acridoides, P. natalensis, Ptychadena anchietae, Chiromantis petersii, Hyperolius viridiflavus goetzei, Phrynomerus bifasciatus)* were heard calling from a shallow, temporary pool in the gravel pit. Situated at the "Dikdik corner" between Seronera and the Research Institute the pond contains little aquatic and marginal vegetation. The *Hyperolius* were sitting above the water (up to 50 cm), clinging to grass stems. *Phrynobatrachus natalensis* sat, partly submerged, near the edge or under plant cover near the middle of the pond. *Cacosternum* called just above water level, or

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

floating, supported by vegetation. *Chiromantis* and *Ptychadena* were sitting on bare ground along the edge, more or less exposed. *Phrynomerus* may be found sitting on the soil between grass clumps, in the entrance to a rodent's burrow or the chimney of a termite mound, but they also called from underneath a log and while floating in the water among some vegetation.

The 6th March, 1975, a brief, weak chirp or buzz, probably *Hyperolius nasutus* Günther, 1864, was heard from a mat of *Pistia stratiotes* covering a deep, permanent pool in the riverbed of a tributary of the Ruwana River near the Kirawira Research Station, about 1 km downstream from the abandoned guardpost. Reed patches grow in the water. The banks are partly devoid of any vegetation due to the frequent trampling by game coming to drink here. There are however, er, some trees and bushes along the bank. At the time, early evening, several *Hyperolius viridiflavus goetzei* had started to call. Later, about 24^h55 *Bufo regularis gutturalis*, one *Dicroglossus occipitalis* (Günther, 1858) and *Ptychadena anchietae* were also calling. The toads were sitting partly submerged near the edges, the *Ptychadena* kept to the edges and the *Dicroglossus* was floating on the water surface, swimming every so often from one side of the pool to another, calling from different positions.

During the same evening *Ptychadena floweri* (Boulenger, 1917) was heard from a shallow, temporary puddle surrounded by grassland, on the open plain near Kirawira. The frog sat partly submerged, at the base of a grass tussock at the edge of the puddle.

Another water hole, at Kirawira, close to a thicket and some *Acacia* trees, served as a wallow and drinking place for various ungulates, resulting in many hoofprints in the mud. These hoofprints, in that they often hold water, may enable tadpoles to metamorphose all the same. At 23^h00 *Cacosternum boettgeri, Ptychadena anchietae, Tomopterna marmorata* (Peters, 1854) and *Phrynomerus bifasciatus* were calling. The *Tomopterna* were on the ground between clumps of short grass close to the puddle's edge, the *Ptychadena* sat on bare mud more or less exposed. The *Cacosternum* called from a grass clump near the edge and *Phrynomerus* sat on the ground near the puddle but also farther afield. A mating pair of *Kassina senegalensis* was noted, but none were calling at the time.

2. Species accounts

During the past years new information has become available on the genus *Xenopus* and several taxonomic problems were solved (Tymowska 1976; Tinsley et al. 1979; Vigny 1977). A survey of the mating calls of 12 *Xenopus* species was presented by Vigny (1979).

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

The calls recorded at Seronera (Plate I, fig. A) at approx. 16° C are very similar to those depicted by Vigny (1979) as short calls by X. *muelleri* (Peters, 1844), but the repetition rate and the absence of trills indicate them to belong to X. *borealis*. Acoustically they make the impression of constantly repeated ting, ting, ting sounds. Their fundamental frequency lies between 1000—1300 Hz, the number of calls/min is ca. 128—132. A comparison of the calls with those already published, recorded at 25° C WT, shows a negative correlation of interval length and water temperature. This was demonstrated experimentally under laboratory conditions, using X. *borealis,* too. No excitement calls were heard.

According to Vigny (1977) X. *borealis* only occurs in Kenya, the Tanzania species being X. *muelleri*. It may well be, therefore, that X. *borealis* reaches its southernmost distributional limit in the Serengeti. X. *muelleri* is known to occur south of Lake Victoria and east of the Rift extending across the border into southern Kenya. More intensive collecting in the Serengeti might show X. *borealis* and X. *muelleri* populations, otherwise allopatric, to come into contact here. Should sympatric populations exist, this would support the claim that mating calls of sympatric species are often more differentiated than those of closely related allopatric ones, the mating call of X. *borealis* consisting of a simple pulse train whereas the X. *muelleri* call is a complex pulse train.

Bufo regularis gutturalis was long known from the literature as „*Bufo regularis* East". Field work proved it to be identical with *Bufo gutturalis* (Tandy et al., 1976). It is known from western Uganda eastwards and from there south to Natal. The mating call recorded (Plate I, fig. B) does not deviate from the normal range of 11—26 passive pulses per pulse train (Tandy and Keith, 1972). The number of pulse trains per complex pulse train is variable (21—36 calls/min for the Serengeti material). Wickler and Seibt (1974) described calling and answering behaviour among ♂ of the Serengeti population.

The genus *Cacosternum* is basically non-tropical with five forms occurring in southern Africa and one, *C. leleupi* Laurent, in Katanga. Relic populations of *C. boettgeri* exist in the East African highlands. The mating call (Plate I, fig. C) has been described for South West Africa material (van den Elzen and van den Elzen, 1977). In the Serengeti 11—20 calls/min are the average. Each call is composed of approximately 6—8 double or triple pulses, the first 3 of a pulse train being double, the last ones sometimes are triple. No territorial or aggressive calls were heard. The pulses have a frequency intensity maximum at 4500 Hz. Calls last an average 0.8 sec, the interval between consecutive calls is 2.2 secs.

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

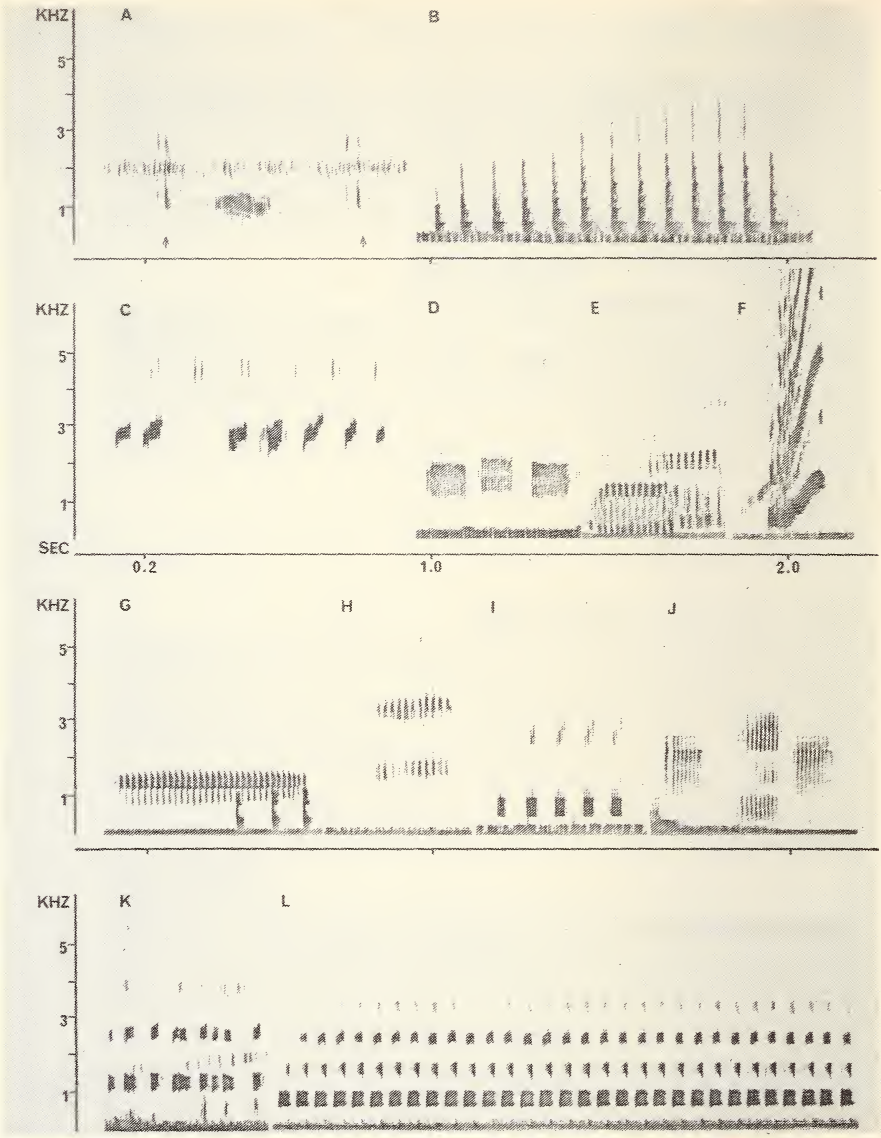

Plate I Sonagrams of the mating calls of some Serengeti amphibians. A. Two *Xenopus borealis* „clicks" and one *Leptopelis bocagei* call. B. *Buto regularis gutturalis.* C. *Hyperolius viridiflavus goetzei, Cacosternum boettgeri* at 5 kHz. D. *Phrynobatrachus acridoides.* E. *Dicroglossus occipitalis* F. *Kassina senegalensis.* G. *Phrynobatrachus natalensis.* H. *Ptychadena anchietae.* I. *Ptychadena floweri.* J. *Ptychadena mascareniensis* (middle call) and *Phrynobatrachus acridoides.* K. *Tomopterna marmorata.* L. *Phrynomerus bifasciatus.*

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

Dicroglossus occipitalis occurs from Senegal to East Africa and Angola in open savanna country. Its mating call (Plate I, fig. E) is known for Cameroon material (Amiet, 1974) and shows the following characteristics: 12 pulses/call, duration 0.2 sec, intervals 0.2 sec, fundamental frequency 400—1100 Hz with an emphasized harmonic at 3000 Hz. Serengeti specimens call 36—44 times per minute, a call lasts 0.2 sec and the intervals between successive calls vary in length from 1.1—1.4 secs. Each call is composed of 12 pulses. The frequency intensity maximum is at 1000—1500 Hz with an energy band at approximately 500 Hz.

The call of *Phrynobatrachus acridoides*, (Plate I, fig. D) which ranges from the northern Zululand coast through East Africa north to Kenya, is a loud, raucous, hoarse "waak-waak-waak-waak" (Stewart, 1967). The species may be heard day and night, unlike *P. natalensis* which calls more often during late afternoon and long into the night. The call is composed of many figures repeated at a rate of 192—216 per minute. The frequency intensity maximum lies between 1400—1600 Hz. Each figure, or pulse train, lasts approx. 0.23 sec with an interval length of 0.31 sec. The species also seems to have a chorus call which is shorter, lasting 0.12 sec with an interval of 0.25 sec between consecutive figures.

Phrynobatrachus natalensis, practically ubiquitous in savanna regions south of the Sahara, excepting the southwestern Cape Province and the Moçambique plain, utters a call which is somewhat similar to that of *Bufo regularis* Reuss, 1834, but not so loud and heavy; it reminds of *P. acridoides,* the repetition rate being much slower though. Sierra Leone specimens (Schiøtz, 1964) utter a series of deep buzzes in unmeasured rhythm. Each motif consists of 35—40 figures, the duration is 0.3 sec with a frequency intensity maximum at 1500 Hz. Serengeti specimens (Plate I, fig. G) call at a rate of 48—56 pulse trains/min, the frequency intensity maximum is at 1100—1500 Hz and each pulse train consists of 33—44 pulses. One motif lasts on average 0.62 sec with a 0.69 sec interval between consecutive motifs.

The call of *Phrynobatrachus ukingensis mababiensis* (Plate II, fig. A) reminds one of *P. calcaratus* (Peters, 1863) from Ghana. This species also has a very high-pitched buzzing call. Wager (1965) describes the call as sounding somewhat like a cricket, each trill lasting from 30—60 secs. Stewart (1967) gives a similar account for this species, which ranges from southeastern Africa to Tanzania and westward across northern Botswana to the northern parts of South West Africa (Namibia) and southern Angola. The available material does not permit a detailed analysis but the trill consists of a pulse train emitted at the rate of 25—49 pulses/sec *(P.*

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

calcaratus has a repetition rate of approx. 100 pulses/sec.). The frequency intensity maximum is situated between 5000—5500 Hz.

Several papers have been published on the vocalisations of members of the genus *Ptychadena* (Amiet, 1974; Passmore 1976, 1977; Schiøtz, 1964). Some deal with west African material, others with specimens from southern Africa.

The mating call of *Ptychadena anchietae* (Plate I, fig. H), which is distributed from eastern Natal to Eritrea, gives the impression of a high-pitched screech, much like rusty hinges being turned at a fast pace. Stewart (1967) finds it to be similar to that of *Phrynobatrachus natalensis* and *Ptychadena oxyrhynchus* (Smith, 1884). The calls follow each other at one second intervals. Passmore (1977) notes a frequency range of 1600—2200 Hz and remarks that, in the chorus call, the duration is decreased and the repetition rate accelerated. An analysis of the material available to us showed that the species vocalises at a rate of 56—96 calls/min, each call is built up of 12—45 pulses and it lasts an average 0.3 sec. The intervals last 0.93 sec. The fundamental frequency lies between 1500—2000 Hz, harmonics are situated at the 3400 Hz, 5000 Hz and 7000 Hz marks.

The mating call of *Ptychadena floweri* (Plate I, fig. I) was first published from Ghana as *Abrana floweri* (Schiøtz, 1964). It sounds like a dry rattle or a machine-gun. Each call is composed of 6—7 short figures with 5—6 segments. The frequency-intensity maximum is at 3000—4000 Hz, the depicted call demonstrates a fundamental frequency of approx. 500 Hz. Amiet (1974) confirms these data from Cameroon, his calls show a frequency maximum at 2000—3000 Hz. The species is able to call in a floating position, spread-eagled on the water surface (Amiet, 1974; Stevens, 1974), an unusual attitude for members of the genus during calling. Our material shows that the species calls at a rate of 32—36 calls/min. The calls are composed of an average 5.8 (4—7) pulse trains per call, which pulse trains are themselves built up of 7 pulses, the first pulse train of such a complex call usually being the shortest and consisting of 5 pulses. The duration of such a complex pulse train is 0.36 sec and the frequency shows a distinct high-intensity band between 400—900 Hz with a harmonic at approx. 2500 Hz. *P. floweri* is known eastwards from Ghana to the Sudan and south till Moçambique.

Ptychadena mascareniensis is a savanna species widely distributed throughout tropical Africa and Madagascar; several subspecies are recognised. Amiet (1974) gives the following information on Cameroon material: call duration 0.15—0.20 sec; intervals approx. 0.30 sec; 22 pulses/call; frequency maximum at 1300—2300 Hz. He further remarks that the species calls during early dawn

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

and morning. Passmore (1977) writes that the Cameroon call seems identical to those obtained at KwaMbonambi, Zululand. His call shows the following characteristics: call duration 0.17 sec; 16 pulses/call; frequency maximum between 2300—3000 Hz. Our material (Plate I, fig. J) shows 12 pulses/call, a duration of 0.12 sec and a fundamental frequency band between 500—1200 Hz with a corresponding harmonic of similar intensity at 2300—3000 Hz. Differences between the various parameters discussed may be due to geographical variation but are certainly a result of the different recording temperatures.

Data on the vocalisations of the genus *Tomopterna* have recently been published (van den Elzen, 1978; van den Elzen and van den Elzen, 1976 b, 1977; Passmore, 1976; Passmore and Carruthers 1975). Serengeti material has already been analysed (van den Elzen, 1978). We only mention the most important parameters of the *T. marmorata* mating call (Plate I, fig. K): duration 0.03 sec, interval 0.11 sec, fundamental frequency 1000—1500 Hz at a temperature of 19.5° C .

The mating call of *Chiromantis rufescens* (Günther, 1868), which ranges from the Nimba Mountain, Guinea, to Uganda, has been described as quiet, inconspicuous, composed of two motifs (Schiøtz, 1967). The first motif consists of a series of clicks, whereas the second is a buzzing, a repetition of approximately 30 pulses. The fundamental frequency is indistinct. Wager (1965) describes the call of *C. xerampelina* Peters, 1854, as a subdued, squeaking noise sounding like "chick — chick — a — chick-chick". This species is known from northern Zululand northwards to coastal Kenya. The quality of the recorded *C. petersii* calls is poor and allows only for a general description. There is a short "creak" motif, consisting of 3—6 pulses. The indistinct fundamental frequency lies between 1000—1500 Hz.

The calls of *Hyperolius viridiflavus goetzei* (Plate I, fig. C) are similar to those of the other forms of the *viridiflavus* superspecies (Schiøtz 1971, 1975). It is a short (0.05 sec) shrill, high-pitched whistle, repeated at approximately 0.6 sec intervals, with a frequency intensity maximum at 2500—3000 Hz. A different call was recorded, which probably belongs to *H. nasutus*. The acoustical impression is a high-pitched, raspy creak repeated at a rate of 40—44 calls/min. The frequency-intensity maximum is between 4000—4500 Hz. The first part of the call is composed of a succession of rapidly rising pulses (9—10 pulses) followed by several double pulses at the level of highest intensity. The species called at Kirawira together with *H. viridiflavus goetzei* on the 6th March, 1975, during early evening.

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

The voice of *Leptopelis bocagei* is a slow, unmelodic "woi" or "wah" repeated at irregular intervals. The sonagram (Plate I, fig. A) shows a call lasting 0.15 sec with a frequency maximum at 1000 Hz. This is a very inconspicuous species, it is terrestrial and fossorial.

The *Kassina senegalensis* from the Serengeti are acoustically similar to Form 2 of Schiøtz (1975) as their mating calls have a long initial motif broken up into segments. The species emits 7—11 calls/min., which are typical (Plate I, fig. F). Sonagrams of mating calls of the species, sensu lato, have been published Channing, 1976 b; van den Elzen and van den Elzen, 1977; Largen, 1975; Schiøtz, 1967, 1975; Wickler and Seibt, 1974).

Phrynomerus bifasciatus ranges from northern Zululand to Kenya and westward via Botswana to Angola. The length of a mating call (Plate I, fig. L) is variable but usually lasts approximately 2 secs. Up to 12 calls are emitted per minute. The voice is a high-pitched trill with a frequency-intensity maximum at 1000 Hz and 4 harmonics. A pulse train is composed of 31—43 pulse groups, with one pulse group lasting 0.033 sec and the interval between the passive pulses being 0.020 sec.

A comparison with *P. microps* (Peters, 1875), an allopatric West African form shows that its mating call is also a deep, melodious trill, consisting of a long repercussion of short figures (Schiøtz, 1964). It is very similar to the call of *P. bifasciatus* with a frequency-intensity maximum at 1250 Hz and four harmonics. The pulse groups last 0.020 sec and the intervals between the pulses last 0.020 sec as well. The mating call of a third *Phrynomerus, P. annectens* (Werner, 1910), known from Angola and South West Africa (Namibia), has been described by Channing (1976 a). The call is a trill lasting up to 12 secs, the frequency-intensity maximum lies at approx. 2500 Hz. Contrary to *P. bifasciatus* and *P. microps* the complex pulse train is not composed of passive pulses, but is subdivided into pulse trains each consisting of 4—5 pulses; pulses number one and four cover a narrower spectrum than pulses two and three do. The simple pulse trains last 0.023 sec and the intervals between these 0.010 sec. It is interesting to note that the ♂ of this species are extremely territorial, in the Namib, actively attacking any ♂ coming too close and emitting a characteristic territorial call.

3. The chorus

African savanna amphibians are explosive breeders, gathering at suitable spawning grounds after the first rains, the numbers are directly dependent on rainfall and temperature. In such a situation

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

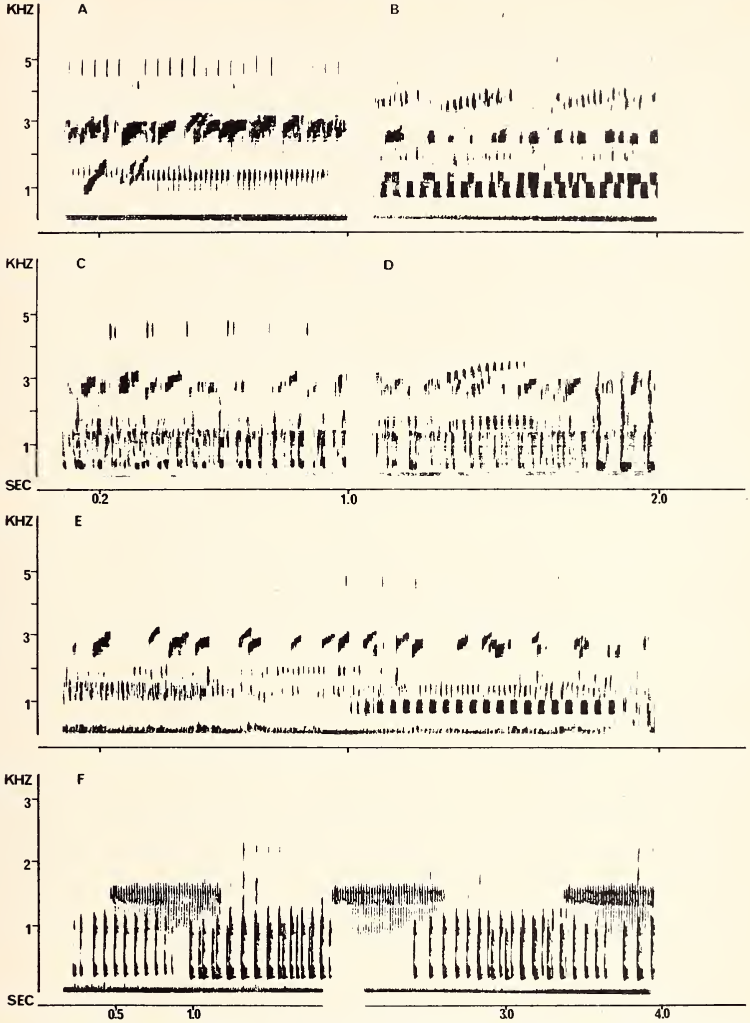

Plate II Sonagrams of some chorus compositions of Serengeti anurans. Species indicated from the lowest frequency up. A. Seronera 22. IV. 1971 *Kassina senegalensis* (glissando figures), *Phrynobatrachus natalensis, Hyperolius viridiflavus goetzei, Phrynobatrachus ukingensis mababiensis.* B. Kirawira 6. III. 1975 *Phrynomerus bifasciatus, Tomopterna marmorata, Ptychadena anchietae.* C. Seronera 22. IV. 1971 *Bufo regularis gutturalis, Hyperolius viridiflavus goetzei, Cacosternum boettgeri.* D. Seronera 22. IV. 1971 *Bufo regularis gutturalis, Ptychadena anchietae, Hyperolius viridiflavus goetzei.* E. Seronera 5. III. 1975 *Phrynomerus bifasciatus, Phrynobatrachus natalensis, Hyperolius viridiflavus goetzei, Cacosternum boettgeri.* F. Seronera 3. XII. 1970 *Bufo regularis gutturalis, Phrynobatrachus natalensis.*

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

low-density species would be at a disadvantage as they are not only limited by the bi-annual rain cycle and the usually temporary nature of the breeding pans, but they must also find a mate which can prove difficult in aggregations of up to 15 species, time being a limiting factor. Bowker and Bowker (1979) found that there is no significant spatio-temporal overlap in the numerically important species gathered at one pond, however.

The choruses presented (Plate II, figs. A—F) give an impression of the sonic background from which the gathered species must be able to select the species-specific call. They illustrate the existence of different acoustical niches. The peripheral auditory systems of amphibians are specialised to detect the major spectral and temporal components of a ♂ mating call (Capranica, 1976; Narins and Capranica, 1976). It seems logical that the frequential and temporal features of a call should be directed towards a channelisation of species-specific sounds to avoid interference.

Five rules of association-competition amongst animals whose periods of acoustic activity are superimposed in time have been defined (Leroy, 1978). Association-competition results in a distribution of the vocalisations within the overall frequency range, it operates upon signals of differing temporal structure, it may oppose a monotonous, regular and continuous signal to one which is of complex structure, it may operate upon signals of different amplitude and it can produce mechanisms of a different nature e. g. the inhibition of the signals of one species by those of another. All anuran signals so far examined by the senior author in Africa fall within the first four categories or show spatio-temporal isolation, none is inhibited in its calling activity by another as far as we presently know. Spatial separation strongly reinforces the functioning of the mating call as a primary species identification signal among anuran species from central Amazonian floating meadows (Hödl, 1977).

An interesting aspect is the problem of sound attenuation in an acoustic environment, which encompasses all relationships within and between faunistic groups and their characteristic habitats or climatic regions, such as an open country savanna.

Fellers (1979) writes that ♀ *Hyla versicolor* Le Conte, 1825, choose the loudest sound cue when presented a choice. Successful ♂ occupied horizontal perches with less surrounding vegetation causing sound attenuation. Such perches were occupied earlier in the season and used more often than others. A horizontal position allows for a uniform spreading of the call and as ♂ base their territorial system on sound pressure levels an acoustically unobstructed territory should be larger, thus increasing the chance that a ♀ reaches such a ♂ without being drawn away in her phonotactic behaviour

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

by other calling ♂. The same principle applies to complex chorusing communities of anurans spatially isolated around and in or above a temporary pool.

Many species, such as *Bufo, Tomopterna, Kassina,* can be heard over long distances and their calls become more or less attenuated and reflected depending on which habitat is crossed. In dry air the sound energy of a 1 kHz sound is halved at 60 m, a 10 kHz sound at 15 m and that of a 150 kHz sound at 1 m. The degree of attenuation varies with temperature, air humidity, environmental structure (Jilka and Leisler, 1974) and frequency. A sound wave hitting an even surface is reflected if the average diameter of the obstacle is greater than the wavelength of the sound. Reflections should be kept to a minimum, hence in a tropical forest system the frequencies of animal vocalisations are usually lower than those of savanna system species (Chappuis, 1971). The low-intensity clicks and buzzes of *Chiromantis rufescens, Hyperolius bobirensis* Schiøtz, 1967 and *H. zonatus* Laurent, 1958, are also adaptations to the quiet forest where breeding aggregations are small (Schiøtz, 1967, 1973). The high-intensity calling savanna species cover a relatively broad spectrum, in accordance with the habitat colonised, but each occupies its spectral and temporal niche which enables the ♂ and the ♀ to extract the species-specific information from the chorus.

Acknowledgements

It is a pleasure to express our gratitude to the following persons and organisations: the Trustees of the Tanzania National Parks; the Director of the Serengeti Research Institute; Prof. Dr. G. P. Baerends; the Netherlands Foundation for the Advancement of Tropical Research (W.O.T.R.O.); A. Duff-Mackay; T. Jager and H. de Wit; Prof. Dr. W. Graf (Österreichische Akademie der Wissenschaften, Kommission für Schallforschung); the Institut für Phonetik, Universität Bonn.

Summary

The mating calls of some anurans from the Serengeti are presented. Some of the species form choruses. Information is presented on the sites chosen for breeding and the choruses are briefly discussed in relation to the acoustic environment.

Zusammenfassung

Die Paarungsrufe einiger Anuren der Serengeti werden beschrieben. Manche davon bilden Chöre während der kurzen Zeit, in der Wasser zur Verfügung steht. Die Rufplätze werden beschrieben und die Chöre werden kurz in Beziehung zur Geräuschkulisse gebracht.

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

Résumé

Les signaux d'appel de plusieurs espèces savanicoles d'amphibiens du Serengeti sont présentées et comparées à d'autres données disponibles. Quelques unes de ces espèces faisaient partie des choeurs rassemblés dans les frayères. Les rassemblements à grand nombre d'individus sont à mettre en relation avec le caractère temporaire des lieux de reproduction, qui sont brièvement décrits. Les choeurs et l'ambiance sonore sont discutés.

Samevatting

Die paar-roepe van verskeie paddaspesies wat in die Serengeti gebied voorkom word bespreek. Enkele van hulle vorm roepgeselskappe wat ontstaan deurdat hulle broeiplekke net 'n kort tyd van water voorsien is en almal dan daar saamkom. Die verskeie spesies is egter so georganiseer dat hulle mekaar nie sal steur nie. Die roepplekke van die spesies word kort beskryf en die koor word in verhouding tot die gehele akoestiese agtergrond bespreek.

References

Amiet, J.-L. (1973): Voix d'Amphibiens camerounais. II. Arthroleptinae: gen. *Cardioglossa*. Ann. Fac. Sc. Cameroun 14: 149—163.

— (1974): Voix d'Amphibiens camerounais. IV. Raninae: genres *Ptychadena, Hildebrandtia* et *Dicroglossus*. Ann. Fac. Sc. Cameroun 18: 109—128.

— (1976): Voix d'Amphibiens camerounais. V. Bufonidae: genres *Bufo, Werneria* et *Nectophryne*. Ann. Fac. Sc. Cameroun 21/22: 139—157.

Amiet, J.-L., and A. Schiøtz (1972): Voix d'Amphibiens comerounais. I. Astylosterninae; gen. *Leptodactylodon, Scotobleps* et *Nyctibates*. Ann. Fac. Sc. Cameroun 12: 79—100.

— (1974): Voix d'Amphibiens camerounais. III. Hyperoliinae: genre *Leptopelis*. Ann. Fac. Sc. Cameroun 17: 131—163.

Bowker, R. G., and M. H. Bowker (1979): Abundance and distribution of Anurans in a Kenyan Pond. Copeia, 1979, 2: 278—285.

Capranica, R. R. (1976): The auditory System. In: Physiology of the Amphibia, III (Lofts ed.): 443—466. New York and London.

Channing, A. (1976 a): Life Histories of Frogs in the Namib Desert. Zool. Africana 11, 2: 299—312.

— (1976 b): Pre-mating Isolation in the Genus *Kassina* (Amphibia, Anura, Rhacophoridae) in Southern Africa. J. Herpetol. 10, 1: 19—23.

Chappuis, Cl. (1971): Un exemple de l'influence du milieu sur les émissions vocales des oiseaux: l'évolution des chants en forêt équatoriale. Terre et Vie: 183—202.

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

Dubois, A. (1975): Un nouveau complexe d'espèces jumelles distinguées par le chant: les Grenouilles du Népal voisines de *Rana limnocharis* Boie (Amphibiens, Anoures). C. R. Acad. Sc. Paris, t. 281, sér. D: 1717—1720.

Elzen, P. van den (1978): Observations sur l'Herpétofaune du Waterberg (Namibie). Bonn. zool. Beitr. 29, 1—3: 171—182.

Elzen, P. van den, and R. van den Elzen (1976 a): Paarungsrufe von *Breviceps a. adspersus* Peters, 1882 (Amphibia, Anura, Microhylidae), in Südwestafrika. Bonn. zool. Beitr. 27, 3/4: 252—257.

— — (1976 b): *Tomopterna* cf. *marmorata* (Peters, 1854) aus Südwestafrika (Amphibia, Salientia, Ranidae). Salamandra, 12, 4: 202—204.

— — (1977): Untersuchungen zur Chorstruktur südwestafrikanischer Anuren: erste Ergebnisse. Bonn. zool. Beitr. 28, 1/2: 108—116.

Fellers, G. M. (1979): Mate Selection in the Gray Treefrog, *Hyla versicolor*. Copeia, 1979, 2: 286—290.

Herlocker, D. (1975): Woody Vegetation of the Serengeti National Park. Kleberg Studies in Natural Resources. Texas A & M University, College Station.

Hödl, W. (1977): Call Differences and calling Site Segregation in anuran Species from Central Amazonian floating Meadows. Oecologia (Berl.), 28: 351—363.

Jilka, A., and B. Leisler (1974): Die Einpassung dreier Rohrsängerarten *(Acrocephalus schoenobaenus, A. scirpaceus, A. arundinaceus)* in ihre Lebensräume in Bezug auf das Frequenzspektrum ihrer Reviergesänge. J. Orn., 115, 2: 192—212.

Keith, R. (1968): A new Species of *Bufo* from Africa, with Comments on the Toads of the *Bufo regularis* Complex. Amer. Mus. Novitates 2345: 1—22.

Largen, M. J. (1975): The Status of the Genus *Kassina* (Amphibia, Anura, Hyperoliidae) in Ethiopia. Monit. zool. Ital., N. S., Suppl. VI, 1: 1—28.

Leroy, Y. (1978): Analysis of the acoustic Environment. Biophon, VI, 2: 6—7.

Menzies, J. I., and R. G. Zweifel (1974): Systematics of *Litoria arfakiana* of New Guinea and sibling Species (Salientia, Hylidae). Amer. Mus. Novitates 2558: 1—16.

Narins, P. M., and R. R. Capranica (1976): Sexual Differences in the auditory System of the Tree Frog *Eleutherodactylus coqui*. Science 192: 378—380.

Norton-Griffiths, M., D. Herlocker and L. Pennycuick (1975): The Patterns of Rainfall in the Serengeti Ecosystem, Tanzania. E. Afr. Wildl. J. 13: 347—374.

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

Passmore, N. I. (1972): Intergrading between members of the "*regularis* group" of Toads in South Africa. J. Zool., Lond., 167: 143—151.

— (1976): Vocalizations and breeding Behaviour of *Ptychadena taenioscelis* (Anura: Ranidae). Zool. Africana 11, 2: 339—347.

— (1977): Mating Calls and other Vocalizations of five Species of *Ptychadena* (Anura: Ranidae). S. A. J. Science 73, 7: 212—214.

Passmore, N. I., and V. C. Carruthers (1975): A new Species of *Tomopterna* (Anura: Ranidae) from the Kruger National Park, with Notes on related Species. Koedoe 18: 31—50.

Pennycuick, L., and M. Norton-Griffiths (1976): Fluctuations in the Rainfall of the Serengeti Ecosystem, Tanzania. J. Biogeography, 3: 125—140.

Schiøtz, A. (1964): The Voices of some West African Amphibians. Vidensk. Medd. fra Dansk naturh. Foren. 127: 35—83.

— (1967): The Treefrogs (Rhacophoridae) of West Africa. Spolia zool. Mus. haun. 25: 1—346.

— (1971): The Superspecies *Hyperolius viridiflavus* (Anura). Vidensk. Medd. fra Dansk. naturh. Foren. 134: 21—76.

— (1973): Evolution of Anuran Mating Calls: ecological Aspects. Ch. 9: 311—319. In: Evolutionary Biology of the Anurans. Contemporary Research on major Problems. J. L. Vial ed. Univ. Missouri Press, Columbia.

— (1975): The Treefrogs of Eastern Africa: Steenstrupia: 1—232.

Schmidt, W. (1975): Plant Communities on permanent Plots of the Serengeti Plains. Vegetatio 30: 133—145.

Stevens, R. A. (1974): An annotated Check List of the Amphibians and Reptiles known to occur in South-Eastern Malawi. Arnoldia, 6, 30: 1—22.

Stewart, M. M. (1967): Amphibians of Malawi, ix, 1—163. New York.

Tandy, M., and R. Keith (1972): *Bufo* of Africa. Ch. 9: 119—170. In: Evolution in the Genus *Bufo*. W. F. Blair ed. Austin and Lond.

Tandy, M., and J. Tandy (1976): Evolution of acoustic Behaviour in African *Bufo* (Anura: Bufonidae). Zool. Africana, 11, 2: 349—368.

Tandy, M., J. Tandy, R. Keith and A. Duff-MacKay (1976): A new Species of *Bufo* (Anura: Bufonidae) from Africa's dry Savannas. Pearce-Sellards Series, Texas Mem. Mus. 24: 1—20.

Tinsley, R. C., H. R. Kobel and M. Fischberg (1979): The Biology and Systematics of a new Species of *Xenopus* (Anura: Pipidae) from the Highlands of Central Africa. J. Zool., Lond., 188: 69—102.

Tymowska, J. (1976): A Karyotype Analysis of the Genus *Xenopus* (Anura, Pipidae). Thèse no. 1781: 1—142. Genève.

© Biodiversity Heritage Library, http://www.biodiversitylibrary.org/; www.zoologicalbulletin.de; www.biologiezentrum.at

Vigny, C. (1977): Etude comparée de 12 Espèces et Sous-Espèces du Genre *Xenopus*. Thèse no. 1770: 1—180. Genève.

— (1979): The mating Calls of 12 Species and Subspecies of the Genus *Xenopus* (Amphibia: Anura). J. Zool., Lond., 188: 103—122.

Wager, V. A. (1965): The Frogs of South Africa. 1—242. Cape Town and Johannesburg.

Wickler, W., and U. Seibt (1974): Rufen und Antworten bei *Kassina senegalensis, Bufo regularis* und anderen Anuren. Z. Tierpsychol. 34: 524—537.

Addresses of the authors: P. van den Elzen, Zoologisches Forschungsinstitut und Museum A. Koenig, Adenauerallee 150—164, 5300 Bonn 1, W. Germany; D. A. Kreulen, P.O. Box 128, Haren (Gn.) 9750 AC, Netherlands.

ZOBODAT - www.zobodat.at

Zoologisch-Botanische Datenbank/Zoological-Botanical Database

Digitale Literatur/Digital Literature

Zeitschrift/Journal: Bonn zoological Bulletin - früher Bonner Zoologische Beiträge.

Jahr/Year: 1979

Band/Volume: 30

Autor(en)/Author(s): Elzen Paul van den, Kreulen D. A.

Artikel/Article: Notes on the Vocalisations of some Amphibians from the Serengeti National Park, Tanzania 385-403