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LIFE HISTORIES OF FROGS IN THE NAMIB DESERT

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ABSTRACT

Four anuran taxa inhabit the central Namib: *Xenopus laevis, Tomopterna delalandei cryptotis, Phrynomerus annectens* and *Bufo vertebralis hoeschi*. *Xenopus* is confined to permanent pools in the Kuiseb river canyon. *Tomopterna* extends further into the Namib, but is restricted to the Kuiseb river bed. The Kuiseb is normally dry, receiving water only briefly (as floods) during the rainy season. These floods are responsible for moving adults and larvae. *Phrynomerus* and *Bufo* occur on granite inselbergs. The inselbergs provide shelter mainly in the form of cracks under granite exfoliations. Large runoff surfaces collect the low rainfall (25 mm per year) in depressions in which the frogs breed. *Phrynomerus* is only active at night; males are aggressive towards one another; oviposition takes place in deep pools and development takes at least eight weeks. *Bufo* is active during the heat of the day; oviposition takes place in warm shallow pools; development takes about three weeks.

INTRODUCTION

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Southern Africa possesses a diverse anuran fauna, many representatives of which occur in arid areas. However, to date no studies have been published on the biology of southern African Anura in low-rainfall areas.

This study was carried out in the field for the duration of one rainy season (January to March 1974) based at the Namib Desert Research Station at Gobabeb (23°30′S/15°05′E) in the central Namib. The area studied is situated within typical 'plain' Namib. This is an area of accumulation of wind-blown rock-debris and sand. A number of inselbergs and small domes of granite project above the plain (Gevers 1936).

Descriptions of the climate of the area and of Gobabeb have been published by Schulze (1965, 1969). Of particular importance to studies on anurans is the very low rainfall which averages less than 24 mm per year. Only 0,6 days per year receive 10 mm or more precipitation.

Gobabeb is situated on the Kuiseb river, the dry sandy bed of which receives flood water annually from rains further inland. These floods are limited to the short rainy season and are sometimes insignificant. Fortunately 1974 proved to be a wet year with extended floods (102 days) and frequent showers on the plains, which enabled me to spend time examining both the plains and the river habitats.

Four anuran taxa have ranges which extend from the central highlands of South West Africa into the central Namib. These are *Xenopus laevis* Daudin, *Bufo vertebralis hoeschi* Ahl, *Phrynomerus annectens* (Werner) and *Tomopterna delalandei cryptotis* (Boulenger). *Xenopus*

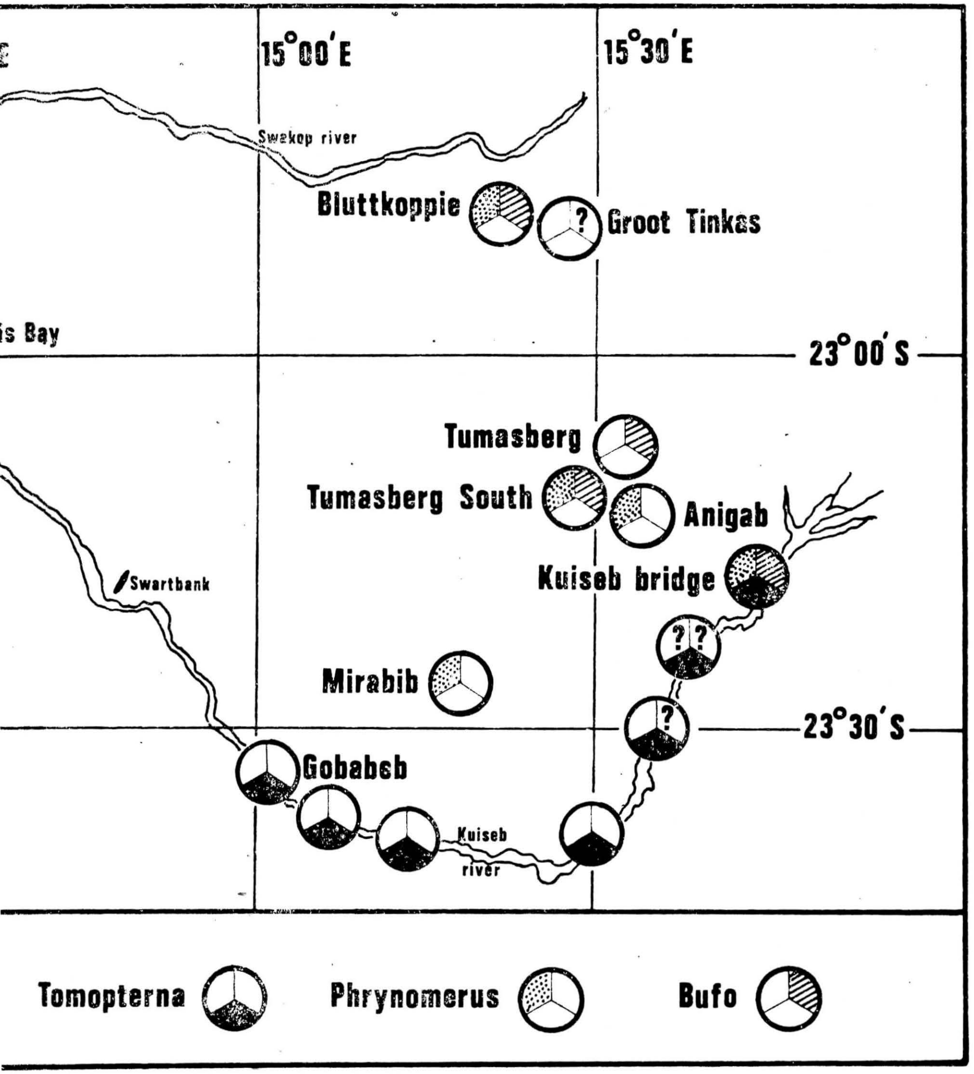

FIGURE 1
...tribution of breeding populations of frogs (excluding *Xenopus*) in the central Namib.

laevis occurs in permanent pools in the Kuiseb Canyon. Although the canyon reaches into the central Namib, *Xenopus* is restricted to pools which effectively remove it from an otherwise arid environment. However, the annual floods may carry adults and larvae downstream to temporary pools where they survive until the water dries up. In wet years when the river-bed contains a number of pools these animals may exist for some months to the west of their permanent range. The extreme western records for *Xenopus* in the central Namib Park (Poynton 1964; Channing & Van Dijk 1976) may be explained in terms of temporary pools of this nature. As *Xenopus* is not a permanent resident within the central Namib proper, its biology will not be considered in this paper.

Tomopterna

Of the three taxa which occur permanently within this extremely arid area, *Tomopterna* is confined to the Kuiseb river-bed, while the other two live on outcrops on the gravel plains.

Size and distribution of Tomopterna *populations*

The distribution of *Tomopterna* populations in the area is shown in Figure 1. No *Tomopterna* were ever found away from the river. Small groups of three to five animals occurred almost as far west as Swartbank (Figure 1). These animals were only found where rocks and/or vegetation were present along pool margins. No frogs were found west of Swartbank until after the twelfth flood, when the river had been flowing for eight weeks. After this flood one subadult was collected in the Kuiseb delta. To the best of my knowledge this is the only specimen which has been taken so far west.

To determine population movements, two pool complexes near Gobabeb were surveyed every evening when possible (Figure 2). At each visit all the frogs in the vicinity were caught, measured, toe-clipped and released. The two pool complexes were chosen because they possessed the largest populations in the area after the initial floods.

Fifty males and fifteen females were marked between 25 January and the end of March. The ratio of males to females in this small sample is about 3 : 1.

The capture-recapture data for males is presented in Figure 2. New animals tended to appear in groups after floods while previously marked frogs were rarely recaptured. Individuals at the study pools never remained longer than 14 days. Of the 65 individuals marked, 45 were never recovered. The low recapture rate is probably not due to disturbance of the animals by toe-clipping, as males continued to call within seconds of being released. New captures were always made after a flood. Flooding of the river appears to be the direct cause of the movement of individuals from and into pools. The absolute number of frogs present declined steadily during the season, suggesting that the 'resident' population was gradually thinned out and washed downstream. The annual flow of the Kuiseb is not always of the magnitude recorded during this study (102 days in 1974; six days in 1975) so the movement of animals in years of little flooding would be much less.

Breeding of Tomopterna

Male *Tomopterna* were heard calling every evening when observations were made (Figure 2) except at the periods of heavy flooding. The males call from the edge of pools, frequently under vegetation. As the pools form against rock outcrops, both sandy and rocky edges were available and used as calling sites.

Females appeared at the pools erratically throughout the season. Although the small number of females observed and marked prohibits any definite conclusions, one point is of interest. Females were observed on 13 nights, but females in amplexus were seen on only six of those occasions. On each of those six nights all the females in the area, *without exception*, were in amplexus. These periods of breeding occurred after floods, but could not be correlated with any climatic factor.

Many eggs must have been laid during the season, but no tadpoles were seen until 25 February, when one young tadpole was found at Nara Valley, south of Gobabeb. A week later, after the tenth flood, many fish, *Xenopus* adults, *Xenopus* tadpoles and *Tomopterna* tadpoles were found at Gobabeb. As these were not present before the flood, they must have been washed down from the permanent pools upriver.

Once the river had stopped flowing tadpoles were found in all the pools near Gobabeb. The first juvenile was seen on 3 March. Others appeared, mostly after the eleventh flood (on 12 March), so that by the end of March about 90 juveniles were present in the vicinity of the study pools. This indicates a small breeding population (or low breeding success), as a similar sized area near Keetmanshoop examined in 1971 contained almost 3 000 juvenile *Tomopterna*. The

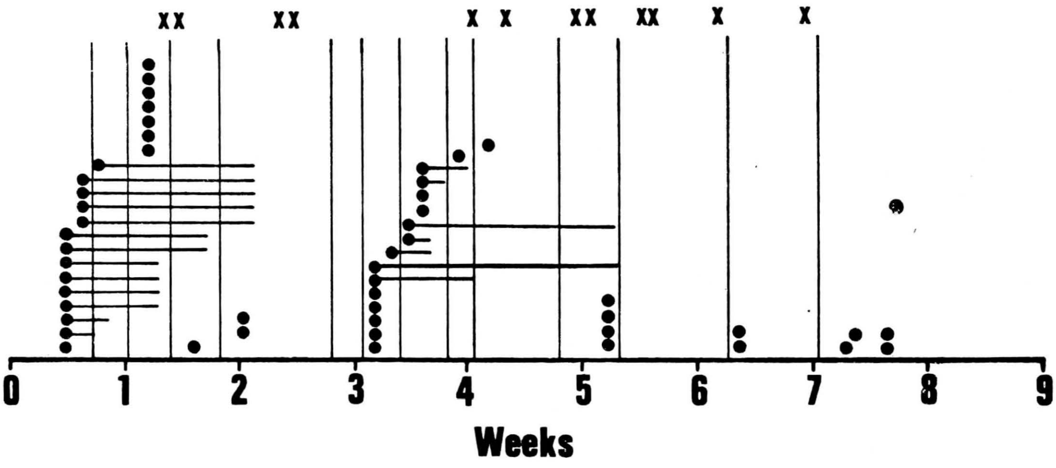

FIGURE 2

Capture-recapture data for male *Tomopterna*.

Dots: initial capture of an individual. *Horizontal line:* time until last recapture.

Vertical lines: flooding peaks in the Kuiseb at Gobabeb.

X: Day when no observations were made.

number of juveniles at Gobabeb was augmented later, however, by small numbers of tadpoles which metamorphosed after the river had ceased to flow and more stable pools had formed. The distribution of *Tomopterna* in the Namib is limited to the Kuiseb river-bed, especially areas where rocks and/or sufficient vegetation are present at the edges of pools. Swartbank represents the westernmost limit of breeding populations, probably correlated with the unsuitable habitat further west, largely sandy waste with few trees and other vegetation. This limit may exist because trees and other riverine vegetation offer cover for calling males and shade for pools containing tadpoles. In addition, west of Swartbank the chances of river flow (and hence pool availability) decrease towards the coast.

The ability of Tomopterna *to survive in the Namib*

Tomopterna avoids the dry hot periods of the Namib by remaining in burrows. During the dry season the adults are known to emerge, probably to feed, as they have been found on the surface in late June by Mr C. T. Stuart. Mr Stuart has also dug up specimens from 8 cm below the surface.

The tadpoles of *Tomopterna* are solitary and bottom-dwelling, and tend to cover themselves with mud. In a 15-cm deep pool near Gobabeb in which tadpoles were found, the water temperature reached 40°C during the hottest part of the day, while the bottom mud around the tadpoles was only 38°C. It is thermally advantageous to remain motionless in relatively cooler mud when the pool water is near the thermal limit for the animals. In the laboratory tadpoles subjected to an increase in temperature (28–42°C in 90 minutes) were found to withstand water temperatures of up to 42°C before half of them became ataxic.

The rate of development of *Tomopterna* is not particularly fast as at least eight weeks are required for development from egg to juvenile.

Phrynomerus annectens

Distribution

The distribution of *Phrynomerus* populations in the central Namib is shown in Figure 1. The populations of this frog within the area are confined to granite inselbergs. These populations, which are at the edge of their range, are apparently restricted to the inselbergs because the granite provides a suitable habitat. The exfoliations provide cracks within which the adults shelter while the typical rock depressions are filled by run-off from the surrounding areas after very little rainfall. These water-filled depressions attract insects and serve as breeding pools.

Breeding

Phrynomerus males congregate around the breeding pools after nightfall. They call from rocky edges near pools and often conceal themselves under overhanging granite or under rocks. In pools with both rocky and sandy edges males typically call from rock. The males were always situated within 20 cm of the edge of the pool, although many called while partly in the water. The males did not call from just any position around the edge of the pool, but always from particular 'preferred' sites. The positions of the preferred calling sites around the pool could be

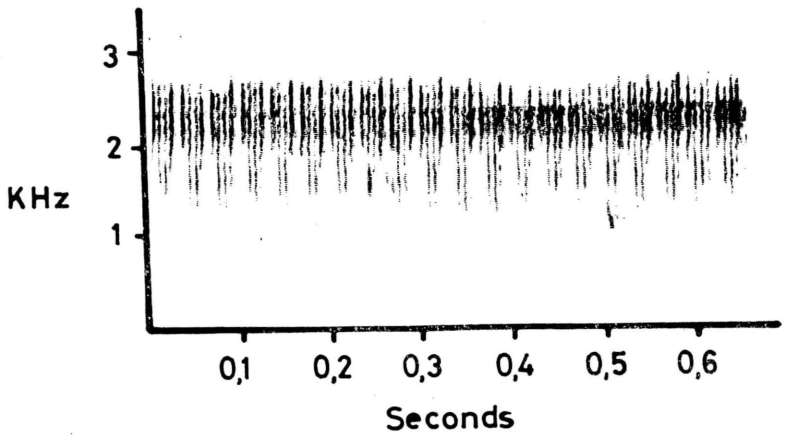

FIGURE 3
Mating call of *Phrynomerus annectens*.

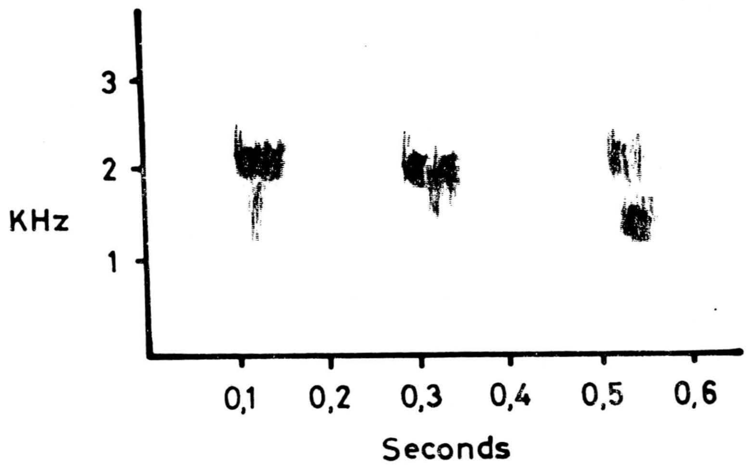

FIGURE 4
Aggression call of *Phrynomerus annectens*. Two individuals produce this call almost simultaneously. The third call shows both participants clearly.

easily ascertained by a few minutes' observation, although I could see no difference between calling sites and the rest of the pool margin. It is not known how the frogs recognize the sites although the same sites are used throughout the breeding season.

The mating call (Figure 3) consists of a train of vocalizations with a duration of up to 12 seconds. The frequency of the mating call is about 2,25 KHz, although the frequencies of some individuals' mating calls were 200–300 Hz higher or lower. *Phrynomerus* males display aggressive behaviour and produce an aggression call. Aggression results when an intruding male approaches an established calling male at a calling site. If the intruder remains more than 10–15 cm away from the established male, even if both are calling, no obvious interaction occurs. However, if the intruder approaches the established male within this 'critical' distance, the established male will immediately start the aggression call and attack the intruder.

The fight consists of face-to-face wrestling in water and takes place 20–30 cm from the calling site. Frequently, fighting was observed in deep water. During the fight both males utter the aggression call almost simultaneously, which results in repeated short bursts of noise at the mating-call frequency. The duration of the combined call (both frogs calling) is about 0,07–0,1 sec. The combined calls are separated by an intercall interval of 0,12–0,2 sec. The intercall interval is nearly constant for any one pair of fighting frogs. Figure 4 is a sonagram of the aggression call. Aggression lasts from 2–14 sec. (average of 25 consecutive observations: 6 sec.) during which time the aggression call is voiced continuously. I have not determined what terminates the aggression, nor what constitutes 'victory', but in all my observations it is the established male that returns to the calling site after a fight and immediately recommences the mating call.

After the fight the intruder either swims to a new site or returns to the site where the established male is calling. If the intruder returns, he remains silent and at a distance from the established male before starting the mating call. The aggression sequence may be initiated again if he moves to within the critical distance of the established calling male. On the other hand, if the intruder moves to another site he will commence calling; if the site is occupied by another male an aggression cycle may result. Figure 5 is a diagram of the sequence of events in aggression. Established males do not hold any particular territory for any length of time, but frequently move from one site to another. Movement only occurs between the preferred calling sites. Males were never observed calling from intermediate positions around the pool. Aggressive behaviour in anurans is always associated with territorial behaviour (Whitford 1967; Goodman 1971). Several types of aggression have been reported in anurans: butting (*Phyllobates panamansis*: Duellman 1966), wrestling while standing upright (*P. trinitatis*: Test 1954, Sexton 1960; *Rana clamitans*: Brode 1959). Only *Pyxicephalus adspersus* (Grobler 1972) and *Hyla faber* (Lutz 1960) are known to injure and possibly kill during intraspecific aggression.

Aggression in *Phrynomerus annectens* may be selectively advantageous by increasing the efficiency of the breeding system. The direct result of inter-male aggression is the inhibition of the mating call in the 'intruder' after the fight. As the established male recommences the mating call immediately after a fight, he appears to have an advantage in terms of female attraction, as he is calling while his opponent is either silently positioned nearby, or silently swimming to a new site. The duration of *P. annectens* mating calls may be up to 12 sec. If five or six males are calling simultaneously around a pool, the particular frequency utilized by this species is effectively blanketed by continuous sound. The constant re-positioning of males and the periods of aggres-

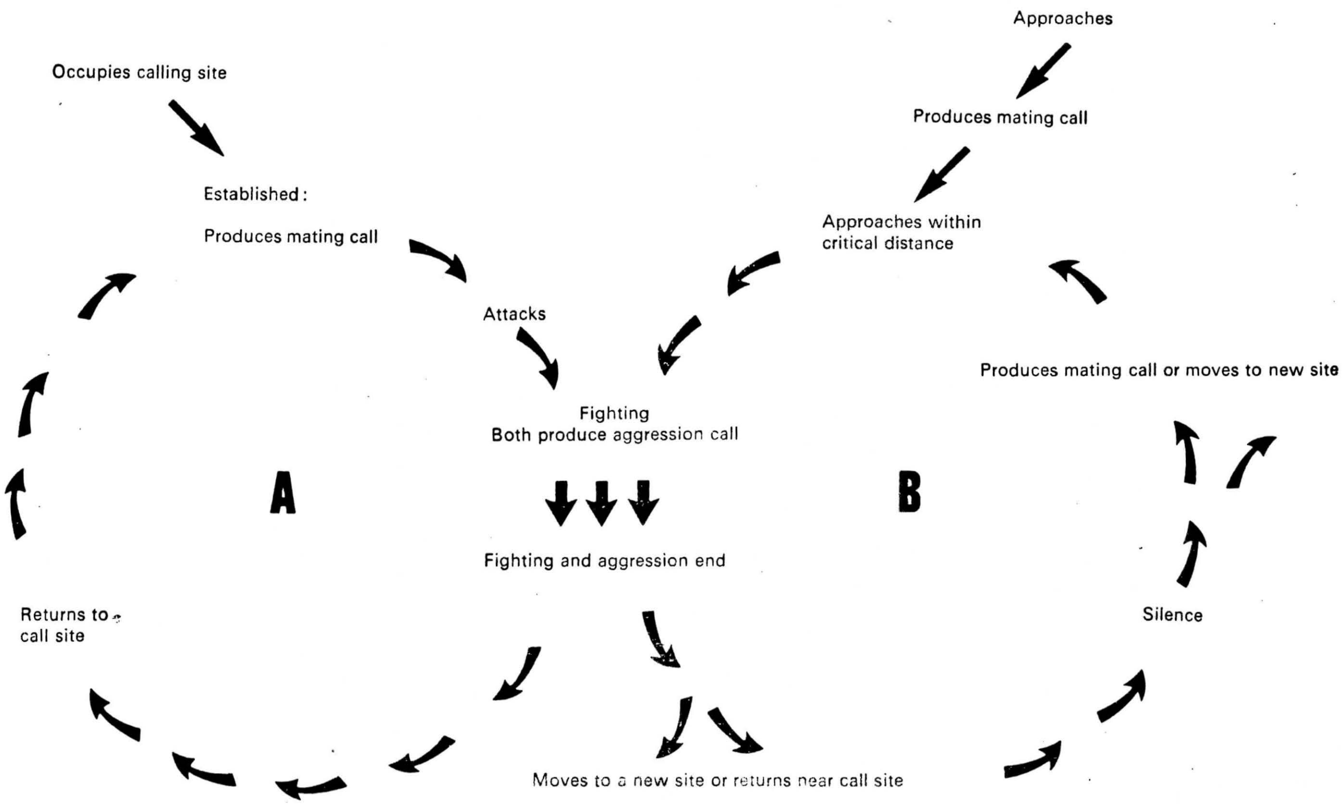

FIGURE 5
The sequence of aggression at preferred calling sites of male *Phrynomerus*. A: established male. B: intruding male.

sion result in temporal gaps in the sound environment. These temporal gaps therefore effectively emphasize the mating calls of males which remain calling.

Amplexus is axillary. Each female lays 80–100 eggs, usually deposited in small groups of two to eight. Oviposition occurs on submerged rock or vegetation usually 5–30 cm below water level. The eggs hatch into free-swimming tadpoles within 18–36 hours. Between 2–5 per cent of the eggs observed did not develop. The eggs are laid in deep pools with (typically) steep rocky sides. These hollows in the granite are surrounded by large catchment areas which effectively concentrate even a very low rainfall. The tadpoles thus stand a better change of avoiding desiccation in this extremely arid area. The tadpoles require at least eight weeks before metamorphosis. The pools in which *Phrynomerus* tadpoles were found reached a maximum daily temperature of 28°C.

Phrynomerus tadpoles are gregarious midwater filter feeders. They congregate in groups of four to 80, usually three or four tadpoles deep in the centre of the mass, and up to 50 or more side by side, swimming in the same direction. The group swims slowly below the surface, occasionally breaking up and re-forming. Groups consist of tadpoles of more than one size. During daylight the animals remain gregarious in deep water, but at night they become more solitary, with individuals occurring throughout the pool in both deep and shallow water. The tadpoles in all the pools examined had a high mortality rate. Predation by dragonfly nymphs accounted for over 90 per cent of many batches. One dragonfly nymph consumed 30 three-centimetre tadpoles in 56 hours.

Phrynomerus is one of only four southern African genera known to possess gregarious tadpoles. The others are *Xenopus*, *Pyxicephalus* and *Schismaderma* (if this is accepted as a genus distinct from *Bufo*). When a group of tadpoles is separated by disturbing the pool, they immediately reform by swimming towards the largest fraction of the original group. The fact that they swim through disturbed water when reforming eliminates thermal factors (Brattstrom 1962) or chemical factors (Black 1970) which have been suggested as causing aggregation. Both may be important, however, in maintaining cohesion. During darkness the tadpoles become solitary and disperse into shallow water. It therefore appears that the stimulus which maintains aggregation in *Phrynomerus* is primarily visual. The advantages of gregariousness may not lie in reduction of predation, as dragonfly nymphs were observed to prey on both individual tadpoles and tadpoles in a group. It seems likely, however, that swimming slowly in a common direction may offer advantages in utilizing the available water for feeding.

Existence in the Namib

Phrynomerus adults remain within cracks in exfoliating granite during the day, emerging to feed and breed after sundown. During the dry season they are not known to leave the shelter of granite exfoliations. *Phrynomerus* is able to walk sideways and backwards, which together with its dorsoventrally flattened body and short legs enables the animal to make use of even the narrowest crevices. The crevices within which these animals shelter provide an even temperature and relatively high humidity. When subjected to heating in the laboratory, animals on a moist substrate pressed their bodies against the substrate, inflated their thoracic and abdominal body walls and extended their limbs. The limbs are normally kept tucked against the body.

Bufo vertebralis hoeschi

Distribution

Populations of *Bufo* were found at the localities indicated in Figure 1. These small toads are confined to the granite outcrops on the plains. Channing & Stuart (in press) have examined the distribution of *B. v. hoeschi* in the Namib Desert Park. Knowledge of this toad is scanty, yet it may prove to be the most interesting anuran within the central Namib. This toad shelters in cracks or under rocks where leaf litter and other dead plant material is available.

Breeding

Breeding records are based only on the presence of eggs and tadpoles. No breeding pairs were observed, as the northern areas where this frog occurs were not visited as frequently as areas closer to Gobabeb. Oviposition takes place in shallow (5–10 cm) sandy-bottomed pools. The eggs are laid in strings of about 400. Oviposition may take place after each rainfall, as all stages of development were present in various pools at Bluttkoppie at the same time; newly laid eggs and toadlets with tails were found together. The pools in which oviposition takes place may be shaded or exposed to full sunlight.

Eggs develop into free-swimming larvae within 48 hours. The tadpoles are solitary and bottom-dwelling, feeding at the bottom of the pool. Pools in full sunlight may reach high temperatures: for example the water temperature in a pool at Blutkoppie containing *Bufo* tadpoles was 36°C. Development from egg to toadlet is rapid. Many newly metamorphosed toads were recorded at Bluttkoppie on 22 February. As there were newly laid eggs in the area 24 days previously, but no developing stages, *Bufo* appears to require less than 24 days to develop from egg to toadlet. It is possible that other batches were laid in the interim, in which case the development of this toad would be even faster.

Bufo in the Namib

The adults shelter under rocks, or in crevices where these contain leaf litter. These shelters provide relatively even, low temperatures during the day. Adults and sub-adults were frequently active during the daytime, even at midday. They were observed on many occasions moving actively on bare granite in full sunlight. When disturbed they would remain motionless, or hop to the shelter of a rock. *Bufo* may avoid competition for food by feeding during the day while *Phrynomerus* is sheltering.

Unfortunately no information is available on the body temperatures of *Bufo* active during the day. Cloudsley-Thompson (1967) showed that *B. regularis* survives in hot areas by efficient evaporative cooling during pulmonary ventilation. Providing that substrate moisture is available, the sculptured integument in *Bufo* acts to permit passive water movement by capillarity over the external body-surface from the substrate (Lillywhite & Licht 1974). Evaporative cooling from the integument therefore puts little stress on the physiology of the animal if it is in contact with a moist substrate. The ability of young toadlets to forage during the heat of the day would warrant further study.

The oviposition sites of this toad – shallow exposed pools which rapidly dry up – seems at first glance an unorthodox approach to the problems encountered in hot arid areas. But these shallow pools maintain higher temperatures than deeper bodies of water (*Phrynomerus* breeding pool: 28°C maximum) with resultant faster rates of development of tadpoles. No macroscopic algae were visible in any of the pools containing *Bufo* tadpoles, nor were any dragonfly nymphs found in these pools. Possibly the toads avoid predation of the larval stages by breeding in pools which are not selected by dragonflies for oviposition.

DISCUSSION

No complete life-history of any southern African frog from an arid area has yet been published. Warburg (1972) mentions that the South African Leptodactylidae inhabit xeric areas. This is not accurate, however, as the only South African leptodactylid genus, *Heleophryne*, is confined to high rainfall areas with permanent streams (Poynton 1964).

It appears from studies elsewhere in the world that burrowing is the most common method of avoiding extremes of climate in desert anurans. In Australia all the amphibia from arid areas are suspected of burrowing (Main *et al.* 1959) although species like *Hyla rubella*, which is restricted to permanent water-holes, may survive for a few months under loose rocks, logs and plant debris where the soil remains damp. The burrowing habit in arid areas is also known from North America in *Bufo hemiophrys* (Breckenridge & Tester 1961); *Scaphiopus* (Ruibal *et al.* 1969; Shoemaker *et al.* 1969; Mayhew 1965; McClanahan 1967). *Tomopterna* burrows in the Kuiseb river-bed during the dry season in the Namib. Burrowing appears to be the most important reason for the success of desert frogs, together with their ability to remain quiescent for long periods (Chew 1961).

A few records are available of frogs which inhabit rock crevices. *Hyla arenicola* and *H. caerulea* have been found in crevices in Arizona (Warburg 1972), while in Mexico *Eleutherodactylus vocalis* has been found in a small crevice of a mine shaft (Hardy & McDiarmid 1969). *Bufo punctatus* of North America inhabits rocky desert canyons (McClanahan & Baldwin 1969) and may inhabit crevices. However, it is not known whether any of these frogs make extensive use of rock crevices in the way that *Phrynomerus annectens* and *Bufo vertebralis hoeschi* do in the Namib for protection in this extremely arid area.

The influence of heavy river-flooding on population movement has been reported previously. Metter *et al.* (1970) suggested that the North American arid-area frogs *Scaphiopus bombifrons*, *Bufo cognatus* and *Gastrophryne olivacea* were dispersed down the Missouri River by floods. They are believed to flourish for a few years in central Missouri and then disappear. In the Namib it would appear that *Tomopterna* similarly exists only briefly west of Swartbank after heavy floods in the Kuiseb.

Certain frogs, particularly subadults, are known to elevate their body temperatures by basking. In North America *Bufo boreas* (Lilywhite *et al.* 1973) and *B. woodhousei fowleri* (Hadfield 1966) bask, which presumably increases the rate of digestion by elevating body temperature. Activity of *B. vertebralis hoeschi* during the heat of the day in the Namib may also facilitate digestion and decrease the time required to reach adult size.

Tomopterna is able to lower its body temperature by postural thermoregulation. *Rana catesbeiana* from North America is known to cool posturally in a similar way, by holding itself progressively more upright; in the extreme position the fore-limbs are completely outstretched with most of the ventral surface held off the ground (Lillywhite 1970). The Namib *Tomopterna* differs in that its ventral surface remains closely applied to the substrate, even when the fore-limbs are completely outstretched.

Bufo viridis (Nevo 1972) and *Acris crepitans* (Nevo 1973) are larger in arid areas. Nevo (1973) believes this is because large frogs have a relatively low surface-to-volume ratio and correspondingly low rates of water loss. However, Main *et al.* (1959) point out that in Australia in the genus *Pseudophryne* the smaller *P. occidentalis* occupies the southern drier interior of Western Australia, while the larger *P. guentheri* occupies the more coastal regions enjoying a typical Mediterranean climate. Although in southern Africa the trend towards increase in size in arid areas is apparent within some species (*Kassina senegalensis* for example: Channing 1976), the smallest members of two genera (*Phrynomerus annectens* and *Bufo vertebralis hoeschi*) occur in the driest habitats. Possibly the smallest frogs are selected for rapid development and ability to seek shelter in the narrowest crevices, although as Main *et al.* (1959) point out, many factors may be of selective advantage.

The three Namib frogs all oviposit in temporary water, although *Tomopterna* will oviposit in permanent water in other parts of its range when this is available. Temporary pools may not exist for prolonged periods in dry years. It is therefore important for desert frogs to be able to develop from egg to metamorphosed juvenile relatively quickly. In the Colorado desert *Scaphiopus couchi* can develop remarkably quickly: the eggs hatch within 48 hours, legs are developed within 10 days and growth to half adult size requires only three months (Mayhew 1965). Under adverse conditions the tadpoles do not develop quickly: up to 145 days from eggs to metamorphosis (Bragg 1966).

Brown (1969) found that *Scaphiopus couchi* tadpoles can withstand high temperatures (41°C) which enables them to colonize successfully the desert environment. *S. hammondi* tadpoles may be exposed to water temperatures above 39°C. Rapid development is advantageous in removing the more heat-sensitive embryonic stages from exposure to excessively high environmental temperatures (Brown 1967). *Tomopterna* and *Phrynomerus* tadpoles in the Namib can withstand temperatures up to 42°C. This is similar to the limits for *Bufo exsul* tadpoles from North America (41–42°C: Straw 1958). Extremely hot water may be a limiting factor in desert anurans. *Heleioporus* in Australia requires low water temperatures during larval life (Main *et al.* 1959). The distribution of *Tomopterna* west of Swartbank may be partly limited by the high temperatures in the pools there, compared to the cooler shaded pools in the more vegetated area further east.

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