THE REPRODUCTIVE ECOLOGY OF AMPHIBIANS OF THE TRANSVAAL HIGHVELD

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The composition of the amphibian fauna of southern Africa is at present quite well known, due to the older work of Smith (1838-49), Boulenger (1910) and the more recent work of Hewitt and Power (1913), Hewitt (1926, 1932), Power (1927c), FitzSimons (1947, 1948), Bush (1952), Poynton (1964) and others. A great deal of information on the biology of South African toads and frogs has also been accumulated, mainly through the efforts of Power (1926, 1927a, b, c), de Villiers (1929), Rose (1929, 1962), Wager (1965) and van Dijk (1966). Nevertheless, the coverage has been rather unequal. Much information has been collected on amphibians inhabiting the western Cape Province and the lowlands in Natal and Transkei, very little has been done on the biology of frogs in the Transvaal, and in particular in the Transvaal highveld. As the ecological conditions on the highveld are quite distinct from those in the south and in the eastern lowlands, it seems desirable to present some data on amphibian life in the Transvaal. During the years 1949-1960 I had an opportunity to study the amphibians in the vicinity of Johannesburg, and the present publication is the outcome. The investigation was concerned mainly with the following topics:

(1) Composition of the highveld fauna and distribution of the species in various biotopes.
(2) Peculiarities of the juvenile forms of the species studied (a key for distinguishing of eggs and tadpoles is supplied).
(3) Breeding seasons and relation of breeding to climatic factors.
(4) Temperature tolerance and rate of development, in relation to climatic factors.
(5) Conditions of survival of juvenile stages in nature.

Some preliminary data of this investigation have been presented at congresses of the South African Association for the Advancement of Science in 1955 and 1957 (see Balinsky 1957).

LOCALITIES AND METHODS OF STUDY

Most of the observations were made in a restricted area on the northern outskirts of Johannesburg which is now a part of the township of Blairgowrie. When my observations were made the township had been laid out, the roads constructed, but building was delayed for several years due to absence of light and water. The area slopes towards the east and north—to the Braamfontein river. At several points water seepage occurred; part forming a little stream running into the Braamfontein river, and part was caught in small dams used for watering cattle when the area was being farmed (Figs. 1, 2). Even during the course of the present investigation there was a moderate amount of grazing by cattle in the area. Besides dams, some of which retained water throughout the year, whilst others dried up in winter, numerous temporary pools formed in the excavations, or depressions resulting from soil erosion (Figs. 3, 4, 5). I also surveyed the amphibian population of the adjacent parts of the northern

Figure 1. Small disused dam – the largest body of water in the area under observation. The dam wall is on the right. Pairing and spawning of *P. adspersus* was observed repeatedly in this dam. It also served as breeding place for *P. delalandii*, *B. carens*, *Phrynobatrachus*, *Xenopus* and *Kassina*. In most years the dam dried up in winter, but in the years 1957 to 1959 water remained in the dam through the winter and it then became a breeding place for *Rana angolensis* and *Rana fasciata*.

Figure 2. The same dam as in Figure 1, photographed in the opposite direction. In the distance – grazing cattle, and further still – the suburbs of Johannesburg.

Figure 3. Temporary rain pool in area under observation – a favourite breeding place of *Pyxicephalus delalandii*.

Figure 4. Small but relatively deep pool in area under observation; has often been used for breeding by *Bufo carens.*

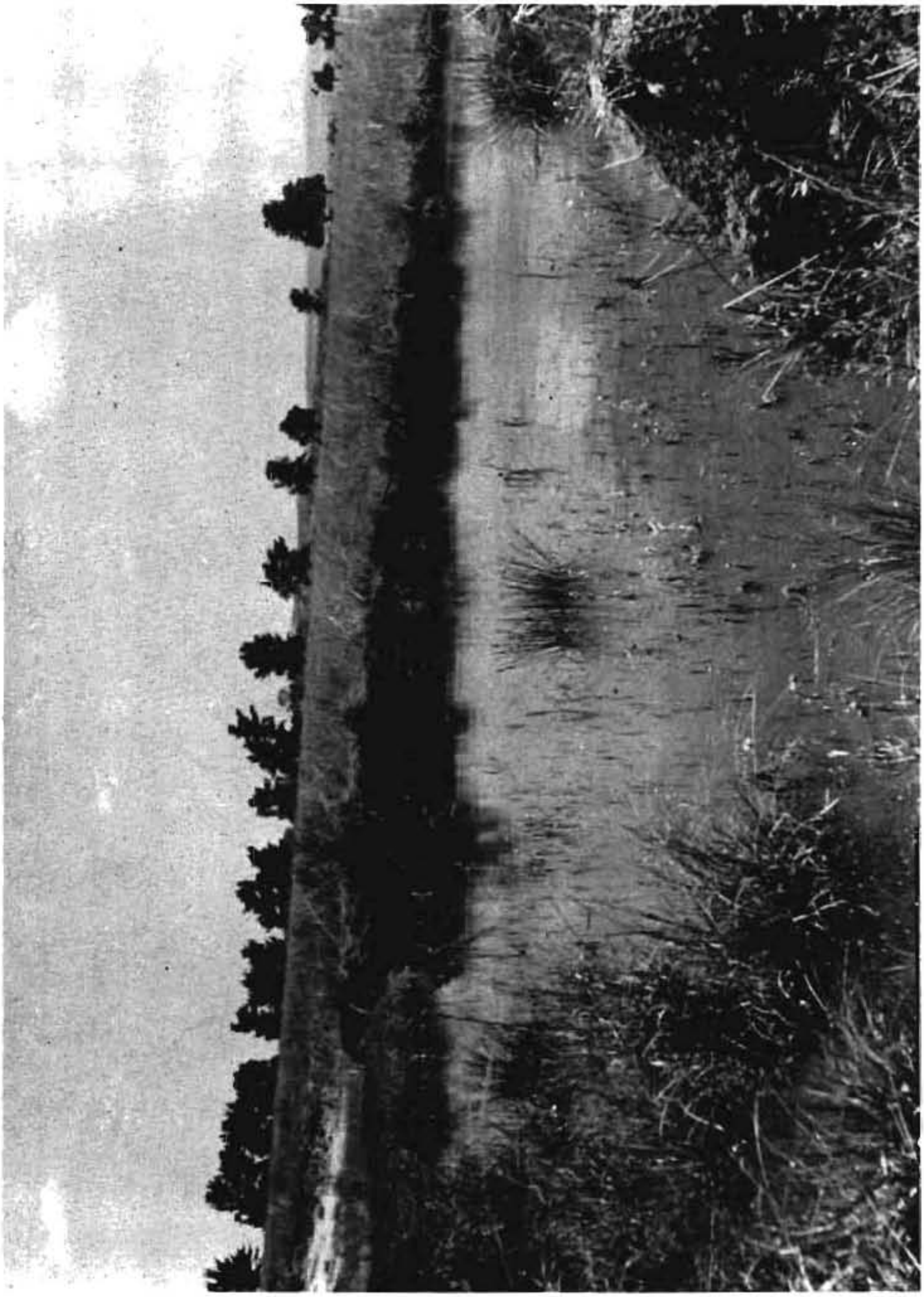

Figure 5. Very small rain pool in area under observation where a brood of *Pyxicephalus adspersus* successfully completed metamorphosis.

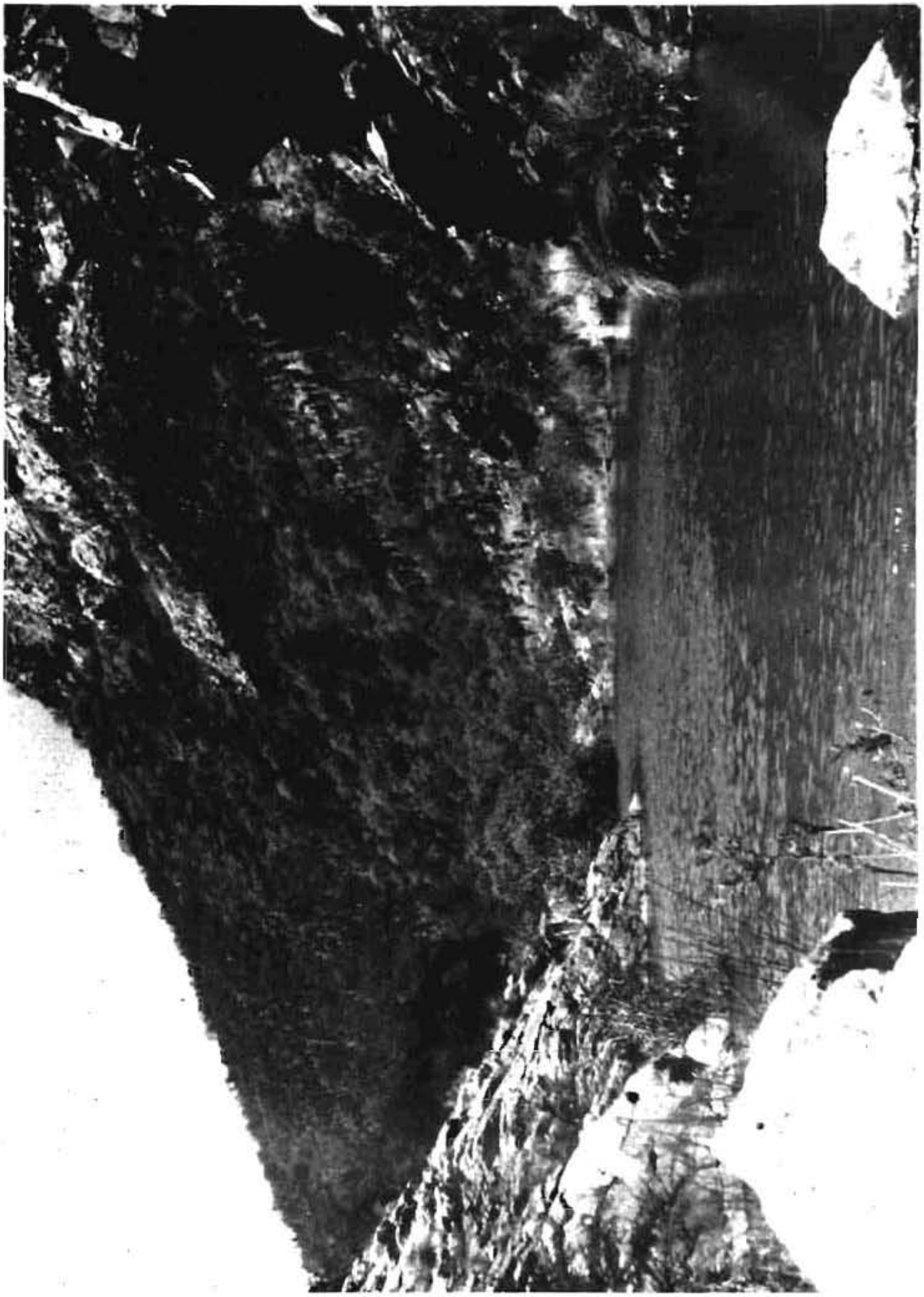

Figure 6. River at "Swartkop" – breeding place of *Rana angolensis*.

suburbs, and made excursions to dams and rivers further afield. The following should be specifically mentioned: a big dam on the Klein Jukskei river near "Boskop" hill to the north west of Johannesburg (the "Boskopdam"), the "Kings Kloof" area on the upper reaches of the Crocodile River, and the "Swartkop" picnic resort, lower down on the Crocodile river (Fig. 6), both within 25 miles N.W. of Johannesburg. Other localities will be mentioned in appropriate places.

In the beginning of 1960 water and electricity were laid on in the main area of my observations. In the process some of the larger pools were drained. Building progressed very rapidly in subsequent years. At the time of writing the area has become closely populated and further observations of amphibian life are no longer possible.

Observations and collecting were carried out at different times of day from early morning to late at night. Presence of adults, their calls, presence of eggs and tadpoles and their stages of development were noted. Eggs and tadpoles were collected and kept in aquaria to ensure identification and to make observations on their rate of development.

COMPOSITION OF THE FAUNA AND PECULIARITIES OF THE BREEDING HABITS

The following species of toads and frogs were observed in Johannesburg and its vicinity*: (1) *Xenopus laevis* (Daudin). (2) *Bufo regularis* Reuss. (3) *Bufo rangeri* Hewitt. (4) *Bufo carens* Smith. (5) *Pyxicephalus adspersus* Tschudi. (6) *Pyxicephalus delalandii* Tschudi. (7) *Pyxicephalus natalensis* Smith. (8) *Rana angolensis* Bocage. (9) *Rana fasciata* Smith. (10) *Phrynobatrachus natalensis* (Smith). (11) *Cacosternum boettgeri* (Boulenger). (12) *Kassina senegalensis* (Duméril and Bibron).

Information concerning the breeding seasons of frogs may be obtained in several ways:

1. By observing the actual mating.
2. By finding freshly laid eggs.
3. By finding young tadpoles (knowing the average rate of development it is possible to make conclusions about the date of egg-laying).
4. By observing older tadpoles (these give only a very approximate indication about the dates of mating and egg-laying).
5. By recording the calls of the frogs; some species call only at the time of mating though others call over an extended period of time. Even in the latter case, however, the mating time would fall within the period when the calls can be heard.

The record of the actual dates of egg-laying for each species, obtained by methods 1, 2 or 3 is given in Appendix 1.

A summary of my observations concerning the breeding habits of the frogs around Johannesburg is given in the following paragraphs.

Xenopus laevis. The clawed toad is ubiquitous on the highveld and is found in practically every type of water, from mountain streams, where it keeps to the deeper pools with slow currents (as in the Crocodile river in King's Kloof, Fig. 6), to the smallest rain pools. It is not averse to very stagnant and polluted water, but is most abundant in dams, both large and

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*Nomenclature following Poynton, 1964.

small. Breeding takes place in pools and dams, and probably in stagnant parts of rivers, but it is doubtful whether the frog can breed in more rapid streams with stony beds, as the eggs are dispersed on submerged vegetation and the tadpoles are planktonic. The breeding season extends from the beginning of September (young tadpoles found on 13th September—actual egg-laying not observed) to middle of March (tadpoles just emerged, found on 17th March, eggs must have been laid on the 15th). The breeding season of *Xenopus* which extends over 6½ months is the longest of all spring-and-summer breeding species (see, however, notes on *Rana angolensis* and *Rana fasciata*).

The spawning usually occurs during the night, so that freshly laid eggs can be found early in the morning; pairs in amplexus, apparently in the process of spawning have occasionally been observed during the day.

Bufo regularis. The leopard toad is probably the most widespread species of amphibian on the African continent. It is often seen in cultivated lands and in gardens, but also near ponds and rivers or in swamps throughout a large part of the year. Breeding occurs in two widely different types of biotope: in rivers and streams on the one hand (including fast running mountain streams such as those of the Magaliesberg range N.W. of Pretoria), and on the other hand, in dams, especially in the bigger ones which do not dry up in winter. Temporary rain pools are very rarely used for breeding by *Bufo regularis*. Cement tanks and fishponds within built up areas are a favourite place for spawning.

Breeding may start near the end of August (earliest observation 22 Aug.), and continues until early January (latest record 10 Jan.). The toads go into amplexus during the night or in the early morning, but the actual spawning usually occurs later in the morning or during the day.

Bufo rangeri. The presence of a second toad close to *Bufo regularis* was noted early in this investigation by its distinctive call but at the time, the relations between *B. regularis* and *B. rangeri* were not clearly understood (see Poynton 1964). As a consequence the breeding habits or life cycles of the two species were not distinguished. *B. rangeri* is found side by side with *B. regularis*, but the latter species is more numerous, and it may be assumed that in most cases the references to *B. regularis* in the subsequent pages, actually concern that species and not *B. rangeri*.

Bufo carens. Outside of its breeding season the red toad is even more terrestrial than the leopard toad. Often found in gardens, it is scarcely ever seen near water, except when it comes there to breed. The preferred breeding places of the red toad are temporary bodies of water created by the spring and summer rains, and smaller dams. These occasionally dry up in winter, but not every year. *Bufo carens* was never seen spawning in streams or in larger lakes, and only once in a larger dam (Boskop dam N.W. of Johannesburg).

The breeding season of *Bufo carens* starts rather late, in the middle of October (earliest record 11th Oct.), after the advent of heavy spring rains. The latest spawning observed was about the 10th of February. After heavy rains the calling of males can be heard during the day, and by the late evening pairs may be found in amplexus. Spawning, however, normally takes place next day in broad daylight (Fig. 7).

Figure 7. *Bufo carens* spawning in a temporary rain pool in area of observation.

Pyxicephalus adspersus. The South African bullfrog breeds in bodies of standing water, both large and small. The natural breeding places are the "pans"—depressions having no outflow which usually dry up in the winter. There were no such pans in the area under observation, but bullfrog tadpoles have been observed by myself and my collaborator John Balinsky in large pans both on the highveld e.g. in a pan near Bapsfontein, some 15 miles east of Johannesburg and further afield near Beit Bridge in southern Rhodesia, and on Inhaca Island, Mocambique. Bullfrogs were breeding regularly in small rain pools in Blairgowrie, some no more than three yards across and very shallow (less than 30 cm deep).

Spawning has been described in a previous paper (Balinsky and Balinsky 1954). The breeding season is the shortest of all highveld species and takes place at the height of summer (earliest observation ± 19 October, latest 29th January). As reported, pairing and spawning occur in broad daylight in very shallow water and the male remains with the eggs and tadpoles until the latter metamorphose.

Pyxicephalus delalandii. This species spends its life burrowing underground and it is only found in water when it comes to breed. Breeding is restricted to rain pools, or at least basins which are completely dry in winter. For several years (1950-1956) with subaverage rainfall, which allowed the dam to dry up in winter a small dam (Figs. 1, 2) in my observation area was used for spawning by *P. delalandii*. During 1957-1959 the rainfall was higher and the dam remained at least partly full in winter. As a result *P. delalandii* spawned there only once in 1957 and not at all in 1958 and 1959 although this species was breeding abundantly in temporary rain pools in the same area. Instead the dam was used for breeding by *Rana angolensis* and *Rana fasciata!*

In one exceptional year spawning of *P. delalandii* occurred before the 10th of September (young tadpoles found on that date), but normally the breeding season near Johannesburg starts about the middle of October and may continue until the middle of February (latest record 11 February). Pairing and spawning take place during the night and fresh eggs may be found in the early morning.

Pyxicephalus natalensis. This species, the smallest of the three burrowing frogs of the genus *Pyxicephalus* in the vicinity of Johannesburg, breeds exclusively in small streams, preferably those with a stony or sandy bottom. In sharp contrast to the previous species these frogs were never found in rain pools or in other standing waters. Spawning was noted from the middle of November to the middle of December, but my observations on this species are probably not extensive enough.

Rana angolensis. This is the typical South African water frog which remains in or near water throughout the year. It lives in large and small rivers and in permanent ponds and dams. The eggs are laid in the same bodies of water. *R. angolensis* can establish itself in small cement fishponds in gardens and breeds regularly in these conditions but it is never found in temporary rain pools nor does it breed in such waters.

In contrast to all the species mentioned earlier, the breeding of *R. angolensis* is not restricted to spring and summer. I have direct proof that this species spawns in April, May, August, September, October and November. Whether this means that breeding may take place throughout the year, or whether it means that there are two breeding seasons, one in spring and one in autumn is not certain. Amplexus was observed in daytime on the 14th of May and eggs were laid during the subsequent night.

Rana fasciata. The South African striped frog is an extremely secretive animal and out of the breeding season it lives in swampy areas covered with abundant vegetation such as tall grass and sedges, where the frogs can easily conceal themselves. Although the call of the male frog carries very far and is often heard, it is difficult to find the frogs when they are not breeding. I have the impression that the striped frogs are especially abundant in hilly or mountainous country such as the Drakensberg and Zoutpansberg mountains in eastern and northern Transvaal, where they live in the grass on hill slopes oozing with spring water.

R. fasciata breeds in permanent waters with abundant vegetation such as swamps, dams and lakes. In the observation area this species was found breeding in artificial water holes, some of them quite small, but deep and permanent.

Only two direct observations of spawning of *R. fasciata* were made: one in Zoutpansberg in September and one in Eastern Transvaal in November. These data are obviously insufficient. In Johannesburg calling of *R. fasciata* is most often heard in winter and early spring. Like *Rana angolensis*, *R. fasciata* probably has an extended breeding season.

Phrynobatrachus natalensis. This species has been called the "puddle frog" by Wager (1965) and this is very appropriate for the breeding localities of this little frog. *P. natalensis* spawns in temporary rain pools, but occasionally too in pools and shallow eddies along the course of small streams and in areas flooded by the streams and rivers in the rainy season.

The breeding season extends from the end of September (earliest record 29 Sept.) to the middle of February (latest record 10 Feb.). Pairing occurs at night and spawning in the early morning. The eggs are laid almost simultaneously by all breeding pairs since all the batches of eggs found in the morning are approximately in the same stage of development. (In this frog one can easily distinguish batches of eggs laid by different females.)

Cacosternum boettgeri. After heavy rains the calls of this tiny frog are heard far and wide on the highveld grasslands. They can be traced to depressions, where water accumulates between tussocks of grass, and to small pans and ditches by the roadside, filled with rain. The eggs are very difficult to find, as the batch consists of only a few dozen inconspicuous eggs attached beneath the water to blades of grass. I have often found the eggs in temporary rain pools on the outskirts of Johannesburg.

The breeding season extends from the middle of October (earliest record 20 Oct.) to the beginning of February (latest record 2 Feb.).

Kassina senegalensis. According to Eloff (1952) out of breeding season this frog lives in the burrows of mole rats. In the breeding season *Kassina* returns to larger bodies of standing water, preferably to ponds and dams, but occasionally it breeds in temporary rain pools. In addition to observations in the vicinity of Johannesburg, I have encountered mating *Kassinas* in large ponds in the Haenertsburg area in the Drakensberg mountains.

The breeding season starts near the end of September (earliest record 25 Sept.) and continues to the middle of February (latest record 15 Feb.). On several occasions *Kassinas* were found in amplexus late at night (9.30-10 p.m.). When brought home and put in an aquarium the frogs laid eggs before morning. The total number of eggs on one occasion was estimated as between 150 and 200. Considering the size of the female this is a very large number, and it is obvious that the whole complement of eggs is laid in one night. In nature the eggs of *Kassina* are never found in large batches and one might presume that a female lays its eggs over an extended period, but this is obviously not the case.

PECULIARITIES OF THE JUVENILE STAGES OF THE SPECIES STUDIED

In the course of this work it was necessary to distinguish the eggs and tadpoles of the various species. Comprehensive descriptions of the tadpoles of all South African amphibians can be found in Wager (1965) and van Dijk (1966). Wager (l.c. pp. 217-225) provides tabulated descriptions of both eggs and developed tadpoles of all known species, and van Dijk gives keys for classifying adult (pre-metamorphic) tadpoles. As these publications were not available when my field work was performed I compiled my own keys for species in the Johannesburg area partly from earlier literature (see lists in Wager and van Dijk) but mainly from my own observations. Since these keys are restricted to a small number of local species they may be more useful to workers in the highveld. Further, both Wager and van Dijk deal predominantly with adult tadpoles, close to metamorphosis, in studying breeding behaviour, however, it is often necessary to identify very young, newly hatched, tadpoles. Keys for very young, newly emerged tadpoles are therefore provided as well as keys for eggs and for advanced tadpoles.

EGGS

1. Eggs connected together by slime to form long strings (Bufonidae) 2
— Eggs joined by slime into a common mass 3
— Eggs seldom joined to other eggs but attached singly to submerged plants or lying free on the bottom 4
2. Eggs black, diameter 1·4-1·5 mm. .. *Bufo regularis* (and *Bufo rangeri* see p. 45)
— Eggs grayish, diameter 1·5-1·6 mm. .. .. *Bufo carens*
3. Egg mass in the form of a flat cake spreading on the surface of the water (occasionally submerged, if attached to vegetation and the water level rises). Each egg mass contains a few hundred eggs .. ..*Phrynobatrachus natalensis*
— Egg mass very small containing ± 20 eggs, attached to blades of grass below the surface of the water .. .. *Cacosternum boettgeri*
4. Slime capsule of the egg with a distinct hardened outer surface; the egg itself is 1·4-1·7 mm. in diameter .. .. *Kassina senegalensis*
— External layer of slime surrounding the egg softer than the internal layers .. 5
5. Diameter of the slimy capsule less than twice the diameter of the egg *Xenopus laevis*
— Diameter of the slimy capsule more than twice the diameter of the egg 6
6. Colour of the egg appears jet black (actually is very dark brown as can be seen when the eggs are examined under a binocular microscope with bright illumination 7
— Colour of the egg grey; diameter 1·1-1·4 mm. .. .. *Pyxicephalus delalandii*

— Colour of the egg coffee brown 8
7. Eggs small, diameter 0·8-1·1 mm. .. .. *Pyxicephalus natalensis*
— Eggs large, diameter 1·6-1·8 mm. .. .. *Pyxicephalus adspersus*
8. Diameter of egg 1·1-1·2 mm. .. .. *Rana angolensis*
— Diameter of egg 1·4-1·6 mm. .. .. *Rana fasciata*

YOUNG TADPOLES (WITH EXTERNAL GILLS AND ADHESIVE ORGANS)

1. A single obtuse conical adhesive organ below the mouth .. .. *Xenopus laevis*
— A V-shaped adhesive organ, consisting of a deep V-shaped groove with thickened and projecting edges 2
— A pair of more or less conical adhesive organs below the mouth 3
2. Tadpoles grey; 3 pairs of external gills (third pair smaller than the rest) *Bufo carens*
— Tadpoles black; 2 pairs of external gills .. .. *Bufo regularis*
— Tadpoles black; 1 pair of fan-shaped external gills .. .. *Pyxicephalus adspersus*
3. Head and body conspicuously bloated, external gills with a short proximal part bearing a bunch of long filaments .. .. *Kassina senegalensis*
— Head and body not conspicuously bloated, external gills pectinate, with a long shaft, and short lateral outgrowths (filaments) 4
4. Tadpoles jet black .. .. *Pyxicephalus natalensis*
— Tadpoles grey .. .. *Pyxicephalus delalandii*
— Tadpoles brownish or yellowish 5
5. Tadpoles very small (under 6 mm. long) 6
— Tadpoles larger (above 7 mm. long) 7
6. Pigmentation heavier, the abdominal cavity covered with an uninterrupted layer of melanophores .. .. *Phrynobatrachus natalensis*
Pigmentation lighter, abdominal cavity covered only with scattered melanophores .. .. *Cacosternum boettgeri*
7. External gills well developed .. .. *Rana angolensis*
External gills lacking or rudimentary .. .. *Rana fasciata*

ADVANCED TADPOLES

1. Edges of mouth without horny jaws ("rostrodonts"—van Dijk, 1966) or horny teeth ("keratodonts"—van Dijk, 1966) (Pipidae) .. .. .. *Xenopus laevis*
— Edges of mouth with horny jaws (rostrodonts) a perioral disc surrounding the mouth bears several rows of horny teeth (keratodonts) 2
2. Perioral disc bears fleshy papillae only on the sides, but not on the lower edge. Anus located symmetrically at the lower edge of the tail fin (Bufonidae) 3
— Perioral disc with papillae on the sides and all along the lower edge. Anus located asymmetrically, on the right of the tail fin (Ranidae) 4

3\. A horse-shoe shaped fold of skin dorsally at the posterior edge of the head. 2 uninterrupted rows of teeth (keratodonts) on the upper lip .. .. *Bufo carens*
— No horse-shoe shaped fold of skin dorsally. 1 uninterrupted and 1 interrupted row of teeth (keratodonts) on the upper lip .. .. *Bufo regularis*
4\. Anus does not reach by far the edge of the tail fin. Eyes wide, or very wide apart (inter-ocular distance considerably larger than distance from inner edge of eye to edge of head) 5
— Anus reaches or nearly reaches the edge of the tail fin. Eyes not wide apart (inter-ocular distance equal to or slightly larger than distance from inner edge of eye to the edge of head) 6
5\. Only one row of teeth in the upper lip. Eyes on the lateral surface of the head. Large tadpoles (up to 76 mm. with tail) .. .. .. *Kassina senegalensis*
— More than one row of teeth on the upper lip. Eyes on the dorsal surface of head, though fairly wide apart. Smaller tadpoles (up to 24 mm. with tail) *Cacosternum boettgeri*
6\. Two complete uninterrupted rows of teeth on upper lip (with, in addition, up to two interrupted rows) .. .. *Pyxicephalus adspersus*
— Only one complete uninterrupted row of teeth on the upper lip 7
7\. Some of the papillae along the posterior edge of the oral disc very much longer than others. The length of the former exceeds their breadth 3 times or more *Phrynobatrachus natalensis*
— Papillae along posterior edge of oral disc of fairly uniform length, in none of them does the length exceed breadth 3 times 8
8\. Thickness of the tail at the base equal to or less than ⅓ of breadth of the body .. 9[*]
— Thickness of the tail at the base equal to about ½ of the breadth of the body .. 10[*]
9\. Upper lip with 4-5 rows of teeth .. .. *Pyxicephalus natalensis*
— Upper lip with no more than 3 rows of teeth .. .. *Pyxicephalus delalandii*
10\. Length up to 44 mm. Distal part of tail tends to be jet black. .. *Rana fasciata*
— Length up to 130 mm. Distal part of tail not appreciably darker than the proximal part .. .. *Rana angolensis*

Remark to key for advanced tadpoles

Van Dijk (1966) claims that tadpoles of *Pyxicephalus natalensis* and *Pyxicephalus delalandii* may be distinguished from those of the genus *Rana* by the relative length of head plus body to length of tail. He states that in the two species of *Pyxicephalus* the tail is not longer than 5/3 (or 1·67) of the length of head plus body. According to van Dijk in *Rana* tadpoles the tail is more than 5/3 (or 1·67) times the length of head plus body. My own

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[*] Whilst the tadpoles of *Pyxicephalus delalandii* and *Rana angolensis* can be very easily distinguished from one another by the relative breadth of the tail, the tadpoles of *Pyxicephalus natalensis* and *Rana fasciata* tend to be somewhat intermediate in this respect. In doubtful cases an examination of the teeth on the upper lip will help in identification. Fully developed tadpoles of *Rana fasciata* have 4 rows of teeth, while equally developed tadpoles of *Pyxicephalus natalensis* have 5 rows of teeth.

measurements of the head and body and of the tail do not confirm van Dijk's statement. They are as follows:

Species	*No. of specimens measured*	*Average ratio of tail to body length in %*	*Range of variation*
Pyxicephalus delalandii	39	1·65	1·25 - 2·11
Pyxicephalus natalensis	21	1·95	1·57 - 2·33
Rana fasciata	11	1·93	1·50 - 2·21
Rana angolensis	37	2·08	1·68 - 2·64

It is evident that an average tadpole of *Pyxicephalus natalensis* would be classified as a *Rana* tadpole when using van Dijk's key. Furthermore the range of variation is such that even some *Pyxicephalus delalandii* tadpoles might be classified as *Rana* tadpoles, whilst many *Rana fasciata* tadpoles fall in the range supposedly characteristic of *Pyxicephalus* tadpoles.

DEPENDENCE OF BREEDING ON ENVIRONMENTAL CONDITIONS

The dependence of the behaviour of amphibians on climatic factors is well known. Breeding often takes place in a specific season and field observations suggest that the weather on the days when spawning takes place or during preceding days plays an important part in triggering the process of reproduction. The relationships are simplified in species which spawn only once a year, as happens in some frogs of the northern hemisphere. The spawning of the European grass frog *Rana temporaria* has been analysed in detail by Savage (1961) but even there a very complicated dependence was discovered in which no single environmental factor appears to be wholly responsible for the time of spawning. In frogs with an extended breeding season which includes all South African species, the problem is even more complicated, as it involves two different aspects namely:

(*a*) the control of the breeding season, i.e. the beginning and the end of the period during which spawning may take place, and

(*b*) the control of the time (date) within the breeding season when the actual spawning occurs.

Even casual observations show that the spawning does not occur regularly throughout the breeding season, but takes place on some days but not on others. It is this discontinuity of the breeding within the reproductive season that has attracted my special attention and which I attempt to explain in the following pages.

It has often been noticed that the spawning of a number of frogs follows a spell of rainy weather. In the highveld most of the rains occur in the spring and summer months. Furthermore, the rains usually take the form of heavy showers often on consecutive days separated by days or weeks of dry weather, even at the height of the rainy season. After one or several showers closely following one another, low lying parts of the veld, including the larger pans, become filled with rain, and this is the time when the breeding activity of the frogs becomes most conspicuous. Loud calls can often be heard in the evening of the day on which a heavy shower has occurred. In Johannesburg the species heard calling are mainly *Pyxicephalus delalandii, Kassina senegalensis* and *Bufo regularis*. Nearer the rainwater one also hears the softer voices of *Phrynobatrachus natalensis, Cacosternum boettgeri*, and *Xenopus laevis*. By morning masses of eggs of all these species may be found. Other species start breeding after some delay.

As stated previously, *Bufo carens* and *Pyxicephalus adspersus* pair and spawn in broad daylight.

The observed breeding sequence of the various species suggests that weather changes may.be the immediate cause of egg laying on any particular day within the breeding season. To check the influence of climatic factors on the reproductive behaviour of frogs the rainfall was measured throughout the years 1951-1960 with an automatically recording rain-gauge, placed in the township of Blairgowrie about 1·3 km. from the main area of observation. In view of the often very local rainfall in the highveld this was considered preferable to using the official data of the meteorological station in Johannesburg which is several kilometres from the area. Similarly maximum and minimum shade temperatures were taken at the same point in Blairgowrie.

From these records I have worked out temperature and rainfall average profiles for the days immediately preceding egg laying of those species for which I have the most complete set of observations. Figures 8 and 9 show the average maximum and minimum temperatures and the average rainfall for 5 days preceding egg laying (days −5 to −1) as well as for the day on which the eggs were actually laid (day 0). Eggs laid during the night were considered to be laid on the subsequent day.

The weather profile for the spawning of *Pyxicephalus adspersus* offers the clearest picture. During the 5 days preceding spawning there is a steady increase of rainfall culminating in a maximum on the day prior to spawning (−1 day). On the day of spawning there is a sharp decrease of rainfall (Fig. 8a). The maximum day temperature is no less characteristic. The cycle begins with a rise in temperature to a maximum on days −4 and −3. As the rainfall increases, the temperature drops and reaches the lowest level on the day preceding spawning (coincident with the maximum rainfall). Further decrease of temperature stops at the end of the rains and on the day of spawning there may even be a slight rise. This is not present in the weather profile for *Pyxicephalus adspersus*, but is distinct in the similar profiles for other species, e.g. in Fig. 8b. The minimum (night) temperatures follow the changes of maximum (day) temperatures.

The weather profiles for *Pyxicephalus delalandii* (Fig. 8b), *Phrynobatrachus natalensis* (Fig. 8c) and *Xenopus laevis* (Fig. 8d) are very similar to that for *Pyxicephalus adspersus*, except that the rise in rainfall is not as great, though in all of them there is a distinct peak on the day preceding egg laying.

The weather profile for *Bufo carens* shows a different pattern (Fig. 9a). The egg laying of *Bufo carens* occurs one day after the spawning of other species. Thus the maximum rainfall in the case of *Bufo carens* is on day −2, i.e. two days preceding egg laying. Egg laying in respect of temperature changes is displaced similarly. The weather profile for *Kassina*

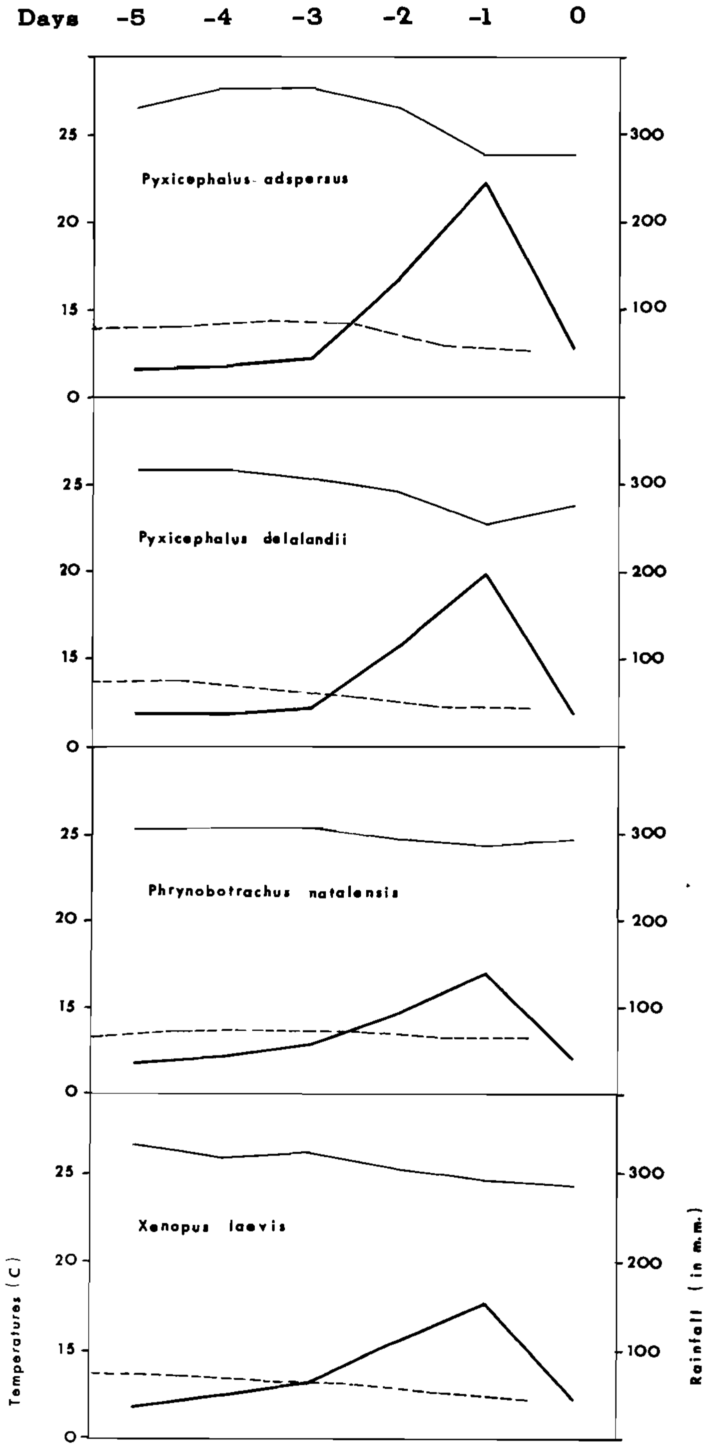

Figure 8. Profiles of weather preceding and accompanying spawning in four species of highveld frogs. Thick lines – average rainfall on day of spawning (day "0") and the five preceding days (days −1 to −5). Thin continuous line ≠ average maximum temperature; thin dashes ≠ average minimum temperature. The maximum and minimum temperatures have been arbitrarily allocated to midday and midnight respectively.

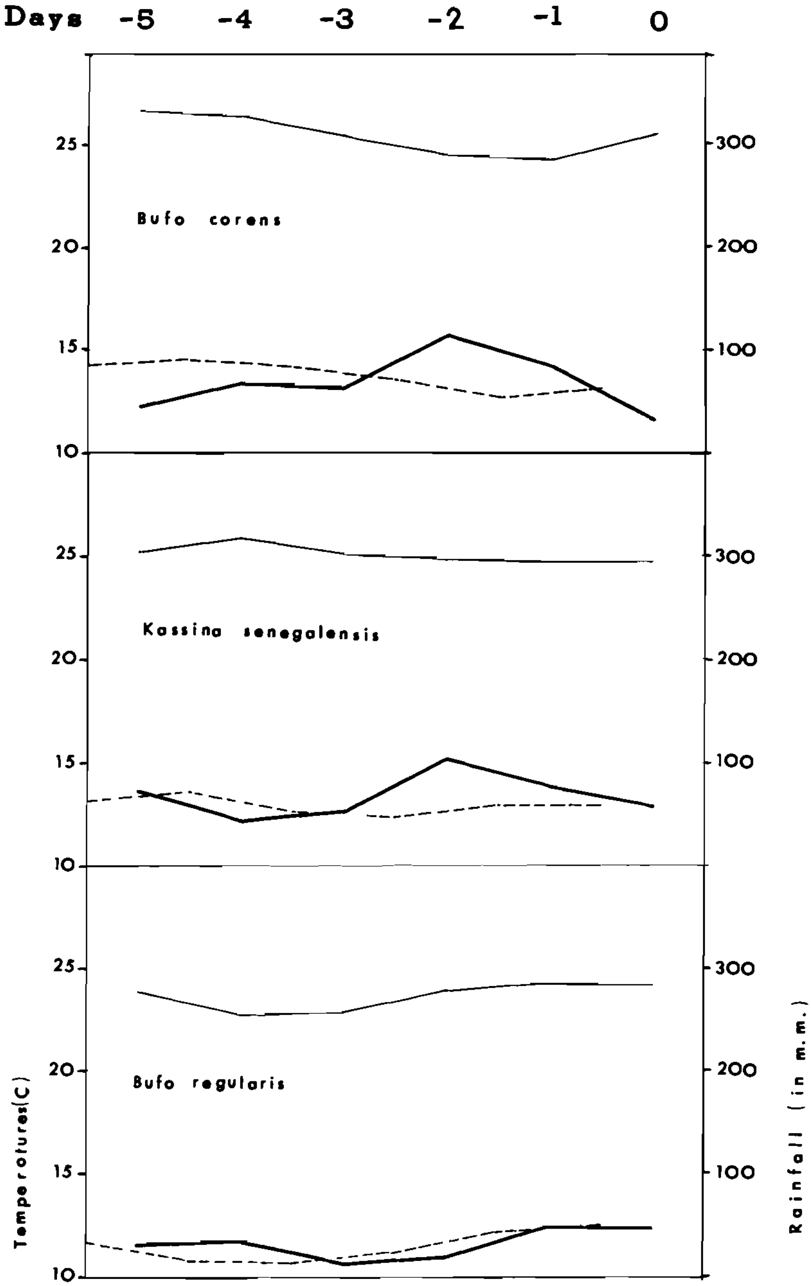

Figure 9. Profiles of weather similar to those in Figure 8, but for three further frog species.

senegalensis (Fig. 9b) resembles that of *Bufo carens* but the curve is less distinct, probably because there are fewer observations on this species.

Lastly, the weather profile for *Bufo regularis* (Fig. 9c) does not resemble either that of *Pyxicephalus adspersus* or *Bufo carens*. The average rainfall throughout is very low and there is no peak preceding egg laying. The temperature changes are also different: the temperature rises continuously (in spite of some rainfall) from day −4 to day −1 with a slight drop on the actual date of egg laying.

While the profiles of average climatic factors in the days preceding egg laying agree with direct observations of the weather, they also show that rainfall is not the only variable favourable for breeding. Changes in rainfall are accompanied by inverse changes in temperature, an increase in rainfall coinciding with a drop in temperature. In fact Kalk (1960) has suggested that the drop in temperature is the factor that triggers reproductive behaviour in at least one species with which my investigation is concerned, namely *Xenopus laevis.*

Obviously the weather profiles as presented in Figs. 8 and 9 are not sufficient to differentiate between the variables included in the graphs, nor do they, in themselves, prove that there is a significant relationship between egg laying and rainfall or temperature changes.

More careful statistical analyses are required to differentiate between the factors involved and to determine the significance of the relationships. The method used was the study of multiple regression.

Egg laying was taken to be the dependent variable and rainfall and temperature were assumed to be two independent variables. To present egg laying in a quantitative form two different procedures were adopted. For those species in which large numbers of pairs sometimes spawned simultaneously (*Pyxicephalus adspersus*, *Pyxicephalus delalandii*, *Phrynobatrachus natalensis*, *Xenopus laevis*), the abundance of spawning was arbitrarily divided in three classes:

class 0 — no spawning
class 1 — single records of spawning
class 2 — a few pairs spawning
class 3 — mass spawning (many pairs)

For species in which most observations were of single spawning pairs or those in which the few observations did not justify sub-division into several classes, (*Bufo regularis*, *Bufo carens*) only two classes were used:

class 0 — no spawning recorded
class 1 — spawning recorded

Rainfall is naturally given in quantitative form—in inches or in hundredth parts of an inch.* It was necessary to decide, however, for what period the rainfall acted as an independent variable.

Initially the rainfall on the date preceding spawning (day −1) was used. Subsequently it was found advisable to sum the rainfall of two or more preceding days.

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* The rain-gauge and the maximum and minimum thermometers used were marked in inches and degrees Fahrenheit. These units were not changed for statistical analysis since a change to metric units would have introduced an error when rounding off the recalculated values.

Temperature as the second independent variable presented more problems. The actual temperature in degrees Fahrenheit* on the day preceding spawning was used in some calculations. However, practically all species spawn at different temperatures in the course of the spring and summer. It was therefore more important to check the relation of spawning to the *changes* in temperature, rather than the actual level of temperature. The regression was therefore calculated on the *increase* in temperature from the day −2 to the day −1. A fall of temperature during the same period was treated as a negative value. The temperature and rainfall on the actual date of spawning was ignored on the assumption that by that time the behaviour of the animals was irrevocably determined by factors operating previously. The regression on the minimum (night) temperatures was not tested, as these follow very closely the maximum (day) temperatures.

A few words must be devoted to controls, that is the days on which no spawning was recorded. Naturally only those days were considered on which the localities in which spawning usually occurs were searched for signs of breeding. During very dry weather it was useless to inspect the area, as it was known that all possible places for egg laying were dry. During more favourable weather I was often prevented from going out by the pressure of other work. Sometimes spawning on such missed days could be recorded by finding developmental stages on subsequent days, as explained on p. 44. There were, however, many days on which no fresh eggs could be found, sometimes because it was too early or too late in the year, or because weather conditions were not quite suitable. Again on some days fresh eggs of some species of frogs were found but not others. Such days could be taken as negative or control days for the species which had not spawned. All in all, there was no shortage of negative or control days even in the height of the breeding season.

The calculations of multiple regression with two independent variables were carried out following Snedecor (1946). Coding was used to avoid negative values of temperature change and zero values of rainfall and spawning. Multiple regression with more than two independent variables could have been used for simultaneous testing of several combinations of climatic factors as done by Savage (1961) when he analysed the factors determining the spawning of *Rana temporaria* in England. I decided, however, to limit the analysis to two independent variables at a time, so as not to complicate the calculations, and to test different combinations of factors separately.

The analysis of multiple regression leads to the calculation for each set of variables of "standard partial regression coefficients". In the case of two independent variables the coefficients may be designated as

$$b'_{Y1\cdot2} \quad \text{and} \quad b'_{Y2\cdot1}$$

These coefficients show the regression of the dependent variable (y) on each of the independent variables X_1 and X_2 (indicated in the designation of the regression coefficient simply as 1 and 2) independently of each other, and expressed in units of standard deviations. In the following calculations, therefore, $b'_{Y1\cdot2}$ means "the standard partial regression coefficient of spawning on rainfall (as the first independent variable) independent of temperature change". $b'_{Y2\cdot1}$ then means "the standard partial regression coefficient of spawning on temperature change (as the second independent variable) independent of rainfall".

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* See footnote on p. 56.

The method further allows one to show the dependence of spawning on both factors by an equation of the form:

$$\hat{Y} = a + bX_1 + cX_2$$

where $\hat{Y}$ is the probability of spawning expressed quantitatively, X_1 and X_2 are the independent variables (rainfall and temperature change) and a, b and c are constants.

For *Xenopus laevis* the equation was calculated as follows:

$$\hat{Y} = 0{\cdot}2077 + 0{\cdot}0084\ X_1 + 0{\cdot}0273\ X_2$$

This means that for every 0·01″ rainfall the probability of spawning increases by 0·0084 of a unit. By simple calculation one can see that 1·19″ of rain is needed to attain 1 unit of spawning probability (that is attain the probability of a weak spawning reaction). However, the first constant, 0·2077 is independent of both rain and temperature change, and may therefore be considered as a measure of "background" against which the reaction to climatic factors takes place. It shows that even without rain or temperature change there is roughly 20% probability that spawning will occur. Thus the rainfall need raise the probability of spawning not from a zero level, but only from the "background" level of 0·2077 to the effective 100% level. 1—0·2077 = 0·7923 and this divided by 0·0084 gives 0·94″, which is the average rainfall needed to produce a weak spawning reaction. This amount of rain on one day occurs fairly frequently, and is sometimes surpassed, which may account for some cases of very abundant spawning.

Similarly it may be shown that 1 unit of spawning probability may be attained independent of the rainfall, by a temperature rise of 36°F. If the "background" is taken into consideration, the necessary rise of temperature becomes 29°F (0·7923 : 0·0273). An increase of maximum temperature by this value from one day to the next would be extremely rare, but in nature rain and change of temperature occur simultaneously and their relative importance can be best evaluated by the standard partial regression coefficients.

For *Xenopus laevis* these are

$$b'_{Y1\cdot 2} = 0{\cdot}4420$$
$$b'_{Y2\cdot 1} = 0{\cdot}1649$$

The standard error of the partial regression coefficients (which is common to both $b's$) is in this case $S_{b'} = 0{\cdot}812$†

The ratio $b'_{Y1\cdot 2}/S_{b'} = 5{\cdot}45^{**}$

$b'_{Y2\cdot 1}/S_{b'} = 2{\cdot}03^{*}$

Thus the standard partial regression coefficient of spawning on rainfall is highly significant, whilst the standard partial regression coefficient of spawning on the change (increase!) of temperature is significant only at a 5% level.

The multiple regression coefficient, R^2, which may be calculated from the partial regression coefficients is a measure of the part of the variance of the dependent variable which is accounted for by the multiple regression. In the case of *Xenopus laevis* $R^2 = 0{\cdot}1692$, which

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† In the following, one asterisk (*) indicates significance at 5% level, double asterisks (**) indicate high significance—at level of 1% or less.

means that about 17% of the total variance in the spawning of this species is accounted for by the regression on rainfall in the last day before spawning, and on temperature.

ANALYSIS OF INDEPENDENT VARIABLES

In the foregoing calculation the change (increase) of the maximum temperature from day −2 to day −1 was used. If the actual maximum temperature on the day preceding spawning is taken as the second independent variable the results are less satisfactory. In Table 1, lines 1 and 2, the two methods are compared to show the multiple regression of spawning of *Xenopus laevis* on rainfall and temperature in the month of December. The data were restricted to the records for one month to simplify calculations.

The advantage of taking temperature increase as the independent variable is obvious. Due to the fewer observations in the December sample the regression on temperature increase has ceased to be significant, but the regression on maximum temperature is even smaller. The regression on rainfall on the other hand remains highly significant or significant even in the smaller sample. The advantage of dealing with temperature increase rather than with absolute temperature is evident also from the higher value of R^2 in the first case. This indicates that the proportion of variance accounted for by the regression on rainfall and temperature increase is greater than the regression on rainfall and absolute temperature. Similar results were obtained with data on the spawning of *Pyxicephalus delalandii.*

A further question is whether it is correct to consider only the rainfall on the last day preceding spawning, as rain on previous days may have a cumulative effect, for releasing the breeding reaction of the frogs. Again to save labour calculations were made on subsamples of data relating to one month only. In Table 1 line 3 both independent variables are represented by rainfall, namely the rainfall on the last day (day —1) and the rainfall on the two preceding days (day —2 and day —3 together).

The partial regression coefficient for rainfall on days —2 plus —3 is almost exactly the same as the partial regression coefficient for rainfall on day —1. This means that the rain falling on the third plus second day before the actual spawning is as much responsible for the breeding reaction, as the rain falling on the last day. In other words the action of the rainfall throughout the last 3 days before spawning is cumulative.

Table 1 line 4 compares regression on the rainfall in the last 3 days as against the rainfall on days —4 and —5. The regression of spawning on the rainfall in days —4 and —5 is obviously smaller than on the rainfall in the last 3 days. Thus the breeding reaction is mainly dependent on the weather conditions of the last 3 days. The rainfall in previous days appears, however, to have some, if weaker influence on the animals. Although the partial regression coefficient in this case does not quite reach the significance level, it comes rather close to it. Furthermore the increased R^2 when rainfall in the last 5 days is taken into account as compared with calculations relating to the last 3 days shows that rain falling 4 and 5 days before spawning contributes to the release of the breeding reaction.

The greatest proportion of variance in the breeding reaction is accounted for by taking rainfall in the last 5 days and the increase in temperature as the independent variables, as shown in line 5 of Table 1.

TABLE 1

ANALYSIS OF INDEPENDENT VARIABLES (ASTERISKS EXPLAINED IN THE TEXT P. 58)

Line	*Species*	*No. of observations*	*Independent variables*		$b'_{Y1\cdot 2}$	$b'_{Y1\cdot 2}/S_{b'}$	$b'_{Y2\cdot 1}$	$b'_{Y2\cdot 1}/S_{b'}$	R^2
			X_1	X_2					
1	*Xenopus laevis* (December observations only)	39	Rain on last day	Temperature increase	0·4596	2·70**	0·2469	1·45	0·1708
2	—	39	Rain on last day	Maximum temperature	0·3595	2·35*	0·0509	0·33	0·1245
3	—	39	Rain on last day	Rain on days −2 and −3	0·3859	2·68*<**	0·3742	2·60*<**	0·2607
4	—	39	Rain on days −1, −2 and −3 together	Rain on days −4 and −5	0·4787	3·47**	0·2614	1·89*	0·3192
5	—	39	Rain on last 5 days	Temperature increase	0·6568	4·87**	0·2282	1·69	0·3983
6	*Phrynobatrachus natalensis* (November observations only)	59	Rain on last day	Temperature increase	0·2572	1·89	0·2609	1·92	0·0875
7	—	59	Rain on last 3 days	Temperature increase	0·4703	4·05**	0·2028	1·75	0·2496
8	—	59	Rain on last 5 days	Temperature increase	0·4417	3·75**	0·1783	1·51	0·2244

While these conditions account for just under 40% of the variance in spawning, the result is not unsatisfactory. In the very extensive observations used by Savage, which cover 11 independent variables, only 51% of the variance in spawning was accounted for; my results, with only 2 variables, are clearly of the same order of magnitude. In this connection Savage (1961, p. 144) points out that in laboratory biochemical reactions often as much as 25% of the variance is not accounted for, and in processes taking place in nature a much greater random variation may be reasonably expected.

To corroborate data obtained for *Xenopus* similar results with *Phrynobatrachus natalensis* for November are quoted in Table 1, lines 6, 7 and 8. The calculations show clearly a cumulative effect of rain falling on the last 3 days before spawning, but they also show that the rainfall on days —4 and —5 does not add to the determination of the spawning reaction and that the greatest proportion of the variance in spawning is accounted for by a multiple regression on weather conditions during the last 3 days before egg laying.

The reaction to weather conditions in those species for which there is sufficient data may now be compared. The comparison is best made by using regression equations, rather than partial regression coefficients. With the exception of *Bufo regularis* the data in Table 2 are based on the temperature increase from day —2 to day —1 as the second independent variable while the first independent variable is the rainfall recorded in days preceding spawning. The number of days considered varies from 1 to 5 depending on which number shows the regression most effectively.

Strictly speaking the asterisks in Table 2 refer not to the degree of significance of the coefficients of X_1 and X_2 which were not calculated directly, but to the partial regression coefficients ($b'_{Y1\cdot 2}$ and $b'_{Y2\cdot 1}$) from which the coefficient of X_1 and X_2 are derived. In the first five species included in the table there is thus a significant or highly significant regression of spawning on rainfall, but there is no significant regression on change in temperature.

In the last species, *Bufo regularis* spawning does not show a significant regression either on rainfall or temperature change; the partial regression coefficient of spawning on rainfall is actually negative. The regression coefficients are not statistically significant, however, and the regression may actually be zero or even slightly positive. This corresponds well with observations that *Bufo regularis* often spawns very early in the year, before the first spring rains.

The results for *Bufo carens* should also be noted. In addition to data presented in Table 2 the regression of spawning on the rainfall two days before spawning (day —2) and on the rainfall on the eve of spawning (day —1) has also been calculated and compared. The corresponding partial regression coefficients are:

$$b'_{Y1\cdot 2} \text{ (rain on day } -2) = 0{\cdot}2645^{**}$$

$$b'_{Y2\cdot 1} \text{ (rain on day } -1) = 0{\cdot}0192$$

Whilst the regression on the rainfall on day —2 is highly significant, the rainfall on the eve of spawning is not significant at all. As mentioned earlier *Bufo carens* usually spawns not on the day after a heavy rain, as do most other frogs, but on the next day. Presumably a heavy rain triggers a breeding reaction which takes 2 days to become overt, and is consum-

TABLE 2

COMPARISON OF REGRESSION EQUATIONS IN DIFFERENT SPECIES (ASTERISKS EXPLAINED IN THE TEXT, P.58)

Species	*No. of observations*	*X_1 expressed in 0·01″ of rain*	*X_2 in degrees F.*	*Regression equation*
Xenopus laevis	162	Rainfall in last 5 days	Temp. rise from day −2 to day −1	$\hat{Y} = 0{\cdot}0096 + 0{\cdot}0045X_1^{**} + 0{\cdot}0086X_2$
Phrynobatrachus natalensis	181	Rainfall in last 3 days	,, ,,	$\hat{Y} = 0{\cdot}4143 + 0{\cdot}0065X_1^{**} + 0{\cdot}0126X_2$
Pyxicephalus delalandii	148	Rainfall in last 3 days	,, ,,	$\hat{Y} = -0{\cdot}0516 + 0{\cdot}0069X_1^{**} - 0{\cdot}0266X_2$
Pyxicephalus adspersus	49	Rainfall in last day	,, ,,	$\hat{Y} = -0{\cdot}0884 + 0{\cdot}0123X_1^{**} - 0{\cdot}0199X_2$
Bufo carens	86	Rainfall in last 2 days	,, ,,	$\hat{Y} = 0{\cdot}1330 + 0{\cdot}0018X_1^{*} + 0{\cdot}0090X_2$
Bufo regularis	63	Rainfall in last 3 days	Temp. rise from day −3 to day 0	$\hat{Y} = 0{\cdot}4833 - 0{\cdot}0018X_1 + 0{\cdot}0125X_2$

TABLE 3

REGRESSION EQUATIONS OF SPAWNING ON RAINFALL AND TEMPERATURE BY MONTHS

Species	*Month*	*No. of observations*	*Regression equation*
Xenopus laevis (rain in 5 days and temperature increase) ..	September	15	$\hat{Y} = 0{\cdot}1104 + 0{\cdot}0051X_1 + 0{\cdot}0592X_2$
	October	26	$\hat{Y} = -0{\cdot}1059 + 0{\cdot}0063X_1^{**} - 0{\cdot}0032X_2$
	November	48	$\hat{Y} = -0{\cdot}1017 + 0{\cdot}0054X_1^{**} - 0{\cdot}0017X_2$
	December	39	$\hat{Y} = -0{\cdot}3262 + 0{\cdot}0079X_1^{**} + 0{\cdot}0358X_2$
	Jan./Feb.	34	$\hat{Y} = 0{\cdot}1628 + 0{\cdot}0019X_1 - 0{\cdot}0187X_2$
Phrynobatrachus natalensis (rain in 3 days and temperature increase)	October	30	$\hat{Y} = 0{\cdot}5096 + 0{\cdot}0032X_1 + 0{\cdot}0061X_2$
	November	59	$\hat{Y} = 0{\cdot}2610 + 0{\cdot}0073X_1^{**} + 0{\cdot}0296X_2$
	December	53	$\hat{Y} = 0{\cdot}7017 + 0{\cdot}0061X_1^{*} - 0{\cdot}0032X_2$
	Jan./Feb.	39	$\hat{Y} = 0{\cdot}1424 + 0{\cdot}0078X_1^{*} + 0{\cdot}0127X_2$
Pyxicephalus delalandii (rain in 1 day and temperature increase)	October	29	$\hat{Y} = 0{\cdot}4478 + 0{\cdot}0066X_1 + 0{\cdot}0065X_2$
	November	46	$\hat{Y} = 0{\cdot}0658 + 0{\cdot}0147X_1^{**} - 0{\cdot}0040X_2$
	December	38	$\hat{Y} = -0{\cdot}0641 + 0{\cdot}0166X_1^{**} - 0{\cdot}0196X_2$
	Jan./Feb.	33	$\hat{Y} = 0{\cdot}0328 + 0{\cdot}0035X_1 + 0{\cdot}0206X_2$

mated largely independently of what happens in the interval. This probably accounts for the low level of the coefficient of X_1 recorded in Table 2.

The next feature shown in Table 2 is the occasional high value of the first constant in the equation (the constant not multiplied by either X_1 or X_2). This first constant is a measure of the probability of spawning when both independent variables are 0 i.e. no rainfall and no change in temperature. In *Xenopus*, *Pyxicephalus delalandii* and *Pyxicephalus adspersus* the first constant is close to zero, suggesting that these species do not spawn without some sort of provocation. In *Phrynobatrachus* and *Bufo regularis* on the other hand the first constant is nearly 50% suggesting that with the inevitable fluctuations, spawning may occur "spontaneously" without any extrinsic cause. This agrees with direct observation, for *Bufo regularis* is a species which spawns ahead of the spring rains, and *Phrynobatrachus* spawns frequently, often on days when no other frog is breeding. The first constant may thus be regarded as an indication of the preparedness of a species to breed without regard to external conditions or at least independent of the two factors, rainfall and temperature which have been investigated. The first constant will therefore be termed the "preparedness factor". The level of this factor is obviously important in facilitating the breeding response. As breeding in most or possibly all frogs in the highveld is restricted to a fairly well defined season, in spite of the fact that conditions of rainfall and temperature favourable to spawning occur at other times, it may be presumed that the degree of preparedness changes during the year, and possibly accounts for the very existence of the breeding seasons. Heavy rains occur in the Transvaal highveld not only during the months of September to January, but quite often in February and even in March. Nevertheless the late rains do not appear to elicit a breeding response or do so very rarely.

As regression equations of the type presented in Table 2 would have no meaning if they were to be calculated for periods in which no spawning occurs, it is not possible to calculate the preparedness of a species for periods out of the breeding season. It is possible, however, to compare the factor of preparedness at various periods within the breeding season, provided that there are sufficient observations to give significant values when divided into smaller groups. This condition is satisfied in three species: *Xenopus*, *Phrynobatrachus* and *Pyxicephalus delalandii*. The regression equations for these species are presented in Table 3.

A general trend seems to emerge from the data presented in Table 3. Preparedness appears to be highest at the beginning of the breeding season, and falls off towards the end. This is very clear in the case of *Pyxicephalus delalandii*. In *Phrynobatrachus* and *Xenopus* the figures fluctuate too much, but in *Phrynobatrachus* the figure for January-February is distinctly lower than for the preceding months. In *Xenopus* the factor of preparedness decreases from September to December (becoming negative), but increases again in January-February; the latter increase cannot be explained at present.

A further trend is that the reactivity to rainfall appears to be low at the beginning of the breeding season but increases to a maximum in the middle of the season and falls off at the end. This is evident both from the degree of statistical significance of the partial coefficients of regression which is indicated by asterisks in the table and from the actual value of the constant by which X_1 (rainfall) is multiplied in the formula.

The two factors combined may account for the beginning and end of the breeding season of each species. It may be noted that in *Xenopus* the anomalously high factor of preparedness in January-February is more than compensated for by a sharp fall of the regression coefficient (as reflected in the constant multiplying X_1).

CONDITIONS OF SURVIVAL OF JUVENILE STAGES OF HIGHVELD AMPHIBIANS

Survival under natural conditions is dependent on the one side on the biological properties of the organism and on the other side on its environment. The environment may be conveniently subdivided into the biotic environment and the physical or abiotic environment. In this study no data have been obtained concerning effect of the biotic environment on the reproduction of frogs, but some information has been collected concerning the physical conditions of survival particularly temperature and availability of water.

TEMPERATURE

It is well known that the temperature tolerance of organisms, and of the eggs and embryos of amphibians in particular, bears a relation to the prevailing temperatures in their habitats. (See Moore 1949, Ballinger and McKinney 1966.) To investigate the temperature adaptations of South African frogs the temperature tolerance of young embryos of some of the species occurring in the highveld was tested. Freshly collected eggs usually in the early cleavage stages were placed in dishes and kept at temperatures adjusted for ± 5°C intervals, in some experiments from 5°C to 45°C, until the stage of swimming larvae or until they died.

The actual records are given in Appendix 2.

TABLE 4

SUMMARY OF EXPERIMENTAL RESULTS ON TEMPERATURE TOLERANCE

Species	*Lower lethal*	*Lower vital*	*Upper vital*	*Upper lethal*
Xenopus laevis	10°	11°	30°	35°
Bufo regularis	13·5°	15°	36°—	36°+
Bufo carens	9°	15·5°	29°	35·5°
Phrynobatrachus natalensis ..	11°	13°	34°	36°
Pyxicephalus adspersus	10·5°	15°	38·5°—	38·5°+
Pyxicephalus delalandii	7°	10°	36°—	36°+

The temperature tolerances of the different species may now be compared with the water temperatures in the pools and dams in which the eggs and embryos were found.

Temperatures in small bodies of water change very considerably during the day especially at the surface and in the shallows as shown by the graph given in Fig. 10 which is based on recordings made in an artificial fish pond. Temperatures taken on the same day show that in shallow natural pools the variation of temperatures is even greater than shown in Fig. 10.

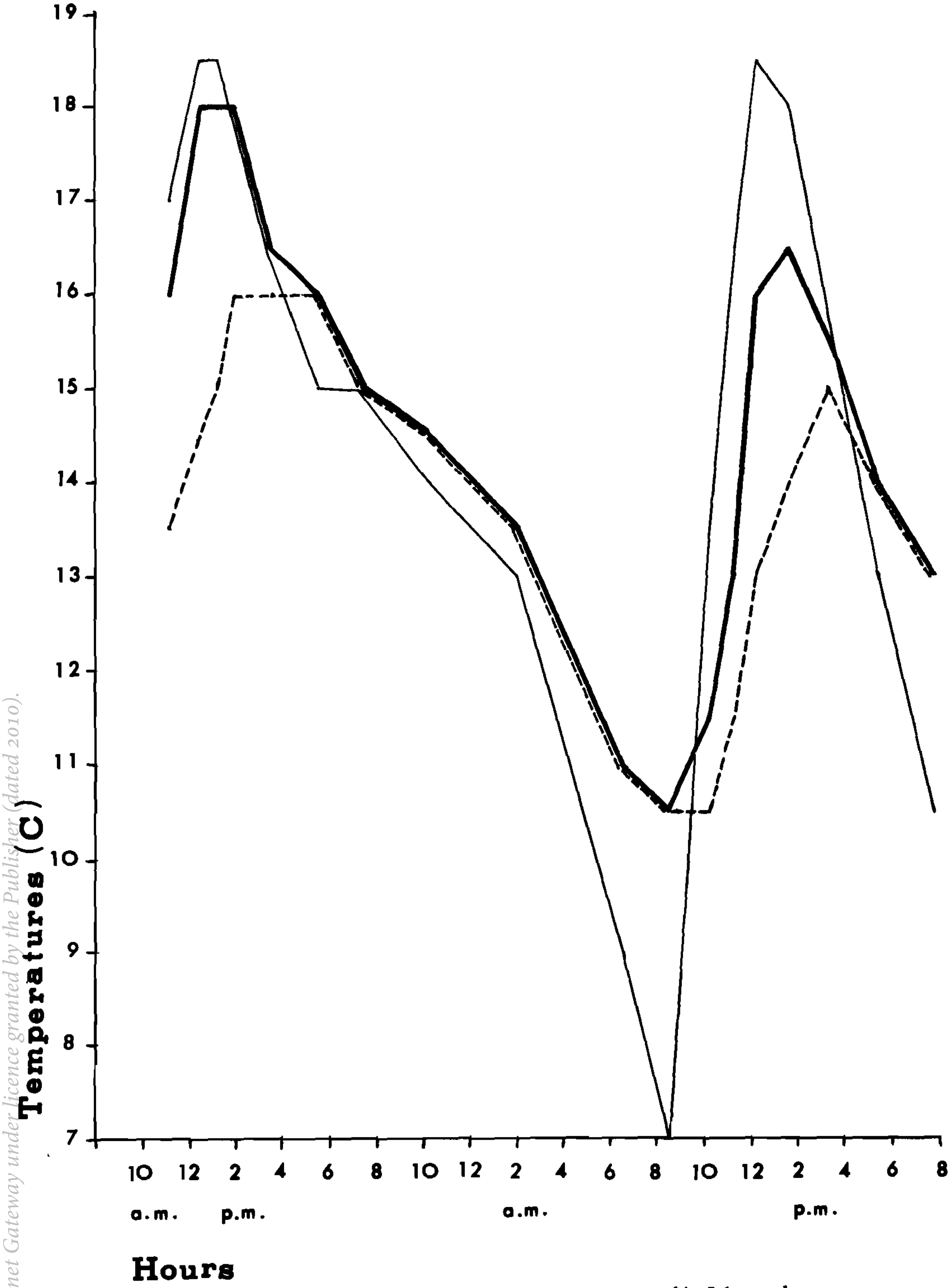


Figure 10. Diurnal temperature fluctuations in a small artificial fish pond in Johannesburg, measurements taken on 31 August to 1 September 1958. Thick line = surface temperature in open water. Thick dashes = temperature at a depth of 40 cm. Thin line = temperature at edge of pool amongst vegetation.

Thus at 12.30 on the 1st of September the reading in a shallow pool was 22° instead of 18·5° in the fish pond. However, the temperature at 40 cm. below the surface was practically identical: 11·5° in the fish pond and 12·5° in the natural pool. The main result of twenty-four hour series of measurements shows that minimum temperatures in water are observed about 2 hours after sunrise, and maximum temperatures are reached in the early afternoon. Excursions to the field of observation were often made in the early morning and at various times during the afternoon. Thus temperature records made during the excursions would often include both the minimum and the maximum water temperatures. Since the temperatures fluctuate, there is little point in calculating averages; only the extremes are important for the survival of frog eggs and larvae. These are given in Fig. 11 which shows the average range of water temperature for each month over several years. There are few records between February and August and none for July but this whole period is out of the breeding season. Nevertheless it is probably true to say that temperature fluctuations in the months February to May are limited, and that the greatest fluctuations occur in the spring months, from September to November.

Apart from the range of temperature, Fig. 11 shows the upper and lower lethal limits for eggs and embryos. It is clear that there is practically no danger that eggs or embryos of any species of frog will be killed by high temperatures, as the lethal temperatures of all species are above, or well above the highest temperatures recorded in nature. On the other hand there is a real danger that some batches of eggs and embryos will be destroyed by low temperatures, especially in the species which start breeding early in September e.g. *Bufo regularis*, *Xenopus laevis* and *Pyxicephalus delalandii*, or those that have a low tolerance for cold such as *Bufo regularis* whose lethal temperature is 13·5°C.

Dead or abnormally developed eggs are seldom found in nature. In a laboratory experiment the eggs are exposed to the lethal low temperature for lengthy periods (30 hours in the case of the experiment with *Bufo regularis* eggs) whereas in nature the minimum temperatures last for a few hours only, and the much higher day temperatures may allow partial or complete recuperation. Nevertheless eggs of *Bufo regularis* presumably damaged by cold were observed at least on two occasions.

(1) Batches of *Bufo regularis* eggs laid on the 15th and 16th of Sept., 1956, had not developed beyond neurula stage when found on the 20th. Some were arrested as gastrulae, and others were exogastrulating. The minimum (air) temperature dropped to 7°C on the 17th, remaining at 9°C on the 18th—sufficiently low to cause developmental arrest or abnormal development. Compare these results with those of laboratory experiments given in Appendix 2, p. 88.

(2) A batch of *Bufo regularis* eggs was found on the 21st Oct., 1953; all of them were dead. Although water temperature was not recorded the previous night the air temperature had dropped to 5°C.

RELATION OF DEVELOPMENT RATE TO AVAILABILITY OF WATER

The permanence of the bodies of water in which they breed may be more important for highveld amphibians than the temperature fluctuations. Rain pools and even the smaller pans and

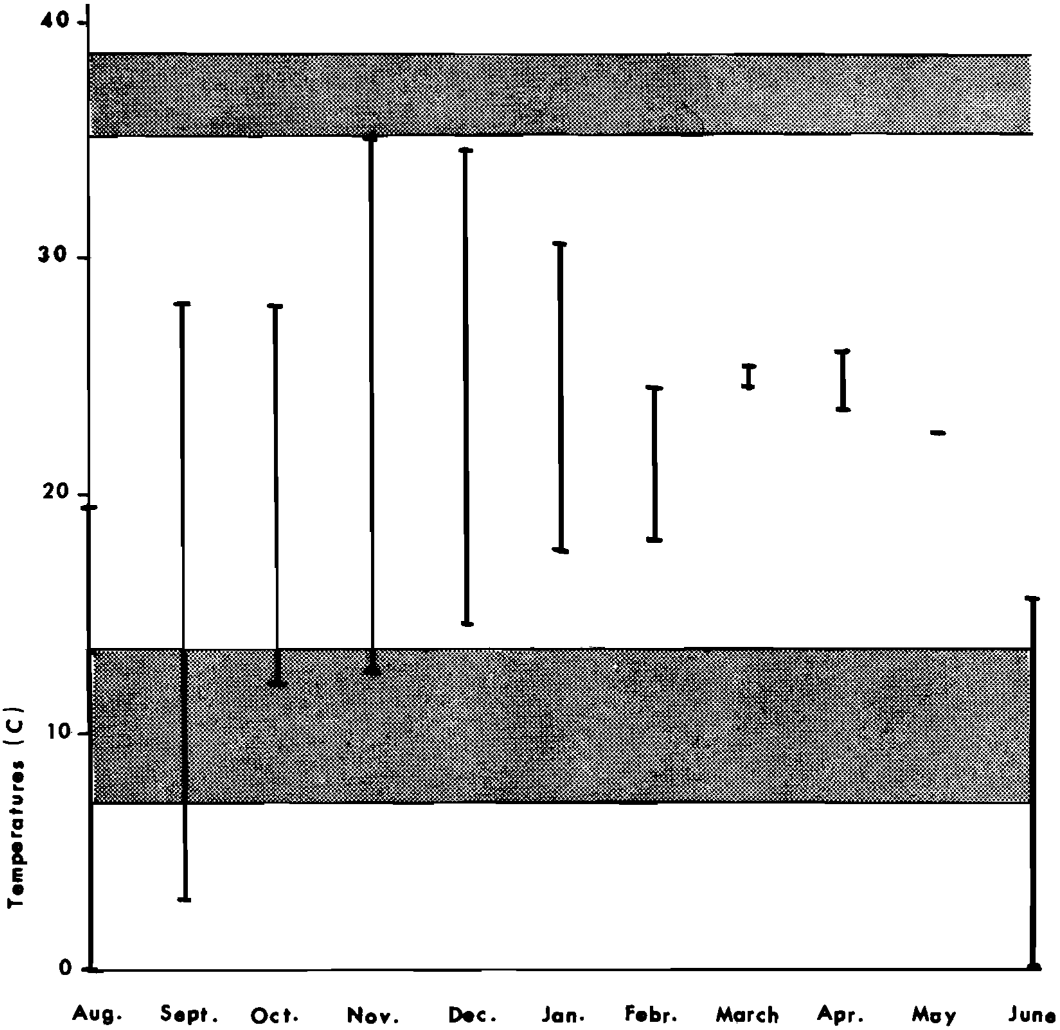


Figure 11. Monthly range of water temperatures measured in pools in area of observation. The stippled bands show the temperature tolerances of frog species of the highveld: the breadth of the stippled band corresponds to the range of tolerances, as between the most hardy species (uppermost for heat and lowermost for cold) and the most sensitive species (lowermost for heat and uppermost for cold). (Compare with Table 4).

ponds frequently dry up, and unless the development of the tadpoles is completed, these die. The following data are presented in this connection:

(*a*) The duration of development up to metamorphosis of the various species.

(*b*) The rate of growth of the tadpoles.

(*c*) Duration of existence of some bodies of water in the area of observation as dependent on rainfall.

(*d*) Actual records of tadpoles destroyed by drying up of bodies of water.

DURATION OF DEVELOPMENT TO METAMORPHOSIS AND RATE OF GROWTH

For this purpose data derived from breeding tadpoles in aquaria or even observations made in climatic conditions differing from those of the highveld are quite useless. The data had to be collected under natural conditions, and specifically under conditions prevailing in the area under observation. Fortunately it was possible to gain this information as the time when frog eggs were first laid in a particular pool was recorded and the earliest emergence of metamorphosed froglets was noted. By measuring samples of tadpoles from such a population their rate of growth was determined.

The data obtained are shown on Table 5.

The following remarks should be made in addition to Table 5.

The data for *Bufo regularis* are not reliable, but as breeding starts in the beginning of September and no metamorphosis was observed earlier than the second half of November, it appears that development is extended over a period of about 2½ months. Hewitt and Power (1913) give the length of development of this species as 73 days.

For *Bufo carens* Power (1926) gives the length of development as 41 days.

Power (1927) gives 114 days as the time of development to metamorphosis of *Phrynobatrachus natalensis* which is definitely too long, and must have been caused by unfavourable conditions. Although my data of 27 and 29 days are somewhat doubtful, the records of 32 and 33 days are quite reliable since the pools were dry before the development, and no earlier batches of eggs could have caused confusion.

The data for *Kassina senegalensis* are not reliable as the batches could not be traced throughout the period of development. Power (1926) observed metamorphosis 90 days after laying, but his larvae were kept in a small aquarium, and it is likely that in nature development proceeds faster.

I have only a very doubtful record of the duration of development of *Cacosternum boettgeri*. Hewitt and Power (1913) have observed that in an aquarium metamorphosis occurs 37 days after egg-laying.

Hewitt and Power (1913) observed metamorphosis of *Pyxicephalus delalandii*, in an aquarium, 36 days after egg-laying.

My data for *Pyxicephalus adspersus* are quite exact, since the tadpoles are gregarious and under the supervision of the male. Individual families could thus be traced throughout the whole time of development. Power (1927) reports that in an aquarium development to metamorphosis took 47 days; evidence that development in nature may proceed at a considerably higher pace.

No new data is available for *Rana fasciata* but according to Wager (1965) metamorphosis occurs after four to five months, or sometimes longer.

Also for *Rana angolensis* no data are available from Johannesburg. Power (1927) states that the nearly related *Rana fuscigula* metamorphoses after 3 months, but may remain in a

TABLE 5.

Duration of development as observed in nature.

Species	*Eggs laid*	*Metamorphosis*	*Duration of development*
Xenopus laevis	27.XI.1950	19.1.1951	53 days
	15.III.1951	6.V.1951	52
	18.X.1952	16.XII.1952	59 ,,
	6.XI.1952	25.XII.1952	49 ,,
	22.I.1955	27.III.1955	64 ,,
Bufo regularis	±12.X.1949	26.XII.1949	±74 ,,
	beginning of September?	19.XI.1952	±75 ,,
	?	27.XI.1954	?
Bufo carens	29.XI.1950	7.I.1951	39 ,,
	3.I.1951	24.II.1951	52 ,,
	12.XII.1952	28.I.1953	47 ,,
	30.XII.1954	11.II.1955	43 ,,
	4.I.1955	10.II.1955	37 ,,
Phrynobatrachus natalensis ..	27 XI 1950	29.XII.1950	32 ,,
	3.XII.1951(?)	30.XII.1951	27 ,,
	27.I.1952	8.III.1952	40 ,,
	28.XI.1953(?)	27.XII.1953	29 ,, (?)
	28.XII.1954	30.I.1955	33 ,,
Kassina senegalensis	27.XI.1950(?) not earlier	19.I.1951	52 ,, at most
	22 or 29.I.1955 not earlier	27.III.1955	57-64 (?) days
Cacosternum boettgeri	4.I.1955(?)	after 10.II.1955	37+ days (?)
Pyxicephalus delalandii	27.XI.1950	26.XII.1950	29 days
	14.X.1951	18.XI.1951	35 ,,
	21.X.1954	20.XI.1954	30 ,,
	6.XI.1954	5.XII.1954	29 ,,
	28.XII.1954	22.I.1955	25 ,,
	28.XII.1954	30.I.1955	33 ,,
	4.I.1955	30.I.1955	26 ,,
	5.XI.1958	10.XII.1958	35 ,,
Pyxicephalus adspersus	11.XII.1952	11.I.1953	31 ,,
	19.XII.1953	19.I.1954	31 ,,
	3.I.1955	5.II.1955	33 ,,
	26.I.1955	26.II.1955	31 ,,

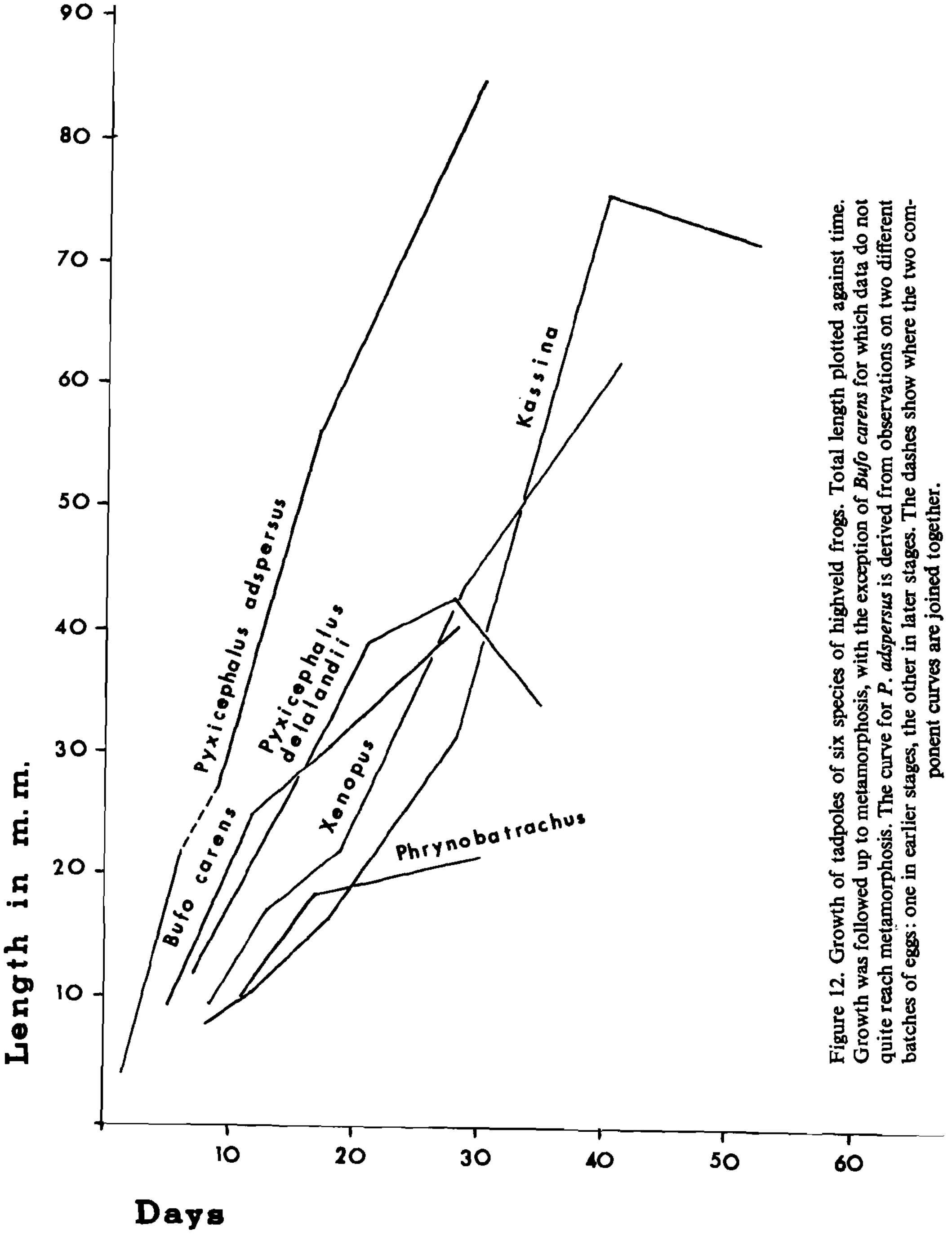
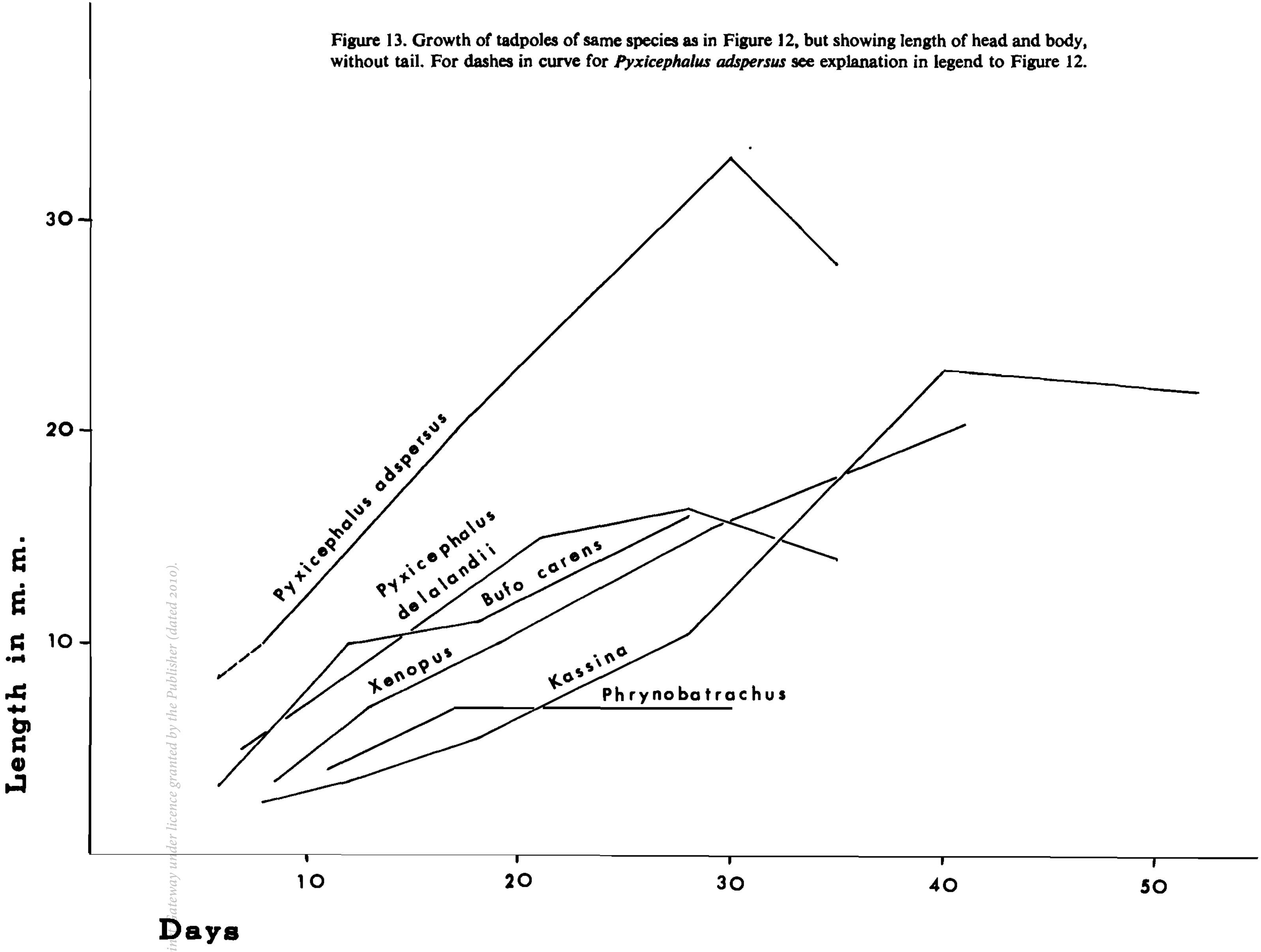


Figure 12. Growth of tadpoles of six species of highveld frogs. Total length plotted against time. Growth was followed up to metamorphosis, with the exception of *Bufo carens* for which data do not quite reach metamorphosis. The curve for *P. adspersus* is derived from observations on two different batches of eggs: one in earlier stages, the other in later stages. The dashes show where the two component curves are joined together.

Figure 13. Growth of tadpoles of same species as in Figure 12, but showing length of head and body, without tail. For dashes in curve for *Pyxicephalus adspersus* see explanation in legend to Figure 12.



larval stage very much longer even 3 years or more. He reports that in captivity metamorphosis occurred after 81 days in water averaging 37°C (range 25-40°C!). Wager (1965) writes that the metamorphosis of *Rana angolensis* usually occurs after nine months, but may take up to 2 years or more.

The rate of development is closely related to the rate of growth as early metamorphosis in larger species requires rapid growth whilst extended larval life allows for a slow growth over an extended period. A limited amount of information on the rate of growth of some species has been obtained by measuring samples of tadpoles which the evidence suggested had developed from batches of eggs laid on known days (though they were not necessarily the offspring of a single pair). These measurements are presented in the form of graphs in Figs. 12 and 13. The data are insufficient for a mathematical treatment, but obviously the steeper slopes of the curves correspond to more rapid growth, and the flatter slopes to slower growth.

Development has not been followed through to metamorphosis for all species. If the right halves of the curves which are affected by impending metamorphosis are ignored the species may be put in the following order in respect of increasing rate of growth:

Kassina — *Phrynobatrachus* — *Xenopus* — *Bufo carens* — *Pyxicephalus delalandii* — *Pyxicephalus adspersus*.

The extremely rapid growth of the bullfrog tadpoles stands out even from the meagre information available.

The actual conditions in which the development and growth of the tadpoles had to proceed in the area under observation will now be considered. Table 6 summarises my records of the rainfall between 1951 and 1961. The seasonal changes are shown by the average for each month. The breeding season of most frogs ends early in February and the rainfall in subsequent months is therefore unimportant for breeding. The crucial months are August to January, and the rainfall in these months makes or breaks a good breeding season for the frogs. By summing the averages for the months August-January a figure of 49·7 cm. is obtained as the average rainfall for these months in the area under observation. The actual rainfall in different years for the same six months is shown in the bottom line of Table 6. Thus the years 1951/52, 1952/53, 1959/60 were years with below-average rainfall, whilst the years 1953/54, 1954/55, 1957/58 and 1958/59 were years with above-average rainfall. My records show that many pools and waterholes were repeatedly filled and dried up in the course of a breeding season.

Table 7 shows the duration of bodies of water (9 pools and waterholes, including the small dam mentioned on p. 37) which were under observation. The records have been arbitrarily divided in four groups:

1st group: water held for 1 to 20 days
2nd group: water held for 21 to 45 days
3rd group: water held for 46 to 90 days
4th group: water held for over 90 days.

TABLE 6

RAINFALL AS RECORDED IN BLAIRGOWRIE (JOHANNESBURG) (IN CENTIMETERS)

	1951	1952	1953	1954	1955	1956	1957	1958	1959	1960	1961	*Total for all years/ number of months recorded*	*Aver-age*
Jan.	—	10·05	4·11	16·31	26·26	—	15·47+	12·01+	8·59+	3·78+	—	96·58/$_8$	12·07
Feb. ..	—	11·28	15·34	8·00	25·50	—	12·85	10·72	6·32	7·95	—	97·96/$_8$	12·24
March ..	—	6·20	8·38	5·41	2·82	—	7·65	9·04	3·61	5·79+	—	48·90/$_8$	6·11
Apr... ..	—	4·88	4·47	3·94	6·65	—	2·90	8·71+	2·39	8·48	—	42·42/$_8$	5·30
May.. ..	—	0·58	1·50	1·90	7·24	—	0·79	0·74+	6·83	0·58	—	20·16/$_8$	2·52
June.. ..	—	0·61	0·00	0·05	0·18	—	5·41	0·13	0·18	0·20	—	6·76/$_8$	0·84
July	—	5·05	0·00	0·00	0·00	—	8·51+	0·00	1·17	0·00+	—	14·83/$_8$	1·85
Aug. ..	2·23	0·00	0·00	0·03	0·38	—	4·55	0·00	0·00	0·96	—	8·15/$_9$	0·91
Sept. ..	1·60	0·05	0·00	2·36	0·23	2·39	11·46	7·72	0·36+	0·43	—	26·60/$_{10}$	2·66
Oct... ..	14·63	2·84	5·23	5·05	7·04	7·80	10·34	3·17	4·52	5·59	—	66·21/$_{10}$	6·62
Nov. ..	2·00	15·49	14·63	14·20	12·70	7·34	6·40+	14·48	11·23	16·13	12·09	126·69/$_{11}$	11·52
Dec... ..	11·15	17·25	12·17	5·38	11·66	8·03+	2·69+	17·96	10·97+	11·33	9·55	118·14/$_{11}$	10·74
Aug.-Jan. of next year..	41·68	39·75	48·33	53·29	32·00+	41·02+	47·45+	51·92+	30·86+	34·44+	—	—	44·52

A plus indicates that the data for a particular month or group of months are incomplete.

TABLE 7.

Relation of duration of existence of bodies of water and mortality of tadpoles to rainfall by years.

Years	*Rainfall during Aug./Jan.*	*Frequency of duration of water in pools*				*Eggs drying up*	*Tadpoles drying up*	*Tadpoles dying due to partial drying and pollution of water*
		1–20 days	*21–45 days*	*46–90 days*	*90+ days*			
1951-52 ..	41·68	14	6	5	0	1	8	6
1952-53 ..	39·75	5	0	1	2	1	3	2
1953-54 ..	48·33	5	0	4	2	1	2	0
1954-55 ..	53·29	8	2	1	7	1	4	1
1955-56 ..	32·00*	5	1	2	1	0	3	0
1956-57 ..	41·02**	15	0	2	4	1	5	0
1957-58 ..	47·45	0	0	0	8	0	0	2
1958-59 ..	51·92	0	4	0	2	0	0	0
1959-60 ..	30·86	0	4	0	1	0	2	0

*Data for August-December only.
**Data for September-January only.

The figures show the frequency of occurrence of each type of duration. Different pools observed simultaneously were counted as so many occurrences, and of course the same pool could figure several times in the same year if it dried up and was refilled repeatedly. The figures show the preponderance of pools with short duration in dry years, and of pools with long duration in wet years. This is even more clearly shown in Fig. 14 which contrasts the bodies of water in dry and wet years.

As mentioned earlier (p. 47) in 1957-1958-1959 the small dam and some of the pools did not dry up in the winter thus creating an entirely different type of biotope.

The grouping of duration of pools and waterholes was made in relation to the length of larval life of the species of frogs on the highveld. Pools that last less than 20 days do not give any species an opportunity to metamorphose, and any tadpoles that develop in such pools inevitably die when the pools dry up. Pools lasting up to 45 days enable some species with a short larval life to metamorphose. These include *Pyxicephalus delalandii*, *Pyxicephalus adspersus*, *Phrynobatrachus natalensis*, *Cacosternum boettgeri* and *Bufo carens*, but not *Xenopus laevis*, *Kassina senegalensis* or *Bufo regularis*. Bodies of water lasting up to 90 days would enable *Xenopus laevis*, *Kassina senegalensis* and *Bufo regularis* to complete their development. Lastly, *Rana angolensis* and *Rana fasciata* can only metamorphose in permanent or very long lasting bodies of water.

In itself this does not prove that death by desiccation occurs in nature as it is conceivable that breeding frogs might avoid unsuitable pools. I have, however, many observations of such occurrences. Rain pools containing tadpoles often dry up long before the tadpoles have time to metamorphose, and masses of living and dying tadpoles have also been found at the bottom of pools when all the water had disappeared, and crusts of dried tadpoles have been found on earth which a few days earlier was the bottom of a pool. Table 7, columns 8-9

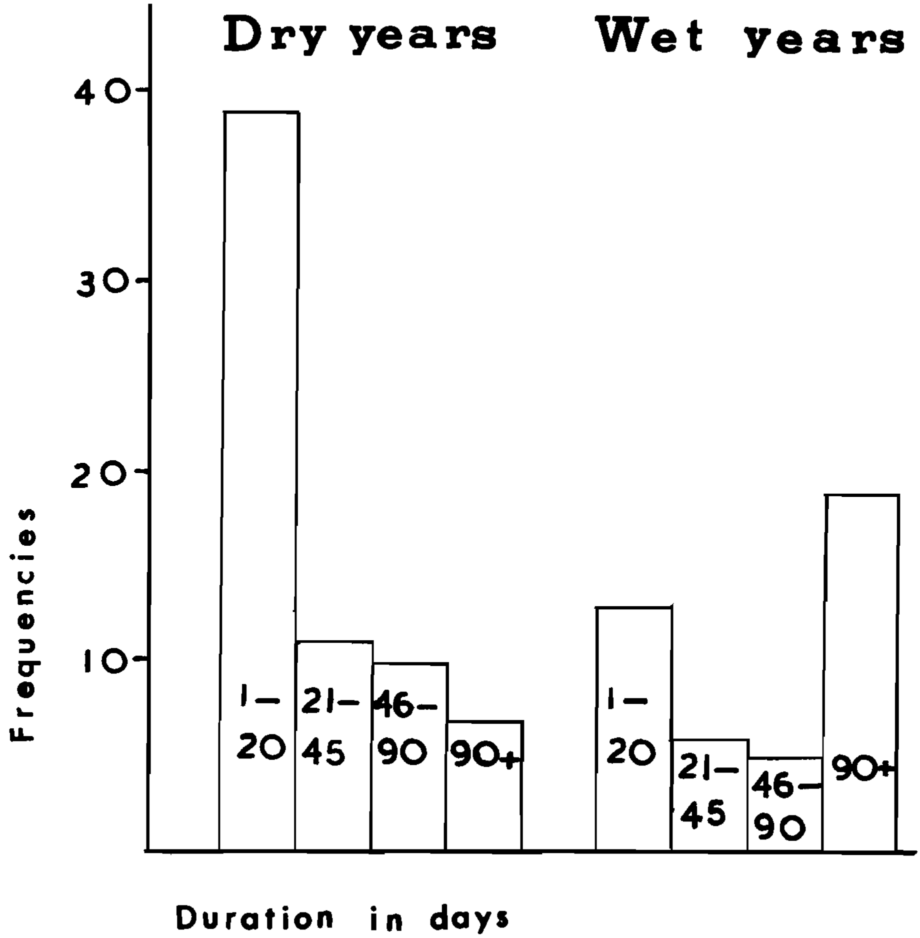


Figure 14. Comparison of frequencies of different duration of bodies of water in dry years (left) and in wet years (right). Data correspond to Table 7.

present records of deaths of tadpoles. In addition to deaths by straight-forward desiccation the table also shows cases of tadpoles dying as the result of extreme pollution which often occurs when the water in a pool is drastically reduced even if it has not dried up completely. Column 7 records cases of eggs drying up. This may occur even if the pool is not dry but the level of the water sinks and eggs in the shallows are exposed. Apart from one case of *Bufo regularis* eggs all the other cases refer to eggs of *Pyxicephalus adspersus* which are usually laid in very shallow water at the edges of pools. When compiling Table 7 all observations of tadpoles drying up on the same day whether in one pool or many, were counted as one case.

The table shows that destruction of eggs and tadpoles through the drying up of pools is infrequent in nature. The largest number of such observations was made in the summer of 1951/52, when the rainfall was particularly irregular, but cases were observed every year with the exception of summer, 1958/59. It is noteworthy that death of tadpoles by desiccation occurred both in dry years, when this would be expected and in some years with very good rainfall. The latter case was due to irregular rains, which allowed the pools to dry up completely or to be reduced in volume, which led to fouling of the remaining water.

The records for the particularly bad year 1951/52 show that several species failed to metamorphose at all in the area under observation. These species are: *Xenopus laevis*, *Bufo carens*, *Kassina senegalensis* and *Pyxicephalus adspersus*. Two other species, namely, *Pyxicephalus delalandii* and *Phrynobatrachus natalensis* managed to metamorphose, although many of their tadpoles dried up.

In the case of *Pyxicephalus adspersus* it was possible to keep records of individual batches of tadpoles, partly because there were few breeding individuals, partly because the tadpoles are gregarious, and partly due to the presence of the male guarding each tadpole group. The observations are summarized in Table 8.

TABLE 8.

Fate of batches of *Pyxicephalus adspersus* eggs.

Seasons	*Total of batches followed*	*Dried up as eggs*	*Dried up as tadpoles*	*Died as result of pollution in drying up pools*	*Metamorphosed*	*Probably metamorphosed*
1950-51	1	0	0	1	0	0
1951-52	3	1	1	1	0	0
1952-53	7	1	1	4	1	0
1953-54	7	0	4	1	1	1
1954-55	8	4	0	0	4	0
All years	26	6	6	7	6	1

The years 1950/51 and 1951/52 were the worst. As is seen in Table 6. 1951/52 was a year with below average rainfall (no records for 1950/51). The favourable years 1953/54 and 1954/55 were years of abundant rainfall.

DISCUSSION

The observations recorded in earlier sections of this paper show clearly that in respect of their breeding habits the frogs of the highveld fall into three distinct ecological types.

1. Breeders in temporary rain pools including *Bufo carens*, *Pyxicephalus adspersus*, *Pyxicephalus delalandii*, *Phrynobatrachus natalensis* and *Cacosternum boettgeri*. Apart from small

pools these species occur in the larger "pans" which usually dry up in winter and are filled again by spring and summer rains. Occasionally members of this group are found in different biotopes, thus *Bufo carens* may breed in dams, and *Phrynobatrachus natalensis* may spawn in shallow bywaters connected to streams and rivers, but for reproduction these species are adapted to temporary bodies of water. The main adaptation is the rapid larval development, which allows the tadpoles to metamorphose before the water dries up.

2. Breeders in semipermanent and permanent bodies of water. This group comprises *Xenopus laevis*, *Bufo regularis* and *Kassina senegalensis*. These species are adapted to breeding in the larger dams, streams and rivers. It is worth noting, that in South Africa a river is not necessarily a permanent body of water, even large rivers may dry up partially or completely. The species of this group especially *Xenopus laevis*, may spawn in quite small bodies of water such as rain pools, but their larval life is longer than that of the first group and their chances of survival in temporary bodies of water are reduced. *Bufo rangeri* probably belongs to this group too. Its eggs and tadpoles could not be distinguished from those of *Bufo regularis*. *Pyxicephalus natalensis* which breeds in streams may be another member of the same group, but there are no data about the duration of larval development.

3. Breeders in permanent waters such as large dams, rivers and swamps. To this group belong *Rana angolensis* and *Rana fasciata*, which both have a long larval development.

In addition to the duration of larval life, other features of reproductive biology are in accordance with the main adaptive trait of the three groups of species.

First, species which spawn in temporary bodies of water must have their breeding season in spring and summer, as it is at this time in the South African highveld that depressions are filled by the rains. Thus species of the first group normally breed from October to the middle of February. Species belonging to the second group breed in permanent or semipermanent bodies of water as well as in temporary rain pools, and their breeding season starts earlier, from the beginning of September, in the case of *Xenopus laevis*, or even in August, in the case of *Bufo regularis*. Species of the third group which breed in permanent bodies of water, are not limited to the spring and summer, but breed in autumn and winter, and possibly even throughout the year (e.g. *Rana angolensis*).

For those species which breed in temporary bodies of water, it should be important to lay eggs as soon as the pools are full, as this gives the tadpoles the best chance of completing their development before the pools dry up. This in itself suggests that the rainfall may act as a releaser for spawning as well as providing the aquatic medium without which, of course, no spawning can take place. Observation shows that the same species may spawn repeatedly in the same body of water. If the first cycle is released by the presence of water alone, the subsequent cycles must be caused by some additional factor or factors. Furthermore, some species, notably *Xenopus*, remain in water as long as any water is available, and yet their spawning occurs periodically, and must be released by some external or possibly internal factors.

The factors supposed to cause spawning in amphibians will now be considered. The recorded observations and theories apply mainly to two species namely *Rana temporaria* and *Xenopus laevis*. The spawning of the European grass frog, *Rana temporaria*, has been extensively studied by Savage (1961). Savage concludes that while many factors may influence the onset of spawning, among which the rise of temperature at the end of winter may be the most important, none of the climatic or geographical factors act directly. He suggests that their action on the breeding frog population is indirect through the growth of algae in the water. The abundant algal flora is necessary for the feeding of tadpoles, and the frogs (*Rana temporaria*) presumably have some means of detecting the onset of "flowering" of the water. There is no direct proof that the frogs react to algal growth and in any case this explanation would not be applicable to highveld frogs of the first ecological type. Spawning may occur the day after the pools have been filled by a heavy rain, before any algal growth could take place. Savage's explanation might apply to frogs of the third ecological type which breed in permanent waters, but here again there are difficulties, since spawning is not restricted to one particular season. Thus whatever causes spawning must occur repeatedly in the course of the year.

The spawning of *Xenopus laevis* has been investigated by many authors, and there is some experimental work as well as observations in the field. Both rainfall and temperature were considered in this connection. Several authors who kept *Xenopus* in captivity claimed to have elicited a breeding reaction by raising the water temperature by 5—6°C (Bles 1904, Kotthaus 1933, Vanderplank 1936). Artificial rain was also used to supplement the raising of temperature by Bles (1904) and Vanderplank (1936).

Hey (1949) claimed, on the other hand, that at the Jonkershoek Hatcheries in the Western Cape spawning of *Xenopus* follows a slight lowering of temperature. At the same time he mentions that the regular practice for inducing breeding at the Hatcheries is to fill ponds which had been kept dry for some time and to fertilise the water, whereupon the frogs start breeding abundantly in 2 to 3 days.

A similar procedure has been reported by Du Plessis (1966) working at Lydenburg Fisheries in Eastern Transvaal. Here the ponds stand dry in winter, and, when needed, are filled with water and fertilised with fowl manure. Within 2—3 days *Xenopus* accumulate in the fertilised ponds and immediately start spawning.

It is rather interesting to note that in both places *Xenopus* breeds readily in ponds that had been standing dry for some time, and are filled with water. In this way conditions are created which resemble the natural filling of pools and pans by the spring rains.

Berk (1938) compared the records of rainfall and temperature in the Western Cape with the onset of mating and breeding of *Xenopus* under natural conditions, and came to the conclusion that the mating signal is a rise in temperatures at the end of winter accompanied by continuing heavy rains. His data refer, however, only to the onset of the breeding season as a whole and not to the eliciting of spawning on any particular day within the breeding season. No observations of spawning on specific days are quoted.

Kalk (1960) compared the dates of spawning of *Xenopus* in Johannesburg with the occurrence of rainfall and with the daily temperatures. She found that spawning coincides with the end of a heavy rainfall or occurs just after it. She argues, that as *Xenopus* does not leave the water, rainfall *per se* could scarcely have a direct effect i.e. the frogs cannot get any wetter than they are before the rain. She, therefore, comes to the conclusion that rainfall acts by *lowering the temperature of the water.* Apart from this argument Kalk was not able to find any means of differentiating between the action of rainfall and the accompanying temperature changes.

It is here that the statistical methods used in the present work provide a deeper insight into the correlation of the variables concerned. The importance of a statistical approach to the problem of initiation of the frog breeding season has been very clearly put by Savage who used it in his own study mentioned earlier. Savage writes (1961 p. 120): "It is an illusion to consider that a statistical treatment of this subject is optional. No human mind can disentangle such a web of interacting factors without the aid of statistics".

In this work the method of multiple regression has been used to evaluate the regression of spawning on any two factors *independent of one another.* The analysis shows unequivocally that there is in *Xenopus* and in several other species which belong to the first ecological type a significant or even highly significant regression of spawning on rainfall independent of the change in temperature. On the other hand there is in the same species no statistically significant regression of spawning on decrease in temperature. The level of temperature on the day preceding spawning was also tested in the same way and no significant relation to spawning (independent of rainfall) could be detected.

The calculated regression of spawning on temperature change (independent of rainfall) was in most cases positive, that is with the same amount of rainfall the chances of spawning were greater if there was a rise and not a fall in temperature or if the fall in temperature was smaller. The figures for temperature are not statistically significant, however, and no further conclusion from them need be made here.

The statistical analysis of the relation of spawning to temperature and to rainfall has revealed some further facts of importance. First, the influence of rainfall was found in several instances to be cumulative, that is the spawning is dependent not only on the rain falling on the day immediately preceding the day on which spawning was released, but also on the rain in the previous 2-3 days. Furthermore there is in some species (notably *Bufo carens*) a latent period, the rain releasing spawning after 2 days. However, the delayed and cumulative action of rainfall does not go beyond a few days, and the regression falls off rapidly when calculated in respect of rainfall 5 days before spawning.

Another noteworthy result was the difference in reactivity to rain of the several species studied. Whilst *Xenopus laevis, Bufo carens, Phrynobatrachus natalensis, Pyxicephalus delalandii* and *Pyxicephalus adspersus* showed a statistically significant regression of spawning on rainfall, *Bufo regularis* did not show such a regression at all. It is thus obvious, that the releasing mechanism of spawning need not be the same in different species. It may even be suggested that this mechanism is different in the highveld population of *Xenopus* which live in conditions of summer rainfall and the Cape populations of *Xenopus* which live in a winter rainfall area.

As for *Bufo regularis*, this is a representative of the second ecological type: breeding occurs in permanent or semipermanent bodies of water which are available to the animals regardless of rainfall, and the necessity for them to breed at the onset of rainy weather so as to utilise the pools before they dry up does not exist. It may be stressed that *Bufo regularis* may be found spawning in Johannesburg very early in spring, before the first spring rains.

The reaction to rain of one and the same species appears to vary within the limits of the breeding season, and occurs with greater facility at the beginning of the breeding season, rather than later on (see p. 63 and Table 3). It is thus necessary to introduce the concept of "preparedness" of the animals for breeding. The preparedness might be directly related to the ripeness of eggs in the females, but in a more general way it would be dependent on the state of the endocrine glands in the last instance. It stands to reason that the general endocrinological state of the animals of which the condition of the gonads is but one expression, is gradually built up in the interval between the breeding seasons, and is at a peak towards the start of the new season, awaiting only the external stimulus (rain?) to initiate the spawning reaction.

Whilst the statistical significance of the regression of breeding on rainfall independent of any changes of temperature that may occur is clearly established, the purely mathematical analysis does not give an indication that rain as such is the direct cause of spawning. For a species living in water, as does *Xenopus laevis*, more water cannot make a difference unless it changes the composition of the water already present, or introduces some new factor, which was not there before. Quite a number of such changes or additional factors could be envisaged; some of these are—

(*a*) Increase in humidity of the air. This factor obviously could not affect an aquatic species, such as *Xenopus laevis*, or a species which normally keeps close to water, as *Phrynobatrachus*. It could perhaps be of significance for a terrestrial species, such as *Bufo carens* which shows a distinct reaction to rain, or to a lesser degree for the burrowing frogs *Pyxicephalus delalandii* and *Pyxicephalus adspersus*.

(*b*) Lowering the salt concentration in pond water through dilution by rain. Whether such a dilution actually occurs, I do not know, the opposite may even be the case, as shown later.

(*c*) Enrichment of pond and pool water with substances either organic or inorganic leached out by the rain from the surrounding soil and washed into the water. This could also change the pH of water. A factor of this nature might conceivably affect an aquatic species, but not a terrestrial or a burrowing species, which only enters the water after rain.

(*d*) Ionization of the atmosphere and of the water during the thunderstorms which accompany heavy rainfall in the highveld. Whether amphibia are able to detect such ionization is questionable.

(*e*) The patter of falling rain. Since amphibia can hear, this factor cannot be ignored completely, and could affect both terrestrial and aquatic species. If the animals need a signal that would give them an indication that eggs laid at a certain time are likely to develop successfully to metamorphosis, the sound of rainfall would be as good a one as any other, and could evoke an inherited reflex reaction on the part of those animals whose gonads are in a suitable condition for breeding.

It is not my intention at this stage to decide how rain elicits spawning. This would need many experiments in the laboratory, whilst this paper is mainly based on field observations. That rain is not the only factor which controls breeding is evident from the variance of spawning in relation to the regression of spawning upon rainfall. As has been shown already, regression on rainfall accounts for only a part of the variance in spawning. In *Xenopus laevis* (see p. 61) only about 40% of the variance is accounted for by regression on the rainfall. In *Pyxicephalus adspersus* the corresponding figure is 53%. This is quite a satisfactory figure, in view of the great variation to be expected in the field. Nevertheless the random variations themselves may have been due to causes which were not noticed.

While temperature did not elicit breeding in the species studied, temperature is important in determining the conditions under which development takes place. Extensive studies on temperature tolerance of eggs of different species and races of American frogs, by Moore (1939, 1949); Volpe (1957); Ballinger and McKinney (1966) have shown that the temperature tolerances bear a definite relationship to the prevailing environment. Species from high latitudes are tolerant to lower temperatures and intolerant to higher temperatures, compared to species from low latitudes. For eggs of *Bufo leutkeni* from Guatemala the lethal temperatures are ± 20·2°C and ± 40·0°C, whilst for the eggs of *Bufo americanus* living in Canada the lethal temperatures are 10°C and 31°C. (Ballinger and McKinney, 1966.)

The temperature tolerances of *Rana temporaria*, however, are much lower than those of *Bufo americanus*; the eggs develop, with slight abnormalities, even at 4·1°C, and at 24·6°C part of the embryos were damaged by heat showing that this was a nearly lethal temperature (Moore 1951).

From data recorded on p. 64 and Table 4 it is evident that the frogs of the South African highveld are intermediate between the tropical *Bufo leutkeni* and the northern *Rana temporaria*.

Of all South African species *Pyxicephalus delalandii* has the greatest tolerance to low temperatures (10°C is still a vital temperature), followed by *Xenopus laevis* (11°C vital). It is noteworthy that of the six highveld species for which I have obtained temperature tolerance data, only these two species reach the Western Cape (Poynton 1964). *Bufo regularis* with a lower lethal temperature of 13·5°C extends over the whole of equatorial Africa, and reaches West Africa and Egypt; thus its temperature adaptations are those of a tropical species, for which the South African highveld is a marginal area.

Bufo regularis also is tolerant to high temperatures (36°C marginal). However, the best tolerance to high temperatures is found in *Pyxicephalus adspersus*, which, with a marginal temperature of 38·5°C, almost matches the Guatemalan *Bufo leutkeni*. As will be shown, there is probably a special reason for tolerance to high temperatures in this case.

From my observations in nature it would appear that the temperature tolerance of highveld amphibians protects them from temperature fluctuations. It was very rare to find eggs probably damaged by marginal temperatures. The only authenticated cases of temperature damage were *Bufo regularis* eggs damaged by cold. This was the combined result of poor tolerance to cold, and early spawning.

Temperature is also a factor which influences the rate of development of eggs and tadpoles.

Frogs of the first ecological type which breed in rain pools and similar temporary waters may not be able to complete metamorphosis before the water dries (see Tables 7 and 8). Obviously there is a premium on a short larval life and early metamorphosis. Actually the larval development of this group of frogs is in the range of 30—40 days; frogs breeding in more permanent bodies of water (second ecological group), develop slower, taking 50—75 days to complete metamorphosis, while frogs of the third type, which breed in permanent bodies of water take several months to reach metamorphosis.

Rapid metamorphosis must be correlated with rapid growth, if the metamorphosing froglets are not to be of very small size. This is not important in miniature frogs such as *Phrynobatrachus natalensis* and *Cacosternum boettgeri*, but is quite important in larger species. Data on the rate of growth of tadpoles in nature, though very fragmentary, show that the rate of growth of *Pyxicephalus delalandii* (metamorphosis in ±30 days) and *Bufo carens* (metamorphosis in ±40 days) is more rapid than that of *Kassina senegalensis* or *Xenopus laevis* (metamorphosis in 50—60 days). The most critical situation is found in *Pyxicephalus adspersus*, the South African bullfrog. Males of this species reach a length of nearly 200 mm. At metamorphosis the little frogs are 26—29 mm. long which is the size of small adult *Phrynobatrachus natalensis*! Nevertheless the full development from egg laying to metamorphosis in *Pyxicephalus adspersus* is regularly completed in 31—33 days. The larval development of the North American bullfrog, *Rana catesbeiana*, an animal of comparable size takes just over two years (Smith and Smith, 1949). The rapid development of *Pyxicephalus adspersus* involves very rapid growth of the tadpoles which exceeds by far the rate of growth of all other local species.

This is achieved not only by an intrinsic high growth rate, but also by the breeding habits of the bullfrog. These include:

(*a*) Spawning at the height of summer, when water temperatures are highest.

(*b*) Spawning in very shallow water which becomes very warm, often several degrees higher than the deeper parts of the same pool.

(*c*) The gregarious tadpoles keep to the shallows among tufts of grass where the water is warmest. As high temperatures accelerate all biological processes including growth (van't Hoff's rule), this allows the bullfrog to develop in waters having a short existence. Coupled with behavioural adaptations are some physiological and morphological adaptations.

(*d*) To use the warmest parts of a pool requires a tolerance of high temperatures, which explains the fact noted on p. 81 that the bullfrog's tolerance of high temperatures is the greatest of all highveld frogs.

(*e*) The eggs of the bullfrog which measure 1.6—1.8 mm. are amongst the largest and allow growth to start from a greater initial size.

(*f*) As heated water loses oxygen, and the shortage is further enhanced by the gregariousness of the tadpoles, the respiratory apparatus of the early tadpoles has marked peculiarities which facilitate the uptake of oxygen. The external gills are large and fan-like with a maximum of 17 gill filaments on each side. The fans are spread on the ventral side of the tadpole and in this stage the tadpoles swim upside down, belly uppermost. As they usually remain near the surface, their gill filaments are pressed against the surface film in the best position to take up oxygen (Balinsky 1955).

Bufo carens somewhat resembles the bullfrog in its adaptations for rapid development. It breeds in late spring and at the height of summer when the water becomes very warm. The eggs are only slightly smaller than those of *Pyxicephalus adspersus*, namely 1.5—1.8 mm. in diameter and provide a good start for growth. The tadpoles are gregarious, like those of the bullfrog and swim in large compact masses. The external gills are not as well developed as those of the bullfrog, but they are relatively larger and have more gill filaments than those of *Bufo regularis* (Balinsky 1965, p. 509). In addition *Bufo carens* tadpoles at later stages of development possess a peculiar structure namely a skin fold on the nape of their neck. When the tadpoles swim near the surface, the skin fold is pressed against the air-water interface and probably serves as a supplementary respiratory organ. This enables the tadpoles to live in shallow pools with water depleted of oxygen through heating and pollution, while the high temperature favours rapid growth and development.

The pattern of reproduction among highveld frogs is conspicuous for the extended breeding seasons and repeated spawning of the same species of frogs in the same bodies of water. This is by no means a general feature in the order Anura. In temperate countries where there is no shortage of water, e.g. Europe and North America, each species of frog has a fairly limited breeding season, while different species spawn earlier or later in the year depending on their particular temperature tolerances and biological preferences. To illustrate this the data of Moore (1942) for North American frogs may be quoted:

Species	*Breeding season*
Rana sylvatica	mid March
Rana pipiens	early April
Rana palustris	mid April
Rana clamitans	May
Rana catesbeiana	June

In contrast to this the breeding seasons of South African highveld frogs overlap, and are extended over 3½—5½ months. This may be at least in part due to the ever-present danger in the highveld of the bodies of water drying up. When this happens all the eggs or tadpoles perish. This is what Schmalhausen has called "elemental elimination" (1940) which is the destruction of life by an overwhelming force of nature. Such a force often kills all individuals so that individual peculiarities cannot contribute towards survival or destruction. Such elimination is essentially non-selective.

Schmalhausen claimed (1940) that the trend of evolution depends on the type of elimination to which animals are mainly subjected. Not only selective elimination but also non-selective elimination may, indirectly, lead to adaptations of species. This is particularly the case when non-selective elimination operates in particular phases of the life cycle. Schmalhausen wrote "Non-selective destruction of larvae and young. In the case of predominant destruction of the young, those animals have the greater chance of leaving a progeny which produce the greatest number of offspring. Of importance is not only the total number of offspring, but also repeated reproduction. Non-selective elimination has often a global character, so that not individuals but whole broods or, during unfavourable years, many sets of broods become destroyed. If the destruction of the young takes great proportions, periodical reproduction, repeated spawning, and prolongation of life of the adults become important. Animals having such an ability have the greatest chance of leaving offspring" (1940, p. 180).

The pertinence of these views to the breeding ecology of frogs in the highveld is obvious. Frequent non-selective destruction of whole batches of offspring has caused the summer breeding highveld species, particularly of the first ecological type, but to a certain extent also of the second ecological type to develop repetitive spawning over an extended period, with a corresponding mechanism of reacting to favourable environmental conditions (rainfall). It does not matter in this connection, whether repeated spawning is performed by the same progenitors, or by different groups of progenitors.

To this basic adaptive feature are added further adaptations which could have been due to the more classic type of "selection of the fittest". The main one of these is rapid development enabling the tadpoles to complete their metamorphosis during the ephemeral existence of rain pools and pans, and this in turn is supported by rapid growth, utilisation of the warmer, shallow parts of the pools, high temperature tolerance and specialisation in larval respiratory organs.

SUMMARY

The present communication is based on more than 10 years of observations on frogs breeding in an area on the outskirts of Johannesburg. Twelve species of frogs and toads are recorded, and keys are given for the recognition of their eggs and tadpoles.

Records were made of the dates of spawning and of the rainfall and temperatures during the same period. In most species there is a distinct breeding season in the spring and summer months.

Statistical methods were employed to establish the relation of egg-laying to environmental conditions. By the method of multiple regression it was established that there is a highly significant dependence of spawning on rainfall in most species, but that there is no significant dependence on temperature, either on the level of temperature, or on the changes (rise or fall) of temperature. Specific differences were found to exist in the reactivity of frogs to rainfall, and there is evidence that the reactivity to rainfall changes in the course of the year, being higher at the beginning of the breeding season than later on.

The tolerance of eggs and embryos to different temperatures was tested in laboratory experiments, and this was compared with the actual water temperatures observed in nature. It was found that the tolerance to high temperatures is quite sufficient to cope with the warming up of water even on the hottest summer days, but that the tolerance to low temperatures

is not quite adequate for highveld conditions, with the result that damage by cold occasionally takes place in nature.

The rate of development (duration of larval life) and the rate of growth were studied in nature, and it was found that both are unusually high in some species. This is considered to be in direct relation to the brief duration of rain pools, small dams and pans which are regularly used for spawning by a number of species. The danger of death by desiccation of eggs and tadpoles in the highveld is very real, as is shown by a comparison of length of larval life with the duration of bodies of water in the study area, as well as by field observations of drying up of eggs and tadpoles. The danger is greatest in years with subaverage rainfall.

It is concluded that several features of reproductive ecology of highveld amphibians have been developed as adaptations to the different bodies of water in which they breed, ranging from permanent or semipermanent lakes, rivers and swamps to pans and rain pools filled with water for a comparatively short time during the summer rainy season.

(See following pages for Appendices I and II and References.)

APPENDIX 1.

Records of Dates of Spawning.

	1949-50	50-51	51-52	52-53	53-54	54-55	55-56	56-57	57-58	58-59	59-60	60-61	61-62	62-63	63-64
Xenopus laevis:	12.XI 15.XI 18.XII	before 24.IX 27.XI 15.XII 16.XII 22.XII 24.XII 25.XII 26.XII 28.XII 29.XII 30.XII 1.I early March	20.IX 21.IX 22.IX 23.IX 30.X 3.XI 19.XII 11.II 12.II 13.II	before 13.IX 17.X 6.XI 2.XII 3.XII 5.XII 11.XII	21.X 28.XI 1.XII 6.XII 19.XII 20.XII 4.I	6.XI 7.XI 12.XI 13.XI 30.XII 31.XII 3.I 4.I 13.I 22.I 29.I	24.XI	29.X 30.X 22.XI	before 15.IX 15.IX 25.IX	5.XI					
Bufo regularis:	12.XI 13.XI 15.XI 20.XI 13.XII 10.I	22.IX 2.XI 5.XI	26.IX 30.IX 19.X	17.X 18.X 6.XI	13.X 14.X 15.X	IX(?) 28.XII	4.X 5.X	3.IX 15.IX 16.IX 20.IX 25.XI	9.IX 10.IX 26.IX 1.X	14.IX		18.X 17.XII	29.VIII 20.X 25.X	24.IX	12.IX
Bufo carens:	4.XII	29.X 30.X 28.XI 29.XI 24.XII 3.I	4.XI 4.XII 12.II	6.XI 11.XI 12.XII 14.XII 31.XII ±10.II	6.XII 12.I	7.XI 13.XI 28.XII 30.XII 31.XII 4.I	±20.X	24.XI 6.XII ± 7.XII ±14.I	11.X 19.X 25.XI 20.I		21.XI				
Rana angolensis:	18.XI 9.IV 16.IV		±25.IX	VIII(?) 6.X 18.X	end of IX(?)	15.V							2.VIII(?) 29.VIII 25.X	6-7.VIII	
Rana fasciata:				25.IX			11.XI								
Pyxicephalus adspersus:		±28.XI	4.XI 3.XII	6.XI 11.XII	±27.XI 6.XII 19.XII 3.I	3.I 4.I 26.I(?) 29.I	±19.X	±28.XI 3.XII 13.I 14.I	25.XI		±11.XI				

Pyxicephalus delalandii:

1949-50	50-51	51-52	52-53	53-54	54-55	55-56	56-57	57-58	58-59	59-60	60-61	61-62	62-63	63-64
	27.XI	13.X 14.X 29.X 30.X 3.XII 27.I(?) 11.II	3.XI 4.XI 6.XI ±30.XI 11.XII I(?)	21.X 11.XI 28.XI 1.XII 6.XII 7.XII 18.XII 19.XII	6.XI 7.XI 29.XII 3.I 4.I 12.I	±14.X 19.X 23.XI 24.XI	27.X 29.X 30.X 1.XI 22.XI 25.XI 3.XII	before 10.IX 14.IX 1.X 3.X 12.X 25.XI			14.XI			
Pyxicephalus natalensis:														
13.XI 15.XI 20.XI 26.XI 13.XII			2.XII											
Phrynobatrachus natalensis:														
11.XI 12.XI 13.XI 20.XI	29.XI 30.XI 3.XII 5.XII 6.XII 15.XII 16.XII 22.XII 23.XII 24.XII 25.XII 26.XII 28.XII 29.XII 30.XII 31.XII 1.I 7.I 19.I	30.X 3.XI 6.XI 3.XII 4.XII 5.XII 19.XII 14.I 27.I 11.II	1.XII 2.XII 12.XII 20.XII II(?)	28.XI 1.XII 2.XII 6.XII 7.XII 19.XII 4.I 11.I	7.XI 13.XI 19.XI 28.XII 30.XII 31.XII 3.I 4.I 12.I 13.I 22.I 24.I 29.I 30.I 1.II 2.II 5.II 10.II	24.XI 15.XII 16.XII	27.X 31.X 1.XI 2.XI 22.XI 23.XI 24.XI 30.XI 1.XII 3.XII 7.XII 15.XII 16.XII 13.I 14.I	29.IX 1.X 8.X 11.X 12.X 18.X 19.X 21.X 22.X 25.XI 1.XII 6.I 20.I	10.XII	13.XI 14.XI 16.XI 19.XI 6.XII 8.XII 10.XII	14.XI 20.XII 21.XII 22.XII	16.XI		
Cacosternum boettgeri:														
		30.X 4.XII 27.I	± 2.II	19.XII	9.XI 28.XII 29.XII 30.XII 4.I 22.I	±20.X			± 9.XII	14.XI				
Kassina senegalensis:														
	28.XI 6.XII 16.XII 24.XII 29.XII 31.XII	before 4.XI 15.II	6.XI 2.XII	29.XI 19.XII 4.I	12.XI 13.XI 18.XI 19.XI 30.XII	11.XI		25.IX 26.IX	6.XI					

APPENDIX 2

RECORDS OF TEMPERATURE TOLERANCE EXPERIMENTS ON EARLY EMBRYOS

Xenopus laevis

2.10.1956	Temperature	Result
	5·0°	after 2 days retarded
	10·0°	after 2 days retarded
	15·5°	retarded but eventually normal
	20·5°	retarded but eventually normal
	25·5°	good development
	30·0°	good development
	35·0°	all dead after 1 day
	40·0°	all dead

Lots from first two chambers transferred after two days to chamber at 25°C. After a further 8 days all embryos held at 5° were found to be dead in early stages. Of the embryos held at 10°C one normal larva and one deformed larva survived.

29.10.1956	Temperature	Result
	4°	started cleavage but later all dead
	7°	started cleavage but later all dead
	11°	retarded but eventually normal
	15°	retarded but eventually normal
	20°	normal development
	25°	normal development
	29·5°	rapid and normal development
	36°	cleavage till large-celled blastula, then dead.
	38·5°	cleavage till 32-64 blastomeres, then dead

Bufo regularis

25.11.1955	Temperature	Result
	4·5°	all dead, no development
	6·5°	all dead, no development
	13·5°	cleavage started but later dead
	15°	retarded but normal
	19·5°	normal development
	22·5°	good development
	30°	good development
	36°	developed to swimming larvae then most died, but 1 survived
	40°	developed to tail bud later all dead

Bufo carens

24.11.1956	Temperature	Result
	5°	some cleavage, later all dead
	6·5°	some cleavage, later all dead
	9°	reached gastrulation, later dead

	15·5°	some retarded, others developed normally
	20°	normal development
	22·5°	normal development
	29·°	normal development
	35·5°	reached early tail bud, later all dead
	40°	after 1 day all dead
Phrynobatrachus natalensis		
22.1.1955	Temperature	Result
	21·5°	normal development
	25·5°	normal development
	32°→34°*	normal development
	35°→38°	reached tail bud stage, then all dead
	40°	reached tail bud stage, then all dead
2.2.1955	Temperature	Result
	17°→13°	after 1 day retarded, transferred to room temperature, subsequently developed normally
	18°→14°	after 1 day retarded, transferred to room temperature, subsequently developed normally
	23°→21·5°	normal development
	26°→28·5°	normal development
	33°→33·5°	many dead, but rest developed normally
	35·5°→36·5°	reached late neurula, then all dead
10.2.1955	Temperature	Result
	6°	dead
	8·5°	dead
	19°	retarded, but later normal
	21·5°	normal development
	28°	good development
	34°	mostly dead, but a few survived and developed into swimming larvae
	36·5°	reached late tail bud but later all dead
31.10.1956	Temperature	Result
	4·5°	some cleavage but later all dead
	7°	some cleavage but later all dead
	11°	abnormal, most embryos developed spina bifida
	15°	retarded but normal
	19·5°	normal development
	22·5°	normal development
	30°	good development
	36°	abnormal larvae, curved and do not swim
	39·5°	all dead

*The arrow indicates a change of temperature in the course of the experiment.

3.12.1956	Temperature	Result
	4·5°	some cleavage but later all dead
	7°	some cleavage but later all dead
	10·5°	some cleavage but later all dead
	15°	retarded, but later normal
	20°	normal development
	24·5°	normal development
	29°	good development
	36°	a few became swimming larvae, but most dead or deformed
	40·7°	some cleavage but later all dead

Pyxicephalus adspersus

3.12.1956	Temperature	Result
	4·5°	some cleavage, after 1 day all dead
	7°	some cleavage, after 1 day all dead
	10·5°	some cleavage, after 1 day all dead
	15°	retarded, but later normal development
	20°	normal development
	24°	normal development
	28·5°	normal development
	36°	excellent development
	38·5°	a few normal, but majority misshapen, some dead.

Pyxicephalus delalandii

19.10.1955	Temperature	Result
	7°	some abnormal cleavage but eventually all dead
	12°→11°	retarded but eventually normal tadpoles
	15·5°	normal development
	21°	normal development
	25°	normal development
	29·5°	good development
	35°→36°	cleavage abnormal, after 1 day all dead
	37·5°→38°	cleavage abnormal, after 1 day all dead

29.10.1956	Temperature	Result
	4°	some cleavage later all dead
	7°	some cleavage but later all dead
	10°→11°	markedly retarded but eventually normal development
	15°	normal development
	20°	normal development
	22°	normal development
	29°→30°	normal development
	36°	a few reached tadpole stage, some abnormal, about half dead
	38°→40°	reached late neurula stage, later all dead

31.10.1956	Temperature	Result
	15°	retarded but normal
	19·5°	normal development
	22·5°	normal development
	30°	good development
	36°	swimming tadpoles, slightly abnormal
	39·5°	all dead

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