STRATEGIES OF WATER CONSERVATION IN SOUTHERN AFRICAN FROGS

J. P. LOVERIDGE

Department of Zoology, University of Rhodesia

ABSTRACT

In arid or semi-arid areas of southern Africa, frogs are typically active nocturnally and seasonally. They may adopt a variety of strategies to conserve water during the day or during the unfavourable part of the year. Aquatic frogs (e.g. *Xenopus*, most species of *Rana, Ptychadena* and *Phrynobatrachus*) do not normally have a water conservation problem except when the water in or near which they are living dries up. Burrowing frogs (e.g. *Bufo, Pyxicephalus, Tomopterna* and *Breviceps*) are able to select microhabitats in the soil which reduce evaporative water loss. Burrowing may, in particular cases, be associated with the formation of a keratinized cocoon of stratum corneum which appears to offer a barrier to outward water movement. In arboreal frogs (*Chiromantis xerampelina* and *Hyperolius* spp.) the most interesting adaptations are found. Evidence is given in the case of *Hyperolius nasutus* for low evaporative water losses at the end of the dry season, when the frogs sit exposed to the sun and dry air, in flowers. During the rains when *H. nasutus* is in breeding aggregation the evaporative water losses are high. *Chiromantis xerampelina* is uricotelic and resistant to desiccation.

The three approaches which anurans have adopted in response to water conservation problems have their correlates in bladder size and function, hormonal regulation of water balance and the extent to which water loss can be tolerated. The potential that the southern African amphibian fauna offers for physiological research is emphasized.

INTRODUCTION

Recent years have seen great advances in studies of the taxonomy and zoogeography of southern African Anura (Poynton 1964; Van Dijk 1971a). Although not all the taxonomic problems have been resolved, the time is now ripe for an intensive research programme into the biology of the southern African frogs. Invaluable biological notes have been given by Poynton (1964) and Wager (1965), but relatively few attempts, notably those of Cott (1932) and Van Dijk (1971b), have been made to survey the adaptations of southern African Anura. In this paper I attempt to examine the water conservation strategies of the frogs of the southern African subcontinent in the geographical region covered by Poynton (1964).

Until comparatively recently it has been widely acknowledged that all Amphibia have a very permeable skin, thus making them ill-adapted for survival in dry atmospheres. Many recent text-books have claimed, as has Porter (1972), that 'all available evidence indicates the adult amphibian skin is a semi-permeable membrane that unquestionably prevents the entrance or exit of some solutes but has little effect on the passage of water'. However, Porter (1972) has urged caution in making such generalizations on the basis of work primarily on a few north temperate genera, and Bentley (1966) was prompted to write that in hot, dry habitats '. . . the most valuable evolutionary novelty which they could invent to assist their survival would be a more impermeable integument'.

This survey is confined to adult Anura which in seasonally arid regions such as southern Africa are seasonally active (during the rains) and frequently cryptic during the day or nocturnally active even during the rains. As Poynton (1964:212) has remarked, problems arise in the use of the terms 'aestivation' and 'hibernation'. So little is known in southern African frogs (and other animals) of the causes of dormant periods, that a more neutral terminology, not implying causal factors or metabolic consequences, is desirable. Such a word, 'retraherence', is available (Goin & Goin 1962; Porter 1972) and is defined by Porter (1972:288) as temporary retreat from adverse weather. Retraherence, as defined above, will be used in this paper.

Three main strategies of water conservation are evident in the Anura, these being correlated to a large extent with aquatic, fossorial and arboreal adaptations. As is frequently the case in most generalizations, many genera and even species of southern African frogs do not neatly fall into a single group. In particular, both aquatic and arboreal forms frequently undergo retraherence in some sort of fossorial habitat.

AQUATIC ANURANS

As might be expected in an area marked by the seasonal occurrence of its rains and the associated fluctuation in level of standing or running water, aquatic adaptations have evolved in rather few southern African frogs. The genera *Xenopus, Rana, Hylarana, Heleophryne, Phrynobatrachus* and *Ptychadena* have to a lesser or greater extent some dependence on year-round free water. The most aquatic genus in feeding and locomotion is *Xenopus* (Van Dijk 1971b), yet even these frogs are known to migrate overland in response to drying of the water (Hewitt & Power 1913; Loveridge 1953). This phenomenon has been observed in the case of *Xenopus laevis* in Rhodesia in recent years. On 10 April 1970 at Noro Dam, Chesa, at about 09h00 several *X. laevis* were seen migrating along a path towards the dam, the weather being overcast after light rain the previous night. At 06h30 on 13 April 1970, again overcast weather, a *Xenopus laevis* was seen hopping through short grass down a slope toward Nyadekese Dam, Chesa. At 08h00 on 25 April 1975 a *Xenopus* was seen on the University of Rhodesia campus, Salisbury, hopping across a road towards a roadside ditch. It is perhaps significant that all these instances occurred at the start of the dry season, when temporary pools or flooded areas would be drying, and that the *Xenopus* were migrating toward more permanent bodies of water.

Migration is not always the final strategy, as it has been noted that *Xenopus laevis* can burrow into the drying mud at the bottom of pools or pans (Alexander & Bellerby 1938; Tasman 1956; Balinsky *et al.* 1967). During the period of retraherence the normally ammonotelic frog stores large quantities of urea in the tissues (Balinsky *et al.* 1967), a common feature of the metabolism of some fossorial anurans (McClanahan 1967) as well as those adapted to living in saline water (Gordon *et al.* 1961). Very little is known of the water balance of the other southern African aquatic genera. *Heleophryne rosei* adults are difficult to find and may hide in crevices or in caves but close to water and in cool environments (Gow 1963). *Rana angolensis* in the Salisbury area are active the year round, always on the banks of permanent streams. This is true of *R. angolensis* in the Transvaal highveld (Balinsky 1969) and is probably true of the montane forms (*Rana fasciata, R. grayi, R. johnstoni inyangae* and *R. vertebralis*) and of *R. fuscigula*. Less is

known of *Hylarana*, but *H. darlingi* is found in vlei grassland during the rains and on the grassy margins of river pools at the end of the dry season in Rhodesia and *H. galamensis bravana* is found in swamps in Moçambique so presumably they are tied, too, to permanent water. *Ptychadena* spp. are found in drier areas than *Rana* spp., but remain active where permanent water persists (for example in October 1971 and 1975 *Ptychadena anchietae* was found on the shore at Sinamwenda, Lake Kariba). Dr D. G. Broadley (*in litt.*) found *Phrynobatrachus ukingensis mababiensis* and *P. acridoides* under piles of palm fronds at Fort Johnston, Malawi, on 16 December 1962, but before the rains had started. On Lake Kariba *Phrynobatrachus natalensis* is frequently found amongst the aquatic fern *Salvinia molesta*, and is active throughout the year in many of the warmer areas of Rhodesia on the margins of artificial water bodies. As a generalization it seems that the genera mentioned would remain close to water provided the water does not dry up. Retraherence would then take place by burrowing into semi-liquid mud (*Xenopus*) or hiding under leaves, logs or other debris that provides a moist microclimate (*Rana, Hylarana, Ptychadena, Phrynobatrachus*) or entering cool, moist crevices or caves (*Heleophryne*).

Little is known of the physiological adaptations of the aquatic group apart from *Xenopus laevis*, which has been well-studied (e.g. Balinsky 1970; Schlisio *et al.* 1975). Water-balance studies of north temperate *Rana* spp. (Thorson & Svilha 1943; Schmid 1965) indicate that they have a permeable skin and a low tolerance to water loss, the lethal weight-loss being 28–38 per cent of body weight. The absorption of liquid water in *Rana* after desiccation proceeds slowly, as it does in *Xenopus laevis* (Ewer 1952) and the bladder volume is small. Limited information on the weight losses of *Rana angolensis* (Loveridge 1970) shows basic agreement with studies on north temperate frogs, but this is a field wide open for detailed investigation.

FOSSORIAL ANURANS

This group contains the majority of genera and species of southern African Anura and is well represented elsewhere in the world. It can be subdivided into those frogs which dig their own burrows and those that utilize spaces under rocks, or holes made by other animals.

It is well known (Schmidt-Nielsen & Schmidt-Nielsen 1950) that retraherence below the ground, even in desert areas, assures a microclimate of cool temperatures (see also Figure 4) and high relative humidities, and it is not surprising that the majority of anurans in arid and semi-arid areas adopt the fossorial strategy. The physiology of some of the North American and Australian fossorial forms has been studied (McClanahan 1967; Seymour 1973a, b; Main & Bentley 1964), but the interesting African genera such as *Tomopterna* and *Pyxicephalus* have been neglected.

Kassina, Phrynomerus, Bufo, Cacosternum and *Arthroleptis* appear to be genera that make use of burrows formed by other animals or natural crevices (Tasman 1956). Eloff (1952) excavated *Kassina senegalensis* from the burrows of the mole-rat, *Cryptomys hottentotus*. Branch & Patterson (1975) found *Cacosternum boettgeri* and *Kassina wealii* in the burrows of the lizard *Cordylus giganteus* in the Orange Free State in the dry season. *Phrynomerus bifasciatus* is commonly found in termitaria (Mitchell 1946) or in holes at the base of rotting tree-stumps (Tasman

1956), and *Bufo regularis* uses termite holes in Salisbury as well as hiding under rocks (Branch & Patterson 1975) or logs. In the Namib *Phrynomerus annectens* and *Bufo vertebralis* shelter under rock exfoliations on granite inselbergs (Channing 1976). *Bufo carens* is commonly found in abandoned termitaria in the Salisbury area. *Kassina* (*Hylambates*) *maculata*, on the other hand, appears to use an arboreal retraherence site, favouring the axils of banana leaves (Mitchell 1950; Poynton 1964).

Among the genera that dig their own burrows are *Breviceps, Tomopterna, Pyxicephalus, Hildebrandtia, Hemisus* and *Anhydrophryne*. The burrows of *Breviceps verrucosus* and *B. adspersus* have been studied by Poynton & Pritchard (1976). The burrowing habits of *Pyxicephalus adspersus* are well known (Loveridge 1950; Poynton 1964) but it is surprising that this large frog (up to 1 kg weight) has not been studied in the laboratory. Preliminary experiments indicate that it is no more tolerant to desiccation in air than many species of north-temperate *Rana*. On 2 April 1968 a 961 g animal was allowed to burrow into wet clay soil, and the clay allowed to dry out slowly at room temperature. After 229 days the dry clay was broken open to reveal the frog in a cavity (Figure 1). It had lost 45 g (4,6 per cent of body weight) in 229 days. D. K. Blake did a similar experiment in a sandy substrate using a cabinet 895 × 595 × 153 mm with one side constructed of glass so that the bullfrog could be examined at intervals. The glass side was, at other times, covered with a wooden sliding door. Figure 3 presents the results of this work which shows that the animal moved around between 2 June 1969, when it was put into the container, and 5 December 1969, when it was removed, penetrating to a depth of some 300 mm.

Some Anura such as *Scaphiopus couchi* (Mayhew 1968), *Cyclorana* spp., *Limnodynastes spenceri* and *Neobatrachus pictus* (Lee & Mercer 1967) form cocoons of shed stratum corneum during retraherence underground. This adaptation has not, to my knowledge, been recorded for any southern African frog. Dr D. G. Broadley (*in litt.*) found a cocoon surrounding a *Pyxicephalus adspersus* which was 3–4 cm below the surface in sandy soil near Bulawayo in October 1959. R. Francis (personal communication) found a number of *Pyxicephalus adspersus* in cocoons in Mana Pools game reserve, Rhodesia, and cocoon formation in this species is confirmed by J. Visser (*in litt.*). Yet in neither of the experiments quoted above (see Figure 1) was cocoon formation seen. There is no doubt that a study of the physiology of retraherence in *Pyxicephalus adspersus* would be most rewarding. *Leptopelis viridis* in West Africa is known to form a cocoon (Dr A. Schiøtz, personal communication), so cocoon formation might be expected to occur in the southern African *Leptopelis bocagei*.

Tomopterna marmorata (and probably other *Tomopterna* species) forms burrows in sandy soil. This species has been excavated on several occasions on the Sengwa and Mwenda estuaries, Lake Kariba, when crocodile eggs were being dug up. *Hemisus marmoratus* has been found once in a crocodile nest, and on other occasions in rather shallow burrows under logs. Mitchell (1950) found them in termite mounds. *Tomopterna delalandei cryptotis* lives in burrows in the sandy Kuiseb River bed, Namib Desert (Channing 1976), and according to Balinsky (1969) spends its non-breeding life underground.

Most of the burrowing forms are hyperactive under desiccating conditions as exemplified by experiments on *Tomopterna natalensis* under different humidity conditions (Poynton 1964: 218). Their increased activity in dry air probably represents attempts to escape dry conditions. Cloudsley-Thomson (1967) has shown that *Bufo regularis* has an endogenous activity rhythm

FIGURE 1
Photograph of *Pyxicephalus adspersus* after retraherence for 229 days in drying clay.

FIGURE 2
Hyperolius nasutus roosting in a lily flower (*Hemerocallis*) in a garden in Salisbury, Rhodesia,
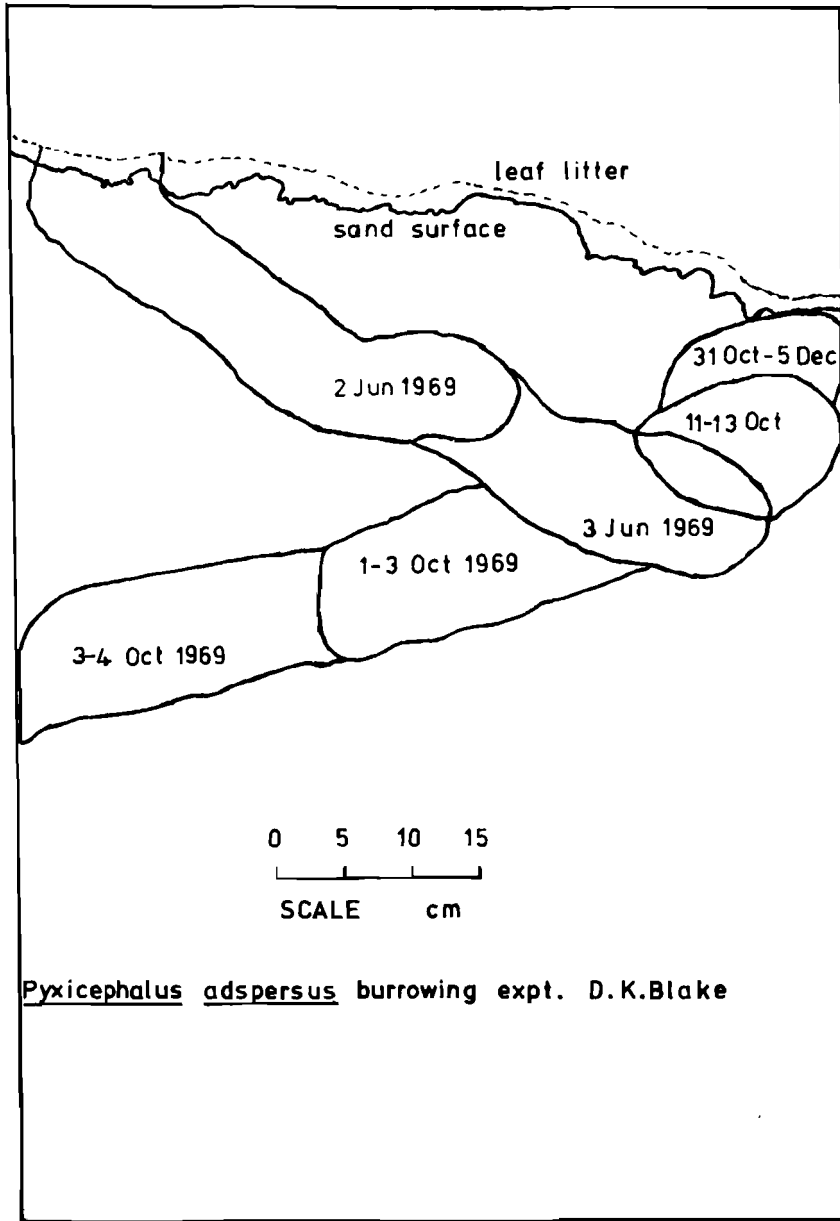8 November 1974.

FIGURE 3

Movement of *Pyxicephalus adspersus* between 2 June 1969 and 5 December 1969 while burrowing in sand (data of D. K. Blake).

which is strongly nocturnal. Experiments on American (Thorson & Svilha 1943) and Australian (Bentley *et al.* 1958) burrowing frogs have shown that they have a permeable skin and are very tolerant to desiccation (38–48 per cent body weight can be lost before death). The water absorption response is strong, increasing when the frogs are partially dehydrated or injected with vasotocin (Bentley 1966). These data have received confirmation for African frogs only in the case of *Bufo regularis*, *B. carens* and *B. mauritanicus* (Cloudsley-Thompson 1967, 1974; Ewer 1952). Most burrowing frogs have large bladders, which serve to store water during retraherence. No data are available for southern African forms, but *Bufo cognatus* can store up to 30 per cent of its body weight as bladder water (Ruibal 1962) and *Notaden nichollsi*, *Cyclorana platycephalus* and *Neobatrachus wilsmorei* can increase their body weight by as much as 50 per cent with water stored in the bladder (Main & Bentley 1964).

ARBOREAL ANURANS

At first sight the arboreal frogs show few morphological or behavioural adaptations which fit them to survive desiccation during dry weather, yet on several occasions it has been remarked that they remain exposed for long periods in direct sunlight and in dry air. Cott (1932) noted this behaviour in *Hyperolius argus* females and *H. marmoratus taeniatus* near the Zambezi delta. Similar behaviour is seen in some other *Hyperolius*, for example *H. horstocki* (Wager 1965). Loveridge (1953) remarked on the apparent avoidance of rain by *Chiromantis xerampelina* at the end of the dry season at Chitala, Malawi, and Mitchell (1946) noted how they live many miles from water, sitting on branches of trees exposed to the sun.

In an investigation into the water relations of *Chiromantis xerampelina* (Loveridge 1970) it has been shown that this tree frog has remarkable powers of resistance to desiccation, and is uricotelic. *Phyllomedusa sauvagei* of Argentina has been shown to be remarkably similar (Shoemaker *et al.* 1972). Investigations in Rhodesia have continued, centred mainly on *Chiromantis xerampelina* and *Hyperolius* spp. In this preliminary account some bioclimatic and weight-loss data are given for the small reed-frog *Hyperolius nasutus* which weighs only 0,3–0,6 g.

In Salisbury *H. nasutus* makes its appearance in gardens toward the end of the dry season (late October) before the rains have started. During the day it is commonly seen in lily (*Hemerocallis* or *Zantedeschia*) flowers often exposed to direct sunlight for at least part of the day (Figure 2). In order to ascertain the microclimatic conditions experienced by these frogs, recordings were made of temperature (Grant miniature multi-channel temperature recorder) and relative humidity (Hygrodynamics Inc. portable electric hygrosensor) in the flower next to the frog and at ground level, a black bulb temperature near the flower, and a temperature 28 cm down an old termite hole being used by a *Bufo regularis*. Windspeed at flower level was measured using a Casella air meter. The results are presented in Figures 4 and 5. On 11 November 1974 the *Hyperolius nasutus* appeared in the flower at 06h35 and left it at 18h20 descending down to the vegetation at ground level and disappearing from sight of the observer with binoculars sitting 5 m away. Between these times it sat motionless in the flower with air temperature in excess of 30°C for 6h (Figure 4) and relative humidity less than 50 per cent for 7h (Figure 5). In addition windspeeds in excess of 20 m min^{-1} from 07h00 to 13h00 (Figure 5) combined with the high tempera-
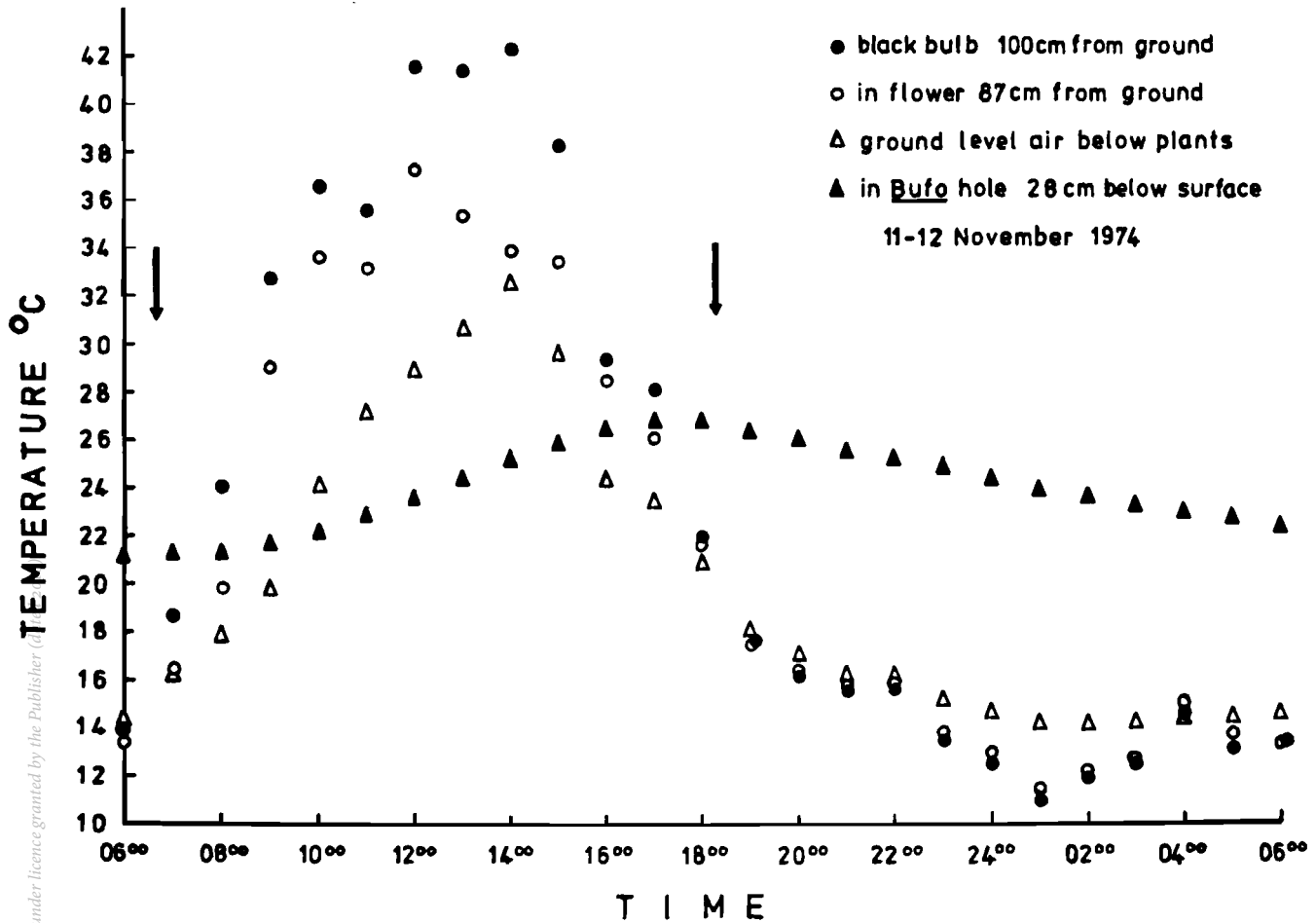
FIGURE 4

Fluctuations in temperature conditions in two frog microhabitats in a garden in Salisbury, Rhodesia, over 24 hours (11–12 November 1974). The arrows indicate time of appearance in the morning and disappearance in the evening of a *Hyperolius nasutus* individual.
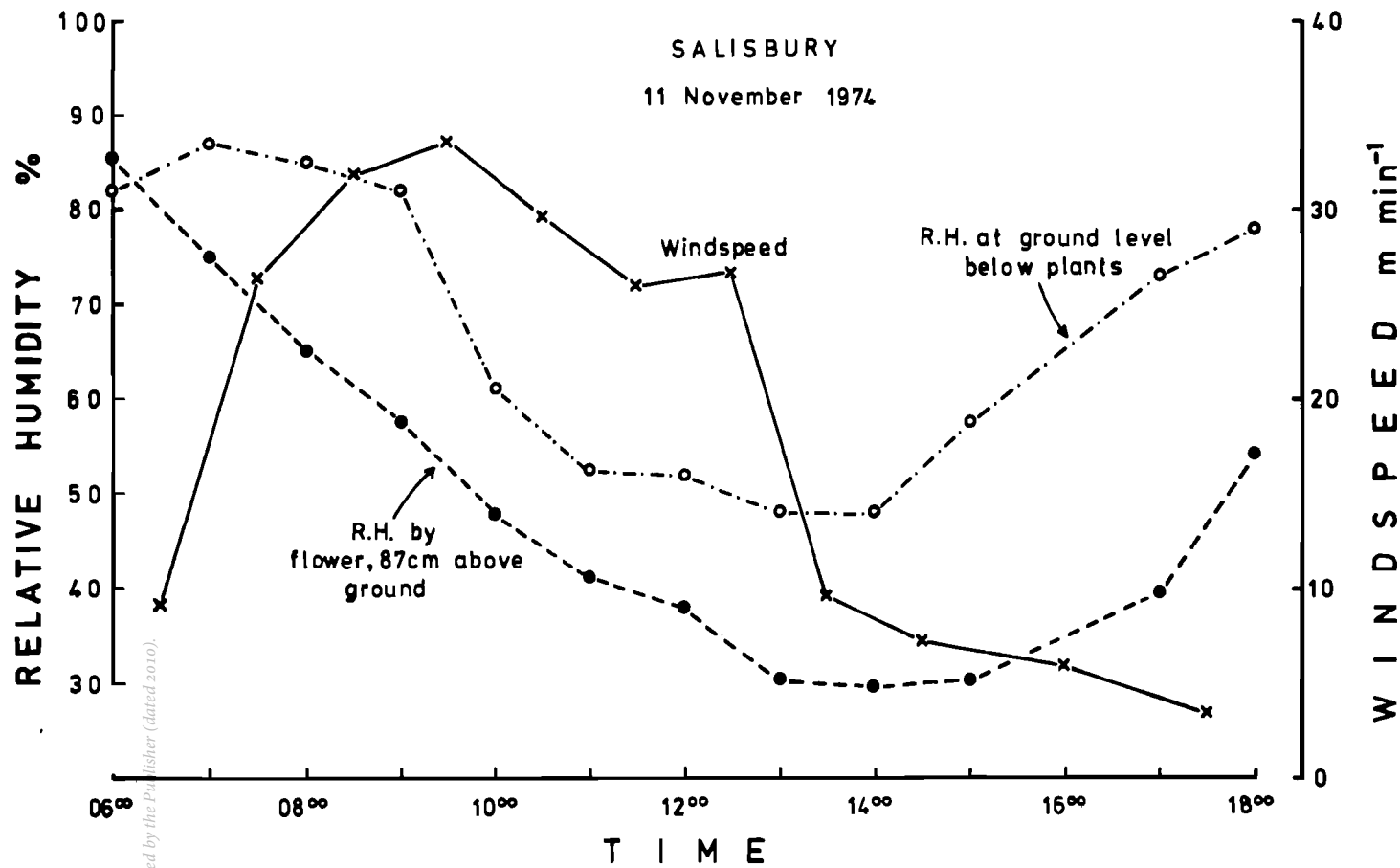
SALISBURY

11 November 1974

RELATIVE HUMIDITY %

WINDSPEED m min⁻¹

Windspeed

R.H. at ground level
below plants

R.H. by
flower, 87cm above
ground

TIME

FIGURE 5

Fluctuations in relative humidity and windspeed in a *Hyperolius nasutus* microhabitat in a garden in Salisbury, Rhodesia, 11 November 1974, over 12 hours.

ture and low relative humidity mean a very high potential evaporation. Yet the frog selected the exposed site in preference to the cooler, more humid one at ground level below plant leaves or the very much more thermally stable microclimate provided by a hole in the ground.

Two *Hyperolius nasutus* collected in November 1974 and exposed to 25°C, 48–56 per cent RH in pre-weighed gauze-covered 75 × 25 mm glass tubes were weighed twice daily in the tube over a period of 15 days. Initially both lost weight fairly rapidly (Figure 6) and this was associated with some nocturnal activity as assessed by movement from a mark made at each weighing on the tube at the tip of the snout. The average weight loss of the two frogs over the whole period was only 0,6 mg g body wt^{-1} h^{-1} and was evidently less than that toward the fifteenth day. Both frogs were in good health at the end of that time.

When the rains start, *Hyperolius nasutus* disappears from the gardens and aggregates for breeding in water-flooded grassland and vlei areas about 1 km or more away. The weight-loss experiment was repeated during January 1975 using 10 *H. nasutus* collected from a breeding site. This time the relative humidity was slightly lower (46–50 per cent) but the temperature and techniques were the same. The results are presented in Figure 7, which shows two representative weight-loss curves of 'wet season' frogs and the initial part of the curve for 'dry season' frogs (Figure 6) for comparison. The 'wet season' frogs were highly active and all had died from
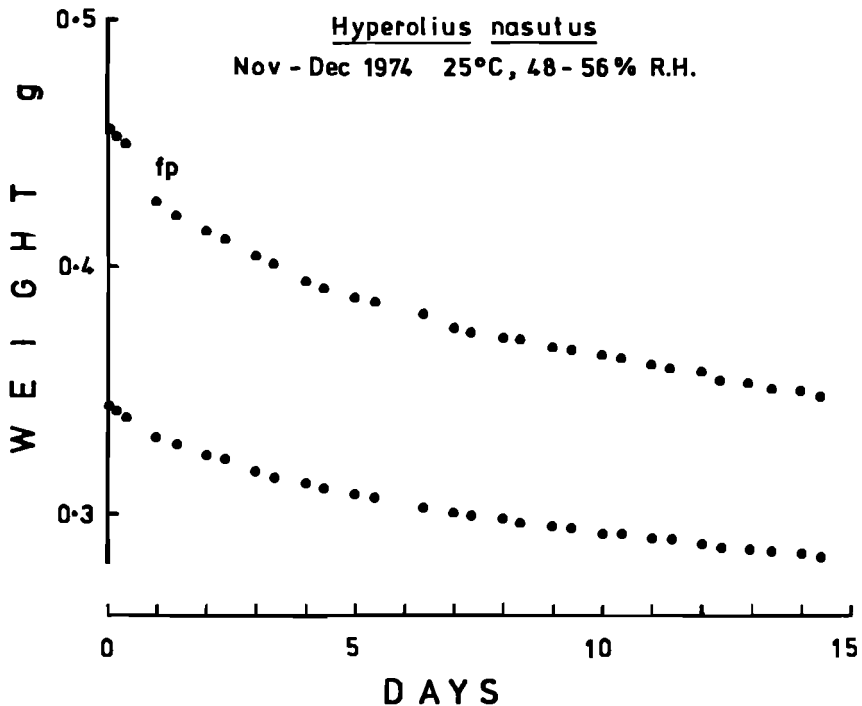

FIGURE 6
Weight changes of two "dry season" *Hyperolius nasutus* in open vials in the laboratory. Production of a faecal pellet by the larger frog indicated by "fp".

desiccation within 2,5 days. The average weight loss (10 animals) was 11,7 mg g body wt^{-1} h^{-1}, a figure about twenty times the 'dry season' frog weight loss. There is evidently a seasonal change in the permeability of the skin of *H. nasutus* increasing in the actively breeding individuals and decreasing to low levels in the animals living in flowers during the late dry season. The habits of this species during the cool dry season are unknown but it is likely that they are more cryptic, if observations on other *Hyperolius* species are any indication. *H. marmoratus broadleyi* was found
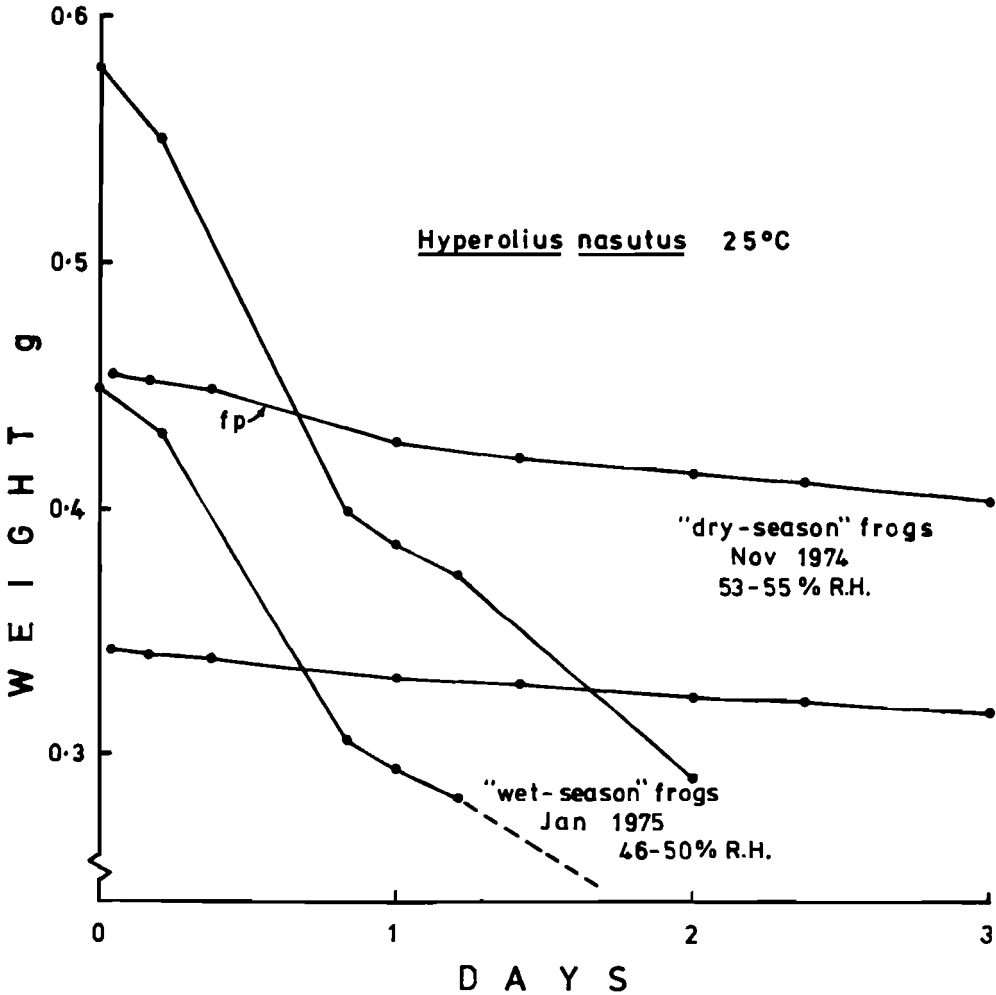

FIGURE 7

Weight changes of two "wet season" *Hyperolius nasutus* in open vials in the laboratory, with the initial parts of the curves for "dry season" frogs (Figure 6) for comparison.

by C. R. Parry (personal communication) on 15 July 1975 and again on 10 August 1975 at Inyanga, Rhodesia, under the bark of poles used for a car-port. Dr C. B. Cottrell (personal communication) found two *H. marmoratus marginatus* under bark of a dead *Monotes* tree on a wooded ridge above the upper Mazoe valley, Rhodesia, about 0,5 km from the nearest water on 21 November 1975. A juvenile *H. marmoratus marginatus* was collected in an ablution block at Mana Pools game reserve, Rhodesia, on 8 June 1972, together with several *Chiromantis xerampelina*. Dr D. G. Broadley (*in litt.*) found *Hyperolius tuberilinguis* under piles of palm fronds at Fort Johnston, Malawi, on 16 December 1962, before the rains had started. Available evidence seems to indicate that southern African *Hyperolius* and *Chiromantis xerampelina* are able to survive the dry season in arboreal situations, probably under loose bark, and are assisted in this by the habit of inactivity and low skin permeability.

Little appears to be known about the retraherence of *Leptopelis natalensis*, which is, in part of its range at least, a forest form. *Afrixalus fornasinii* and *A. brachycnemis brachycnemis* are known to favour the moist leaf-bases of banana plants (Cott 1932; Mitchell 1946), presumably the same microhabitat selected by *Kassina* (*Hylambates*) *maculata* (Mitchell 1950). *Afrixalus brachycnemis knysnae* is found in arum (*Zantedeschia*) inflorescences (Poynton 1964). Nothing is known of the water balance of these forms, but it should prove to be of interest.

It is evident that, from the physiologist's point of view, the southern African arboreal frogs present a diversity of adaptations. The genera *Hyperolius* and *Leptopelis* alone provide a wide diversity of forms inhabiting different climatic regions and with different morphological adaptations, and a study of their water and thermal relations should be rewarding. Some species of tree and reed frog – *Hyperolius nasutus, Chiromantis xerampelina* (Loveridge 1970) and *Phyllomedusa sauvagei* (Shoemaker *et al.* 1972) have relatively impermeable skin. The measurements reported in this paper for *Hyperolius nasutus* show the existence of seasonal differences which should be carefully investigated, particularly in those arboreal species which have been reported to have no desiccation resistance, observations perhaps based on material collected in the breeding season. Some species of *Hyla* have a high tolerance to desiccation (between 31 and 45 per cent of weight can be lost before death: Schmid 1965; Main & Bentley 1964) and *Chiromantis xerampelina* can tolerate the loss of more than 60 per cent of its body weight over several months and recover fully when rehydrated and fed (Loveridge 1970). Two uricotelic species – *Phyllomedusa sauvagei* (Shoemaker *et al.* 1972) and *Chiromantis xerampelina* (Loveridge 1970) are known. The water absorption response is strong in some Australian species of *Hyla* (Main & Bentley 1964) and in *Chiromantis xerampelina* (Loveridge 1970). The bladder volume in *Hyla moorei* and *H. latopalmata* allows storage of water amounting to 20–30 per cent body weight (Main & Bentley 1964). No data are available for the bladder volumes of southern African tree and reed frogs.

DISCUSSION

Physiological studies on the southern African Anura are hampered by the lack of published information on their biology, particularly their selection of sites for retraherence. In this paper whole genera (*Microbatrachella, Anhydrophryne, Natalobatrachus, Arthroleptella*) have not been

mentioned for lack of published information on their biology. Other genera (*Heleophryne*, *Arthroelptis*, *Cacosternum*, *Leptopelis*) are poorly known from a biological point of view, and even the conspicuous *Pyxicephalus adspersus*, *Hyperolius*, *Bufo* and *Rana* have not been thoroughly studied, information on their mode of retraherence being little more than anecdotal. The cocoon formation of *Pyxicephalus adspersus* should be investigated, as should the possibility of cocoon formation in fossorial *Leptopelis* such as *L. bocagei*. The genus *Leptopelis* as a whole, with some arboreal and some fossorial forms, presents a challenge to the physiologist interested in a comparative study of water relations. The physiology of retraherence in *Pyxicephalus adspersus* is surely worthy of intensive study, and species in the genus *Tomopterna* would probably also make rewarding subjects. The diverse species in the colourful and taxonomically confusing genus *Hyperolius* must have interesting thermal and water relations which have only been briefly touched upon in this paper.

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