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Adaptations of the reed frog *Hyperolius viridiflavus* (Amphibia, Anura, Hyperoliidae) to its arid environment

IV. Ecological significance of water economy with comments on thermoregulation and energy allocation

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Summary. After breeding African savanna dwelling reedfrogs of the "superspecies" *Hyperolius viridiflavus* face a severe dry season. The frogs withstand the adverse abiotic conditions in exposed positions, clinging to dry vegetation. Only juveniles (300–700 mg) are able to adjust water economy and metabolism to a prolonged dry season. Wet season frogs attain low levels of evaporative water loss (EWL) within 6–8 days after incipient water shortage. This time course is mainly determined by the animal's ability to lower metabolism and activity level to the minimum demands of a dry season. Barriers against diffusion of water which most probably are built up by the stratum corneum and/or the overlying film of dried mucus seem not to be essentially modified during adjustment to dry season conditions. Changeover to dry season physiology is greatly accelerated through preconditioning frogs to water shortage. Adult *Hyperolius* are unable to reduce activity and metabolism as fast and effectively as juveniles. Most probably these are the main reasons for their very restricted survival capability under dry season conditions; the generally poor energy reserves after the breeding period may further shorten their survival time. At the critical thermal maximum (CTM) *Hyperolius* uses skin gland secretions for evaporative cooling. Acclimation effects and regulation of evaporative cooling within some 1/10° C help to employ limited water reserves very economically. Dry adapted, dehydrated frogs take up water, whenever available, via specialized skin areas. Rate of uptake is high and is mainly determined by the actual stage of dehydration. The onset of the water-balance-response is also affected by preconditioning. Survival time of small (<500 mg) estivating *Hyperolius* is limited by their water reserves. Due to their unfavourable surface to volume ratio they lose relatively more water by evaporation than larger conspecifics. Therefore, smaller specimens should allocate energy preferably to growth, until reducing EWL so far to survive the average periods between the rare precipitations. In larger frogs (>500 mg) the amount of stored energy determines maximal survival time. When a critical size is reached in postmetamorphic growth, a change in energy allocation from body growth to energy storage would improve prospects of survival and should therefore be expected. Species specific differences in regard to EWL and CTM indicate a strong correlation between physiological properties and ecological demands.

Key words: Estivation – Water-balance – Thermoregulation – Hyperolius

With progressive adaptation to terrestrial life, the differentiation of the anuran skin into two functionally diverging types becomes ever more evident. Exposed ("dorsal") skin areas function as diffusion barrier against evaporative water loss (EWL; Warburg 1972; Withers et al. 1984; Wygoda 1984; Duellman and Trueb 1986). "Ventral" or pelvic skin areas, on the contrary, often are highly permeable ensuring fast absorption of water (Fair 1970; Baldwin 1974; Christensen 1974; Yorio and Bentley 1977; Berkum et al. 1982) and mediating regulation of ion exchange with the surroundings (Katz 1979). Generally, these highly permeable skin areas are behaviorally protected against EWL by tight contact with the substratum.

During dry seasons savanna inhabiting members of the African species-group *Hyperolius viridiflavus* do not avoid the hot and dry climate by burrowing into the ground, but estivate in exposed positions on dry plants (Withers et al. 1982b; Geise and Linsenmair 1986; Kobelt and Linsenmair 1986). *Chiromantis, Phyllomedusa* and *Hyperolius nasutus* evolved very similar estivation modes (Loveridge 1970; Shoemaker et al. 1972; Drewes et al. 1977; Withers et al. 1982a, b). To survive in exposed positions even under extremely dry conditions especially high demands are placed on water economy. In these species the functional dichotomy of the "dorsal" and "ventral" skin, respectively, is very pronounced (Drewes et al. 1977; Geise and Linsenmair 1986).

Besides energy reserves (Geise and Linsenmair, in preparation) successful estivation during prolonged periods without water supply depends upon the amount of stored water and its most economical use. Movements should be avoided otherwise high water losses via the exposed permeable "ventral" skin areas cannot be prevented (Withers et al. 1982a; Wygoda 1984; Geise and Linsenmair 1986). Transpiratory and respiratory water losses should be minimized. Furthermore, the water dependent excretion of nitrogenous wastes as well as defecation should be greatly diminished or totally cease under water deprivation. This problem,

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Abbreviations: EWL = evaporative water loss; CTM = critical thermal maximum; WSF = wet season frog; TSF = transitional season frog; DSF = dry season frog; SD = saturation deficit

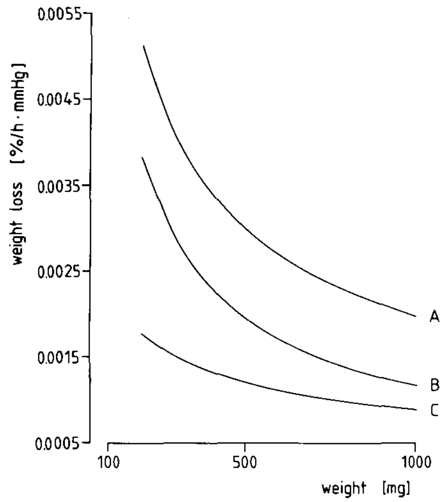

Fig. 11. Species specific differences of evaporative water loss in *H. v. taeniatus* (*A*), *H. v. ommatostictus* (*B*) and *H. v. nitidulus* (*C*). Taken from Fig. 5b and d, but converted to 1 mmHgSD

creased 2–5 fold (Fig. 9). What are the reasons for this unexpected result? Video observations revealed a rise in activity level of DSF under high humidity (Geise and Linsenmair, in preparation). Activity surely leads to higher losses of water. But since the frogs were video controlled, we could select EWL-values from those individuals which stayed inactive during the whole experiment. These values are considered solely in Fig. 9. The distinct increase in EWL in inactive DSF points to properties of the evaporation barrier being changed at high humidities ($SD < 10$ mmHg) toward lower resistance against EWL.

Comparison of species

Weight specific EWL, converted to losses in %/h/mmHgSD are summarized for *H. v. taeniatus*, *H.v.ommatostictus* and *H. v. nitidulus* in Fig. 11 (taken from Fig. 5b, d). Of these the West African *H. v. nitidulus* has developed the best protection against evaporation, followed by the East African *H. v. ommatostictus*. *H.v.taeniatus* from Mozambique has, under comparable conditions (size, humidity, temperature) the highest EWL. At 500 mg body weight, values are 2.5 times higher than in *H. v. nitidulus*.

Critial thermal maximum and evaporative cooling

H. viridiflavus spp. experience a sharp increase in water loss, after reaching a certain high temperature (Fig. 12). Increase factors of 3–10 were measured in *H. v. nitidulus* (Geise and Linsenmair 1986) and *H. v. taeniatus*. Water loss is no longer continuous, but rather becomes irregular. The skin loses its parchment-like appearance and becomes wet and shiny. During this phase, the animals stay motionless in their resting position. At a temperature increase of about 0.5° C above the CTM, the animals showed bursts of activity, suggesting an escape behavior.

The temperature to which the DSF were acclimated during the dry season affected the height of CTM. Species show definite differences in their thermal acclimation (Table 1).

During evaporative cooling, skin temperature at the head of two *H. v. taeniatus* was occasionally measured and was found to be 2–5° C below the surrounding temperature.

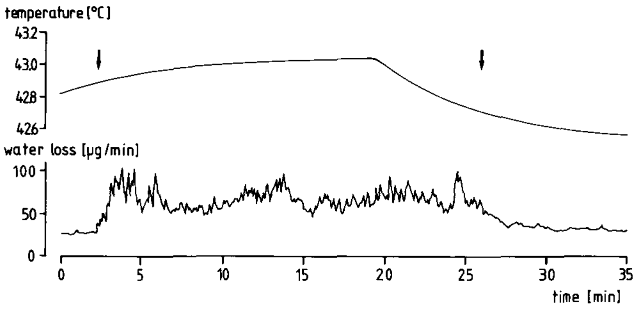

Fig. 12. Evaporative cooling in a *H. v. taeniatus* dry season frog. Arrows indicate onset and end of active mucus secretion. Measurement of air temperature is given by the upper curve; the critical thermal maximum lies at 42.9° C

Table 1. Critical thermal maximum (CTM) and its dependency on acclimation temperature

No.	Acclimation temperature (°C)	Critical thermal maximum			U-test	
		n	Mean	±	No. tested	$P<$
H. v. nitidulus						
1	27	9	42.3	0.46	1/2	0.005
2	35	7	43.9	0.65	3/4	0.01
					4/5	0.05
H. v. taeniatus					5/6	0.03
3	25	9	40.46	0.61	3/5	0.001
4	30	4	41.95	0.24	2/5	0.005
5	35	8	42.34	0.38	4/7	0.02
6	40	9	42.89	0.47		
H. tuberilinguis						
7	30	5	40.52	0.044		

Once evaporative cooling has begun, it will stop if the surrounding temperature is lowered to some 1/10° C below CTM (mean for *H. v. taeniatus*: 0.31 ± 0.22° C, $N=18$). These results show that *H. viridiflavus* is able to measure temperature very exactly and to accordingly adjust its water expenditure for evaporative cooling in such a way as to minimize water losses.

Water uptake

The distinct dependency of the rehydration rate on the actual stage of dehydration and on the time of exposure is demonstrated with high significance for *H. v. taeniatus* in Fig. 13a, b and for *H. tuberilinguis* in Fig. 14. Rehydration rates clearly increased with progressive stages of dehydration and are highest in the beginning of exposure to water.

In DSF of *H. v. taeniatus* at about the 35% stage of dehydration, after repeated (5 x) 15min-exposures to water within 4 hours, urine excretion could be observed for the first time after frogs had reached a maximum weight increase of 51.6 ± 7.3% ($N=9$) relative to the weight before the first rehydration.

Regardless of the time of exposure to water (5–30 min), urine excretion was frequently observed in WSF as well as in DSF when the stage of dehydration before water offering was less than 10%. All cases of a negative weight balance after exposure to water indicated urination and were

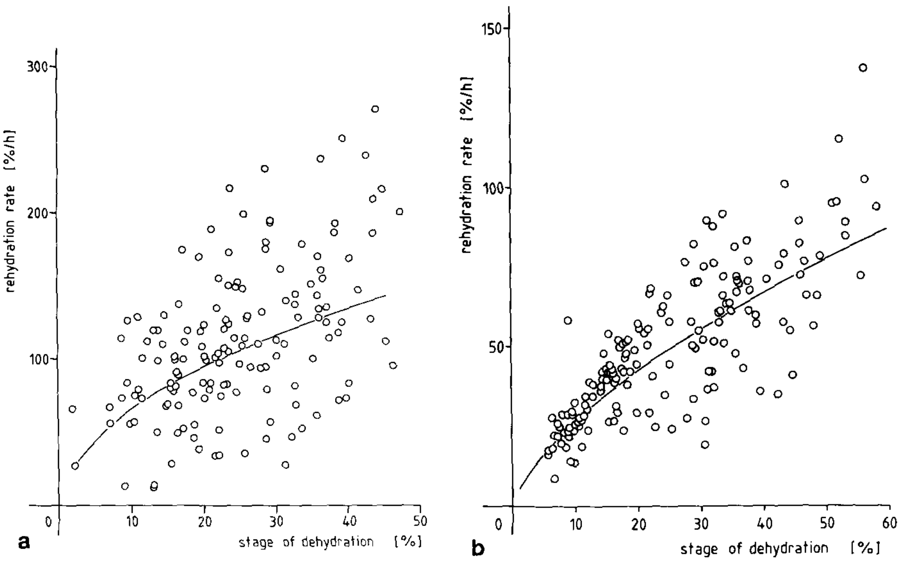

Fig. 13a, b. Dependency of rehydration rate on the stage of dehydration in dry season frogs of *H. v. taeniatus*.
a Administration of water for 5 min. Regression equation: rehydration $\text{rate}_{(\%/h)} = 20.77 \times \text{stage of dehydration}_{(\%)}^{0.508}$; $r = 0.48$; $N = 147$.
b Administration of water for 30 min. Regression equation: rehydration $\text{rate}_{(\%/h)} = 6.09 \times \text{stage of dehydration}_{(\%)}^{0.65}$; $r = 0.803$; $N = 169$

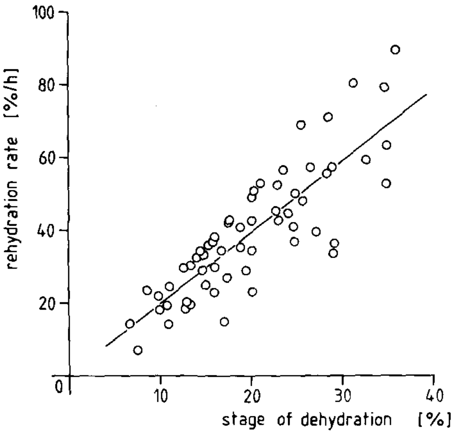

Fig. 14. Dependency of rehydration rate on the stage of dehydration in dry season frogs of *H. tuberilinguis*. Administration of water for 30 min. Regression equation: rehydration $\text{rate}_{(\%/h)} = 1.77 \times \text{stage of dehydration}_{(\%)}^{1.029}$; $r = 0.843$; $N = 64$

Table 2. Dependency of rehydration rates on stages of dehydration in Hyperolius viridiflavus taeniatus

No.	Stage of dehydration classes (%)	Stage of dehydration means of classes (%)			Rehydration rate (%/h)		U-test	
		N	Mean	±	Mean	±	No. tested	*P*<
Wet season frogs								
1	0 – 2.5	25	1.49	0.6	10.01	9.52	3/9	0.05
2	2.5– 5	26	3.64	0.8	12.01	10.99	4/10	n.s.
3	5 – 7.5	22	6.6	0.78	14.8	8.96	5/11	0.001
4	7.5–10	32	8.83	0.72	17.8	8.26	6/12	0.001
5	10 –12.5	47	11.33	0.82	20.2	7.51	7/13	0.001
6	12.5–15	25	13.62	0.6	24.64	7.01	8/14	n.s.
7	15 –17.5	25	16.13	0.82	26.4	11.2		
8	17.5–20	19	18.7	0.66	38.1	12.4		
Dry season frogs								
9	5 – 7.5	13	6.27	0.82	20.36	5.75		
10	7.5–10	17	8.85	0.75	22.94	12.05		
11	10 –12.5	14	11.07	0.83	28.5	4.97		
12	12.5–15	12	14.13	0.72	37.72	4.43		
13	15 –17.5	22	16.15	0.68	36.99	11.84		
14	17.5–20	14	18.44	0.72	37.69	15.3		

not taken into account when calculating the regression equations. Urination which did not conspicuously affect weight balance was disregarded here and may impose some, although insignificant, errors on regression equations.

Those animals, which had to be given water because of poor condition or which had to be taken out of the experiment had lost 45–50% of their initial (maximum) body weight.

Water balance response

As it was shown for the adjustment of low EWL, preconditioning to water shortage also affected the onset of physiological mechanisms known as the "water-balance-response" which enhances water uptake. Differences in the rehydration rates of equally dehydrated TSF and WSF of *H. v. taeniatus* which were directly put into dehydrating conditions could not be conclusively proved through regression analysis due to the extreme scattering of the single data. This was partially caused by the method (see above) and partially had its source in great variations in plasma concentrations at the same stage of dehydration (Schmuck and Linsenmair 1988). Therefore, frogs were separated according to their stage of dehydration and attributed to classes of 2.5%. The means for stages of dehydration and corresponding rehydration rates (water available for 30 min) for each single class were calculated (Table 2). The rehydration rates of TSF assumed significantly higher values, compared with WSF, mainly within the range of 10–17.5% stage of dehydration. Above 20%, WSF had completely turned to the dry season physiology and rates of rehydration did not differ between these two groups.

In order to more closely scrutinize the differing rehydration rates of WSF and DSF in the 10–17.5% stages of dehydration, the differences between means of rehydration

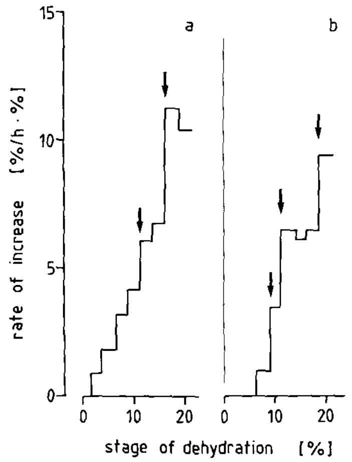

Fig. 15a, b. Rates of increase in rehydration rate in *H. v. taeniatus*, calculated from Table 2 (see text). **a** wet season frogs. **b** transitional season frogs. Arrows point to exceptionally high rates of increase, which occur at lower stages of dehydration in transitional season frogs

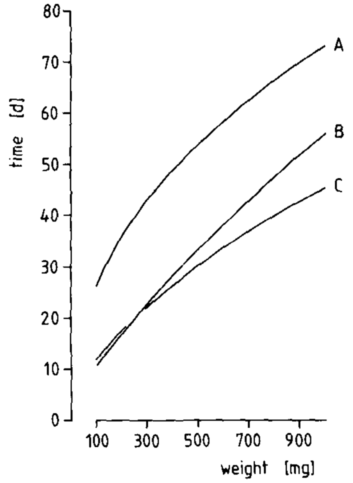

Fig. 16. Time span which *H. viridiflavus spp.* are able to survive until an overall weight loss of 40% is reached. A clear dependency on body weight as well as distinct species specific differences can be seen. *A* = *H. v. nitidulus*; *B* = *H. v. ommatostictus*; *C* = *H.v.taeniatus*

rates of neighbouring classes were divided by those of the corresponding stages of dehydration and thereby the factor of increase (%/h rehydration rate/% stage of dehydration) was obtained. These factors are cumulatively reported in Fig. 15 for each class of dehydrated frogs. Unusual high rates of increase which point to the onset of the water-balance-response are marked with arrows. High rates of increase appear earlier in TSF than in WSF. This leads to significantly higher rehydration rates.

Discussion

Adjustment of low EWL

In amphibians, the development of effective diffusion barriers in their skin is a main device to lower EWL (Seymour and Lee 1974; Blaylock et al. 1976; Yorio and Bentley 1977; Loveridge and Crayé 1979; Wygoda 1984). To reduce the evaporating surface arboreal anurans assume a typical squat resting position (Duellman and Trueb 1986). During movement activity, DSF inevitably expose their highly permeable skin areas at the ventral flanks and the inner sides of their legs. In addition their whole skin surface is wetted by skin gland secretions facilitating mobility and allowing cutaneous respiration. Accordingly, in *H. viridiflavus spp.* under water deprivation a fast decrease in movement activities and a cessation of skin gland secretion are the main devices to reach a low EWL. Delivery of mucus onto the skin surface only takes place when it is absolutely necessary – for thermoregulation at CTM (see below), during molting (Geise and Linsenmair, in preparation) or in escape behavior. The skin itself seems to be rather well protected against evaporation by physiological and morphological means independently of the physiological state (i.e. whether WSF or DSF; Geise and Linsenmair, in preparation). Mechanisms to cope with dry season conditions are well developed even in newly metamorphosed *H. viridiflavus*. Wygoda (1984) emphasized the generally well developed skin resistance against EWL in arboreal frogs.

Apart from the reduction of activity the achievement of low EWL seems to be coupled to lowering the resting rate of metabolism. Previous preconditioning to water shortage improves the ability for fast behavioral and physiological adjustment to dry season conditions.

Apparently, under dry season conditions, mature and reproducing *H. v. taeniatus* are not able to reduce activity such far to reach the low EWL of juvenile DSF. As our field data indicate adult *H. v. nitidulus* do obviously not survive dry seasons; according to our laboratory results the same most probably holds true for the other members of this superspecies living under comparable ecological conditions.

Size and survival time without water uptake

Besides the parameters and mechanisms which influence the gradient for and the resistance against water diffusion, EWL greatly depends on the size of the exposed skin surface in relation to the water storing body volume. Therefore, small DSF are distinctly handicapped concerning their EWL. This correlation should affect developmental patterns.

Based on regression equations for EWL at 35/25° C the graphs in Fig. 16 indicate after how many days DSF of *H. v. nitidulus*, *H.v.ommatostictus* and *H. v. taeniatus* reach a weight loss of 40%, which is assumed to be still well beneath the critical stage of dehydration. Nevertheless, at this stage the animals require water during the next few days otherwise they will reach their lethal dehydration limit. Taking *H. v. taeniatus* as an example, climatic data indicate that in its habitats precipitations occur on average one day out of every 4 weeks (Grünewald 1983; Müller 1983). Figure 16 shows that juvenile *H. v. taeniatus* cannot survive this time span of 4 weeks without replenishing lost water unless they have attained a weight of 400–500 mg (corresponding to a body length of 1.6–1.7 cm), which we therefore consider the minimum weight for a *H. v. taeniatus* to survive an average dry season. It follows, that after metamorphosis *H. v. taeniatus* should expend energy preferably on growth, in order to reach this size as fast as possible. Especially in small frogs (<400 mg), the ratio of exposed surface to body weight will be greatly diminished by further growth. Increase in body size, not the least, makes available larger prey which could improve energy intake, thus fastening growth and the building up of fat reserves.

With progressive growth, the investment of the same energy equivalent in growth yields less and less gain in regard to lowering EWL. At a size of about 500 mg, in *H. v. taeniatus* water reserves are more than sufficient for the average rainless time span of about 4 weeks. Then, the maximal time of survival is no longer determined by water, rather, the new limit is set by the energy supply. Therefore, time of survival at that stage is more effectively increased through augmenting energy reserves than by further growth. Under the conditions assumed here, changing the priority in energy allocation from growth to fat storage should take place in the 400–500 mg weight range. Corresponding data concerning the fat content at various body sizes corroborate our assumptions by pointing to this size-dependent type of energy allocation (Geise and Linsenmair, in preparation).

The actual size range where the shift in energy allocation from growth to fat storage is expected to occur should strongly depend on EWL and on average periods without any precipitations in the field. Under laboratory conditions, these EWL values are probably higher, possibly due to unnatural experimental conditions and frequent manipulations. Extremely low rates of water loss enable equally sized *H. v. nitidulus* to survive much longer than *H. v. taeniatus* without any water uptake (Fig. 16). Precipitations in the distribution area of *H. v. nitidulus* are far more restricted. So there is a very good correlation between ecological demands and physiological properties. Differences between species and populations in the "logistics" of energy allocation are certainly to be expected but have not been examined in any detail until now.

Nature of the diffusion barrier

Assumptions based on experimental evidence concerning the character of the diffusion barrier of anurans which estivate in exposed positions exist for *Phyllomedusa spp.* only. These species protect themselves against EWL by spreading a lipid film over their skin (Blaylock et al. 1976; McClanahan et al. 1978). The corresponding mechanisms in other species like *Chiromantis* or *Hyperolius* remained unexplained until now. Withers et al. (1984) assume an analogy to the findings in mammals and reptiles (Landmann et al. 1981; Roberts and Lillywhite 1983), and, therefore, postulate lipid filaments in the stratum corneum to function as the diffusion barrier for water in anurans, as well.

All data available indicate that EWL is greatly influenced by SD and that temperature effects are negligible. An unexpected increase in EWL (per mmHgSD) of dry adapted *H. v. taeniatus* occurred at very low SD. Very similar results were obtained by Machin (1969) in experiments on *Bufo marinus* and by Mautz (1982) in reptiles. Obviously, at low SD (=high humidity), the properties of the evaporation barrier gradually change. Besides determining the steepness of the diffusion gradient, SD acts on the outermost cell layer, e.g. on the keratin filaments of the stratum corneum. It is known that keratin has a high absorption capacity for H_2O (Mautz 1982), binding H_2O 5 times the dry weight of the stratum corneum. The resulting change in the keratin structure, for instance, could ease the diffusion of water through the keratin filaments. Lillywhite and Maderson (1982) pointed out that wetted reptilian epidermis is more permeable to water. In *Hyperolius* the overlying dried mucus could be hygroscopic as well and lose its waterproofing properties after being soaked with water.

Besides the well documented effects of water on keratin, it is conceivable that even in apparently inactive DSF the skin is slightly moistened by mucus secretion as a preparation for activity under increasing humidity, thus leading to higher EWL. Furthermore, changes in metabolic rate prior to the onset of movement activity may enhance water loss, e.g. by increased ventilation rate. Certainly this subject needs further investigation.

We did not find any hint to a temperature caused change in the structure of the diffusion barrier within the ecologically significant temperature range up to the lethal limit. Even at temperatures up to 44° C and high SD, the evaporation barrier remains intact in *H. viridiflavus spp.*

However, temperature does influence the diffusion barrier in phyllomedusans. McClanahan et al. (1978) found a rapid increase in EWL at temperatures $>35°$ C in *P. sauvagei*. The proposed change in the ordered structure of the lipid molecules (transition point) lies in the temperature range where the animals begin evaporative cooling, thus facilitating active mucus secretion and its spread over the skin surface (McClanahan et al. 1978; Shoemaker et al. 1987). Therefore, a temperature dependent disorder of the lipids' structure seems to be adaptive in this species.

The suggested deterioration of the diffusion barrier at SD <10 mmHg in *H. viridiflavus spp.* certainly is of little, if any, significance to the water economy of DSF. Under natural conditions very low SD usually indicate an imminent condensation of water. Therefore, it is not astonishing that high humidity proved to induce activity in DSF of *H. v. taeniatus*; then, however, the retention of low EWL becomes unimportant.

Evaporative cooling and critical thermal maximum

The use of water from the very limited reserves for evaporative cooling should be restricted to situations when lethal overheating can no longer be avoided by other, less costly means. In contrast to other anurans, *H. viridiflavus* shows an unusually high, long lasting(!) heat tolerance. DSF survive a temperature regime of 40°/30° C and about 30% RH (9:15 h) for many days and weeks until water and energy reserves are exhausted.

Lillywhite (1971, 1975) pointed out the importance of mucus gland secretions for thermoregulation in *Rana catesbeiana*. Evaporative cooling at 35–40° C was reported for *H. nasutus, Chiromantis petersi, Ch. xerampelina* and *Phyllomedusa sauvagei* (Withers et al. 1982a; McClanahan et al. 1978; Shoemaker et al. 1987). At high temperatures $>40°$ C, *H. viridiflavus* also utilizes its limited water reserves to prevent lethal body temperatures (Geise and Linsenmair 1986).

High acclimation temperatures increase the CTM. Especially in *H. v. nitidulus*, these CTM exceed (with up to 44° C) the highest known values of amphibians (Brattstrom 1968; Warburg 1972; Duellman and Trueb 1986) and probably are even still higher in the northern parts of its distribution area. They certainly lie not far from the lethal limit. But it should be stressed that previous investigators defined CTM as the temperature at which the animals showed locomotion disorder, while we defined it by the onset of evaporative cooling. Their examinations had the character of LD50 experiments (Duellman and Trueb 1986). It is certain that the CTMs they reported would have to be lowered when applying our methods. This further emphasizes the special accomplishments of *H. viridiflavus spp.*

WSF of *H. v. taeniatus* also show evaporative cooling, beginning at about 41° C. Climatic analysis reveals that *H. viridiflavus spp.* generally have to deal with temperatures above 40° C not only during the dry season, but also and even more pronounced in the rainy season (Geise 1987). Evaporative cooling, therefore, is not a specific adaptation to dry season conditions.

Nevertheless, under water deprivation *H. viridiflavus* is forced to sparingly use its limited water reserves. Delayed need for evaporative cooling by acclimation to high temperatures surely is of great survival value. In this respect *H. viridiflavus* faces a strong selection pressure and it is, not at all, surprising to find distinct species-specific and – most probably – also population specific differences.

Rehydration rates

The ventral skin of many terrestrial anurans is specialized for rapid water uptake (Fair 1970; Baldwin 1974; Drewes et al. 1977). It is highly sensitive to hormones, such as vasotocin, which affect the skin's permeability (Bentley 1971; Baldwin 1974; Yorio and Bentley 1977). Roth (1973) could show that water uptake is supported by the formation of a well developed capillary network just beneath the epidermis.

In *H. viridiflavus spp.* this highly permeable skin is restricted to the ventral flanks and inner sides of the legs (Geise and Linsenmair 1986). In contrast, in *H. tuberilinguis* and *H. nasutus* the whole ventral skin is highly permeable to water. Furthermore, with exposed ventral side they cannot protect limbs and feet against evaporation by hiding them in skin folds (Geise 1987). As most other anurans these two species are bound to habitat structures which provide impermeable or wet sitting surfaces. In the field, *H. nasutus* was found only on green leaves (personal observations). *H. tuberilinguis* retreats beneath stones at the soil or conceals itself under green leaves at the bottom near permanent water (lakes, streams: Loveridge 1976 and personal laboratory observations). As opposed to *H. viridiflavus spp.* these two species apparently have little chance for survival in areas with completely dried vegetation.

In spite of the comparatively small area of highly permeable skin, *H. v. nitidulus* (Geise and Linsenmair 1986), *H. v. ommatostictus* (R. Schmuck, personal communication) and *H. v. taeniatus* show very high rehydration rates which are not surpassed by any of the hitherto investigated amphibian species. The stage of dehydration greatly influences the steepness of the diffusion gradient and therewith the speed of water uptake. The stage of dehydration affects plasma concentration, i.e. osmotic pressure, which most probably is the most important driving force for water uptake (Schmuck and Linsenmair 1988). With increased water uptake, the plasma concentration decreases and the diffusion process slows down.

Regulation of water uptake

It remains unclear at the moment whether DSF control water uptake during prolonged exposure to water by physiological means, e.g. by changing circulation of capillaries or by changing permeability of the relevant ventral skin (Kobelt and Linsenmair 1986). In contrast to our observations in *H. v. nitidulus* (Geise and Linsenmair 1986), dehydrated *H. v. taeniatus* were never found to die from osmotic shock when supplied with water ad lib. This implies that DSF of *H. v. taeniatus* are able to a fast regulation of water uptake. Continued exposure to water caused multiple urination in *H. v. taeniatus* and *H. tuberilinguis*, as soon as they reached a maximum level of hydration. Schmuck and Linsenmair (1988) observed urination independent of the actual level of hydration at a certain high plasma urea concentration in *H. v. taeniatus* and in *H. v. ommatostictus*, when these were exposed to water for only a few minutes. Especially fast accumulation of urea results when DSF, because of exhausted fat reserves, are forced to gain energy from protein catabolism (Schmuck et al., submitted).

How *H. v. taeniatus* regulates its balance of electrolytes while repeatedly urinating is still an open question. Recovery of lost electrolytes appears difficult during the dry season. It remains to be elucidated, however, whether urination in DSF actually happens in the field. In the laboratory DSF are not allowed to leave the water during a rehydration experiment, so that superhydration may occur. In the field, DSF may actively terminate exposure to water by seeking a drier place.

Ecological significance of high water uptake

While many subterraneously estivating anurans exhibit a relatively good protection against EWL, they do not seem to have developed the ability to rehydrate quickly in comparison to aquatic anurans (McClanahan 1967). However, this is no disadvantage. These anurans do not become active unless extensive precipitations have occurred and puddles and pools built up, which offer good prospects for reproduction. Adaptations, which lead to a high rate of water uptake could, under these conditions, quickly cause a potentially lethal superhydration (Schmid and Barden 1965; Hillyard 1975; Canziani and Cannata 1980). Evolution of adaptations to terrestrialism in anurans must not necessarily lead to a coupled development of effective barriers against water loss and of mechanisms for high rates of water uptake. Both properties may be shaped by differing selection pressures. For example, *H. tuberilinguis* proved to be essentially less resistant to dryness compared to *H. v. taeniatus*, but showed a well developed capability of water uptake. Unlike burrowing species as e.g. *Scaphiopus*, *H. tuberilinguis* as well as *H. viridiflavus* do not retreat for longer periods, but rather utilize every favourable condition for acquiring nourishment. This kind of opportunistic behavior during a dry season is only to be maintained if mechanisms for rapid and effective use of all available sources of water have been developed.

Water balance response

Dehydration in anurans leads to the so called "water-balance-response" (Shoemaker 1965; Baldwin 1974). Changes in hormone action (Bentley 1971), glomerular filtration rate (Shoemaker and Bickler 1979; Cirne et al. 1981), changes in the permeability of skin areas differentiated for water uptake (Bentley and Main 1972; Baldwin 1974; Katz and Graham 1980; Cirne et al. 1981) and an increase in plasma concentration to enhance water uptake are involved (Balinsky et al. 1967; Jungreis 1974). Already at the onset of the water-balance-response elevated plasma concentrations are observed: at first mediated by aminoacids, then by increased urea concentrations accrueing from protein metabolism (Balinsky et al. 1967; Carlisky and Barrio 1972; Jungreis 1974; Katz and Gabbay 1986; Schmuck and Linsenmair 1988).

In TSF of *H. v. taeniatus*, high rates of increase in rehydration rate appeared within a range of 9–14% stage of dehydration . In WSF, the highest rates of increase were measured at the 16–19% stage of dehydration . It has to be concluded that in TSF which were actually hydrated to their maximum weight as well as the WSF, the water-balance-response is switched on earlier. We suppose the delayed response in WSF as resulting from a lack of preconditioning to dryness. The earlier *Hyperolius* adapts itself to water deprivation, the better it is able to use sporadic and slight precipitations to replenish water reserves. Unpredictable and abruptly changing climatic conditions should select for the ability to react very sensible and fast to these changes of environmental parameters which indicate the onset of a dry season.

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