

THERMAL DEPENDENCE OF WATER AND ELECTROLYTE EXCRETION IN TWO SPECIES OF LIZARDS*

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Abstract—1. Lizards with different preferred temperatures were water-loaded, and their ability to excrete excess water and conserve electrolytes was tested at several temperatures.

2. Rates of water excretion were much less temperature dependent in lizards having a low preferred temperature, but were maximal at about 30–35°C in both species.

3. Urinary sodium levels were minimal at temperatures near the respective preferred temperature of each species.

4. Urinary potassium levels were low and apparently not temperature dependent over most of the range studied, but increased as lethal temperatures were approached.

INTRODUCTION

LIZARDS differ conspicuously in their thermal preferences, and it has been assumed that the differences reflect diversity in the physiological adjustments of these animals to temperature (Dawson & Bartholomew, 1958). Over the past decade, numerous studies have been devoted to evaluation of this assumption (see Dawson, 1967). It is now possible to correlate the thermal dependence of several physiological processes with the preferred level of body temperature. Despite the interest in this topic and in the water economy and electrolyte excretion of terrestrial vertebrates, effects of temperature on renal function of lizards have not been investigated until very recently. We demonstrated that several aspects of such function are strongly temperature dependent in the skink *Tiliqua rugosa* (Shoemaker *et al.*, 1966). Information on intraspecific variation in the effects of temperature is obviously needed if meaningful comparisons of renal function are to be made;

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this is particularly important in view of the fact that other studies of urinary excretion in reptiles have been carried out only at single temperatures on species with imprecisely defined thermal preferences. We have therefore extended the studies of water and electrolyte excretion initiated on *T. rugosa* to two other species treated in our analyses of the thermal preferences and heat tolerances of Western Australian lizards (Licht *et al.*, 1966a, b). One of these, a gecko, has a significantly lower preferred temperature and more restricted tolerance to heat than *T. rugosa*. The other, an agamid, is more thermophilic than this skink.

MATERIALS AND METHODS

Lizards used in this study, *Phyllurus milii* (Gekkonidae) and *Amphibolurus barbatus minimus* (Agamidae), were captured on Houtman's Abrolhos Islands off the coast of Western Australia. Adult animals of both sexes were used; the twenty representatives of *P. milii* averaging 10.6 g in weight (range, 6.5–13 g) and the seventeen *A. barbatus* 22.2 g (range, 11–36 g). All animals were studied within 3 weeks after capture. They were kept at 25°C and provided with water while in captivity, but were not fed, since the presence of feces would have interfered with urine collection.

The ability of lizards to excrete a water load was tested at several temperatures ranging from 14° to 36°C for *P. milii* and from 14° to 42.5°C for *A. barbatus*. The upper temperature used for each species approaches its lethal limit (see Licht *et al.*, 1966b). Most individuals were tested at two temperatures, with at least a week between experiments. Water loads were imposed via a single intraperitoneal injection of 0.1 ml of distilled water per g of body weight. The animals were held at 20°C for 1 hr following the injection of water to ensure osmotic equilibration before the tests were begun. One hour had previously been found sufficient for equilibration in a large skink, as indicated by stabilization of the concentration of sodium in the plasma (Shoemaker *et al.*, 1966). At the end of the equilibration period, any accumulated urine was expressed from the cloaca and each animal was weighed to the nearest 0.01 g on a Mettler balance of appropriate sensitivity. (Urine produced during the equilibration period was less than 5 per cent of the injected volume.) In tests involving *A. barbatus*, the cloaca was then sealed by wrapping a strip of masking tape around the base of the tail and the animal was weighed again. Each of these agamids was then placed in a separate container within a thermostatically controlled chamber. After 3 hr, it was weighed with the tape in place. Then the tape was removed and a sample of the accumulated urine was collected by inserting a fire-polished glass capillary into the cloaca. Any remaining urine was expressed and blotted, and the animal was weighed again. Urine production over the 3-hr period was determined from the loss of weight associated with the removal of the urine. The weighing and sampling procedure was repeated in the subsequent 3-hr period so that rates of urine production and urinary Na⁺ and K⁺ concentrations were obtained for a total of 6 hr following equilibration of the water load.

A slightly different procedure was used for *P. milii*, because repeated taping of the cloaca caused these animals to cast their tails. We therefore omitted the taping

procedure in water-loaded geckos, but included several taped controls in each run. The weight losses of these controls over the 6-hr period agreed with the weight losses of the experimental animals during the two 3-hr intervals between weighings. This demonstrated that the water-loaded lizards did not void urine during these periods, even though their cloacas were not sealed.

High humidities were maintained in the constant-temperature chambers to minimize pulmocutaneous water losses. Total non-urinary weight loss over the 6-hr period never exceeded 5 per cent of the water load. Urine samples were sealed in Pyrex capillaries and analyzed within a few days for sodium and potassium using a Coleman flame photometer (model 21).

RESULTS

The gecko and the agamid differed markedly in the rate at which they excreted excess water (see Table 1). At each temperature where data were obtained for both species (14°, 21°, 31°, 36–37°C), *P. milii* produced urine at a significantly higher

TABLE 1—URINE PRODUCTION IN WATER-LOADED LIZARDS AT VARIOUS TEMPERATURES

Temperature (°C)	N	Urine production ml/100 g*		% of load excreted in 6 hr
		0–3 hr	3–6 hr	
<i>Phyllurus milii</i>				
14	5	1.28† (0.6–1.7)‡	1.59 (1.0–2.3)	28.7
21	7	2.28 (1.3–3.2)	1.92 (1.1–2.8)	42.0
26	9	2.88 (1.7–4.9)	2.10 (1.4–4.3)	49.8
31	5	4.26 (2.4–6.8)	2.52 (1.1–3.4)	67.8
36	7	3.86 (2.7–6.6)	2.52 (1.6–5.2)	62.7
<i>Amphibolurus barbatus</i>				
14	4	0.31 (0.17–0.40)	0.36(0.17–0.69)	6.7
21	4	0.82 (0.40–1.0)	0.83 (0.33–1.4)	16.5
31	9	1.78 (0.54–3.7)	1.74 (0.71–2.8)	35.2
37	7	1.76 (0.66–3.7)	1.51 (0.73–2.2)	32.7
42.5	5	0.97 (0.69–1.4)	0.81 (0.42–1.3)	17.8

* Total urine produced in each of the two 3-hr collecting periods.

† Mean. ‡ Range.

rate on a weight-specific basis ($P < 0.05$) than did *A. barbatus*. In fact, the lowest rates observed for the gecko, those at 14°C, were comparable to the highest rates for the agamid which occurred between 31° and 40°C. *A. barbatus* excreted no more than a third of the water load in 6 hr in this thermal range, and rates of urine production were fairly uniform over this period. The gecko excreted a greater fraction of the load, about two-thirds at 31° and 36°C, and in this species rates of urine production tended to decline in the second 3-hr period. Interspecific differences in the thermal dependence of urine production are evident when rates

of production are plotted semi-logarithmically as a function of temperature (Fig. 1). Urine production doubled between 15° and 30°C in *P. milii* and increased fivefold over the same range of temperatures in *A. barbatus*. Between 30° and 35°C rates

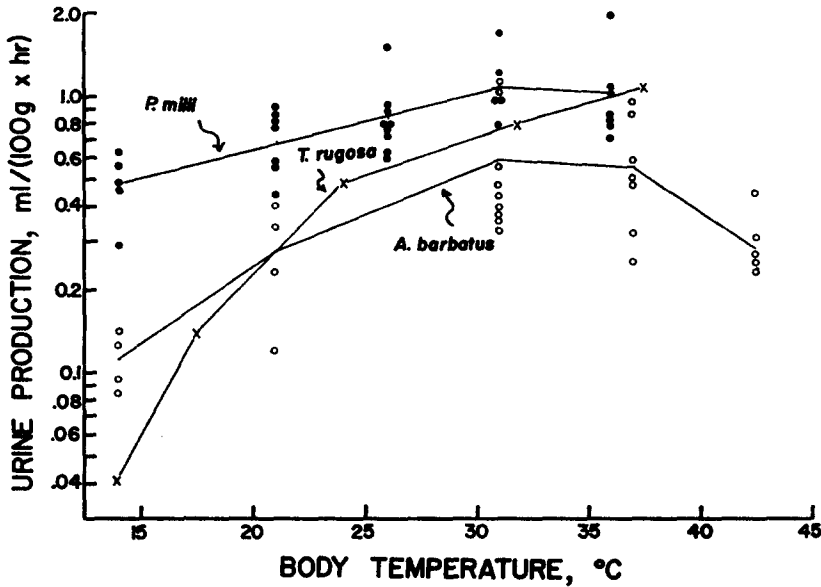


FIG. 1. Effect of temperature on rate of urine production in water-loaded lizards; *Phyllurus milii* (●), *Amphibolurus barbatus* (○), and *Tiliqua rugosa* (×). All rates are based on 6 hr of urine collection. Individual values are shown for *P. milii* and *A. barbatus*. Average values for *T. rugosa* from Shoemaker *et al.* (1966) are included for comparison (semi-logarithmic plot).

of urine production leveled off in both species and, in *A. barbatus*, declined slightly at 42.5°C. These trends may also be seen by examining the temperature coefficients (Q_{10} 's) shown in Table 2. These coefficients were determined graphically from Fig. 1 and are thus based on rates for the entire 6-hr period. Nearly identical values are obtained if only the first 3-hr period is considered.

TABLE 2—TEMPERATURE COEFFICIENTS (Q_{10} 's) FOR RATE OF URINE PRODUCTION IN WATER-LOADED LIZARDS*

Species	Temperature range (°C)			
	15–20	20–25	25–30	30–35
<i>Phyllurus milii</i>	1.6	1.6	1.6	0.9
<i>Amphibolurus barbatus</i>	3.6	2.5	2.3	1.0
<i>Tiliqua rugosa</i> †	14.5	5.1	1.9	1.8

* Based on semi-logarithmic plot of average rates over 6 hr.

† From data of Shoemaker *et al.* (1966).

Temperature also had a marked influence on the ability of water-loaded lizards of both species to conserve sodium while excreting excess water. Urinary sodium levels were highest at 14°C, declining as temperature increased to some intermediate value characteristic of the species, and finally increasing somewhat at the highest temperatures investigated (Fig. 2). Urine of *P. milii* was considerably more

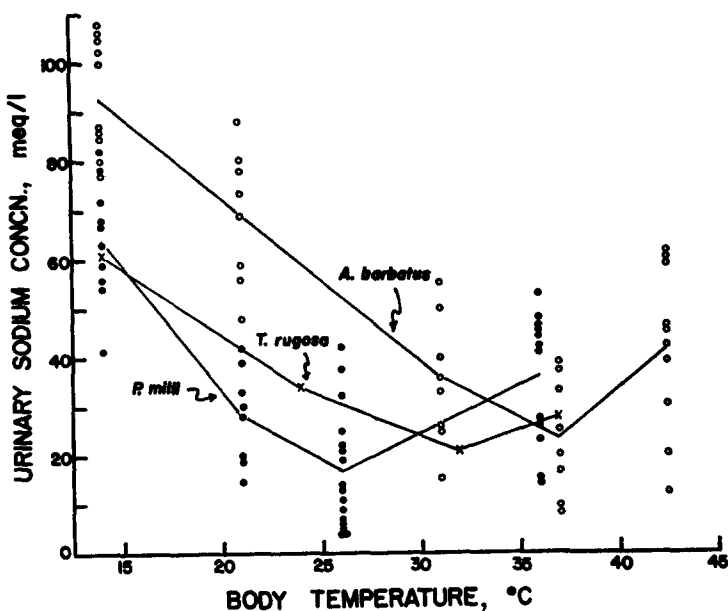


FIG. 2. Effect of temperature on urinary sodium concentration in water-loaded lizards; *P. milii* (●), *A. barbatus* (○), and *T. rugosa* (×). Concentrations of both samples collected from each lizard during the 6-hr period are shown for *P. milii* and *A. barbatus*. Values for *T. rugosa* (Shoemaker *et al.*, 1966) are comparable averages.

dilute than that of *A. barbatus* below 25°C. The lowest mean urinary sodium level observed for *P. milii* (17 mequiv./l) was that at 26°C, whereas the corresponding minimum for *A. barbatus* (23 mequiv./l) was seen at 37°C.

Concentrations of potassium in the urine of water-loaded lizards varied little with body temperature over most of the range studied, but some elevation of urinary potassium levels was apparent at the highest temperature tested for each species. Between 14° and 26°C, urine of *P. milii* averaged 11 mequiv. K⁺/l (range, 6–26 mequiv./l), whereas urine produced by these lizards at 36°C averaged 30 mequiv. K⁺/l (range, 7–58 mequiv./l). At temperatures between 14° and 37°C urinary potassium concentrations for *A. barbatus* averaged 22 mequiv./l (range, 10–44 mequiv./l); at 42.5°C they averaged 46 mequiv./l (range, 26–73 mequiv./l).

At the end of the study, six *P. milii* and eleven *A. barbatus* were sacrificed.

Both kidneys were removed from each lizard and weighed together to the nearest mg. In the gecko the mean fresh weight of the paired kidneys was 6.4 mg/g body wt. (S.E. = 0.038) compared to 3.2 mg/g body wt. (S.E. = 0.025) in the agamid.

DISCUSSION

The mean preferred temperature (i.e. mean body temperature maintained in a thermal gradient) of *P. milii* is quite low compared to that of *A. barbatus* (see Licht *et al.*, 1966a). The former remained at the cool end of a gradient in which 25°C was the lowest temperature available, and their body temperature averaged 21.6°C in a gradient with a range of 15°–35°C. *A. barbatus*, on the other hand, maintained body temperatures between 33° and 39°C with a mean preferred temperature of 36.3°C. Representatives of the two species also differ in heat resistance. *P. milii* survived less than 1 hr at 40.5°C and suffered high mortality following a 3-hr exposure to 37.5°C, whereas *A. barbatus* readily survived 3 hr at 43.5°C (Licht *et al.*, 1966b). Field observations reflect even greater differences in the thermal relations of these species. The gecko is nocturnal and may be found foraging at temperatures below 20°C, whereas the agamid is diurnal and, when active in the field, maintains temperatures near those observed in the laboratory thermal gradient.

Although there was no obvious difference in the body temperature at which maximal rates of water excretion were achieved by the two species, the gecko is less temperature sensitive and has a far greater capacity for water excretion at low temperatures. This difference in renal function is consistent with the tendency of the gecko to be active over a lower and wider range of body temperatures. Temperature dependence of water excretion in the skink *T. rugosa* is even greater than that of the agamid (Fig. 1, Table 2). The skink resembles the agamid in that it maintains a relatively constant body temperature in the field and in laboratory thermal gradients. The mean preferred temperature of the skink (33.8°C) greatly exceeds that of the gecko and is slightly lower than that of *A. barbatus* (Licht *et al.*, 1966a).

We have examined the effect of temperature on renal function in *T. rugosa* in somewhat greater detail (Shoemaker *et al.*, 1966). Water-loaded lizards of this species at 37°C excreted twenty-five times more water during the first 6 hr than they did at 14°C, and there was a corresponding twenty-fivefold increase in glomerular filtration rate. This suggests that interspecific differences in the thermal dependence of water excretion reflect differences in the thermal dependence of factors (e.g. arterial pressure) that influence rates of glomerular filtration. For example, in the iguanid lizard *Sauromalus obesus*, arterial pressure increases between 5° and 25°C with a Q_{10} of 2.4 and is essentially independent of temperature between 25° and 45°C (Templeton, 1964).

The highest rates of urine production attained by *P. milii* were considerably greater than those of *A. barbatus*, and this may be a reflection of the larger weight-relative size of the kidneys in the gecko. Roberts & Schmidt-Nielsen (1966)

compared renal responses of another gecko (*Hemidactylus*) and two iguanids (*Phrynosoma* and *Tropidurus*) to water loading, salt loading and dehydration at about 25°C. The gecko excreted excess water at a rate similar to that observed for *P. milii* at a comparable temperature, and, like the agamid studied here, the iguanids produced urine at a much lower rate. More detailed comparison would be of little value because of differences in the methods of water-loading and urine collection in the two studies. Also, interspecific differences in renal function found by Roberts and Schmidt-Nielsen are probably influenced to some extent by the fact that the temperature employed does not bear the same relation to the preferred level in all three species.

Analysis of the effects of temperature on the ability of lizards to produce urine dilute in sodium is complicated by concomitant changes in the rate of urine flow. However, diuretic water-loaded reptiles appear to resorb a fairly uniform fraction of the filtered water (40–60 per cent) as indicated by studies on water snakes (LeBrie & Sutherland, 1962) and several species of lizards (Roberts & Schmidt-Nielsen, 1966; Shoemaker *et al.*, 1966). Moreover, this fraction is independent of temperature in *T. rugosa* (Shoemaker *et al.*, 1966). It therefore seems reasonable to assume that the temperature at which urinary sodium levels are minimal are those at which the greatest fraction of this solute is resorbed. Although the temperatures employed in this study were too widely spaced to permit precise determination of this temperature, it is clear from Fig. 2 that it is considerably lower in *P. milii* than in *A. barbatus*. In general, lizards appear best able to conserve sodium while excreting excess water when kept at temperatures near their preferred levels, and the gecko was particularly effective in that it excreted the greatest amount of urine at the lowest sodium concentration. In *T. rugosa*, minimal urinary sodium levels were observed at an intermediate temperature (see Fig. 2) corresponding to the intermediate position of its thermal preferendum. The elevation of urinary sodium and potassium levels noted at the highest temperatures examined may reflect impairment of ion transport mechanisms, since these temperatures approach lethal levels.

It is not known whether dilution of the urine with respect to sodium is accomplished by the distal tubules, the cloaca, or both. Data of Roberts & Schmidt-Nielsen (1966) are of interest in this connexion. They collected urine directly from the ureters of water-loaded lizards and observed urinary sodium levels near that of the plasma in contrast to the much lower values reported here. They found urine of the gecko *Hemidactylus* to be somewhat more dilute with respect to sodium (98 mequiv./l) than that of the iguanids *Phrynosoma* (119 mequiv./l) and *Tropidurus* (124 mequiv./l) at about 25°C. Ureteral urine of water-loaded snakes (*Natrix*) at 26°C contains about 40 mequiv. Na⁺ and 10 mequiv. K⁺/l (LeBrie & Sutherland, 1962), and these values approximate concentrations of cloacal urine of the lizards used in this study. The extent to which cloacal resorption accounts for the differences in urine composition of the lizards compared here awaits further investigation. Junqueira *et al.*'s (1966) analysis of the resorptive function of the cloaca in snakes of several genera should give additional impetus for similar studies in lacertelians.

Whatever the role of the cloaca in the total response may be, it is evident that capacities of lizards for excretion of water and resorption of sodium show interspecific differences in thermal dependence that can be correlated with their characteristic body temperatures during activity.

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