Water and Energy Use in a Free-Living Tropical, Carnivorous Lizard, *Tupinambis teguixin*

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There is a reasonable amount of published information on the water and energy requirements of reptiles from arid/semiarid and temperate environments (see reviews by Nagy, 1982a, 1982b; Nagy and Peterson, 1988); however there is a dearth of such information from tropical/equatorial habitats. Much of the tropics is characterized by comparatively uniform daily ambient temperatures, whereas the pattern of rainfall is quite seasonal being confined predominantly to a "wet" season of some five months or so. Outside of the "wet" season, conditions become progressively drier and can become extremely arid toward the end of this period.

It could be expected that the energy expenditures of tropical lizards might be uniform throughout the year, reflecting the comparatively uniform thermal environment, whereas water fluxes might reflect more closely the major seasonal variation in the availability of water in the environment. The present study was undertaken to investigate the extent of the seasonal variations in the rates of water and energy use of free-living tegu lizards *Tupinambis teguixin*, a tropical carnivorous species which is the largest member of the Teiidae.

Subsequent to the commencement of this study, comparative data on the field metabolic rates (FMRs) and water fluxes of some other tropical carnivorous lizards have become available: three species of tropical varanids (*Varanus salvator*, *V. bengalensis*, and *V. scalaris*) and an agamid (*Chlamydosaurus kingii*). The results obtained for *T. teguixin* are compared to these and other tropical and xeric species of carnivorous lizard.

Materials and methods.—The study was conducted at Hato El Frio, Estado Apure (7°46'N, 68°57'W), in the low llanos of Venezuela. This region is tropical floodplain savannah (Herrera and MacDonald, 1989), which undergoes extensive flooding during the wet season that extends from May to late October. With the conclusion of the rainy season, the environment progressively dries out so that, by the end of the dry season in late April, the flood plains are completely dried out with restricted numbers of small waterholes aside from the permanent rivers and creeks.

The animals were captured in wire-mesh cage traps (45 × 15 × 15 cm) that were located on bancos (elevated, rarely flooded areas with a vegetation cover of bushes) or bajios (grass-covered areas that are flooded during the wet season). The traps were baited with a mixture of tinned fish and bananas. On capture, the animals were transferred to cotton bags, weighed with a spring balance, and bled (1 ml) from the ventral tail vein via syringe. The animals were then injected intraperitoneally with 0.5 ml of tritiated water alone (containing 90 MBq activity) or in conjunction with 0.25 ml of 95% atoms excess $H_2^{18}O$. About 5 h was allowed for equilibration of the isotopes (Nagy, 1983) after which the animals were again bled from the tail. During the equilibration period, the animals were fitted with denim harnesses containing radiotransmitters (Biotrack) that measured approximately 3 × 1 × 1 cm. The total mass of transmitter, battery, and harness was less than 15 g. The harnesses were glued to the dorsal pelvic and tail base region with contact adhesive after which the animals were released at their respective points of capture.

Blood samples were refrigerated and frozen until ready for laboratory analysis. Water was extracted from the blood by vacuum sublimation (Vaughan and Boling, 1961), and then 50 µl aliquots of extracts were added to 3 ml of scintillation cocktail (PCS, Amersham) and counted in a Beckman 2800 LSC. Similar-sized aliquots were subjected to Urey exchange with standard charges of CO_2 (Green et al., 1991), after which the CO_2 was drawn off and 46:44 ratios measured with an isotope ratio mass spectrometer (VG Isogas 903).

Body water pool sizes were calculated by comparing isotope activities at equilibration with standard dilutions of the injected isotopes. It was assumed that there were no changes in mass-specific water pools during the experimental periods and that any changes in body mass were linear. Subsequently, rates of water flux and CO_2 production were calculated following Lifson and McClintock (1966) and Nagy (1980).

The first experimental period was in November 1989 in the transition from the wet to the early dry season. However all but one of the animals injected with doubly labeled water lost their transmitters and could not be recaptured. Subsequently, two extra individuals were studied in November 1990 to increase the data on CO_2 production rates at the end of wet season. A further five animals were injected with only tritiated water in December 1989 and recaptured in January 1990. Ten animals were injected with $^3H_2^{18}O$ and released in February and March 1990. Only eight of this group of animals were recaptured

TABLE 1. SEASONAL CHANGES IN WATER AND ENERGY TURNOVER (SAMPLE SIZE) IN *Tupinambis teguixin* AND OTHER TROPICAL CARNIVOROUS LIZARDS.

Species	Wet season		Dry season		Reference
	ml/kg/d	kJ/kg/d	ml/kg/d	kJ/kg/d	
Tupinambis teguixin	59.6 ± 9.5 (8)	183 ± 12 (3)	35.6 ± 6.8 (8)	76 ± 32 (8)	Present study
Varanus salvator	54.4 ± 11.4 (10)	117 ± 58 (6)			Dryden et al. (1992)
Varanus bengalensis	60.5 ± 13.3 (11)	149 ± 51 (6)			Dryden et al. (1992)
Varanus scalaris	60.4 ± 20.2 (13)	128 ± 29 (13)	16.6 ± 7.4 (17)	68 ± 34 (17)	Christian et al. (In press)
Chlamydosaurus kingii	27.5 ± 6.7 (7)	84 ± 18 (7)	6 ± 3 (11)	23 ± 4 (11)	Christian and Green (1994)

to provide FMR and water influx data. Animals injected with tritiated water only were released for about 40 days, but those injected with doubly labeled water were recaptured between six and 18 days after release to ensure that the ^{18}O concentration was sufficiently above background levels to permit accurate evaluation of CO_2 production. A few animals that were recaptured and released were recaptured a second time. In these cases, only data covering the full period between initial release and final recapture were used in the calculation of mean values and statistical analyses.

Tupinambis is predominantly carnivorous, feeding on a mixture of vertebrates, insects, crustaceans, and eggs. Only at the end of the dry season is there any evidence of plant material (mainly fruits) being ingested by some individuals (ER, unpubl.). The diet is therefore effectively protein with some fat; thus, a thermal equivalent of 25.7 kJ/l CO_2 was assumed (Nagy, 1983).

All mean values in the text are given with ± SD, and comparisons between seasons made using Mann-Whitney U-tests. Statistical significance was assumed for *P*-values of < 0.05. Two of the animals studied in February/March had previously provided water turnover data in the December/January period. To satisfy statistical independence, the data for these two animals were excluded from statistical tests but included in the calculation of means.

Results.—The initial body masses of individuals that returned isotope turnover data ranged from 900–1400 g (mean = 1172 ± 190, n = 8) during the November/January period, whereas animals studied in the February/March period ranged from 550–1200 g (mean = 938 ± 201, n = 8). The mean body water pools of tegu lizards estimated by tritiated water dilution was significantly lower (*P* = 0.042) in November/January (727 ±

56 ml/kg body mass, n = 8) than in the February/March period (765 ± 17 ml/kg body mass, n = 8). This pattern of seasonal change in mass-specific body water pools was also shown by two individuals that were studied in both December/January and February/March; an increase from 686–783 ml/kg body mass in one case and from 689–747 ml/kg body mass in the other.

There were no significant or consistent changes in the body masses of individuals during the experimental periods; i.e., body mass changes were within 5% of initial mass and within the range of variation expected for animals at different stages of feeding and gut fill. Thus, it was assumed that the animals were effectively in water and energy balance during the periods of isotope turnover measurements.

The water influx rates of *Tupinambis* were comparatively high (59.6 ± 9.5 ml/kg · day, n = 8) between November and January, the period immediately following the end of the long rainy season in Venezuela. However, during February and March, as conditions became increasingly dry, the water influx rates declined substantially (*P* = 0.003) to 35.6 ± 6.8 ml/kg · day, n = 8 (Table 1). Two individuals that provided water influx data for both seasons showed similar declines in water flux rates as those of the population sample means; from 61.0–27.8 ml/kg · day in one case and from 65.9–34.8 ml/kg · day in the other.

The mean FMR of *Tupinambis* in November/December was 0.297 ± 0.019 ml CO_2/g · h (n = 3), which is equivalent to a metabolizable energy expenditure of 183 kJ/kg · day. However, by February/March mean FMR had declined significantly (*P* = 0.006) to 0.124 ± 0.052 ml CO_2/g · h (n = 8), equivalent to a FMR of 76 kJ/kg · day.

Discussion.—The higher mass-specific body water pools measured in February/March relative to pool sizes in November/January reflect a decline

in body fat reserves of tegu lizards between December and April; from about 3% of body mass in December to less than 1% in April (EH, unpubl. data). The reduced availability of prey in open areas during the tropical dry season (Janzen, 1973) could oblige tegus to utilize body fat reserves in the dry season.

The present study clearly shows that there are significant seasonal differences in the water flux and metabolic rates ($P < 0.01$ in both cases) of a carnivorous lizard inhabiting a tropical environment. The rates measured in the period immediately following the rainy season are similar to those reported for two tropical varanids (*V. salvator* and *V. bengalensis*) under similar climatic conditions; 54 and 61 ml/kg · day, respectively (Dryden et al., 1992). Christian and Green (1994) reported that *Chlamydosaurus kingii*, an Australian tropical carnivorous lizard, also showed higher rates of water turnover in the wet season compared to the dry season (Table 1), although the mass-specific turnover rates for this species are much lower than in *Tupinambis* and the varanids.

Apart from these species, there are limited data on the water fluxes for other tropical reptiles in the field. However, Nagy (1982a) has provided allometric expressions for water influx in free-living reptiles and has suggested that water fluxes of tropical reptiles appear to be higher than those of arid/semiarid species:

Water Influx, (ml/day)
= 20.5 kg$^{0.91}$ arid/semiarid reptiles
= 45.0 kg$^{0.66}$ tropical reptiles.

Using these expressions, the predicted water influx rates for a 950-g lizard inhabiting either arid or tropical areas are 19.6 and 43.5 ml/day, respectively. The actual water influx rates measured for *Tupinambis* at the end of the wet season were substantially higher than either of these estimates, but the dry season water influx rates were intermediate to both of these predictive estimates.

Nagy and Peterson (1988) have proposed the following allometric expressions for water influxes of xeric and nonxeric reptiles:

Xeric: Water Influx (ml/day) = 0.038 g$^{0.79}$
Nonxeric: Water Influx (ml/day) = 0.065 g$^{0.73}$

Using these expressions, the predicted water influx rates for a reptile weighing 950 g in xeric and nonxeric environments are 8.7 and 14.9 ml/day, respectively, much lower than those measured for *Tupinambis* in either season. It appears that the allometric regression for tropical forms proposed by Nagy (1982a) provides a water influx estimate that most closely matches that for

Tupinambis in the dry season. However, the water influxes measured at the end of the wet/early dry season greatly exceed the value derived from this allometric regression.

The differences between water influx rates determined for tegu lizards in the postwet season and predicted values could be a result of the limited data for tropical reptiles available for allometric analysis. Nagy (1982a) used data for only four tropical species, covering both wet and dry conditions, whereas the nonxeric predictive expression of Nagy and Peterson (1988) is based predominantly on mesic species. Clearly, seasonal water influx data from a much broader range of tropical forms is required before reliable allometric analyses can be undertaken.

There are few reports of the field metabolic rates of tropical reptiles. The CO_2 production rates of *Tupinambis* immediately after the wet season were again similar to those of *V. salvator* and *V. bengalensis* under similar seasonal climatic conditions: 0.195 and 0.249 ml CO_2/g · h, respectively (Dryden et al., 1992). However, the lower FMRs in *Tupinambis* during the dry season are similar to those reported for active arid/semiarid varanids (Dryden et al., 1990) and that predicted for an iguanid of similar size, 55.3 kJ/day (Nagy, 1982b). The FMRs of *C. kingii* in the wet season were about five times higher than those measured in the dry season (Christian and Green, 1994), but again the mass-specific FMRs were much lower in both seasons than in *Tupinambis* (Table 1).

It is not known whether the water and energy use of *Tupinambis* declines to even lower values toward the end of the dry season (April/May) or how the activity and behavior patterns of tegus might change especially with respect to any decline in prey availability. It is possible that toward the end of the dry season *Tupinambis* becomes even less active and may spend extensive periods in burrows or other shelter.

Assuming that each gram of the diet of a carnivorous lizard provides 0.85 ml water and 5 kJ of metabolizable energy (Green et al., 1991), the FMRs reported here would require the ingestion of 35 g/kg · day of prey in the postwet season and 15 g/kg · day in the dry season. These rates of prey consumption would in turn generate 29.7 and 12.7 ml/kg · day of water from dietary sources, which represent only 50% and 45% of the total water influxes of the postwet and dry seasons, respectively. Thus a significant fraction of water influx in *Tupinambis* is probably derived from sources other than food; either through drinking or the pulmo-cutaneous exchange of water vapor. Similar values for nondietary water

intake have been reported for two tropical varanids (Dryden et al., 1992).

A water economy index (WEI) has been proposed by Nagy and Peterson (1988) to assess the water fluxes of animals relative to their energy expenditure. For nondrinking, free-living desert reptiles, WEI values are usually about 0.2 ml H_2O/kJ energy metabolized. *Tupinambis* exhibited WEI values of 0.33 and 0.46 in the postwet and dry seasons, respectively, whereas postwet WEI values for *V. salvator* and *V. bengalensis* were 0.44 and 0.39, respectively. The reasons for the higher relative rates of water use by tropical lizards are not known. However, the high availability of water in tropical environments relative to xeric habitats, both as free water bodies and higher atmospheric humidities, would not require tropical reptiles to develop physiological adaptations for water conservation to the same extent as xeric species. For example, the skins of tropical reptiles are generally more permeable to water than the skins of xeric species (Bentley, 1976). Thus, it is possible that exchange of water across the skin and pulmonary surfaces may be elevated in the more humid atmospheres that predominate in the tropics. In addition, the fact that free water is generally available in tropical habitats for much of the year allows the option of drinking, thereby saving the metabolic expenditures that are associated with water conservation via solute-linked reabsorption of water by the kidneys and cloaca.

The pattern of water use found for *Tupinambis* was as predicted; however, the expectation that energy use would be uniform throughout the year was incorrect. There is an obvious need for more extensive research into the seasonal patterns of water and energy use in tropical/equatorial lizards, their activity profiles, and how these parameters are related to prey availability. Only then will there be a better understanding of the relative importance of body size, diet, and behavior as influences on the utilization of water and energy which are two of the most important environmental resources required by animals.

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