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Effects of Season, Temperature, and Body Mass on the Standard Metabolic Rate of Tegu Lizards (*Tupinambis meriana*)

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ABSTRACT

This study examined how the standard metabolic rate of tegu lizards, a species that undergoes large ontogenetic changes in body weight with associated changes in life-history traits, is affected by changes in body mass, body temperature, season, and life-history traits. We measured rates of oxygen consumption ($\dot{V}O_2$) in 90 individuals ranging in body mass from 10.4 g to 3.75 kg at three experimental temperatures (17°, 25°, and 30°C) over the four seasons. We found that standard metabolic rate scaled to the power of 0.84 of body mass at all experimental temperatures in all seasons and that thermal sensitivity of metabolism was relatively low ($Q_{10} \approx 2.0-2.5$) over the range from 17° to 30°C regardless of body size or season. Metabolic rates did vary seasonally, being higher in spring and summer than in autumn and winter at the same temperatures, and this was true regardless of animal size. Finally, in this study, the changes in life-history traits that occurred ontogenetically were not accompanied by significant changes in metabolic rate.

Introduction

Due to their dependence on external heat sources for thermoregulation, many reptiles undergo large fluctuations in body temperature on a daily and a seasonal basis (Cowles and Bogert 1944; Bartholomew 1982; Gregory 1982). For example, when ambient temperature falls at night or during inclement weather, body temperature is usually proportionately lowered (Bennett and Dawson 1976). The preferred body temperature in many

reptile species is also significantly lowered during the winter cold months (e.g., Gregory 1982) in comparison with the hot spring/summer months. Because metabolic rate is inextricably linked to body temperature (Bennett and Dawson 1976), it is not surprising that the circadian and seasonal changes in body temperature are paralleled by concurrent changes in metabolism (Gregory 1982; Boutilier et al. 1997; Andrade et al. 2004). However, besides the direct effect of temperature on metabolic rate, many reptile species also exhibit a seasonal depression in metabolism that brings them into a torpid state (dormancy), producing further temperature-independent decreases in metabolic rate (Gregory 1982; Guppy et al. 1994; Abe 1995).

Such seasonal cycles of activity and dormancy have been documented in reptile species varying widely in body size (Gregory 1982; Abe 1995) as well as in juveniles and adults of the same species (Abe 1995; Andrade and Abe 1999; de Souza et al. 2004). Because body size affects thermal conductance, thermoregulatory behavior, and metabolism per se (McNab 2002), it seems plausible that body size might influence the degree of seasonal change that is seen in metabolism and the magnitude (sensitivity) of this change as a function of body temperature. The consequences of changes in body size on seasonal metabolic depression, however, are poorly documented in reptiles.

The mechanistic basis for the relationship between body mass and metabolism is one of the most controversial, complex, and unresolved issues in comparative animal physiology (Hemmingsen 1960; Kleiber 1961; Heusner 1982, 1984; Gilloly et al. 2001; White and Seymour 2005). In general, the metabolic rate of vertebrates (including squamate reptiles) increases to the power of 0.75 of body mass in interspecific comparisons, whereas in intraspecific comparisons it increases to the lower power of 0.67 (Heusner 1982; Andrews and Pough 1985; Bennett and Dawson 1976). Whatever the mechanistic basis of the scaling in metabolism, it has been clearly demonstrated that this relationship also reflects (to different degrees) variability in ecological traits such as diet, foraging strategy, reproductive state, and so on (Andrews and Pough 1985; McNab 2002). Therefore, during ontogeny, the scaling of metabolism may encompass not only changes in body size but also changes in life-history traits.

Tegu lizards *Tupinambis meriana* hatch with a body mass of approximately 10 g, and during the next 4–5 yr they grow to attain an adult body size of up to 8 kg (Köhler and Langerwerf 2000). Thus, from hatchling to full grown, tegus experience an impressive 800-fold increase in body size. Furthermore, as in many vertebrates, as tegu lizards grow they experience major changes in life-history traits, among which

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there are three that we could identify as likely candidates to affect metabolism: (1) a change in diet from insects to small vertebrates, carrion, eggs, and fruits (occurring between 600 and 750 g; Dessem 1985); (2) the onset of reproductive activity by the third year of life (at a body size of approximately 1.5 kg; Lopes and Abe 1999); and (3) an age-dependent growth rate (greater during the first and second year of life, with growth almost ceasing by 4 yr of age; A. S. Abe, unpublished data).

Tegu lizards also experience a marked circadian and circannual cycle of activity that begins within the first year of life (Köhler and Langerwerf 2000; A. S. Abe, personal observation). During the hot summer months, which in southeastern Brazil extend from mid-September until late May, tegus are active daily, and body temperatures vary from $\sim 36^{\circ}\text{C}$ during the day to $\sim 24^{\circ}\text{C}$ during the night. During the winter months (May–August), the animals retreat into burrows dug in the soil and cease feeding, and daily changes in body temperature are reduced to the thermal profile of the shelter, which is usually stable at around 17°C (Andrade et al. 2004). In our companion article (Milsom et al. 2008) we explore how such behavior (retreat to shelters) and the resulting exposure to continuous “dark and cold” might be involved in the seasonal metabolic depression exhibited by tegu lizards.

In this study, we determined how the standard metabolic rate of tegu lizards is affected by changes in body temperature, body mass, and season. In the process, we hoped (1) to describe the intraspecific scaling of metabolism in a species with a large ontogenetic variation in body size; (2) to examine the effects of temperature and season on the body size/metabolism relationship; (3) to determine whether any of the differences in metabolism related to body size, temperature, and/or season were correlated with changes in life-history traits; and (4) to determine possible causes of the discrepant results seen in the effects of season on metabolic rate in previous studies on this species.

Material and Methods

Animals

The experiments were conducted on 90 specimens of *Tupinambis merianae* of both sexes born in captivity at the Jacarazario, Universidade Estadual Paulista, Rio Claro, São Paulo, southeastern Brazil. Measurements were made over three consecutive years, from July 2000 to July 2002.

Before experimentation, young animals (<500 g) were housed in small groups (three to 10 individuals) kept indoors in plastic boxes (74 cm \times 56 cm \times 41 cm) lined with wood shavings. During the active season, the cages were provided with incandescent lights (10L:14D) to provide a source of radiant heat for thermoregulation, along with sunlight that diffused in from outside. During the night, temperature was allowed to fall to ambient levels (typically around 20°C). During the inactive season (May–September), the lights in the cages were kept off, exposing the young tegus to constant dark at room temperature (16° – 21°C). No food or water was offered

during this period, and the wood shavings lining the cages were kept moist. Older animals (>500 g) were kept in outdoor pens continuously under ambient conditions (see Nimer 1989 for a general characterization of the climate of southeastern Brazil and Pitton and Prochnow 2000 for a more detailed description of the climate in the city of Rio Claro). During the inactive season, these older animals, as is usual for the species, voluntarily retreated into the shelters present in the pens (concrete boxes half buried in the soil), occluded the entrance of the shelters with plant debris, and stopped eating completely. The body temperature variation experienced by adult tegus among the seasons (and also daily), under the same conditions described here, can be found in a study by Andrade et al. (2004).

During the active season, all animals were fed three times a week with minced meat supplemented with fruit, minerals, and vitamins. Water was available ad lib. Animals were fasted for at least 10 d before experimentation, and only individuals that seemed healthy and not molting were used. To control for the fasting period, adult animals were brought from the outdoor pens into the lab, where they were kept under conditions similar to those described above for the juveniles for 10 d before experimentation.

Respirometry

Rates of oxygen consumption ($\dot{V}\text{O}_2$) were measured using a computer-automated closed respirometry setup (TR-RM8, Sable Systems). This system controls pumps and solenoid valves and was programmed to ventilate seven respirometers (acrylic chambers of varying volumes depending on animal size) with fresh air (open phase; 200 mL/min/chamber) for 70 min while measuring the rate of oxygen depletion in one other chamber during a 10-min closed phase, during which the air was recirculated (200 mL/min) through an oxygen analyzer (PA-1, Sable Systems). The output from the gas analyzer was collected on a data acquisition system (DATACAN V, Sable Systems), and $\dot{V}\text{O}_2$ was calculated from the rate of oxygen depletion within the respirometer during the closed phase. As the system alternated between closed and open phases among the eight chambers, one 10-min $\dot{V}\text{O}_2$ measurement was obtained for each individual chamber every 80 min. The fall in oxygen concentration inside the respirometer (generally 0.2%–1.0%) was linear, and $\dot{V}\text{O}_2$ values were calculated as the slope (b value) of the linear regression (least squares method) obtained for all the single measurements recorded during the closed phase (600 data points sampled over 10 min). This regression usually provided r^2 values greater than 0.9. Excurrent flow was passed through a drying column (Drierite) before entering the gas analyzer, and $\dot{V}\text{O}_2$ calculations assumed a respiratory exchange ratio of 1.

Experimental Protocol

Experiments were performed in spring (September–November), summer (December–February), autumn (March–May),

and winter (June–August). The tegus were placed inside the respirometry chambers and placed within a climatic chamber (BOD-37 CD, Fanem, São Paulo) set to 30°C and constant dark. Tegus were allowed to acclimate to this temperature for 12 h, and then their metabolic rates were measured at this temperature overnight (approximately from 2000 until 0600 hours). The next morning (approximately from 0700 until 0900 hours), the temperature was decreased to 25°C, and the animals were left to acclimate for a further 12-h period; at night, their metabolic rates were measured at 25°C. Finally, the temperature was decreased to 17°C, and after a further 12-h acclimation period, the metabolic rates at this temperature were measured overnight. This protocol of temperature change was followed in all seasons except winter. During winter, the daily steps in temperature proceeded from 17° to 25° to 30°C. At the end of

each series of experiments, all animals were removed from the respirometers and returned to the colony.

Data Analysis and Handling

Tegu lizards exhibit circadian variations in metabolism, with metabolic rates being lowest during the nighttime (Milsom et al. 2008). Therefore, we took the average of all $\dot{V}O_2$ measurements collected during the night to represent the standard metabolic rate (SMR).

In total, we obtained 270 measurements from 90 individuals at the three experimental temperatures in each of the four seasons. Although different animals were used in the different seasons, within each season every individual was measured at all three experimental temperatures.

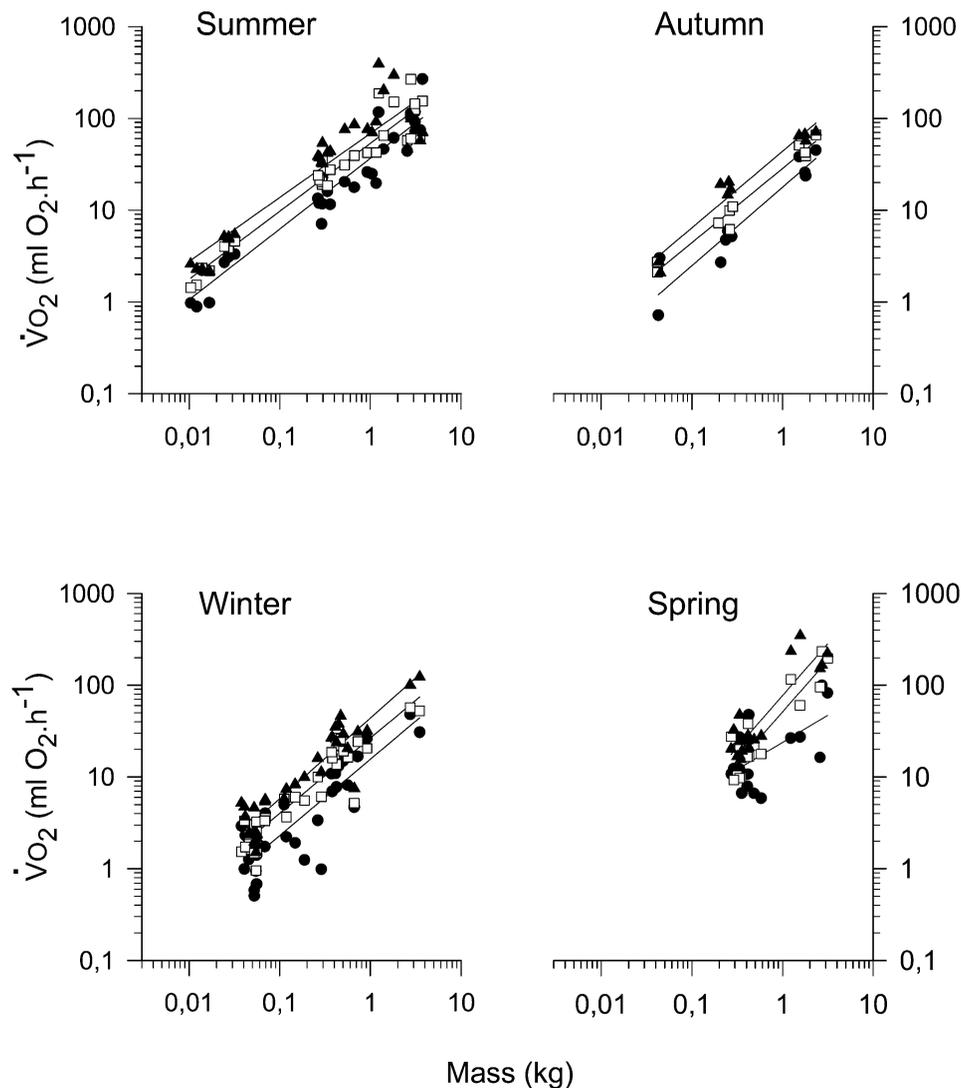


Figure 1. Relationship between resting metabolic rate and body mass for tegu lizards at three different body temperatures (17°C, circles; 25°C, squares; 30°C, triangles) during the four seasons of the year. Lines were fitted by least squares regressions for each temperature. The equations describing the linear regression of $\dot{V}O_2$ against body mass are given in Table 1.

Table 1: Linear regression equations describing oxygen consumption rate as a function of body mass at different temperatures in different seasons

	Temperature (°C)											
	Summer			Autumn			Winter			Spring		
	17	25	30	17	25	30	17	25	30	17	25	30
<i>a</i>	3.6	4	4.2	2.9	3.3	3.8	2.7	3.3	3.8	3.2	3.9	4.3
<i>b</i> (95% CI)	.77 (.68–.86)	.74 (.66–.82)	.70 (.58–.82)	.85 (.62–1.1)	.81 (.71–.92)	.83 (.67–.98)	.83 (.65–1.01)	.82 (.7–.94)	.88 (.75–1)	.59 (.16–1)	1.12 (.85–1.4)	1.13 (.82–1.4)
<i>r</i> ²	.92	.93	.84	.9	.97	.95	.73	.86	.86	.36	.83	.8
Body mass (kg):												
Mean ± SE	1.09 ± .22			.85 ± .28			.42 ± .13			.93 ± .24		
Min–max	.01–3.75			.04–2.35			.03–3.5			.27–3.14		
<i>N</i>	30			10			33			17		

Note. Individual slope values (*b*) are shown for each distinct condition. Because no statistical differences were found among the exponent values as a function of season or temperature, however (see text for details), the mean value of *b* = 0.84 describes the relationship between body mass and metabolism for *Tupinambis merianae* under all conditions. *a* = intercept; CI = confidence interval.

We natural log transformed body mass and $\dot{V}O_2$ and used these data to perform linear regressions using the least squares method for each combination of temperature and season. Thereafter, we applied a homogeneity-of-slopes design to model whether our continuous (body mass) and categorical (experimental temperature and season) parameters interacted to influence the rates of oxygen consumption. Since no interaction was found, we performed the traditional ANCOVA to verify the influence of each of our parameters (season, temperature, and body mass) on $\ln(\dot{V}O_2)$. This was followed by a repeated-measures ANOVA including $\dot{V}O_2$ as the dependent variable, temperature as the repeat variable, and $\ln(\text{mass})$ and season as the effects. Values of Q_{10} were calculated from the slopes obtained from the regression between $\ln(\dot{V}O_2)$ and temperature (see White and Seymour 2005).

All values are presented as mean ± SEM. Differences were considered statistically significant at the level of $P < 0.05$.

Results

The relationships between resting metabolic rate and body mass for tegu lizards at three different body temperatures during the four seasons of the year are depicted in Figure 1, and the equations describing such relationships under each condition are given in Table 1. We found a significant effect of mass on $\dot{V}O_2$ ($F_{1,85} = 826$, $P < 0.0001$) but no interaction between $\ln(\text{mass})$ and temperature or season; that is, the scaling exponents (*b* values) presented in Table 1 did not change significantly between temperatures and seasons (see Fig. 2). Therefore, the rates of oxygen consumption (mL O_2 /h) for *Tupinambis merianae* can be adequately described as $\dot{V}O_2 = aM^{0.84}$, where *M* is body mass in kg and *a* is the intercept value (given in Table 1), which was significantly affected by temperature and season ($F_{3,85} = 11.4$, $P < 0.0001$; see Fig. 3). Thus, rates of oxygen consumption were the lowest during the winter, intermediate during the autumn,

and highest during summer and spring. This pattern was not affected by body mass or temperature.

Temperature significantly affected $\dot{V}O_2$ ($F_{2,84} = 39.3$, $P < 0.0001$), but no significant interactions between temperature and $\ln(\text{mass})$ ($F_{2,84} = 0.036$, $P = 0.97$) or between temperature and season ($F_{6,168} = 0.040$, $P = 0.88$) were found. The sole effect of increasing temperature was to elevate the regression lines (and the values for the intercept, *a*), and this effect was the same for both temperature intervals (17°–25° and 25°–30°C) in all seasons (Fig. 3). Thus, Q_{10} values did not differ between seasons and were not affected by body mass (Fig. 4).

Discussion

Intraspecific Scaling over a Large Ontogenetic Range of Body Sizes

Controversy surrounds the interpretation of the relationship between basal or standard metabolic rate and body mass, specifically around the value of the mass exponent (*b*) in the allometric equation, which, when rewritten to allow the use of oxygen consumption as an indirect measure of metabolism, is $\dot{V}O_2 = aM^b$. In general, the metabolic rate of vertebrates (including squamate reptiles) has been reported to increase to the power of 0.75 of body mass in interspecific comparisons, whereas in intraspecific comparisons it increases to the lower power of 0.67 (Bennett and Dawson 1976; Heusner 1982; Andrews and Pough 1985). In this study we found that metabolism of tegu lizards scaled to the power 0.84 of body mass. While this value is higher than the mean power of 0.67 more commonly reported for intraspecific comparisons in squamate reptiles (17 species; Andrews and Pough 1985), it is well within the broad range of values reported from individual studies (0.58–1.1; Andrews and Pough 1985; Thompson and Withers 1994). Significantly, if we look at the mass exponents (*b* values) obtained in different seasons and at different temperatures for *Tupinambis merianae* in this study (Table 1), we see this same

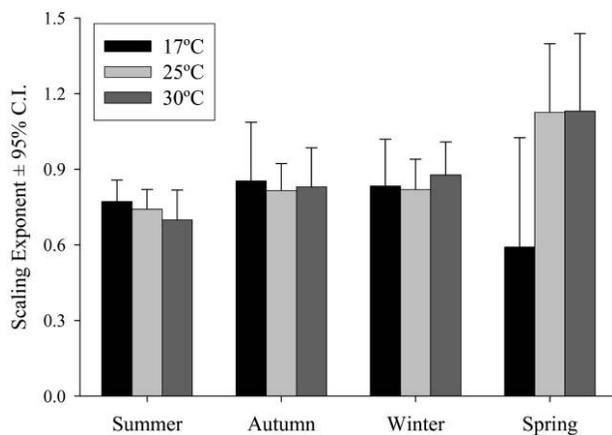


Figure 2. Scaling exponent ($b \pm 95\%$ confidence interval [CI]) for the oxygen consumption rates of *Tupinambis merianae* at different temperatures in different seasons.

range of variation (from 0.59 in spring at 17°C to 1.13 in spring at 30°C). Even though this variation did not attain statistical significance in our study, it clearly indicates that season and/or temperature can produce this same degree of variation in the mass exponent in a single study.

Effects of Temperature and Season on the Body Size/Metabolism Relationship

Despite the variation just noted in mass exponents in different seasons and at different temperatures, we found that there were no significant effects of temperature on the scaling of body mass and metabolic rate, regardless of season. This is consistent with numerous studies on other reptilian species (Chappell and Ellis 1987; Zari 1996a, 1997; Dorcas et al. 2004). Thus, the thermal sensitivity of the physiological processes underlying the determination of metabolic rate in tegu lizards does not appear to change with body mass. Given that ectothermic organisms, such as tegu lizards, do not use endogenously generated heat to regulate body temperature, changes in body size and thermal conductance would not be expected to influence metabolism heavily at different ambient temperatures. This contrasts markedly with what is usually observed in endotherms. However, White and Seymour (2005) have recently shown that if the mass exponent for mammals obtained under different thermal conditions is normalized to a single euthermic temperature, the differences in the scaling exponent (and hence the difference between ectotherms and endotherms) vanish.

We also found no changes with season in the temperature sensitivity of the metabolism of the tegu lizards; in other words, metabolism was elevated to the same extent with changing temperature in the different seasons (as depicted by the constancy of Q_{10} values; Fig. 3). As in other reptile species, however (e.g., Bennett and Dawson 1976; Beyer and Spotila 1994; Zari 1996b; Hailey and Loveridge 1997), and in previous studies in tegu lizards (Abe 1983, 1993, 1995; Andrade and Abe 1999; de

Souza et al. 2004; Milsom et al. 2008), we found that the metabolic rate of *T. merianae*, regardless of temperature, was reduced during the winter relative to the peak in metabolism in spring/summer. This is apparent from the variation in the intercept (a) values. We now add to this that the degree of metabolic suppression during dormancy (or of metabolic increment during the active season) is the same for small and large individuals. Tegus are born at the beginning of spring (roughly mid-September) and go into dormancy at the beginning of the cold season (late May–early June). This timing is apparently not affected by body size (A. S. Abe, personal observation). The mechanisms triggering dormancy in tegu lizards appear, ultimately, to be first expressed as a behavioral decision; that is, the animals confine themselves to their burrows and let their body temperature equilibrate with their surroundings (cold) under dark conditions (Andrade et al. 2004). This, as we show in our companion article (Milsom et al. 2008), is enough to induce metabolic suppression, and the data presented here suggest that this occurs independent of body size.

Reports of the degree to which metabolism is reduced in the fall and winter and the extent to which these reductions are temperature sensitive in tegu lizards are quite discrepant (Abe 1983, 1993, 1995; Andrade and Abe 1999; de Souza et al. 2004; Milsom et al. 2008). For example, Abe (1983, 1993, 1995) and de Souza et al. (2004) found $Q_{10} \approx 3$ between 25° and 17°C during the spring, whereas during the winter, a similar change in temperature yielded a Q_{10} of 1.5. As a result, they described the metabolic rate of dormant tegus as being relatively temperature independent. In another study, however, while similar profound seasonal reductions in metabolism were found, the temperature independence of winter metabolism did not appear to be present (Andrade and Abe 1999). When winter metabolism in this study was compared with the spring/summer metabolism in the study by Abe (1995), the Q_{10} remained constant regardless of season (3.2 and 3.0 for spring and winter, respectively). In this study we also found that the Q_{10} effect

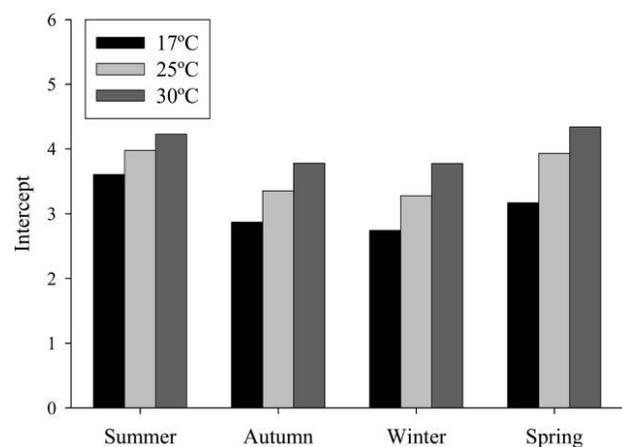


Figure 3. Intercept (a) for the oxygen consumption rates of *Tupinambis merianae* at different temperatures in different seasons.

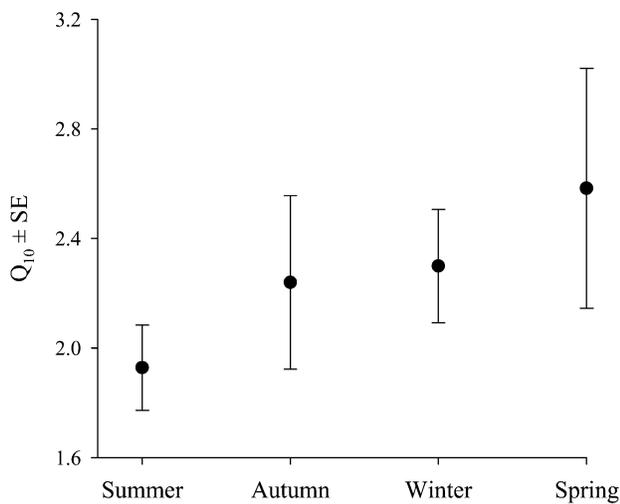


Figure 4. Values of Q_{10} (mean \pm SE) for *Tupinambis merianae* measured in the 17°–30°C interval across the seasons.

remained constant regardless of season, although our Q_{10} values were generally lower (\sim 2.0–2.5) than previously reported.

An explanation of these discrepant results may come from our companion article (Milsom et al. 2008), where it is shown that if enough time was taken, the seasonal reduction in metabolism seen at 17°C in this species disappeared. In this study, seasonal effects similar to those observed by Abe (1995) were seen on metabolic rates of animals at 17°C if the measurements considered were those made over the first 24 h. If the lizards were left to acclimate for prolonged periods (7–10 d) in the dark at a constant 17°C, however, all effects of season disappeared (Milsom et al. 2008). This suggests that metabolism could be suppressed to the same minimum level at 17°C, regardless of the season, if animals were kept long enough in the cold and dark. Thus, discrepancies in measures of the magnitude of the Q_{10} effect over the seasons documented in different studies might well reflect differences in the acclimation time provided for the animals before the measurements were taken.

Effects of Ontogenetic Changes in Life-History Traits

During ontogeny, changes in body size are accompanied by changes in life-history traits, and these in turn can exert a strong influence on metabolism (Andrews and Pough 1985; McNab 2002). In the tegu lizard, there are three major ontogenetic changes in life-history traits that we thought might affect metabolism: (1) a change in diet from insects to small vertebrates, carrion, eggs, and fruits (occurring between 600 and 750 g; Dessem 1985); (2) the onset of reproductive activity by the second to third year of life (at a body size of approximately 1.5 kg; Lopes and Abe 1999); and (3) growth rate (greater during the first and second year of life, with growth almost ceasing by 4 yr of age; A. S. Abe, unpublished data). In this study, changes in life-history traits were not accompanied by

(or causative of) any significant changes in metabolism (see also Chappell and Ellis 1987). This, however, is a weak conclusion because differences in sample size over different parts of the body size range in different seasons precluded us from adequately testing these relationships. We do, however, have observations (W. K. Milsom and D. V. Andrade, unpublished data) that suggest that reproductively active animals might be more responsive than nonreproductive juveniles to temperature changes in early spring, which would help them to readily engage in reproduction as soon as they come out of dormancy (see Lopes and Abe 1999). The validity of this observation and the influence of the other ontogenetic changes in life-history traits that we have identified for the tegus on metabolism remain to be rigorously tested.

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