

Overwintering in Tegu Lizards

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Abstract. The tegu, *Tupinambis merianae*, is a large South American teiid lizard, which is active only during part of the year (hot summer months), spending the cold winter months sheltered in burrows in the ground. This pattern of activity is accompanied by seasonal changes in preferred body temperature, metabolism, and cardiorespiratory function. In the summer months these changes are quite large, but during dormancy, the circadian changes in body temperature observed during the active season are abandoned and the tegus stay in the burrow and allow body temperature to conform to the ambient thermal profile of the shelter. Metabolism is significantly depressed during dormancy and relatively insensitive to alterations in body temperature. As metabolism is lowered, ventilation, gas exchange, and heart rate are adjusted to match the level of metabolic demand, with concomitant changes in blood gases, blood oxygen transport capacity, and acid-base equilibrium.

Seasonality and the Tegu Life Cycle

As with any other ectothermic organism, the tegu lizard, *Tupinambis merianae*, depends on external heat sources to regulate body temperature. Although this type of thermoregulatory strategy conserves energy by avoiding the use of metabolism for heat production (Pough, 1983), it requires that the animal inhabit a suitable thermal environment to sustain activity. When the environment does not provide the range of temperatures that enables the animal to be active year round, many species of ectothermic vertebrates become seasonally inactive (Gregory, 1982). Such a strategy is widespread amongst amphibians and reptiles

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of South America, although it is not always clear whether dormancy occurs in response to low temperature or to the accompanying dryness (Abe, 1995). The main landscape in Brazil, south of the Amazon, is characterized by savannah-like regions, called "Cerrado," alternating with tropical forests (Hueck, 1972). A wide belt of Cerrado crosses South America diagonally from northeastern Brazil to northern Argentina (Ab'Saber, 1977). The Cerrado is characterized by a seasonal climate consisting of alternations of cold, dry months (winter) with hot, rainy months (local summer) (Nimer, 1989). These cycles of rain and temperature dictate the annual pattern of activity for most species of amphibians and reptiles inhabiting the Cerrado (Abe, 1995).

The distribution of the tegu lizard, *T. merianae*, largely overlaps that of the Cerrado formation. Tegus are the largest members of the teiid family, attaining as adults a body length of up to 1.6 m and a body mass of up to 5 kg (Fig. 1). This lizard is an active forager, possessing powerful jaws and feeding on fruits, invertebrates, and small vertebrates (Vanzolini et al., 1980). In southeastern Brazil, tegus are active during the hot rainy season (approximately from August to April) and retreat into shelters, usually burrows dug in the earth, during the cold dry season (May to July) (Abe, 1983). From February onwards, activity and food intake decline markedly until the onset of the dormant season, at which



Fig. 1. An adult male tegu, Tupinambis merianae, pauses while foraging in southeastern Brazil.

time the lizards will retreat permanently into the burrow, occlude the entrance with plant debris, and stop food intake completely. After this time, tegus will not leave the burrow to bask, even on those occasional days when environmental temperatures attain levels equivalent to those seen in summer (Lopes and Abe, 1999). Thus, during dormancy, the marked diurnal cycles in activity, body temperature, and metabolism are abandoned. By the end of August to early September, tegus begin to emerge from dormancy, become progressively more active, and begin to bask and feed again. By this time, tegus in captivity will feed every other day and will gain weight, quickly recovering the losses incurred during dormancy. Breeding takes place approximately one month after the tegus have emerged from dormancy, when pairs are often observed in courtship and mating. By mid-October, females are gravid with extended bellies and egg laying occurs. An adult female may lay from 21 to 52 eggs; with the mass of the clutch being equivalent to 40% of the female's post-partum body mass (see Lopes and Abe, 1999, for more details on the reproductive biology of tegus). Although this represents a large investment in reproduction, females are able to recover the weight loss during the remainder of the active season. During the months leading up to entrance into dormancy, the fatty mass stored in the abdominal cavity increases to about 5% of total body weight. It is estimated that this amount of fat is sufficient to sustain metabolism in dormancy for more than one full year (Abe, 1995).

Temperature and Metabolism

Over the course of a year, tegus show a variable thermal profile that is distinctive for each season (Fig. 2). While active in the summer, body temperature (T_b) rises rapidly in the morning with basking, slowly continues to increase during the day, and then gradually declines once the tegu re-enters the burrow in the evening. This pattern is common throughout the active season, although mean T_b appears to be higher and more variable (has a wider daily range) during spring and summer, than in fall. Interestingly, throughout the active seasons, the daily maximum for T_b is about 35–36° C, a value quite close to the regulated T_b of many endotherms. In the fall, at the onset of dormancy, T_b falls relatively quickly over a short, multiday period. At present, it is unclear whether this is the result of concomitant changes in the weather (e.g., several days of rain), or an active strategy employed by the animal to prepare for entrance into hibernation. During hibernation, the little variation in T_b that remains is assumed to reflect changes in the ambient temperature in the hibernaculum (see Fig. 2).

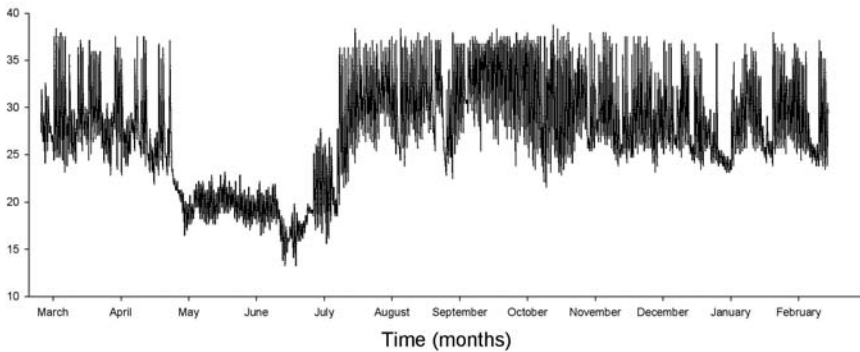


Fig. 2. Body temperature profile of an adult male tegu lizard (~3.5 kg) during one full year of recording with an implantable data logger. Dormancy is clearly distinguishable, from late April to late July. Multiday bouts of inactivity in the burrow can be seen from January until late April. (Recordings taken every 16 minutes, from Elis R. Lopes, unpublished data.)

During the active season, tegus become active each day, not with sunrise, but rather with increases in ambient temperature (Fig. 3). During the night, ambient temperature falls below the temperature of the burrow and the tegu. During the day, once the ambient temperature rises to equal that of the resting tegu, the lizard emerges from the burrow to bask. Basking induces a rapid increase in T_b (~2° C/hr in an ~3.5 kg tegu) to a maximum T_b of ~33–38° C. This is accompanied by parallel increases in metabolism, heart rate (from a resting value of ~10 beats/min to ~70 beats/min) and respiratory frequency (from a resting value of ~2–3 breaths/min to ~12–18 breaths/min). Once warm, the tegus become active and spend the day alternating between periods of basking, foraging, and resting in the burrow, behaviourally maintaining T_b between 32° C and 38° C. Later in the afternoon, the tegu re-enters the burrow to rest for the night. The rate of heat loss (~0.44° C/hr for an ~3.5 kg lizard) throughout the night is slow and appears to be physiologically regulated. A dead tegu of similar mass, under the same environmental conditions, loses body temperature at a rate of ~1.28° C/hr (Colin Sanders, unpublished data).

During hibernation, tegus exhibit a depressed metabolism (Abe, 1983), although the nature and extent of this depression in nature are still unclear. Abe (1983) recorded a Q_{10} for metabolic rate (VO_2) of about 1.1, over a temperature range of 20°–30° C in a hibernating tegu recovered from the wild. This sug-

gested that an absolute level of metabolic suppression had been reached that was temperature independent. In a subsequent study in which hibernation was induced in tegus in captivity, Abe (1983) found a Q_{10} of 2.9 for VO_2 over the same range (20°–30° C). While this suggested that the absolute level of metabolic suppression was not temperature independent, metabolism was nonetheless suppressed compared to that of active tegus during the summer over the same temperature range (inverse acclimation) (Abe, 1995; Andrade and Abe, 1999). Thus, although increases in temperature produce increases in metabolism in dormant tegus, the magnitude of this increase is less than that exhibited by active tegus in the summer over the same temperature range.

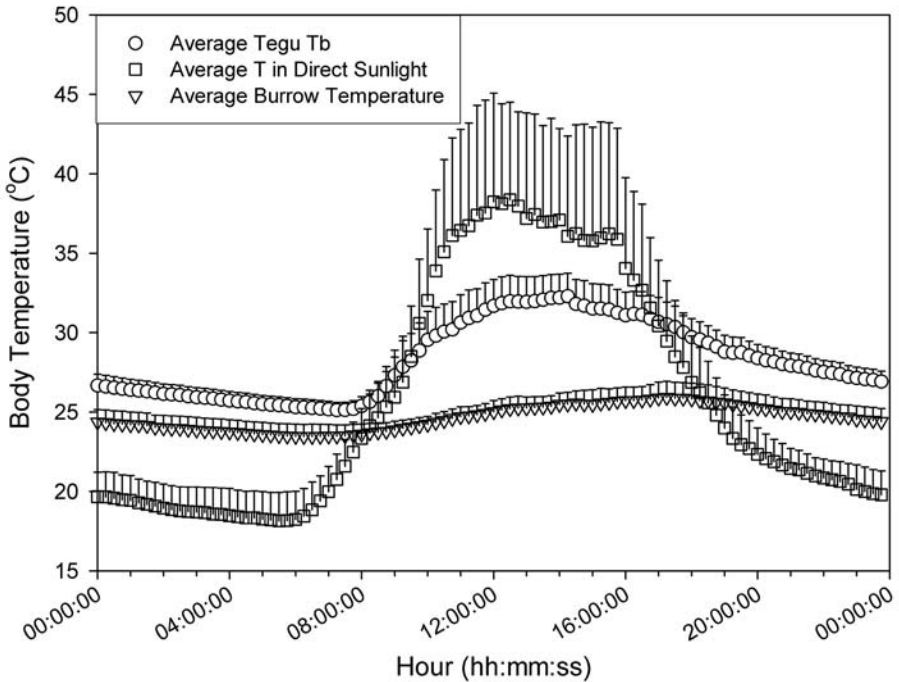


Fig. 3. The average daily thermal profile of a group of adult tegus ($n = 6$, average mass = 3.7 ± 0.33 kg), their burrows, and a data logger in direct sunlight, during days when tegus were active during the month of January 2004. Average values \pm SEM.

Cardiorespiratory Adjustments

The primary function of the cardiorespiratory system is to transport adequate amounts of O_2 from the external environment to the tissues and, conversely, remove the metabolically produced CO_2 from the tissues to the external environment (Hlastala and Berger, 2001). "Adequate" here means that the rate of O_2 delivery and CO_2 removal meet the metabolic demands of the animal and prevent the development of tissue hypoxia/anoxia and/or acidosis and their deleterious consequences. Given that the tegu lizard experiences marked seasonal changes in activity, body temperature, and metabolism, seasonal adjustments in cardiorespiratory function are also expected to occur.

As metabolism is depressed, animals require less O_2 and produce less CO_2 and thus lung ventilation decreases. While an active tegu usually breathes 10 ml/kg/min, a dormant tegu at the same temperature breathes 4 ml/kg/min (Andrade and Abe, 1999). In dormancy, tegus also exhibit a change in ventilatory pattern; at 17°C these lizards breathe episodically, with a few grouped breaths (five to six breaths) separated by periods of apnea as long as 26 minutes; the longer the duration of apnea, the greater the number of breaths in the subsequent breathing episode. O_2 extraction and CO_2 excretion occur at different rates during breath holding in dormant tegus; O_2 is extracted more rapidly from the lungs than CO_2 is eliminated (Andrade and Abe, 1999). As a result, lung volume changes during the breath-holding period, raising the possibility that a mechanical cue is involved in the regulation of the breathing pattern of dormant tegus. The differences in the dynamic of O_2 and CO_2 exchange may also explain why dormant tegus have elevated levels of total CO_2 in the blood, while O_2 content is almost unaltered (Andrade et al., 2004; see below).

Given that tegus do not move around during dormancy, the most conspicuous activity they perform during this period is breathing. Since all other activities shut down during dormancy, the relative cost of the remaining activity will be increased. Thus, it is not surprising that the oxidative cost of breathing of dormant tegus has been estimated to be 52.3% of the total metabolism (Andrade and Abe, 1999). This figure is even higher for hibernating squirrels breathing episodically, where the cost of breathing has been estimated to account for 90% of the total metabolism (Garland and Milsom, 1994). It has been suggested that the change to an episodic breathing pattern during dormancy might, due to mechanical considerations, represent a strategy to minimize the energetic costs of breathing, and this would appear to be a strategy shared by mammals and reptiles (see Milsom, 1991). Interestingly, however, if the temperature of

dormant tegu is increased to 25° C, their breathing becomes regular. In this situation, metabolism is somewhat elevated by the change in temperature, but this increase is accompanied only by an increase in total ventilation with no noticeable change in the air convection requirement. This matching of ventilation to metabolism is caused by reducing the duration of the apneic periods, i.e., by alterations of breathing frequency rather than changes in tidal volume (Andrade and Abe, 1999).

Recently, we (Andrade et al., 2004) extended these studies to address the question of whether the blood characteristics associated with the transport of the respiratory gases also change seasonally. Furthermore, considering that the seasonal adjustments in the cardiorespiratory system aim to maintain adequate levels of blood gases and acid-base equilibrium *in vivo*, we also wondered whether the definition of “adequate levels” might vary seasonally. We found that during dormancy, tegus exhibited a lower blood oxygen-carrying capacity than during the active season, reflecting the need to transport less O₂ to meet the lower metabolic rate typical of dormant tegus. The lower blood oxygen-carrying capacity observed in the dormant tegu was due to concurrent decreases in hemoglobin concentration ([Hb]) and hematocrit (Hct) and an increase in nonfunctional met-hemoglobin content. Dormancy caused blood–oxygen affinity in *T. merrianae* to increase independently of pH and temperature. Increased blood–oxygen affinity is a common feature of metabolic depression (Jokumsen and Weber, 1980; Maginniss and Milsom, 1994) and facilitates pulmonary O₂ loading. In the case of dormant tegus, the left-shift in the oxygen equilibrium curve (O₂EC) might be particularly important because a higher blood oxygen affinity would allow pulmonary O₂ extraction even during the final portion of extended periods of apnea (see also Lapennas and Lutz, 1982). At the same time, a high blood O₂ affinity decreases the capillary-to-tissue oxygen diffusion rate and promotes tissue hypoxia. This has been suggested to be a mechanism involved in the down regulation of aerobic metabolism (see Leggio and Morpurgo, 1968; Jokumsen and Weber, 1980). As reported for other ectothermic vertebrates, the arterial pH decreases with temperature in *T. merrianae*, while arterial O₂ partial pressure (Pa_{O₂}) and arterial CO₂ partial pressure (Pa_{CO₂}) increase. Arterial O₂ content (Ca_{O₂}) and CO₂ content in the plasma (Cpl_{CO₂}) are not altered (Glass et al., 1985; Stinner and Wardle, 1988; Wang et al., 1998). Dormancy is accompanied by an increase in plasma bicarbonate ([HCO-3]pl) and an elevation of Pa_{CO₂} and Cpl_{CO₂}, suggesting that, on a seasonal basis, tegus regulate arterial pH at the expense of changes in Pa_{CO₂} and [HCO-3]pl (see also Rocha and Branco,

1998). As a consequence, at most temperatures, arterial pH (pHa) does not differ between seasons. However, at low temperatures, tegus regulate pHa at a relatively acidic level, suggesting that tissue acidosis may also be involved in the down-regulation of metabolism in these lizards, as has been postulated to occur in other animals (Malan, 1993; Guppy et al., 1994; Boutilier et al., 1997).

Perspectives

Undeniably, the most complete picture of the physiological adjustments accompanying seasonal depression in metabolism has arisen from studies on mammals. However, the study of ectothermic vertebrates might provide a fruitful alternative for such studies, providing a system where one can potentially separate the consequences of altering metabolism and body temperature, since these two functions are not as intricately intertwined in ectotherms as they are in endotherms. Tegus are large animals, which facilitates instrumentation. They breed successfully in captivity, they grow rapidly, and they can be obtained in large numbers. So far, we have documented only a few aspects of the physiological adjustments associated with the metabolic depression experienced by this lizard. We have not even begun to examine the exciting topic of the cues used by this lizard to establish its seasonal cycle nor the proximal factors that trigger dormancy. The humoral, neural, genetic, and molecular basis of the seasonal pattern of activity in *T. merianae* remain unexplored aspects of "life in the cold," taking place south of the Amazon.

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