

Chapter 28

Seasonal Changes in Thermoregulatory Strategies of Tegu Lizards

William K. Milsom, Colin Sanders, Cleo Leite, Augusto S. Abe, Denis V. Andrade and Glenn Tattersall

Abstract During the post-reproductive period (December–March) black and white tegus [*Tupinambis merianae* (Duméril and Bibron)] basked during the day and regulated maximum daily T_b around 33–37°C. Heart rate (HR) and breathing frequency (fR) increased during the day to relatively constant levels. Nighttime values of HR and fR, however, decreased progressively from December to March while nighttime T_b was fairly constant ($\sim 25^\circ\text{C}$). During March to mid-April the lizards slowly entered into hibernation. If HR is correlated to metabolic rate under steady state conditions, declines in nighttime HR at constant T_b would suggest there was a continuum from sleep to nightly torpor to multi-day bouts of torpor to hibernation. During hibernation, tegus in artificial outdoor burrows exhibited periodic bouts of emergence. This was not seen in tegus in natural burrows. During arousal from hibernation there was an increase in preferred day time T_b during periods of emergence and an increase in nighttime T_b that exceeded the increase in nighttime burrow temperature (T_{burrow}). This gave rise to nighttime differences between T_b and T_{burrow} that at their peak were as much as 6–8°C. Differences between T_b and T_{ambient} of 2–4°C could be maintained in an environmental chamber with no bedding for extended periods suggesting that the temperature differential was due in part to either decreased heat loss, increased heat production, or both.

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28.1 Seasonality and the Tegu Lizard Life Cycle

The tegu lizard, *Tupinambis merrianae*, depends largely on external heat sources to regulate body temperature. As a consequence, individuals living in seasonal habitats undergo seasonal changes in body temperature, metabolism and activity. Most terrestrial ectothermic vertebrates employ behavioural and physiological mechanisms to provide some degree of autonomy from environmental change but the extent of this independence is generally small. We have been conducting a long-term study of the black and white tegu lizard in Brazil with a focus on both the strategies employed during the cooler, dryer winter period to reduce metabolism as well as the spring reproductive period to enhance metabolism.

The tegu lizard is an active omnivore that can grow as an adult to over 5 kg body weight. The main habitat of this lizard in Brazil is characterised by savannah-like regions, called ‘Cerrado’ (Hueck 1972). The yearly cycle of the tegu can be divided into five main periods based upon the physiological-behaviour states: the reproductive (early active), post-reproductive (late active), entrance (into hibernation), hibernation and arousal (from hibernation) periods. Mid-September through to December (spring in the southern hemisphere) is a period of high activity associated with courtship and breeding (the reproductive period). December–February is a post-reproductive period of reduced activity. Throughout the reproductive and post-reproductive periods the lizards are foraging and replenishing energy stores. During March to mid April the lizards slowly enter into hibernation. This period is marked by a drastic decrease in activity and complete aphagia (the animals are no longer interested in eating) (Lopes and Abe 1999). Hibernation occurs from mid April through to the end of July during which time the tegus spend almost all their time inactive in their burrows (Abe 1983). In August to mid-September they arouse (Lopes and Abe 1999). During this period the tegus progressively emerge from the burrows with increasing frequency.

28.2 Winter Dormancy (Hibernation)

While many are reluctant to use the term hibernation to describe dormancy in reptiles, in the case of the tegu lizard this is a period of active metabolic suppression (Abe 1983, 1995; de Souza et al. 2004; Andrade and Abe 1999) that occurs seasonally during the winter (Abe 1983; Lopes and Abe 1999). By strictest definition it is a form of active winter sleep [hibernare (*v*) = to winter] and will be referred to as such here.

28.2.1 Anticipatory Decreases in Metabolic Rate: Programmed Nocturnal Torpor?

During the fall (February–April) tegus are still active in the day, warming to usual active temperatures and are still exposed to progressive changes in photoperiod and ambient temperature (Köhler and Langerwerf 2000). During this period, however, nighttime values of heart rate (HR) and breathing frequency (fR) decrease progressively (Fig. 28.1). Minimum nighttime body temperature (T_{bmin}) through December–March, on the other hand, are fairly constant (T_{bmin} hovered around 25°C) (Fig. 28.1) (Sanders et al. 2011). If HR is correlated to metabolic rate under steady state conditions, as suggested by several studies (Butler et al. 2000, 2002; Clark et al. 2004; Piercy et al. 2010), declines in nighttime HR at constant T_{b} would suggest that there is a nightly torpor that increases in magnitude over this period of time. This is consistent with previous studies that have shown that tegus depress metabolism in the autumn in anticipation of the hibernation period when confined in the dark for several days at constant temperature (Abe 1983, 1995; de Souza et al. 2004; Andrade and Abe 1999; Milsom et al. 2008).

As the year progresses, during the late active period and during entrance into hibernation (March and April), tegus emerge from their burrows later in the morning and retreat into their burrows earlier in the afternoon (Fig. 28.2). In most tegus, daytime maximum T_{b} also drops slightly (Fig. 28.1). Daytime maximum levels of HR and breathing show similar trends suggesting that a behavioural metabolic suppression (behavioural selection of lower temperatures or warming for shorter periods) is also occurring during the day late in the active period and during the entrance phase; however, the extent of this is small (Sanders et al. 2011).¹

28.2.2 Daily Torpor/Multi-Day Bouts of Torpor/Hibernation: A Natural Progression?

At the onset of the active period, daytime quiescence is rare and associated with inclement weather. If rainfall only occurs for half a day, tegus still usually emerge once the rain stops. When full days are spent in the burrow due to unfavourable conditions, T_{b} , fR, HR and presumably metabolic rate remain low. T_{b} , however, remains elevated relative to burrow temperature suggesting that this is simple quiescence (Sanders et al. 2011). Throughout the late active period and the period leading up to hibernation the tegus begin to spend more time in the burrow, often for more than one day, even when weather is favourable. As the seasons progress, during

¹ T29F-7B implantable biopotential/temperature amplifier/encoders [5.7 × 2.8 × 0.92 cm; (60 g or roughly 2% of body weight)] (Konigsberg Instruments, Inc., Pasadena, CA, USA) inserted to lie between the fat bodies ventral to the digestive tract in the abdominal cavity were used to monitor T_{b} , HR and breathing frequency.

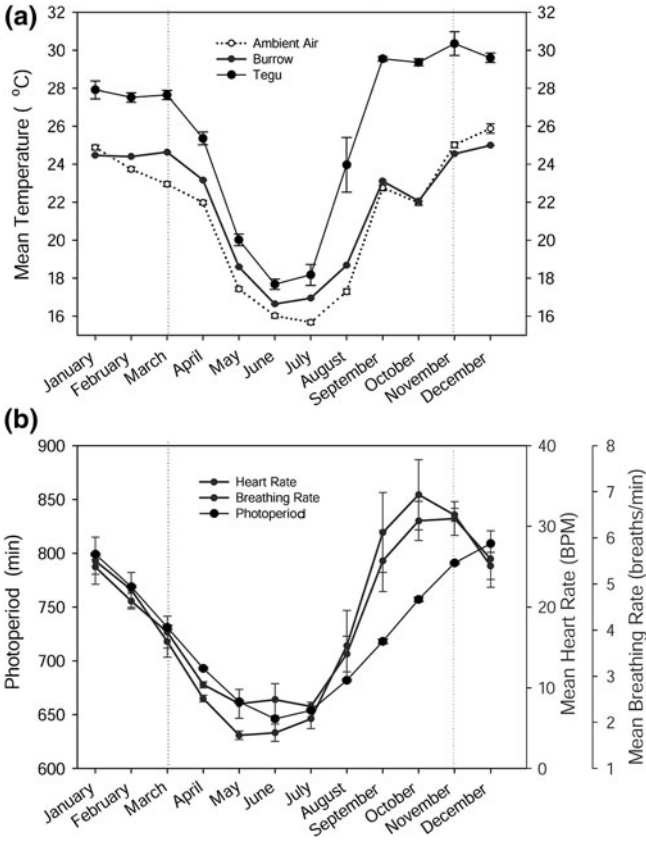
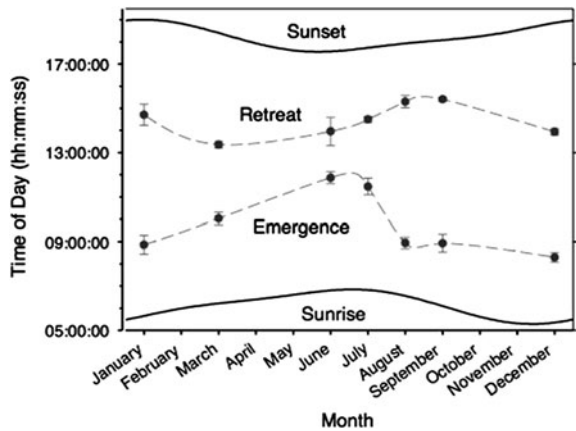


Fig. 28.1 Mean monthly values for **a** ambient and burrow temperatures, and core body temperature, and **b** photoperiod, heart rate and breathing rate for four tegus

Fig. 28.2 Times of sunrise and sunset at the study site (Rio Claro, SP, Brazil) for the study period. Time of emergence from the burrow and retreat into the burrow are also shown for 7 months in the late active season (January), during entrance into hibernation (March), for rare incidents of emergence in hibernation (June, July), during arousal from hibernation (August) and during the early active season (September and December)



these periods T_b falls to the temperature of the burrow. This becomes particularly pronounced in April when, although rainfall is infrequent and light, the tegus spend roughly half the month in their burrows (Sanders et al. 2011). The hallmark of final entrance into hibernation is when the burrow entrances are blocked with detritus and litter, indicating a behavioural commitment to hibernate. This suggests there is a continuum from sleep to nightly torpor to multi-day bouts of torpor to hibernation. This is consistent with a recent report that tegu lizards can reduce their metabolism to the low rates seen in hibernation at all times of the year when given sufficient time in the cold and dark (Milsom et al. 2008). It is also consistent with the views of some (Wilz and Heldmaier 2000; Heldmaier et al. 2004) but not all (Geiser and Ruf 1995; Geiser 2003) studies of mammalian hibernation.

28.2.3 Do Tegus Arouse Periodically During Hibernation?

While there is still much debate over the causes and benefits of periodic arousal from hibernation (Barnes et al. 1993; Wang 1993; van Breukelen and Martin 2002; Carey et al. 2003), it is common to all mammalian hibernators except the bears. Their occurrence is normally very rhythmic with the lengths of the hibernation bouts increasing in the early season and then decreasing again in the spring (Twente and Twente 1967). Most mammals do not leave their burrows during these bouts of periodic arousal (Willis 1982). Whether this occurs in species of reptiles that hibernate in temperate zones is not known. Species of reptiles that hibernate in subtropical regions are less constrained to remain in their burrows during periods of arousal and in a recent study it has been shown that hibernating *Varanus rosenbergi* spontaneously arouse fairly frequently during their hibernating period (Rismiller and McKelvey 2000).

For *Tupinambis merianae*, the data are equivocal. Animals held in artificial burrows exhibit both short bouts of arousal and emergence throughout the hibernation season (Fig. 28.2). These arousals occur randomly, with no distinct pattern in any animal, suggesting that they are not the consequence of an underlying biological rhythm. They also are not tightly correlated to local factors such as temperature change, noise, or disturbance (Sanders et al. 2011). At present it is not clear what the underlying cause of the arousals is. Animals dormant in natural burrows do not emerge over the hibernation season. Whether they undergo periods of arousal without emerging from the burrow is not clear. There is some evidence to indicate that tegus in artificial burrows do arouse on occasion without leaving the burrow.

28.3 Reproductive (Spring) Thermogenesis?

Shortly after emerging from hibernation, the biological priority of the tegu is to reproduce. Activity from September through to November is elevated as tegus not only seek food to replenish stores depleted by hibernation, but also engage in courtship,

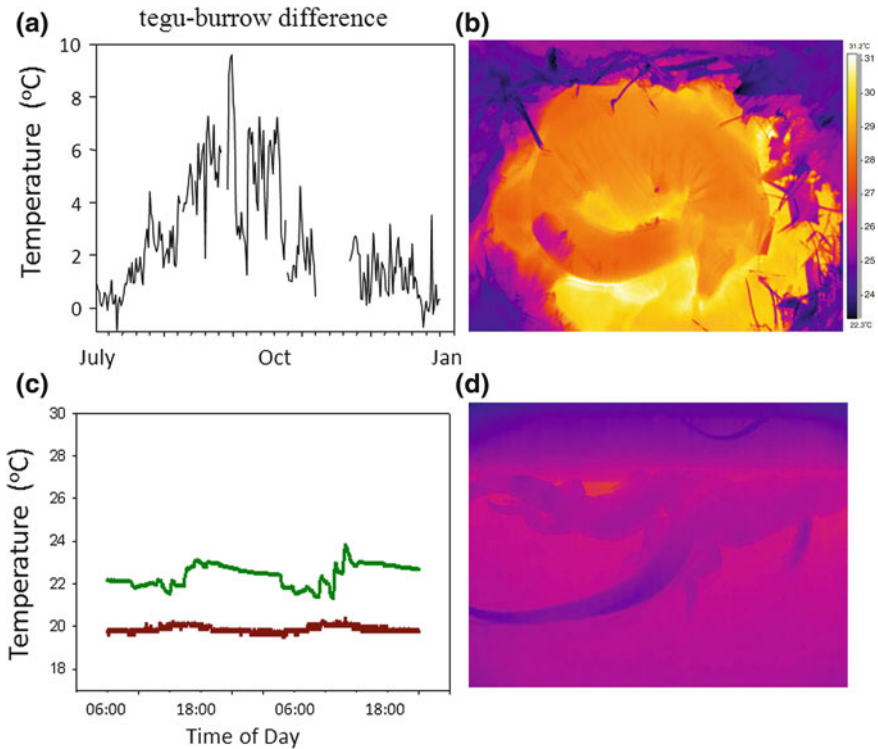


Fig. 28.3 **a** The mean differential between tegu body temperature and burrow temperature during arousal from hibernation and through the reproductive season. **b** Tegus in artificial burrows could be as much as 6°C warmer than the burrow at the end of the night. **c** Tegus inside an environmental chamber remained 2–3°C warmer than the chamber over extended periods. **d** Despite the fact their skin was at or below ambient temperature

mating, nesting and egg laying. Not surprisingly, concomitant with this elevated activity is an elevated metabolism as evidenced by high daytime and nighttime HR and fR (Fig. 28.1) (Sanders et al. 2011). This suite of changes is not uncommon in reptiles (Rismiller and Heldmaier 1991) and can be accompanied by an elevation in preferred T_b and is attributed to ‘mating unrest’ (Rismiller and Heldmaier 1991). Tegus also increase their preferred daytime T_b in August and most notably, increase their nighttime T_b to exceed the increase in nighttime burrow temperature. This gives rise to a nighttime difference between T_b and T_{burrow} that is maintained throughout this period. At its peak, the $T_b - T_{\text{burrow}}$ difference is as much as 6–8°C (Fig. 28.3a) (Sanders et al. 2011).

The underlying cause(s) of this $T_b - T_{\text{burrow}}$ differential is unclear. It has recently been shown that if tegus are maintained in an environmental chamber at constant temperature with normal photoperiod at this time of year, they are capable of maintaining this differential for at least 10 days (length of the study period) (Fig. 28.3) (Milsom et al. 2011). Their ability to do this could not be due to activity as it still occurs during the nighttime quiescent period. Certainly, basic thermal inertia due to body size will

contribute but this too cannot explain their ability to sustain the differential for this period of time. This leaves two possibilities. The first is that it is due to changes in vascular tone and peripheral blood flow acting to decrease thermal conductance. Thermal conductance is inversely proportional to body mass in reptiles (McNab and Auffenberg 1976) and the size of the tegus will be of benefit in this regard. The second is that it reflects some degree of thermogenesis during this period. This remains to be determined. There is no doubt that this would also be enhanced by behavioural means, including the use of bedding/nesting material in the burrows as well as social huddling (Fig. 28.3b).

28.4 Perspective

The ongoing study of the ability of tegu lizards to adapt to seasonal change is providing new insight into the physiological capacity of ectothermic vertebrates to both suppress and enhance their body temperatures and metabolic rates. This will certainly help to conserve energy during periods of environmental challenge and to promote reproductive capacity during the mating season.

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