

Metabolic Response to Feeding in *Tupinambis merianae*: Circadian Rhythm and a Possible Respiratory Constraint

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ABSTRACT

The diurnal tegu lizard *Tupinambis merianae* exhibits a marked circadian variation in metabolism that is characterized by the significant increase in metabolism during part of the day. These increases in metabolic rate, found in the fasting animal, are absent during the first 2 d after meal ingestion but reappear subsequently, and the daily increase in metabolic rate is added to the increase in metabolic rate caused by digestion. During the first 2 d after feeding, priority is given to digestion, while on the third and following days, the metabolic demands are clearly added to each other. This response seems to be a regulated response of the animal, which becomes less active after food ingestion, rather than an inability of the respiratory system to support simultaneous demands at the beginning of digestion. The body cavity of *Tupinambis* is divided into two compartments by a posthepatic septum (PHS). Animals that had their PHS surgically removed showed no significant alteration in the postprandial metabolic response compared to tegus with intact PHS. The maximal metabolic increment during digestion, the relative cost of meal digestion, and the duration of the process were virtually unaffected by the removal of the PHS.

Introduction

The tegu lizard *Tupinambis merianae* is an active forager widespread in South America (Vanzolini et al. 1980; Avila-Pires 1995) that attains a body size of up to 450 mm snout-vent length and a body mass of up to 8 kg (Lopes and Abe 1999). In southeastern Brazil, activity of tegus varies seasonally, animals being active during the summer months (hot and rainy season) and entering into dormancy during the winter (cold and dry season; Abe 1995; Andrade et al. 2004). During dormancy, these lizards retreat into shelters (usually burrows dug in the soil), decrease activity to a minimum, and fast for 3–4 mo (Abe 1995; Andrade and Abe 1999). In middle September (spring), tegus become active again and engage in reproduction and feeding until the onset of the next dormancy season (Abe 1995; Lopes and Abe 1999).

In addition to the seasonal cycle in activity, active *Tupinambis* also exhibit a marked circadian rhythm. During activity, tegus usually leave the burrows where they have spent the night shortly after sunrise and bask until body temperature has reached levels adequate for activity (36°–37°C), which means that they experience a 10°–15°C increase in body temperature in about 5–7 h. During late afternoon and in the evening, body temperature changes (drops) by the same amount, although not as fast as during heating. Therefore, the body temperature of *T. merianae* can vary widely on a diurnal basis (Andrade et al. 2004). Paralleling the circadian variation in body temperature, tegus also show daily increments in metabolism that can elevate metabolic rate by 76% during the active hours; these changes persist even if the animals are kept in continuous dark and constant temperature for up to 10 d (W. K. Milsom, D. V. Andrade, S. P. Brito, L. F. R. Toledo, T. Wang, and A. S. Abe, unpublished article).

Animals in nature are challenged to perform multiple tasks simultaneously, and therefore the metabolic demands from different activities occurring at the same moment must be accommodated by the support system of the organism (Bennett and Hicks 2001). It has been well established that ectothermic organisms, including lizards (Secor and Phillips 1997; Hicks et al. 2000; Iglesias et al. 2003), may experience large increments in metabolism following the ingestion of food, that is, the specific dynamic action (SDA; Kleiber 1961). In the first part of this article, we examine how the increments in metabolism due to the circadian rhythm and the SDA are integrated in digesting tegus. We ask whether the metabolic demands of these two processes are added to each other or whether one activity is

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put aside while the other is given priority (see Bennett and Hicks 2001; Andrade et al. 2005).

In the second part of the article, we investigate the role of an accessory breathing structure in supporting the metabolic increments associated with food digestion in *T. merianae*. Tegu lizards possess a posthepatic septum (PHS) that divides the body cavity into two compartments: a cranial one containing the lungs and liver and a caudal one containing the stomach and the remaining viscera (Duncker 1978; Klein et al. 2000). This septum has been shown to be essential to the maintenance of visceral topology (Klein et al. 2003b) and to facilitate lung ventilation by acting as a mechanical barrier preventing the viscera from moving cranially during physical exertion (Klein et al. 2003a). The increased metabolic demand during SDA can match or even exceed that caused by exercise, and in both cases, concurrent ventilatory adjustments are observed (Overgaard et al. 1999; Hicks et al. 2000; Secor et al. 2000; Wang et al. 2001). Thus, it seems possible that the PHS may contribute to the adequate matching between ventilation and metabolism during the postprandial metabolic response of tegus, as it does during exercise (Klein et al. 2003a). We test this prediction by comparing the postprandial metabolic response between intact lizards and lizards that have had their PHS surgically removed. We anticipate that the PHS may have a greater importance for insuring adequate levels of ventilation during digestion than during locomotion. This idea is based on the observation that feeding results in stomach dilation, which, in the absence of the PHS, will cause the filled stomach to invade the pleural cavity and compress the lungs (Klein et al. 2003b), possibly hindering lung ventilation.

Material and Methods

Animals

All specimens of *Tupinambis merianae* used in this study were captive bred at the Jacarezário, Universidade Estadual Paulista, Rio Claro municipality, São Paulo state, southeastern Brazil. Five individuals had their PHS surgically removed at least 12 mo before experimentation (see Klein et al. 2003a, 2003b for details about the surgical procedure), while in the remaining individuals ($n = 6$), the PHS was intact. We did not dissect the PHS-ectomized animals after experimentation to verify the possible formation of scar or connective tissue because a previous study (Klein et al. 2003b) clearly demonstrated the lack of formation of scar tissue in tegus living 1 yr without a PHS, and this, accompanied by a drastic reorganization of the pleuroperitoneal viscera, precludes any morphological compensation of a removed PHS. Before experimentation, the animals were maintained in individual plastic boxes (74 cm \times 56 cm \times 41 cm) and fed twice a week with minced meat supplemented with minerals and vitamins. Water was available ad lib., and a bulb lamp fixed on the top of the cage provided a source of radiant heat (up to 40°C) for thermoregulation as well as a

12L : 12D cycle. Animals were fasted for at least 10 d before experimentation, and only individuals that seemed healthy and not moulting were used.

Experimental Protocol

The postprandial metabolic response of *T. merianae* was determined by measuring the rates of oxygen uptake ($\dot{V}O_2$) of lizards before (resting metabolic rate [RMR]) and after meal ingestion. Throughout the experiments, the tegus were kept inside respirometry chambers of adequate volumes and maintained within a climatic chamber at 30°C and constant dark. Tegus were allowed to acclimate to experimental temperature for at least 24 h before measurements, and RMR was monitored for no less than 48 h. After that, the respirometers were opened and the tegus offered minced beef ad lib., which they ate spontaneously. Immediately following meal ingestion, the measurements of $\dot{V}O_2$ were restarted and continued until the rate of $\dot{V}O_2$ uptake had returned to the RMR levels.

Respirometry

Oxygen uptake rates were measured using a computer-automated and intermittently closed respirometry setup (TR-RM8, Sable Systems). This system controls pumps and solenoid valves and was programmed to ventilate eight respirometers (six respirometric chambers containing tegus, the remaining two serving as reference chambers) with air (open phase, 200 mL min^{-1}) for 70 min while measuring intermittently the rate of oxygen depletion in each chamber during a 10-min closed phase when the air of a respirometric chamber was recirculated through an oxygen analyzer (PA-1, Sable Systems). As a result, oxygen uptake rates of every animal were measured for 10 min interspaced by 70 min before the next $\dot{V}O_2$ measurement. To remove water vapor, air flowed through a column of silica gel before reaching the respirometric chambers and before passing through the oxygen analyzer. The output from the gas analyzer was collected on a data acquisition system (DATACAN V, Sable Systems), and $\dot{V}O_2$ was calculated from the rate at which oxygen concentration decreased within the respirometer during the closed phase. The fall in oxygen concentration inside the respirometer was linear, and $\dot{V}O_2$ values were calculated as the inclination (b value) of the linear regression (minimum square 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 >0.9 , and the system was able to yield $\dot{V}O_2$ measurements every 80 min.

Data Analysis and Handling

RMR was determined from the $\dot{V}O_2$ measurements taken before feeding. However, whenever a circadian variation in metabolism could be identified, RMR was calculated to include only

$\dot{V}O_2$ measurements taken during the period in which the metabolism was depressed (usually at night). The measurements taken during the period in which metabolism was elevated were used to calculate the activity metabolic rate (AMR). The ratio between AMR and RMR yields the factorial increment in metabolism experienced by the tegus on a daily basis.

Maximal $\dot{V}O_2$ during digestion ($\dot{V}O_{2peak}$), the time to reach it, and the duration of the SDA were inferred by plotting all $\dot{V}O_2$ measurements during digestion and tracing the best curve fit using the software TableCurve 2D (Jandel Scientific). The factorial increment of metabolism was calculated as $\dot{V}O_{2peak}/RMR$. To analyze the parameters associated with digestive energetics, we transformed $\dot{V}O_2$ values and meal mass into energetic equivalents by assuming a caloric content of the meal (CCM) of 5.78 kJ g^{-1} minced beef (Vianna 1999). Furthermore, we assumed a respiratory exchange ratio of 1, which might have introduced a small error in the calculations. Net energetic cost of digestion (E_d) was calculated under the assumption that O_2 volume (total SDA) used in the aerobic metabolism (after subtracting the cost of maintenance during this period, calculated from RMR values) was equivalent to $0.0198 \text{ kJ mL } O_2^{-1}$ (Gessman and Nagy 1988). The SDA coefficient (% E_d ; see Jobling and Davies 1980) was expressed as the percentage of CCM that is allocated for digestion: SDA coefficient = $[(E_d/CCM) \times 100]$. Furthermore, we calculated the mean SDA increase dividing the total SDA by the time of SDA duration and set this value in proportion to RMR (mean SDA/RMR). For the calculation of SDA parameters, we disregarded metabolic increments that could be ascribed to the circadian changes in metabolism.

Daily changes in metabolism were envisaged by the application of a one-way ANOVA for repeated measurements followed by a Student-Newman-Keuls test comparing, along time, the rates measured during the low (RMR) and high (AMR) metabolism periods. By extending this analysis to the postprandial period, we were able to test whether the circadian change in metabolism persists even when metabolic rate is elevated due to the SDA. Differences in the parameters associated to the postprandial metabolic response between septum-removed and intact animals were tested by the application of a *t*-test. Before statistical procedures, we verified the premises of normality and homoscedasticity of the data. All values are presented as mean \pm SEM. Differences were considered to be statistically significant at the level of $P < 0.05$.

Results

Body mass of intact and PHS-removed tegus did not differ significantly (Table 1). PHS-removed tegus consumed a meal equaling $14.4\% \pm 1.4\%$ of their own body mass, whereas tegus with intact PHS ate meals with relative masses equaling $10.9\% \pm 1.2\%$. The larger meal size in PHS-removed tegus was

not significantly different ($P = 0.091$) from that of intact animals.

Circadian Variation in Metabolism

Tegus exhibited a clear diurnal cycle of variation in metabolic rate. This variation, however, was more pronounced in PHS-dissected tegus than in intact animals, as seen in Figures 1 and 2. This was caused mainly by the higher AMR of PHS-removed tegus, since RMR did not differ significantly between PHS-removed and intact lizards. In general, metabolism started to increase by 0900 hours and returned to resting values at about 1900 hours (Table 2). AMR was significantly different from RMR in the days in which the tegus were measured in fasting conditions. In average, the AMRs of fasting tegus were two times higher than RMR, and this increase did not differ between PHS-removed and intact animals.

After feeding, the difference between RMR and AMR was abolished for the two subsequent days in both experimental groups (see Figs. 1, 2). On the third day of the digestive period, a diurnal cycle in metabolic rate again became apparent, and the difference between RMR and AMR regained statistical significance. The reappearance of the circadian increase in metabolism caused the highest increments in metabolism observed during the postprandial period: 3.4- and 4.0-fold above RMR for tegus with and without PHS, respectively.

Postprandial Metabolic Response in PHS-Removed versus Intact Lizards

The maximum rates of oxygen consumption during digestion, the time to reach these rates, and SDA duration showed no significant differences between intact and PHS-removed tegus. Metabolism after feeding, disregarding the metabolic increment associated with AMR (see above), was increased in animals with and without PHS by 2.8- and 3.1-fold above RMR, respectively (Table 1).

Calculating energetics of digestion revealed that both groups of animals showed similar net energetic costs of digestion, but tegus without PHS exhibited significantly greater SDA coefficients. The mean increase in metabolism over the whole SDA response is not significantly different between animals with and without PHS. The relationship mean SDA/RMR, however, is significantly lower in tegus without PHS (Table 1).

Discussion

PHS and Meal Ingestion

Ingested meal masses did not differ statistically between intact and PHS-removed tegus, which makes it seem unlikely that the small difference in relative meal size between the two groups ($\sim 3.5\%$) could significantly affect any of the SDA parameters discussed below. In intact tegus, the PHS divides the visceral

Table 1: Oxygen consumption rates and basic parameters associated with specific dynamic action (SDA) of *Tupinambis merianae* with and without posthepatic septum (PHS) at 30°C

	Intact PHS (N = 6)	PHS Removed (N = 5)	P
Body mass (g) ^a	796.7 ± 65.4	880. ± 90.1	.464
Meal (% MB)	10.9 ± 1.2	14.4 ± 1.4	.091
RMR (mL O ₂ kg ⁻¹ h ⁻¹)	116.0 ± 14.1	137.0 ± 6.1	.204
AMR (mL O ₂ kg ⁻¹ h ⁻¹) ^a	194.3 ± 26.5	268.1 ± 8.1*	.026
$\dot{V}O_{2peak}$ (mL O ₂ kg ⁻¹ h ⁻¹)	321.2 ± 31.6	395.1 ± 14.1	.078
$\dot{V}O_{2peak}$ + AMR (mL O ₂ kg ⁻¹ h ⁻¹) ^b	359.1 ± 35.9	501.3 ± 77.5	.111
SDA duration (h) ^c	113.9 ± 7.9	133.3 ± 5.9	.090
Time to $\dot{V}O_{2peak}$ (h) ^c	33.0 ± 2.7	37.4 ± 1.0	.201
AMR/RMR ^d	2.0 ± .5	1.9 ± .1	.928
$\dot{V}O_{2peak}$ /RMR	2.8 ± .2	3.1 ± .2	.431
$\dot{V}O_{2peak}$ + AMR/RMR ^e	3.4 ± .3	4.0 ± .5	.238
CCM (kJ)	515.4 ± 63.5	716.7 ± 72.8	.066
E _d (kJ)	187.0 ± 24.4	176.7 ± 38.1	.820
% E _d	36.3 ± 2.5	24.9 ± 4.0*	.024
Total SDA (mL O ₂)	9,443.5 ± 1,231.0	8,926.3 ± 1,922.0	.820
Mean SDA increase (mL O ₂ h ⁻¹)	85.3 ± 13.5	69.1 ± 16.0	.458
Mean SDA/RMR	.96 ± .1	.54 ± .1*	.042

Note. Data are presented as means ± SEM. See text for abbreviations.

^a Measured before feeding.

^b AMR at the peak of SDA.

^c Measurements of time include a 35-min error as a result of the respirometry sampling protocol.

^d Relationship determined before feeding for each night and the following day for each animal.

^e Relationship determined by comparing lowest value of RMR with $\dot{V}O_{2peak}$ plus AMR.

* Significant difference to intact tegus.

cavity and helps to maintain visceral topology by keeping the lung and liver separated from the remaining viscera, particularly the stomach and intestines. On the surgical removal of the PHS, Klein et al. (2003b) have shown that the stomach moves cranially and invades the pleuro-hepatic cavity, reducing the space for the lungs. Accordingly, it was suggested that the PHS facilitates ventilation by acting as a mechanical barrier and preserving the integrity of the pleurohepatic cavity, especially during physical exertion (Klein et al. 2003a). Because we found no significant difference in ingested meal masses between the experimental groups, it remains speculative whether removal of the PHS influences the food intake capacity in tegu lizards.

Circadian Changes in Metabolism

Tegus are heliothermic lizards well known for their very marked diurnal cycle of activity. Such a cycle can be characterized by animals spending the night in burrows, basking in the morning, and being active during the hotter hours of the day (Lopes and Abe 1999). Our data show that even when confined in respirometric chambers with no access to environmental cues and at a constant temperature, the metabolic rate of tegus will increase significantly during the day. This is in agreement with

data collected by W. K. Milsom, D. V. Andrade, S. P. Brito, L. F. R. Toledo, T. Wang, and A. S. Abe (unpublished article) and indicates that the establishment of the circadian changes in the metabolism of tegus is not completely dictated by thermoregulatory behavior and changes in body temperature. As true for other reptiles (Iglesias et al. 2003), the establishment of cyclical changes in physiological functions during the day probably involves the participation of endogenous factors.

Because no difference was observed in the pattern of activity between intact and PHS-removed tegus (W. Klein, personal observation), it is not surprising that the circadian change in metabolism was not affected by the removal of the PHS. Independently of the PHS removal, metabolic rate practically doubled during the active hours of the day in comparison with RMR. Nonetheless, septum-removed lizards exhibited AMRs that were considerably higher than intact animals. Our observation, therefore, contradicts previous data showing that metabolism, during rest and exercise, is decreased in PHS-removed tegus (Klein et al. 2003a). Such a difference may be related to methodological differences—Klein et al. (2003a) measured O₂ uptake in masked animals by a flow-through system, while in this study, we used closed respirometry in minimally disturbed

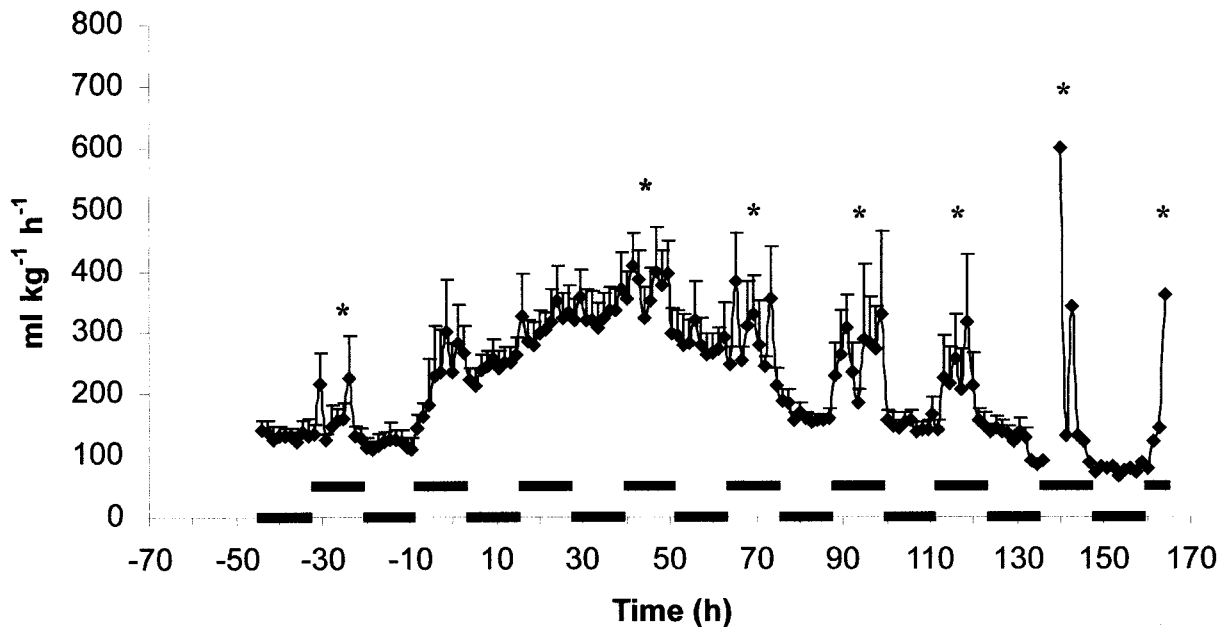


Figure 1. Oxygen consumption rates ($\dot{V}O_2$) in *Tupinambis merianae* with intact posthepatic septum (PHS) in response to the ingestion of a meal representing $10.9\% \pm 1.2\%$ of an animal's body mass. $\dot{V}O_2$ was measured for 2 d preprandial, animals were fed at time 0, and the change in $\dot{V}O_2$ was recorded for the next 160 h. Data are presented as mean \pm SEM. $N = 6$. The black bars indicate a 12L:12D cycle (0700–1900 hours represented by upper bars). An asterisk denotes a significant difference between AMR and RMR of the following day.

animals. Finally, the higher AMRs of PHS-removed tegus found in our study might be caused by a decrease in breathing efficiency (i.e., higher breathing cost; see Klein et al. 2003c), but because RMR remains equal between intact and dissected tegus, other explanations, such as a greater activity of PHS-removed animals inside the respirometric chambers, cannot be excluded.

Postprandial Metabolic Response (SDA)

The magnitude of the postprandial response exhibited by the tegu lizards fits well within the limits reported for frequently feeding lizards (Secor 2001). Tegus are active foragers whose diet, in nature, is probably formed by relatively small items ingested on a daily basis, although large meals are occasionally consumed (Vanzolini et al. 1980; Mercolli and Yanosky 1994; Martuscelli and Olmos 1996; Kiefer and Sazima 2002). In captivity, adult tegus will accept food on a daily basis or larger amounts once or twice a week (A. S. Abe, personal observation). To ensure that our tegus were postabsorptive, the lizards were not fed for 10 d, a long interval for this species, and then were allowed to feed ad lib., which resulted in unusually long fasting intervals and large meal sizes for the species. Thus, the SDA response reported here is probably greater than the one normally experienced by tegus. Even so, the SDA response of tegus was noticeably modest when compared to that exhibited by an infrequently feeding species of *Varanus*, for which the post-

prandial metabolism increased 10-fold after the ingestion of a meal with a relative size of 9.3% (Secor and Phillips 1997).

The difference in the magnitude of the SDA response between frequently and infrequently feeding reptile species has been suggested to be related to differences in the morphological changes of the gut associated with feeding regime (Secor 2001). A species feeding infrequently and experiencing an atrophy of the gut epithelium during extended fasting periods would show large postprandial metabolic responses due to the costly up-regulation of the gut following meal ingestion (Secor 2001). Nonetheless, recent data gathered on snakes have shown that intestinal regeneration contributes little to the overall SDA response (Starck and Beese 2001, 2002; Overgaard et al. 2002; Secor 2003). Thus, it seems unlikely that the difference in the magnitude of the SDA response between frequently and infrequently feeding lizards might be related to differences in intestinal regulation.

Frequently feeding lizards are known to maintain an elevated metabolic rate compared to counterparts that are fed infrequently (Iglesias et al. 2003). As a consequence, the factorial increase in metabolic rate tends to be smaller for these species when compared with infrequently feeding lizards whose low RMR inflates the factorial increment. This observation seems to explain adequately the difference in the postprandial factorial scope between *Tupinambis* (this study) and *Varanus* (Secor and Phillips 1997) because both species attain a postprandial peak

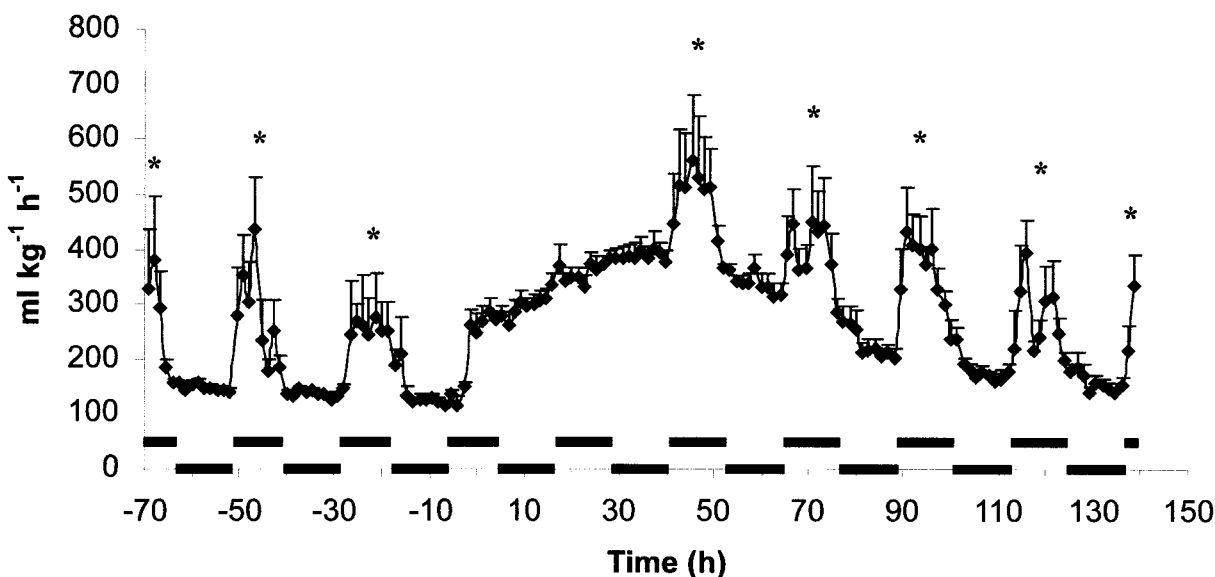


Figure 2. Oxygen consumption rates ($\dot{V}O_2$) in *Tupinambis merianae* with removed posthepatic septum (PHS) in response to the ingestion of a meal representing $14.4\% \pm 1.4\%$ of an animal's body mass. $\dot{V}O_2$ was measured for 3 d preprandial, animals were fed at time 0, and the change in $\dot{V}O_2$ was recorded for the next 140 h. Data are presented as mean \pm SEM. $N = 5$. The black bars indicate a 12L : 12D cycle (0700–1900 hours represented by upper bars). An asterisk denotes a significant difference between AMR and RMR of the following day.

in metabolism that is almost identical ($\sim 350 \text{ mL O}_2 \text{ kg}^{-1} \text{ h}^{-1}$), despite the fact that the resting metabolic rate in *Varanus* ($35 \text{ mL O}_2 \text{ kg}^{-1} \text{ h}^{-1}$; Secor and Phillips 1997) is one-third of that observed for *Tupinambis* ($116 \text{ mL O}_2 \text{ kg}^{-1} \text{ h}^{-1}$; see Table 1). The energetic costs of digestion of *Tupinambis*, on the other hand, are similar to the values found in *Varanus albigularis*, another large carnivorous lizard (Secor and Phillips 1997) and greater than most values measured in frequently feeding reptiles (Secor and Diamond 1997; Secor 2001).

Effects of PHS Removal on SDA

Of the parameters used to describe the postprandial metabolic response, only the SDA coefficient and the relationship mean SDA/RMR differed significantly between septum-removed and intact lizards. The small and not statistically significant differences between experimental groups agree with the pattern usually caused by variation in meal size (Andrade et al. 1997; Secor and Diamond 1997). Accordingly, septum-removed tegus, which were fed with meals 4% larger, exhibited a higher $\dot{V}O_{2\text{peak}}$, which was attained later, and a longer SDA duration. Therefore, it seems unequivocal that the PHS is not vital to ensure adequate levels of ventilation in order to support the increased rates of metabolism during digestion in *Tupinambis merianae*. This observation contradicts our expectation that the removal of the PHS would hinder lung ventilation by the displacement of the stomach, on food intake, toward the pleural cavity.

Septum-removed tegus are unable to attain the same degree of lung ventilation exhibited by intact animals while walking on a treadmill. During locomotion, they are constrained in regard to changes in tidal volume and partially compensate for that by increasing breathing frequency (Klein et al. 2003a). Whether tegus employ the same strategy during digestion remains to be investigated. For animals running on a treadmill, it was suggested that the PHS would help to maintain a minimum space for the lungs, preventing the displacement of the viscera toward the pleural cavity, which otherwise would occur due to the lateral undulation of the trunk during locomotion (Klein et al. 2003a). Digestion does not hinder ventilation as

Table 2: Times of a day when RMR first increased to AMR (arousal) and returned to RMR (return to rest) in *Tupinambis merianae* with and without posthepatic septum (PHS) at 30°C

	Intact PHS ($N = 6$)	PHS Removed ($N = 5$)
AMR	0906 hours \pm 16 min (0620–1300 hours)	0853 hours \pm 7 min (0704–1154 hours)
RMR	1856 hours \pm 17 min (1700–2220 hours)	1905 hours \pm 16 min (1624–2044 hours)

Note. Data are presented as means \pm SEM, with minimum and maximum values in parentheses. The estimates of SEM include a 35-min error due to the sampling protocol (i.e., the half-time between two consecutive $\dot{V}O_2$ measurements for any individual lizard).

the axial constraint caused by lateral undulation during locomotion does and is, in general, accompanied by a decrease in activity (D. V. Andrade, personal observation). This might in part explain why PHS removal did not affect the SDA response of tegus. Finally, experimental data in *Varanus* show that, while exercise is accompanied by hyperventilation, digestion is characterized by a relative hypoventilation (Hicks et al. 2000); that is, for the same level of metabolic increment, the rate of ventilation will be greater during exercise than during digestion. Thus, it seems plausible that the role of the PHS, as an accessory breathing structure, will be more pronounced during exercise than during digestion.

The significantly lower SDA coefficient in tegus with removed PHS may be explained by the greater RMR in animals without PHS. Despite showing a greater $\dot{V}O_{2\text{peak}}$, tegus without PHS exhibited a similar mean increase in SDA during the SDA duration compared with intact tegus, which leads to a significantly lower mean SDA/RMR relationship in tegus without PHS.

Interaction between Postprandial and Circadian Changes in Metabolism

Because animals may become simultaneously engaged in multiple activities, their physiological system must be able to accommodate these concurrent metabolic demands. Such interaction may happen by (1) additivity, meaning that the demands from different activities are added to each other, increasing total metabolism to the level expected by the sum of the demands for each activity; or (2) prioritization, meaning that the support system gives priority to one activity while the other(s) are put aside. Obviously, different degrees of additivity and prioritization might occur simultaneously, and this would cause the metabolic increment to be shared among different demands. Until now, the interaction between different activities in ectothermic vertebrates has been investigated only in regard to exercise and digestion. In all cases, which include toads (Andersen and Wang 2003), snakes (Secor et al. 2000), and lizards (Bennett and Hicks 2001), the metabolic responses to exercise and digestion were added to each other. Unfortunately, we did not monitor the activity of the tegus while determining their $\dot{V}O_2$, but based on occasional observations, we suggest that the greater metabolic rate during the day was accompanied by the animal becoming more active inside the chamber, moving around, and trying to escape from the chamber. Therefore, the physiological basis for the circadian increments in metabolic rate might involve, to a great extent, muscle exercise. In this regard, the data collected on the third and subsequent days postprandial agree well with the notion that the metabolic demands from digestion and exercise are added to each other (Secor et al. 2000; Bennett and Hicks 2001; Andersen and Wang 2003) because daily and cyclical increases in metabolism are clearly distinguishable by that time. On the 2 d immediately

following feeding, however, tegus seem to prioritize digestion to the detriment of the circadian changes in metabolism. Such a response is remarkably similar to that of the snake *Lamprophis fuliginosus*, in which circadian changes in metabolism are abolished during the first 2 d postprandial but are resumed thereafter (Roe et al. 2004). The only significant difference between the responses exhibited by *L. fuliginosus* and tegus is that in the snakes, the maximum metabolic increment recorded on the third and subsequent days postprandial, which include the SDA plus the circadian metabolic increments, are never higher than the peak in metabolic rate recorded between the first and second day after feeding and that are due to SDA only. Such differences preclude us from extending the considerations drawn below to snakes as they are based on our data on *Tupinambis*.

The prioritization of digestion in the first 2 d postprandial is suggested by the absence of cyclical changes in metabolism during this period and by the shape of the SDA curve, which, if drawn without the circadian changes, agrees perfectly with the pattern usually observed in reptiles—the attainment of a peak in metabolism soon after meal ingestion, followed by the progressive and slower return to fasting level (Wang et al. 2001). To obtain the same pattern, assuming that no priority was given to digestion on the first 2 d of digestion, we would have to assume that tegu lizards suppressed the SDA metabolic demand to the same degree that it was increased due to the circadian rhythm. This possibility seems unlikely if we consider that on the third day postprandial, tegus recommence to show the circadian rhythm exhibiting metabolic rates that were significantly higher than the levels observed during the first 2 d of digestion, showing that on the first and second day postprandial, the tegus would be able to increase metabolic rate further, adding metabolic demands of activity and digestion, but they do not. This suggests that the prioritization of digestion in the initial phases of the process is a behaviorally regulated response of the animal, reducing its activity during the first 2 d of digestion. A natural question raised by this consideration is why tegus would shut the circadian rhythm off during the first 2 d postprandial. We cannot offer a definite explanation for that, but many species of reptiles are known to become less active in the days immediately following feeding (Beck 1996; Wang et al. 2003; D. V. Andrade, personal observation), possibly due to the impairment of locomotion shortly after meal ingestion (Garland and Arnold 1983; Ford and Shuttlesworth 1986). Also, there might be no need for the animal to forage on a full stomach until a great part of the meal has been processed. On the other hand, digestion could be a priority for tegus in the first days postprandial, when they need some time to remodel the cardiopulmonary system to increase transport capacity significantly to match the simultaneous demands of circadian and SDA-related metabolic increments during the later phase of the postprandial response (Wang et al. 2005). It remains to be elucidated which might be the causal mechanism for the lack

of circadian variation in tegu metabolism during the first 2 d following feeding.

In conclusion, our data unequivocally show that the interaction between different metabolic demands may be plastic. Tegus favor digestion during the first 2 d postprandial and, thereafter, start to add the metabolic increment caused by circadian changes to the SDA-linked demand.

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