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Digestive state influences the heart rate hysteresis and rates of heat exchange in the varanid lizard *Varanus rosenbergi*

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Summary

To maximize the period where body temperature (T_b) exceeds ambient temperature (T_a), many reptiles have been reported to regulate heart rate (f_H) and peripheral blood flow so that the rate of heat gain in a warming environment occurs more rapidly than the rate of heat loss in a cooling environment. It may be hypothesized that the rate of cooling, particularly at relatively cool T_bs, would be further reduced during postprandial periods when specific dynamic action (SDA) increases endogenous heat production (i.e. the heat increment of feeding). Furthermore, it may also be hypothesized that the increased perfusion of the gastrointestinal organs that occurs during digestion may limit peripheral blood flow and thus compromise the rate of heating. Finally, if the changes in f_H are solely for the purpose of thermoregulation, there should be no associated changes in energy demand and, consequently, no hysteresis in the rate of oxygen consumption ($\dot{V}_{O_2}$). To test these hypotheses, seven individual *Varanus rosenbergi* were heated and cooled between 19°C and 35°C following at least 8 days fasting and then approximately 25 h after consumption of a meal (mean 10% of fasted body mass). For a given T_b between the range of 19–35°C, f_H of fasting lizards was higher during heating than during cooling. Postprandial lizards also displayed a hysteresis in f_H, although the magnitude was reduced in comparison with that of fasting lizards as a result of a higher f_H during cooling in postprandial animals. Both for fasting and postprandial lizards, there was no hysteresis in $\dot{V}_{O_2}$ at any T_b throughout the range although, as a result of SDA, postprandial animals displayed a significantly higher $\dot{V}_{O_2}$ than fasting animals both during heating and during cooling at T_bs above 24°C. The values of f_H during heating at a given T_b were the same for fasting and postprandial animals, which, in combination with a slower rate of heating in postprandial animals, suggests that a prioritization of blood flow to the gastrointestinal organs during digestion is occurring at the expense of higher rates of heating. Additionally, postprandial lizards took longer to cool at T_bs below 23°C, suggesting that the endogenous heat produced during digestion temporarily enhances thermoregulatory ability at lower temperatures, which would presumably assist *V. rosenbergi* during cooler periods in the natural environment by augmenting temperature-dependent physiological processes.

Key words: metabolic rate, metabolism, digestion, rate of oxygen consumption, body temperature, reptile, goanna, fasting, postprandial.

Introduction

Reptiles, as ectotherms, have low endogenous heat production and primarily use behavioural mechanisms to obtain their desired body temperature (T_b), which is almost always above ambient temperature (T_a), to optimize physiological processes (Harlow et al., 1976; Stevenson et al., 1985; Autumn and Denardo, 1995; Busk et al., 2000; Secor, 2003; Toledo et al., 2003). These behavioural mechanisms are often assisted by the phenomenon where heating occurs at a faster rate than cooling (Bartholomew and Tucker, 1963; Grigg and Seebacher, 1999). Enhanced heat transfer between the environment and the core of the body in a warm environment is often accomplished by increased cutaneous perfusion, mediated through increases in heart rate (f_H). Conversely, retention of heat during the cooling period is often assisted by reductions in peripheral blood flow and f_H (Morgareidge and White, 1969; Grigg and Alchin, 1976; Smith et al., 1978). Another avenue of heat available to reptiles is that generated by the increase in metabolic rate associated with digestion [i.e. specific dynamic action (SDA)], and it could be expected that a postprandial reptile, as a consequence of the increased heat production, would have a reduced rate of cooling. Minimizing the rate of cooling would increase the time available where T_b exceeds T_a, thereby augmenting temperature-dependent physiological processes.

A study on the savannah monitor (*Varanus exanthematicus*) reported that the rate of cooling from 35°C to 27°C was not

affected by SDA (Bennett et al., 2000), leading the authors to dismiss the thermoregulatory hypothesis proposed for the evolution of endothermy, which postulates that increments in metabolic rate of ancestral ectotherms elevated T_b and helped to retard changes in T_b in different thermal environments (Ruben, 1995). Nevertheless, in the study by Bennett et al. (2000), the heat increment of feeding of *V. exanthematicus* at 32°C (increase of 0.65°C) was greater than that at 35°C (increase of 0.40°C). Furthermore, the Q_{10} of the metabolic increment associated with digestion in the Burmese python (*Python molurus*) from 25°C to 35°C was less than that of resting metabolic rate (reworked data from Wang et al., 2003), indicating that the relative increase in metabolism associated with digestion is greater at cooler temperatures than at warmer temperatures.

It may be hypothesized, therefore, that the rate of cooling during digestion would be more greatly influenced at lower temperatures when the heat increment of feeding is proportionately greater. Additionally, like other vertebrates, reptiles cannot maximally perfuse all of the circulatory beds at the same time, thus the increased perfusion of the gastrointestinal organs that occurs during digestion may compromise cutaneous perfusion during warming if f_H cannot increase sufficiently to perfuse enough blood to satisfy both processes (see Zaar et al., 2004). Consequently, the rate of heating may be reduced in postprandial animals, although this was reported not to be the case for *V. exanthematicus* over a relatively narrow temperature range (28–38°C; Zaar et al., 2004). Finally, if the changes in f_H are solely for the purpose of modifying peripheral perfusion, there should be no associated changes in energy demand and, consequently, no hysteresis in the rate of oxygen consumption ($\dot{V}_{O_2}$). To test these hypotheses, we measured the rates of heating and cooling, and the associated changes in f_H and $\dot{V}_{O_2}$, in fasting and postprandial *Varanus rosenbergi* Mertens 1957 when given the opportunity to thermoregulate behaviourally over a broad T_b range of 19–35°C, which is within the T_b range (10–38°C) previously reported for this species in the natural environment (Christian and Weavers, 1994; Rismiller and McKelvey, 2000).

Materials and methods

Animals

Data on the rate of oxygen consumption ($\dot{V}_{O_2}$), heart rate (f_H) and body temperature (T_b) were obtained from seven lizards *Varanus rosenbergi* Mertens 1957 with a mean fasted body mass (M_b) ± S.E.M. of 1.35±0.09 kg. Animals were obtained from Kangaroo Island, South Australia and kept in a temperature-controlled holding facility at approximately 28–31°C at La Trobe University and used within 25 days of capture (Animal Ethics Approval Number 99/42L). They had unlimited access to water and were exposed to a 12 h:12 h light:dark cycle with access to a heat lamp during light hours.

Instrumentation

The lizards were instrumented using similar methods to those described in Clark et al. (2005a). Briefly, $\dot{V}_{O_2}$ was obtained by lightly taping a lightweight (approximately 10 g), transparent, loose-fitting mask over the head of the animal. Air was drawn through the mask by a pump (1–4 l min^{-1}), and a subsample of the air leaving the pump was passed through columns containing a drying agent (Drierite; Hammond, Xenia, OH, USA) and a carbon dioxide absorbent (Dragersorb; Lubeck, Germany) and subsequently analysed for the fractional content of oxygen by a calibrated gas analyser (Powerlab ML205; ADInstruments, Sydney, Australia). The rate of oxygen consumption was calculated from airflow through the mask and the difference between incurrent and excurrent fractional concentrations of dry, CO_2-free air (see appendix in Frappell et al., 1992). Values of $\dot{V}_{O_2}$ are expressed at STPD.

Heart rate was determined from an electrocardiogram (ECG). Three leads were attached to the dorsal surface of the animal, in an arrangement that triangulated the heart, by using self-adhesive Ag/AgCl ECG electrode pads (Unilect, Wiltshire, UK). The ECG signal was appropriately amplified (BIO amp; ADInstruments). Body temperature was measured by inserting a calibrated thermocouple (T-type Pod; ADInstruments) 5–6 cm into the cloaca, which remained in position for the duration of the experiment. The outputs from this, the gas analyser and the ECG amplifier were simultaneously collected at 100 Hz (Powerlab 8sp; ADInstruments) and displayed on a computer using Chart software (ADInstruments). Animals were monitored throughout all experiments using a digital computer-linked camera.

Protocol

Heating and cooling in fasting lizards

Animals were fasted for at least 8 days prior to the first series of experiments. Animals were removed from the holding facility (28–31°C), instrumented and placed in a constant temperature room (floor area 1.5 m×2.0 m) at 14°C. When T_b dropped below 19°C, a heat lamp positioned above the floor was switched on. The maximum skin temperature that a lizard could possibly attain under the heat lamp was 43°C [determined during a control experiment when three dead lizards (mean M_b=1.59±0.11 kg) were left under the heat lamp until skin temperature reached a plateau]. Hence, the temperature differential between T_b and T_a (ΔT) was similar when T_b was 29°C during heating (ΔT=43–29=14°C) and 28°C during cooling (ΔT=28–14=14°C) or when T_b was 30°C during heating (ΔT=43–30=13°C) and 27°C during cooling (ΔT=27–14=13°C), and so on. Most lizards voluntarily moved underneath the lamp to bask, although on very few occasions the lizard was initially gently moved by the experimenter. All lizards voluntarily moved from underneath the lamp when they reached a T_b of 33–36°C, and either rested and cooled, or shuttled in and out from underneath the heat lamp. After a few hours, the heat lamp was switched off and the lizards that had shuttled were allowed to cool again to obtain a T_b below 19°C (two fasting

individuals were cooled only to 20°C; see Table 1). The lizard was then removed from the room and returned to the holding facility.

Heating and cooling in postprandial lizards

Five to 10 days after the initial series of experiments, animals in the holding facility were individually fed mice and/or chicken necks to satiation (7–18% of fasted body mass, mean 10±1%; all animals fed voluntarily). Animals were then placed in the constant temperature room at 30±1°C and observed (maximum 5 h) for any food regurgitation, after which time they were instrumented as outlined above. One animal regurgitated part of its meal 3.5 h after feeding, so the mass of the food consumed by that individual was recalculated accordingly. All animals remained relatively quiescent for at least 23 h after consumption of a meal, and any brief periods of activity were excluded from the analysis (see below). After approximately 23 h (in *V. exanthematicus*, postprandial f_H and $\dot{V}_{O_2}$ reach a maximum at ~24 h; Hicks et al., 2000), the room temperature was dropped to 14°C (taking approximately 30 min) and, when T_b dropped below 19°C, the heat lamp was switched on and the heating and cooling protocol followed as outlined above. This protocol made it possible to perform fasting and postprandial heating and cooling experiments on each individual with only small differences in M_b (mean fasting M_b, 1.35±0.09 kg; mean postprandial M_b, 1.34±0.09 kg), given that the increase in M_b that was associated with consumption of a meal was typically countered by the decrease in M_b that had occurred for each individual between the fasting and postprandial experiments (i.e. 5–10 days).

Data analysis and statistics

Body mass was measured immediately prior to each particular experiment, and $\dot{V}_{O_2}$ was normalised using fasting M_b (to account only for metabolizing tissue), while time taken to heat/cool was normalised using total M_b, which included any food that had been consumed (see Discussion). Data for all variables were averaged into 30 s blocks before further analysis. Only data for resting animals were used in the analysis; any periods of activity during the postprandial, heating or cooling periods (determined using the camera and/or interference signals on the ECG trace) were excluded. The dead lizards that were used as a control (see above) were heated and cooled, following the same protocol as outlined above, for comparison with live animals (see Table 1). It should be noted that this study was not undertaken for a comprehensive comparison of heating *versus* cooling rates, but rather to compare fasting and postprandial lizards under an identical experimental setup. Differences in heat exchange, $\dot{V}_{O_2}$ and f_H during heating and cooling for fasting and postprandial animals at each T_b were analysed using two-way analysis of variance (ANOVA) for repeated measures. A Bonferroni *t*-test was applied where appropriate to distinguish mean values that differed significantly. N=7 unless otherwise indicated. All data are presented as means ± S.E.M.

Results

Typical traces of $\dot{V}_{O_2}$, f_H and T_b, both for fasting and postprandial experiments, are given for an individual in Fig. 1 to illustrate the experimental protocol. Six hours after a meal, postprandial lizards (mean T_b, 30.5±0.4°C) displayed $\dot{V}_{O_2}$ and f_H that were 2.0±0.2 ml min^{-1} kg^{-1} and 35±3 beats min^{-1}, respectively. Both variables increased steadily during the postprandial period to reach values of 4.2±0.4 ml min^{-1} kg^{-1} and 50±4 beats min^{-1} at 23 h (P<0.05; Fig. 2). The mean heat increment of feeding determined during this period (6–23 h after prey consumption) was 1.4±0.2°C (P<0.05; Fig. 2C), although individual measurements ranged from 0.5°C to 2.1°C.

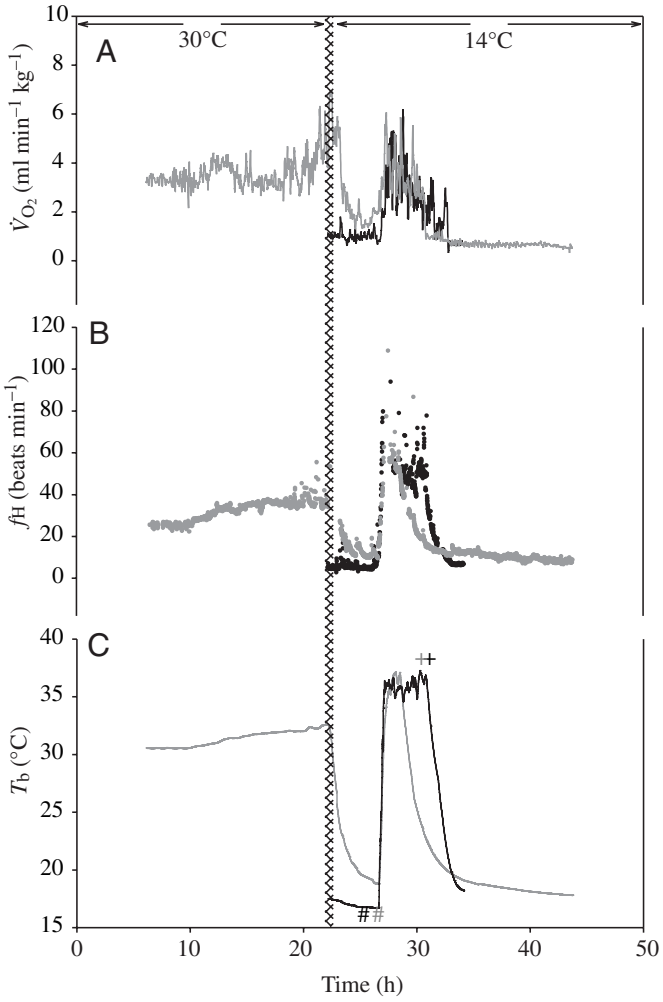

Fig. 1. Representative trace of (A) the rate of oxygen consumption ($\dot{V}_{O_2}$), (B) heart rate (f_H) and (C) body temperature (T_b) measured from a single individual while fasting (black symbols and lines) and while postprandial (grey symbols and lines). Each trace includes the entire period for which the animal was instrumented, and traces for each digestive state have been aligned to coincide with the period when the lizard moved under the heat lamp. Lizard was fed at 0 h. In C, # and + indicate the times at which the heat lamp was switched on and off, respectively. During the postprandial state, the animal remained at an ambient temperature of 30°C until approximately 23 h, after which room temperature was decreased to 14°C (indicated by hatched vertical line).

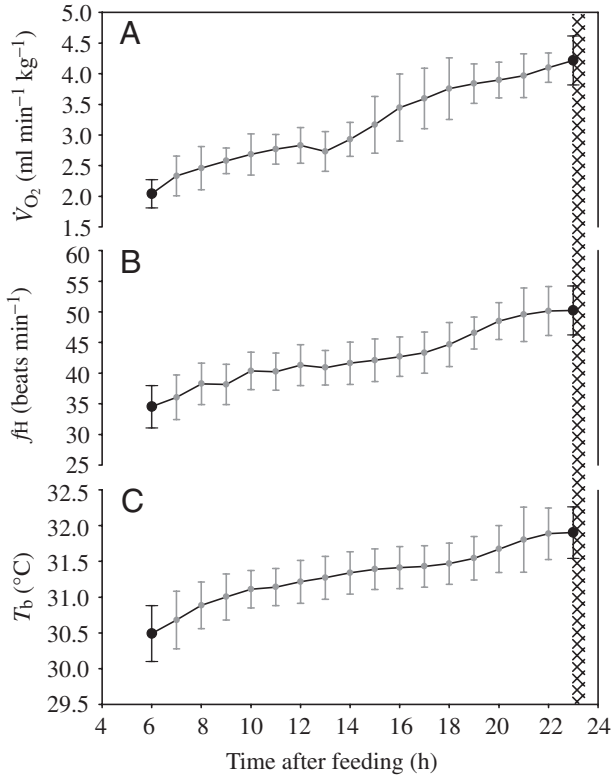

Fig. 2. The changes in (A) the rate of oxygen consumption ($\dot{V}_{O_2}$), (B) heart rate (f_H) and (C) body temperature (T_b) for *V. rosenbergi* at an ambient temperature of 30°C measured every hour between 6 h and 23 h following consumption of a meal (~10% of fasted body mass; see Materials and methods). All parameters were significantly higher at 23 h postprandial than they were at 6 h postprandial (P<0.05; see Results). The hatched vertical bar indicates the time at which room temperature was decreased to 14°C in order to begin the hysteresis experiments. Values are means ± S.E.M.

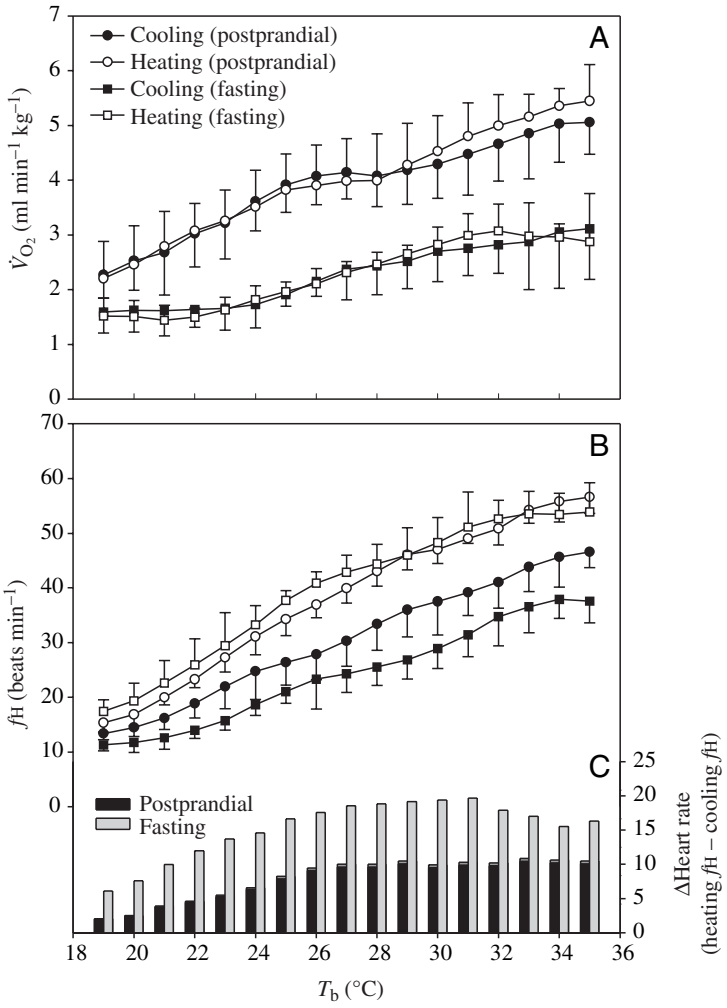

Fig. 3. Relationship for *V. rosenbergi* of (A) the rate of oxygen consumption ($\dot{V}_{O_2}$) and (B) heart rate (f_H) *versus* body temperature (T_b±0.4°C) during heating and cooling in fasting (squares) and postprandial (circles) lizards. Irrespective of digestive state, a hysteresis in $\dot{V}_{O_2}$ during heating and cooling was not observed, although, both during heating and cooling between 25°C and 35°C, $\dot{V}_{O_2}$ was significantly higher in postprandial lizards than in fasting lizards. There was a significant hysteresis in f_H during heating and cooling from 19°C to 35°C in fasting animals although, for postprandial animals, the f_H hysteresis was significant only between 24°C and 35°C. Values are means ± S.E.M. (C) The absolute differences in f_H between heating and cooling for fasting (grey bars) and postprandial (black bars) animals.

Both fasting and postprandial lizards displayed a hysteresis in f_H, with values during cooling being lower than those during heating at a given T_b. Heart rate during heating was the same for each digestive state at any given T_b between 19°C and 35°C (Fig. 3B), although the magnitude of the hysteresis for postprandial lizards was reduced (P<0.05 above 23°C only) in comparison with that of fasting lizards (P<0.05 at all T_bs) as a result of a higher f_H during cooling for a given T_b (Fig. 3B). The mean maximum difference in f_H between cooling and heating for fasting lizards was 19.7 beats min^{-1}, which occurred at 31°C, while the mean maximum difference in f_H for postprandial lizards was only 10.4 beats min^{-1}, which occurred at 33°C (Fig. 3C).

By contrast, no hysteresis existed for $\dot{V}_{O_2}$ in either group at any T_b throughout the range (Fig. 3A). Nevertheless, as a consequence of the metabolic increment associated with feeding, postprandial animals displayed a higher $\dot{V}_{O_2}$ than fasting animals both during heating and during cooling (P<0.05 above 24°C only).

Inverse rates of heating (the time taken per kg for a 1°C change in T_b) for fasting and postprandial animals were temperature independent over the entire range (P>0.05; Table 1), and both fasting and postprandial lizards heated more rapidly than the dead control animals (Table 1; P>0.05). Postprandial lizards tended to heat more slowly than fasting lizards at all T_bs and, consequently, took 1.7× longer than fasting animals to heat from 19°C to 35°C (P=0.043; Table 1). The control animals cooled quicker than live fasting animals under the same experimental conditions, suggesting that the resting heat production of live fasting animals, albeit minor, is

Table 1. *Time taken per kg for a 1°C change in body temperature for* V. rosenbergi *during heating and cooling while fasting and postprandial (25 h after consumption of a meal that was ~10% fasted body mass)*

	Time per unit mass for 1°C change in T_b					
	Fasting		Postprandial		Control animals	
Body temperature (°C)	Heating (min deg.$^{-1}$ kg^{-1})	Cooling (min deg.$^{-1}$ kg^{-1})	Heating (min deg.$^{-1}$ kg^{-1})	Cooling (min deg.$^{-1}$ kg^{-1})	Heating (min deg.$^{-1}$ kg^{-1})	Cooling (min deg.$^{-1}$ kg^{-1})
19	1.7±0.3	13.9±3.2*,†	3.8±1.3	47.4±11.6†,‡	2.9±0.9	9.8±2.4
20	1.4±0.3	10.8±2.9†	3.7±1.3	31.8±8.7†,‡	3.1±0.7	7.7±1.8
21	1.2±0.1	9.0±2.1†	3.6±1.1	18.4±3.4†,‡	3.2±0.6	6.0±1.1
22	1.1±0.2	7.7±1.4†	3.1±1.2	12.3±1.3†,‡	3.3±0.5	5.2±0.9
23	1.5±0.4	6.6±1.4†	2.4±0.6	8.9±1.2†	3.5±0.4	4.4±0.9
24	1.6±0.4	5.8±1.8†	1.8±0.2	7.8±1.1†	4.0±0.3	3.8±0.5
25	1.6±0.3	5.8±2.2†	2.3±0.7	6.5±0.7†	4.1±0.1	3.3±0.4
26	1.8±0.4	4.5±0.7†	2.1±0.6	5.2±0.4†	4.2±0.2	3.1±0.5
27	2.1±0.7	4.1±0.4	2.3±0.7	4.7±0.6†	4.2±0.3	2.6±0.4
28	1.5±0.3	3.5±0.5†	1.9±0.3	4.4±0.4†	4.2±0.3	2.6±0.4
29	2.0±0.4	3.4±0.4	3.1±0.8	4.3±0.6	4.2±0.4	2.2±0.3
30	2.0±0.4	4.0±0.6	2.2±0.4	3.3±0.4	4.2±0.4	2.0±0.3
31	1.9±0.6	3.0±0.5	3.3±0.9	3.2±0.5	4.3±0.6	2.1±0.2
32	1.4±0.6	3.9±0.2	2.8±0.6	2.9±0.5	4.3±0.6	1.8±0.2
33	1.8±0.6	3.2±0.1*	3.6±1.1	3.6±0.4	4.4±0.7	1.9±0.1
34	1.9±1.4*	2.9±0.1*	2.6±0.4	2.9±0.2*	4.5±0.9	2.1±0.2
35	2.6±0.8*	3.1±0.3*	3.5±0.8*	2.6±0.3*	4.6±1.1	2.3±0.2
Total time (min kg^{-1})	29.7±4.0	103.3±10.0	50.8±12.8	165.1±12.7	69.2±6.2	60.1±9.9

Values for heating and cooling for dead individuals are also presented as 'control animals'. Air temperature was 14°C and heating was achieved by basking under a heat lamp. Values are means ± S.E.M.; * signifies N=5 rather than N=7 (see Materials and methods). Repeated-measures comparisons performed on fasting and postprandial animals, †significantly higher than the heating value within the same group (P<0.05), ‡significantly higher than the corresponding value for fasting animals (P<0.05). Total time (min kg^{-1}) indicates the sum of the time taken to heat/cool over the entire temperature range (19–35°C). Control animals: body mass=1.59±0.11 kg (N=3). Body mass for all animals was determined immediately prior to measurements.

sufficient to reduce the rate of cooling. Additionally, the time taken per degree T_b change during cooling below 23°C was greater in postprandial animals than both in fasting animals and in the control animals (P<0.05).

Discussion

Hysteresis of cardio-metabolic variables

A number of laboratory- and field-based studies of reptiles have reported values of f_H for a given T_b that are higher during heating than during cooling, and the associated changes in peripheral blood flow are thought to facilitate faster rates of heating and slower rates of cooling in order to maximize the period of time spent at the preferred T_b (Bartholomew and Tucker, 1963; Smith et al., 1978; Grigg and Seebacher, 1999; Seebacher and Grigg, 2001). Similarly, *V. rosenbergi* in the present study displayed a hysteresis in f_H over a broad range of T_b, where values were higher during heating than during the subsequent cooling period. The hysteresis in f_H in postprandial lizards, however, was not as prominent as that determined for fasting animals as a consequence of a higher f_H during cooling at a given T_b without a correspondingly higher f_H during heating (Fig. 3B). Consequently, it is possible that differences in digestive state may explain the differences in the magnitude of the f_H hysteresis determined between individuals of some species in the wild (e.g. Grigg and Seebacher, 1999; Seebacher and Grigg, 2001).

It is generally accepted that the sympathetic (adrenergic) and parasympathetic (cholinergic) nervous systems are principally responsible for short-term cardiovascular control in vertebrates (Akselrod et al., 1981); however, evidence exists for alternative [i.e. non-adrenergic and non-cholinergic (NANC)] cardiovascular control systems. For example, in the snake *Boa constrictor*, double autonomic block of β-adrenergic and cholinergic systems prevented an increase in f_H during exercise, but not during digestion, so it was subsequently postulated that a circulatory regulatory peptide may exert a positive chronotropic effect on the heart during the postprandial period (Wang et al., 2001a). Furthermore, prostaglandins have been suggested to be primarily responsible for the f_H hysteresis in *Pogona vitticeps* during heating and cooling (Seebacher and Franklin, 2003), given that the f_H hysteresis in the closely related *Pogona barbata* was maintained following double block of the β-adrenergic and cholinergic control systems (Seebacher and Franklin, 2001).

In the present study for *V. rosenbergi*, the inability of

postprandial animals to increase f_H above that of fasting animals during heating at a given T_b suggests that the regulatory system(s) responsible for f_H during digestion and heating in inactive animals may have reached a maximum and may only be increased further by modifying the influence of β-adrenergic and cholinergic control systems, as occurs during exercise, for example (see Wang et al., 2001b and references within). Indeed, Clark et al. (2005a) reported for maximally exercising *V. rosenbergi* at 25°C a f_H of 51.0±0.9 beats min^{-1}, which is greater than that obtained at the same T_b during heating in the present study (see Fig. 3). In this context, postprandial *Python molurus* can achieve a higher f_H during exercise than a similarly exercising individual in a fasting state, although this increase is not enough to demonstrate a complete additive response in f_H for simultaneous digestion and exercise (Secor et al., 2000).

If, indeed, a limit has occurred in f_H during heating in postprandial *V. rosenbergi*, then it is likely that prioritization of blood flow to the periphery or to the gastrointestinal organs would be necessary with a subsequent impairment of the other process (Zaar et al., 2004). It seems as though digestion may have taken at least partial priority over thermoregulation, as indicated by the increased time taken for postprandial animals to heat from 19°C to 35°C (see below; Table 1). Similarly, Axelsson et al. (2002) concluded for sea bass that once food has been eaten, it is digested and absorbed, even at the expense of a reduced oxygen supply to other organs. By contrast, it has recently been reported for *V. exanthematicus* that simultaneous digestion and heating resulted in an additive response in f_H such that f_H during heating was higher in postprandial animals in comparison with that in fasting animals (Zaar et al., 2004) and, consequently, the rate of heating of postprandial animals was not compromised. Further studies on cardiovascular control of reptiles are required to clarify the interaction that exists between exercise, digestion and thermoregulation.

As far as we are aware, there is no study of reptiles that has simultaneously measured $\dot{V}_{O_2}$ with f_H during heating and cooling, and it is evident in the present study that the f_H hysteresis, and the resultant enhancement of thermoregulation, does not have an associated hysteresis in energy demand; that is, f_H and $\dot{V}_{O_2}$ are uncoupled during thermoregulation. Such a dissociation between f_H and $\dot{V}_{O_2}$ would also be expected for a thermally stressed bird or mammal in which peripheral blood flow would increase to enhance heat loss. As a consequence of this uncoupling, a hysteresis must exist in the reverse direction (i.e. higher during cooling) for at least one of the other circulatory variables (i.e. cardiac stroke volume and/or tissue oxygen extraction) in accordance with the Fick equation for the cardiovascular system (see Clark et al., 2005b). Of these other circulatory variables, it may be suggested that the hysteresis exists for tissue oxygen extraction, as a result of there being little or no oxygen extracted from the blood perfusing the periphery during heating (see Baker and White, 1970). Cardiac stroke volume is a structural component that is thought not to change substantially without morphogenetic processes (Hoppeler and Weibel, 2000), and it has been reported for the turtle, *Trachemys scripta*, that cardiac stroke volume remained the same for a given T_b during heating and cooling (Galli et al., 2004). Having said this, quite substantial changes in cardiac stroke volume were reported for *V. rosenbergi* during exercise in an earlier study (see Clark et al., 2005a), implying that further measurements are required to clarify the component(s) of the circulatory system for which a hysteresis exists in the reverse direction to that of f_H.

Heating

It has been suggested that thermoregulation in reptiles is facilitated by the light-sensitive pineal gland situated at the top of the head (Tosini and Menaker, 1996; Tosini, 1997), although there is also evidence that reptiles respond to heat rather than light *per se* (see Seebacher and Franklin, 2001). Nevertheless, the fact that lizards in the present study wore masks that encompassed the head created some concern that the function of the pineal gland may be compromised. In an attempt to counter this, care was taken to ensure that masks were as transparent as possible, and observations of most lizards repositioning themselves under the heat lamp shortly after it was switched on suggested that the mask did not considerably obstruct the ability of the lizards to detect light and/or heat.

Both for fasting and postprandial animals, the time taken to heat between 19°C and 35°C was less than that taken to cool, which is consistent with several previous studies of reptiles (e.g. Bartholomew and Tucker, 1963; Grigg and Seebacher, 1999). Given that ΔT was similar when T_b was 34°C during heating (ΔT=43–34=9°C) and 23°C during cooling (ΔT=23–14=9°C) (see Materials and methods), the variation in the time taken to change T_b by 1°C during heating and cooling at these T_bs (see Table 1) cannot be explained by ΔT alone, thus implying a regulation of thermal conductance by live animals. The fact that the control animals did not heat as rapidly as the live animals suggests that increased blood flow to the periphery (see above) is critical to increase thermal conductance and obtain the fast rate of heating. The speed at which fasting *V. rosenbergi* heated from 19°C to 35°C (1.7 min deg.$^{-1}$ kg^{-1}) is faster than has been reported for several other varanids including *V. exanthematicus* (7.1 min deg.$^{-1}$ kg^{-1} between 28°C and 38°C; calculated from Zaar et al., 2004), *V. gouldii* (2.3 min deg.$^{-1}$ kg^{-1} at 30°C) and *V. varius* (3.0 min deg.$^{-1}$ kg^{-1} at 30°C; calculated from Bartholomew and Tucker, 1964). Differences in operative temperatures and/or digestive state between studies may account for some of the disparity, although the rapid heating of *V. rosenbergi* in the present study is probably assisted by the dark colouration of its skin, which is an adaptation to a high-latitude habitat and has been reported to display a greater absorptance than the skin of any other varanid (Christian et al., 1996).

Interestingly, the period of time taken for postprandial lizards to heat from 19°C to 35°C was compromised when compared with that for fasting animals. Generally speaking, as a consequence of consuming a meal, postprandial lizards would have a reduced surface area to mass ratio (the magnitude of which is dependent on the size of the meal) and a higher

heat capacity and would therefore take longer to warm the entire body. The protocol followed in the present study, however, ensured that each lizard was of similar M_b when in the fasting state and in the postprandial state (see Materials and methods). It is possible that postprandial lizards had a reduced rate of heating due to a decrease in peripheral blood flow during digestion, resulting from a limitation in the f_H response and therefore a prioritization of digestion over thermoregulation (see above). Measurements of blood flow to the gastrointestinal organs and/or the periphery of simultaneously heating and digesting animals are required to investigate this suggestion.

Cooling

This study is the first to report the heat increment of feeding acting to slow the rate of cooling of a reptile. Postprandial lizards with a T_b less than 23°C cooled more slowly than fasting lizards and the control animals, exemplified at 19°C when the mean times taken to cool were 47.4 min deg.$^{-1}$ kg^{-1}, 13.9 min deg.$^{-1}$ kg^{-1} and 9.8 min deg.$^{-1}$ kg^{-1}, respectively (Table 1). It appears as though the rate of decline in T_b is reduced at low temperatures due to the heat increment of feeding being proportionately greater at such low temperatures (see Introduction). Alternatively, it may be suggested that the development of a net right-to-left intracardiac shunt during digestion would produce a similar result by decreasing pulmonary circulation and reducing the heat lost across the surface of the lungs during cooling, although the development of such a shunting pattern during digestion seems unlikely (see Wang et al., 2001b for a review) and shunt patterns are thought to contribute little to heat exchange (Weathers and White, 1971; Galli et al., 2004). Nevertheless, given that the difference in cooling rates of fasting and postprandial lizards was apparent only below 23°C, it is clear why previous studies, which were performed over narrower and higher T_b ranges, have not reported such findings (e.g. Bennett et al., 2000; Zaar et al., 2004).

It appears that the heat increment of feeding temporarily enhances thermoregulatory ability in *V. rosenbergi* at low temperatures, and this would presumably prolong the period for which T_b exceeds ambient temperature throughout cooler periods in the natural environment (e.g. at night), possibly augmenting the rate of digestion and/or digestive efficiency (Harlow et al., 1976; Stevenson et al., 1985; Toledo et al., 2003; see Wang et al., 2003 for a review) and reducing the time required to reheat upon the onset of warmer conditions (e.g. the following morning). Consequently, in addition to considering the effects of M_b and the rate at which an animal moves through a thermal environment (see Seebacher and Shine, 2004), the postprandial influence on rates of cooling must be considered in studies that predict the minimum operative temperature available to an animal in a particular environment.

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