

# Changes in heart rate are important for thermoregulation in the varanid lizard *Varanus varius*

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## Abstract

Laboratory studies and a single field study have shown that heart rate in some reptiles is faster during heating than during cooling at any given body temperature. This phenomenon, which has been shown to reflect changes in peripheral blood flow, is shown here to occur in the lizard *Varanus varius* (lace monitor) in the wild. On a typical clear day, lizards emerged from their shelters in the morning to warm in the sun. Following this, animals were active, moving until they again entered a shelter in the evening. During their period of activity, body temperature was 34–36 °C in all six study animals (4.0–5.6 kg), but the animals rarely shuttled between sun and shade exposure. Heart rate during the morning heating period was significantly faster than during the evening cooling period. However, the ratio of heating to cooling heart rate decreased with increasing body temperature, being close to 2 at body temperatures of 22–24 °C and decreasing to 1.2–1.3 at body temperatures of 34–36 °C. There was a significant decrease in thermal time constants with increasing heart rate during heating and cooling confirming that changes in heart rate are linked to rates of heat exchange.

**Keywords:** Heart rate - Body temperature - Thermoregulation - Lizards - Heat transfer.

**Abbreviations:**  $T_b$  body temperature –  $T_c$  median operative temperature during the heating/cooling period -  $T_i$  initial body temperature at the beginning of heating or cooling episode.

## Introduction

Bartholomew and Tucker (1963) showed that the agamid lizard *Pogona barbata* (previously *Amphibolurus barbatus*) heated more rapidly than it cooled, when exposed in the laboratory to step function changes in air temperature. Concomitant with differential rates of heating and cooling were changes in heart rate, with individuals showing higher rates during heating than during cooling, at the same body temperature ( $T_b$ ). This phenomenon of heating and cooling and heart rate hysteresis is known from a number of reptile species (reviewed by Grigg et al. 1979; Bartholomew 1982). It has been interpreted to be of significance for reptiles because it enables rapid heat gain during basking and reduced rates of heat loss when the individual is in the shade, thereby minimising the amount of time each day that a behaviourally thermoregulating reptile needs to devote to basking (Bartholomew and Tucker 1963; Bartholomew 1982; Seebacher 2000).

In vertebrates other than fish, circulation and its dependent physiological functions are primarily governed by changes in heart rate rather than by changes in stroke volume (Farrell 1991). Also, experimental data show that changes in heart rate are closely linked to changes in peripheral blood flow in reptiles, so that measurements of heart rates may be used as an index of changes in blood flow (Morgareidge and White 1972; Grigg and Alchin 1976; Smith 1976; Smith et al. 1978). For example, wash-out rates of Xe isotope injected under the skin increase dramatically with the application of heat and decrease as the heat source is removed, indicating thermally dependent changes in peripheral blood flow. These changes in blood flow are accompanied by changes in heart rate which increase and decrease proportionally to changes in Xe wash-out rates (Grigg and Alchin 1976; Smith et al. 1978). Moreover, rates of internal heat transfer within an animal body are determined to a large extent by changes in heart rate and blood flow, which explains the differential rates of heating and cooling (Seebacher 2000).

Most of the knowledge of reptilian cardiovascular physiology stems from data collected under laboratory conditions. However, heart rate and blood circulation in vertebrates are controlled by complex humoral and nervous mechanisms (Wilson 1983; Robleto and Herman 1988; Altimiras et al. 1998) and, given this dependency, it is likely that stress under artificial conditions may confound laboratory data. Moreover, absence of stimuli from the animals' natural environment may modify behaviour and physiological responses so that it is important to verify laboratory findings with data collected from undisturbed animals in the wild. The present study is only the second to evaluate whether or not reptiles under field conditions show the heating and cooling hysteresis described under laboratory conditions. Grigg and Seebacher (1999) confirmed Bartholomew and Tucker's (1963) laboratory findings by monitoring heart rates of free-ranging *Pogona*. Moreover,

Grigg and Seebacher (1999) also found a "reverse hysteresis" pattern where, in very hot conditions, lizards decreased heart rates, presumably to decrease rates of heating, and then increased heart rates to dump heat when entering a cooling environment.

It was the aim of the present study to further investigate the occurrence of heart rate hysteresis among undisturbed reptiles in the wild. We used telemetry to investigate the interaction between heart rate,  $T_b$  and behaviour in the varanid lizard *Varanus varius*. Varanid lizards are different from the agamid *Pogona* in their habits. While *Pogona* is a relatively slow, sedentary lizard, varanids are among the most active reptiles (Thompson and Withers 1997); the occurrence of heart rate hysteresis in two different species in the wild could indicate that the phenomenon may be a general reptilian pattern.

## Materials and methods

We hand-captured and monitored six lizards (*V. varius*, 4.0-5.6 kg) on a property near Texas, Queensland (28°46'S, 151°04'E).  $T_b$  and heart rate were recorded by telemetry, and behavioural observations were made whenever possible. Each animal was monitored for 4-13 days.

$T_b$  was measured with temperature-sensitive radio transmitters (Sirtrack, Havelock North, New Zealand), which were surgically implanted into the peritoneal cavity of locally anaesthetised (using Lignomav) lizards. The surgery was performed in the field under sterile conditions, and all lizards healed well. Lizards were allowed to recover for 2 weeks before data were recorded. Radio transmitters, which were encased in non-reactive epoxy resin and weighed less than 1 % of the animals' body mass, were calibrated in a temperature-controlled water bath against a certified thermometer, and were accurate to 0.1 °C.  $T_b$  was determined every 5-10 min during the day by measuring the temperature-dependent time intervals between two transmitted pulses with a digital processor (Telonics, USA) connected to a telemetry receiver (Telonics, USA). At night, transmitter signals were recorded every 15-30 min by a remote system described by Grigg et al. (1992).

Direct observations of the animals' behaviour were recorded continuously with binoculars, approaching as closely as possible without disturbing the animals. During observations, care was taken to remain concealed behind vegetation and to gain a vantage point, for example on top of a hill, whenever possible. Behavioural data were collected at different times of day for periods lasting 0.16-6.48 h [mean 2.03 h  $\pm$  0.18 (SE)], and each animal was observed for 15.58 h ( $\pm$ 3.22 SE, range 4.8-26.3 h). When direct observations were not possible, movement of the animals could be detected by the varying signal strength of a transmitter resulting from the loop antenna changing its plane of transmission.

Lizards were defined to be 'active' when the animals moved without stopping for longer than 5 min. While stationary for longer than 5 min, the animals' behaviour was categorised according to their proportion of surface area exposed to sun (Muth 1977; Seebacher 1999). Hence, when more than 75% of surface area was exposed to sun lizards were deemed to be in the 'sun', 25-75% exposed to sun was defined as 'partial sun', and less than 25% exposed was defined as 'shade'. Lizards were considered to be in a 'shelter' when in a hollow tree or underground burrow.

The proportions of total observation time spent performing each defined behaviour, as well as operative temperatures and  $T_b$  calculated or measured, respectively, at the commencement of a defined behaviour, were compared by one-way analyses of variance followed by Tukey tests (Sokal and Rohlf 1980).

Heart rate transmitters (Sirtrack, New Zealand), which were encased in epoxy resin and weighed less than 1 % of the animals' body mass, had two external contact points for electrode attachment as well as a sensitivity adjustment. Transmitters were taped to the side of the tail at its base, just posterior to the vent. Using a straight surgical needle, one electrode was passed under the skin to a position just ventral to the heart where it was sutured in place. The other electrode was sutured under the skin of the tail near the transmitter. We used temporary myocardial pacing leads (model 6500, Medtronic, France) as electrodes. During transmitter installation, heart rate was also recorded with a MacLab physiograph (AD Instruments, Australia) to verify that transmitted pulses matched heart beats.

Environmental conditions were monitored every 5 min during field work with calibrated sensors connected to a datalogger (Data Electronics, Australia). Air temperature was measured in the shade 1 m above the ground (with a LM335 semiconductor), and ground temperature was measured on a patch of open ground with a sensor (LM335) lightly covered with soil. Solar radiation was measured either with a tube solarimeter (Irricrop Technologies, Australia) or a dome pyranometer (model 80HDX, SolData, Denmark), and wind speed was measured with an anemometer (Pacific Data Systems, Australia). Operative environmental temperatures were calculated, using these environmental measurements, by solving a steady state energy balance equation for  $T_b$  (Bakken and Gates 1975; Tracy 1982). The resulting equation was:

$$T_e = (Q_{abs} + hAT_a + k/LAT_g)/(h_aA + kLA)$$

where  $Q_{abs}$ =absorbed solar radiation,  $h$ =convection coefficient which were calculated according to methods given in Mitchell (1976),  $A$ =body surface area,  $T_a$ =air temperature,  $k$ =conductivity [ $0.45 \text{ Wm}^{-1}\text{C}^{-1}$ ] (Bowman

et al. 1978)],  $L$ =skin thickness, assumed to be  $0.1 \times$  radius of the animal (the radius was calculated from measurements of the diameter of each lizard and we also made direct observations of skin thickness during surgery), and  $T_g$ =ground temperature.

'Heating' and 'cooling' were each defined as a rate of  $T_b$  change at least as great as 5% of the maximum rates of heating and cooling measured in each lizard (Grigg and Seebacher 1999). This definition of heating and cooling was used in order to eliminate noise, but it also excluded periods when  $T_b$  was equal to operative temperature, and changed proportionally to it. For example, after entering shelters in the late afternoon or evening,  $T_b$  would decrease to operative temperature, but operative temperature of the shelter itself would decrease overnight. This night-time period was excluded from the analysis of heart rate hysteresis, because lizards were not thermoregulating as  $T_b$  was restricted by environmental conditions. As a consequence,  $T_b$  values in the analysis of heart rate during cooling were greater than those for heating periods, because shelter temperatures and, therefore  $T_b$ , decreased overnight so that lizards emerged to bask with  $T_b$  near the daily minimum.

$T_b$  was measured at regular intervals for most of the day except for periods of direct observation when sampling intensity was greater. In order to avoid bias in calculations of 'average' daily  $T_b$  towards those periods of greater sampling intensity, 'average' daily  $T_b$  was determined by integrating using Riemann Sums (Stewart 1991), which were then divided by the period of integration. The advantage of this method over arithmetic means is that measurements are weighted according to sampling intensity (Seebacher et al. 1999).

Lizards were always active on clear days, but they stayed in their shelter on cloudy or rainy days when environmental conditions prevented lizards from thermoregulating. Hence, only data from clear days were used in the analysis of thermoregulation (Christian and Weavers 1996).

All statistical tests of the heart rate data were performed on random subsamples (25% of total) to minimise potential problems of dependence between measurements. Least squares methods and model 1 regressions were used in all regressions analyses (Sokal and Rohlf 1980).

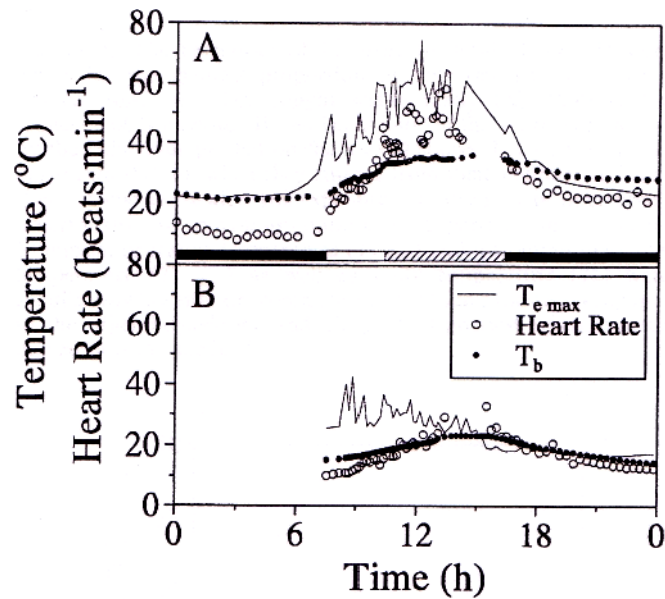
Thermal time constants were calculated as the inverse of the slope of the regression of the natural logarithm of the rate of change in the dimensionless temperature  $\Theta=(T_b-T_e)/(T_i-T_e)$  against time. Regressions used data for the entire heating or cooling episodes, where  $T_e$ =median operative temperature during the heating/cooling period, and  $T_i$ =initial body temperature at the beginning of the heating or cooling episode [time constant=  $-1/(d(\ln\Theta)/dt)$ ; Turner and Tracy 1985; Seebacher 2000].

In the regression of time constants against heart rate, time constants were corrected for the average body mass of the study animals (4.8 kg) by, firstly, regressing time constants against body mass to determine the average change of time constants with body mass. This relationship was then used to correct time constants for mean body mass. For example, the time constants of a 5.8-kg lizard would be greater because of its greater mass alone so that, using the regression of time constants against body mass, it was possible to determine how much greater than average the time constants of the heavier animals were expected to be because of mass alone, and this value was subtracted from the data for the 5.8kg animals. Similar corrections were performed for each animal. Heart rate was expressed as the median heart rate measured during each heating and cooling episode. Time constants are presented as averages for 5 beats  $\text{min}^{-1}$  intervals; for example, all time constants calculated for heating/cooling episodes when the heart rate was 20-25 beats  $\text{min}^{-1}$  were averaged and plotted at 22.5 beats  $\text{min}^{-1}$ .

## Results

Typically, when climatic conditions were such that operative temperatures were high enough for lizards to warm, animals emerged from their shelter, often a hollow tree, in the morning and moved to heat in the sun. Following sun exposure, animals became active and kept moving for most of the day until evening when they again entered a shelter (Fig. 1A).

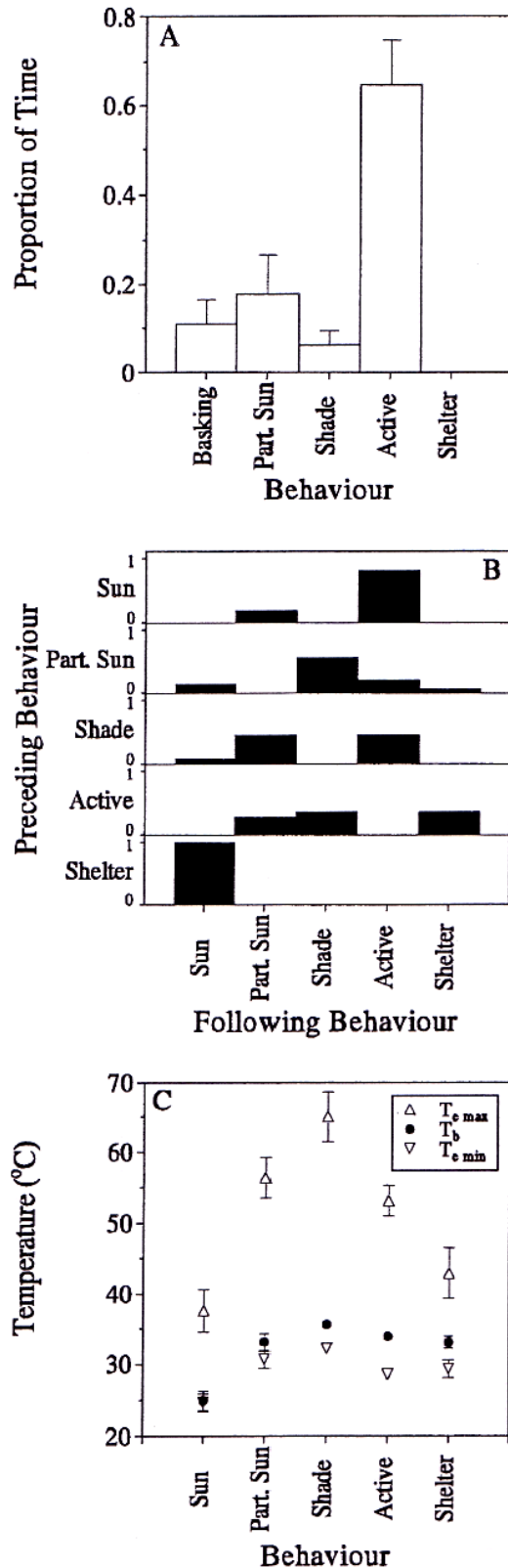
Patterns of behaviour and  $T_b$  changed in the face of unfavourable climatic conditions, and animals remained in their shelter when maximum  $T_e$  ( $T_{e \text{ max}}$ ) was low for most of the day (Fig. 1B). In the following analysis 'activity' on 'clear' days refers to patterns similar to that shown in Fig. 1A.



**Fig. 1A, B** Typical examples of daily patterns of  $T_b$  and heart rate of *Varanus varius* in the field. Maximum operative temperatures ( $T_{e\ max}$ ) are shown. On clear days (A) lizards emerged from their shelter, usually a hollow tree (indicated by the *solid bar* above the x-axis), and heated in the sun (*open bar*) after which they moved actively for most of the day (*hatched bar*) until seeking shelter again in the evening. On cloudy or rainy days, when  $T_{e\ max}$  was low, lizards remained in their shelter all day (B) and  $T_b$  and heart rate remained well below the levels seen on clear days.

Lizards were active for the greatest proportion of time during observations, and they spent relatively little time on sun or shade seeking ( $F_{3,20} = 11.66$ ,  $P < 0.0001$ ; Fig. 2A). In fact, exposure to sun was observed mostly in the mornings after the animals emerged from their shelter, and the animals sought shade rarely at any time of day (Fig. 2A, B). After exposure to sun in the morning, lizards became active (Fig. 2B) and  $T_b$  at the time when animals became active was significantly higher than at the commencement of sun exposure ( $F_{4,92} = 23.49$ ,  $P < 0.0001$ ; Fig. 2C). However, there were no differences in  $T_b$  at the commencement of any of the other behaviours.

Operative temperatures, too, were significantly lower ( $T_{e\ max}$ :  $F_{4,92} = 11.32$ ,  $P < 0.0001$ ;  $T_{e\ min}$ :  $F_{4,92} = 7.48$ ,  $P < 0.0001$ ) when animals emerged to move into the sun in the morning compared to those determined at the commencement of other behaviours during the day, except that lizards retreated into shelters at night when  $T_{e\ max}$  were similar to those measured at the commencement of sun exposure in the morning (Fig. 2C). While being active for most of the day, animals occasionally stayed in partial sun or shade before resuming activity (Fig. 2B), and  $T_{e\ max}$  was significantly higher when animals sought shade compared to when being active (Fig. 2C). Average  $T_b$  during activity was 34-36 °C, and there were no significant differences between lizards ( $F_{5,24} = 1.48$ ,  $P = 0.23$ ; Fig. 3).



**Fig. 2A-C** The behaviour of *V. varius* in the field. Lizards were active for the greatest proportion of time (means  $\pm$  SE) during observations, and they sought shade rarely (**A**) Plotting the sequence of behaviour (**B**) the behaviour on the y-axis is followed by the behaviour plotted on the x-axis) shows that lizards always move into the sun when they emerge from their shelters, and that they become active after sun exposure. Activity may be interrupted occasionally by remaining stationary in partial sun or shade. Minimum operative temperature ( $T_{e \text{ min}}$ ) and maximum operative temperature ( $T_{e \text{ max}}$ ) as well as body temperature ( $T_b$ ) were significantly lower at the commencement of sun exposure compared to the other behaviours, and  $T_e$  max was greatest when animals moved into the shade (**C**)

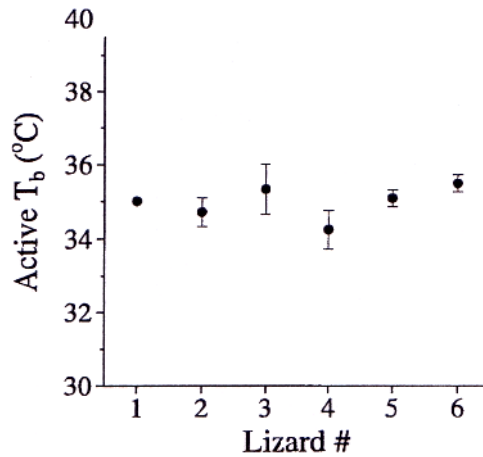


Fig. 3 Average ( $\pm$ SE)  $T_b$  of active *V. varius* in the field. Active  $T_b$  was 34-36 °C in all animals

Heart rate of all lizards was significantly higher at any given  $T_b$  during the warming phase in the morning than during cooling in the evening after lizards had retreated into a shelter (analysis of covariance with  $T_b$  as a covariate:  $F_{1,178}=163.66$ ,  $P<0.0001$ ; Fig. 4). It is interesting to note that heart rates during heating were as high or higher than those during activity (see below) despite the animals being stationary. Further, heart rate increased significantly with the covariate,  $T_b$  (two-tailed  $t$ -test,  $t=15.52$ ,  $df=178$ ,  $P < 0.0001$ ). Note that during heating in the morning and cooling in the evening the animals were stationary so that those heart rates were not confounded by activity.

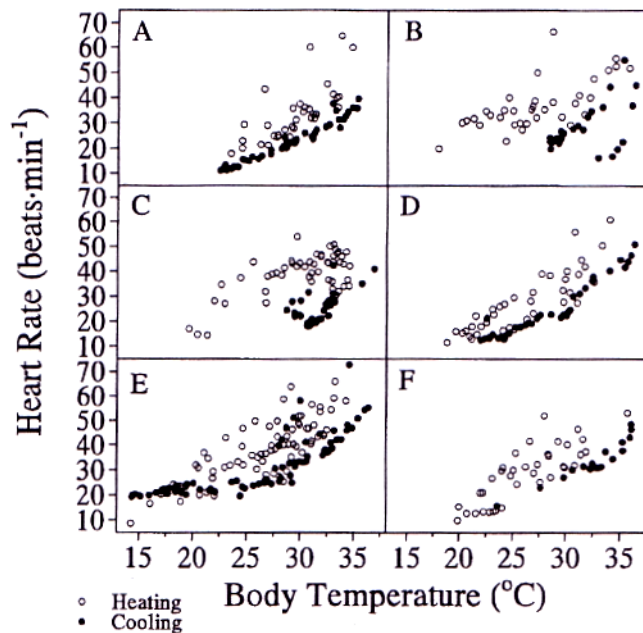
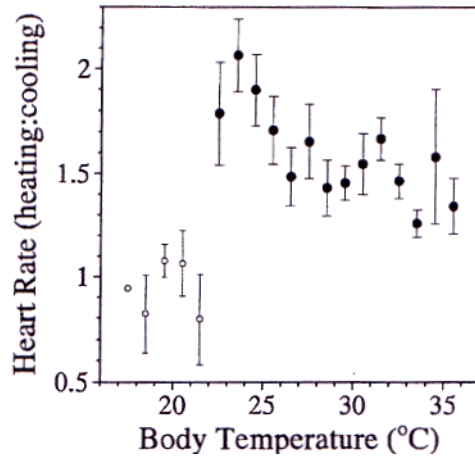


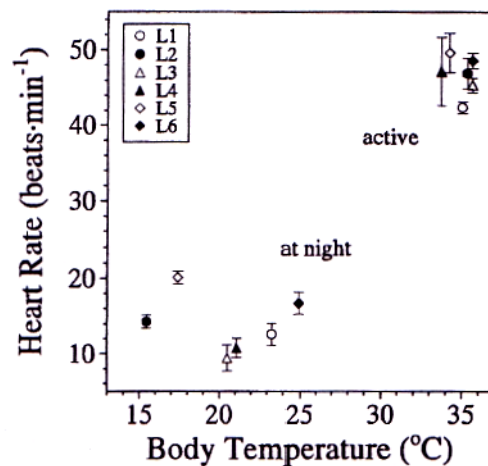
Fig. 4A-F Heart rate during heating, while lizards were basking in the morning was significantly faster than heart rate during cooling in the evening at any given  $T_b$  in all study animals (A L1, 5.6 kg; B L2, 4.7 kg; C L3, 5.5 kg; D L4, 4.5 kg; E L5, 4.0 kg; F L6, 4.2 kg)

The difference between heart rate during heating and during cooling was, however, not constant over the observed range of  $T_b$  (Fig. 5). Heart rate during heating was around twice as high compared to that during cooling at  $T_b$  of 22-25 °C, but the ratio of heating to cooling heart rates decreased as  $T_b$  increased further (regression: heart rate heating:cooling= $2.733-0.0393T_b$ ,  $r^2 = 0.57$ ,  $F_{1,12}=16.08$ ,  $P<0.01$ ) so that at 35-36 °C the ratio was only 1.34 (Fig. 5). Cooling heart rates at  $T_b$  of less than 22 °C were measured in one animal only (lizard 5, Fig. 4E), and at these low temperatures heart rate between heating and cooling did not seem to differ.



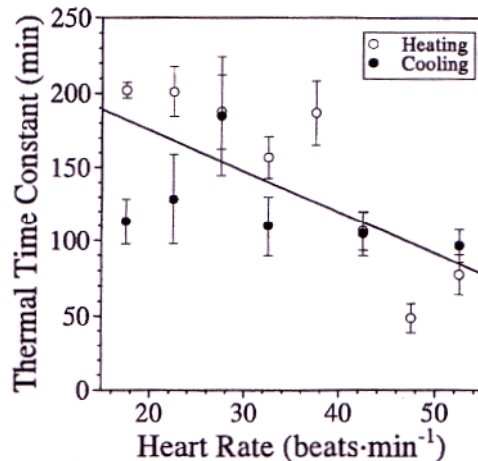
**Fig. 5** The ratio of heart rate during heating:heart rate during cooling decreased with increasing  $T_b$  (solid circles are means from all animals). Data were averaged over 1 °C intervals, and the means ( $\pm$  SE) are plotted at the midpoint of each interval. Note that heart rate during cooling at  $T_b$  of less than 22 °C was observed in one animal only, so that these data are shown separately (open circles). There is an indication that heart rate during heating and cooling are not different at low  $T_b$  (< 22 °C)

It was often difficult to measure heart rate during activity, because muscular activity was registered by the transmitter as well as heart rate. However, when we were able to measure heart rate during activity, for example during brief pauses in an animal's movement, it averaged between 40 beats  $\text{min}^{-1}$  and 50 beats  $\text{min}^{-1}$  (Fig. 6). On the other hand, heart rates of lizards in shelters overnight decreased to between 10 beats  $\text{min}^{-1}$  and 20 beats  $\text{min}^{-1}$  (Fig. 6).



**Fig. 6** Heart rate (means  $\pm$ SE) during activity averaged 40-50 beats  $\text{min}^{-1}$ , while heart rate in *V. varius* resting in their shelters overnight fell on average to 10-20 beats  $\text{min}^{-1}$ .

Heart rate had a pronounced effect on rates of heating and cooling. Thermal time constants decreased significantly with increasing heart rate (linear regression:  $Y = 238.27 - 3.00x$ ,  $r^2 = 0.72$ ,  $F_{1,6} = 18.77$ ,  $P < 0.01$ ; Fig. 7), which means that lizards heated and cooled faster the faster their heart rate. There was no significant difference between time constants during heating and cooling (two tailed  $t = 1.74$ ,  $df = 65$ ,  $P = 0.087$ ; Fig. 7) which was expected because internal heat transfer mechanisms (conduction and convection by blood flow) are the same during heating and cooling (Seebacher 2000).



**Fig. 7** Thermal time constants (means  $\pm$  SE) during heating and cooling decreased with increasing heart rate, confirming that changes in heart rate have a direct effect on rates of heating and cooling. Note that time constants were corrected for the average body mass of 4.8 kg

### Discussion

Lizards in the wild showed a heart rate 'hysteresis' pattern that is characterised by significantly faster heart rates during heating while in the sun in the morning compared to heart rates during cooling in shelters in the evening. Note, however, that heart rates during heating were not greater than during cooling in one lizard at low  $T_b$ . Given the small sample size of heart rates at low  $T_b$ , it is impossible to say if this reflects a general pattern, but it may indicate that there is a temperature threshold for upregulation of heart rate during heating which should be investigated further.

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Unlike *Pogona*, which appears to be a shuttling thermoregulator (Grigg and Seebacher 1999), *V. varius* were active for most of the day, seeking shade rarely, and displaying typical basking behaviour by sun exposure in the morning only. Hence, the thermal significance of modifications in heart rate would be of importance during the heating phase in the morning and during cooling in the evenings, but less so, or not at all, during the day while the animals are active. Varanids are among the most aerobically active reptiles (Thompson and Withers 1997) and the occurrence of the hysteresis pattern of heart rate in lizards as different in habit and taxonomically as the sedentary *Pogona* and *Varanus* may indicate that the phenomenon is typical for reptiles in general. That this is the case has often been assumed in the past (Bartholomew 1982), although heart rate hysteresis remains to be demonstrated in wild reptiles with even more different lifestyles, such as semi-aquatic turtles and crocodiles.

Rates of heating and cooling increased with increasing heart rate, confirming that heart rate hysteresis is of functional significance (see also Seebacher 2000). Note that the internal heat transfer processes are the same during heating and cooling so that changes in heart rate affect rates of heating and cooling to the same extent.

Typically, lizards were active at  $T_b$  of 34–36 °C, so that when  $T_b$  is low on cool mornings, it would be of particular advantage for lizards to increase their heart rate and thereby increase their rate of heating. Hence, it is interesting to note that the extent to which heart rate during heating exceeded heart rate during cooling decreased as the animals warmed. Grigg and Seebacher (1999) also found that the magnitude of the hysteresis depended on  $T_b$  in *Pogona barbata*, in which it decreased with increasing  $T_b$  in a similar way as observed in *V. varius* here. It could be that control of heart rate is determined by the difference between  $T_b$  and operative temperature, so that the heart beats faster the cooler the animals are compared to their environment, resulting in greater rates of heating.

There may be thermal sensors triggering control mechanisms, such as prostaglandins in the skin, but too little is known about the control of heart rate in reptiles and the foregoing remains speculative until more data are gathered.

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