The relationship between heart rate and rate of oxygen consumption in Galapagos marine iguanas (*Amblyrhynchus cristatus*) at two different temperatures

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Summary

To enable the use of heart rate (fH) for estimating field metabolic rate (FMR) in free-ranging Galapagos marine iguanas *Amblyrhynchus cristatus*, we determined the relationships between fH and mass-specific rate of oxygen consumption (sVO₂) in seven iguanas before and during exercise on a treadmill and during the post-exercise period. The experiments were conducted at 27 and 35 °C, which are the temperatures that represent the lowest and highest average body temperatures of these animals in the field during summer. There were linear and significant relationships between fH and sVO₂ at both temperatures (r² = 0.86 and 0.91 at 27 °C and 36 °C, respectively). The slopes of the two regression lines did not differ, but there were significant differences in their intercepts. Thus, while heart rate can be used to predict FMR, the effects of temperature on the intercept of the regression must be taken into account when converting fH to sVO₂. On the basis of our data, this can be achieved by applying the following formula:

\[ s\text{VO}_2 = 0.0113f_H - 0.2983Q_{10}^{(T_b-27)/10}. \]

The increase in sVO₂ with elevated body temperature results from an increase in fH, with no significant change in mass-specific oxygen pulse (sO₂ pulse; cardiac stroke volume times the difference in oxygen content between arterial and mixed venous blood). However, during exercise at both temperatures, increases in fH are insufficient to provide all of the additional O₂ required and there are also significant increases in the sO₂ pulses. This creates the situation whereby the same fH at the two temperatures can represent different values of sVO₂.

Key words: heart rate, rate of oxygen consumption, exercise, Galapagos marine iguana, *Amblyrhynchus cristatus*.

Introduction

The maximisation of net energy gain during a particular activity, such as foraging, has been used to explain some behavioural patterns of animals in their natural environment (Charnov, 1976). However, as pointed out by Speakman (1997), the energetics explanation of observed traits must be supported by measurements of rate of energy expenditure. Also, many models that estimate the food consumption of populations are based on energetics (Weins, 1984; Lavigne et al., 1985). Thus, accurate estimates of the rates of energy expenditure of animals in the field are essential components of many behavioural and ecological studies. Field metabolic rate (FMR) of many species of air-breathing vertebrates has been determined by the doubly labelled water method (DLW; see Nagy et al., 1999). This method estimates the rate of CO₂ production (VCO₂) and is relatively easy to use in the field. However, the DLW method only provides an average value for VCO₂ over the duration of the experiment, which is itself constrained by the biological half-life of ¹⁸O (Nagy, 1983). Thus, it is not easy to obtain estimates of rates of energy expenditure for specific activities such as foraging, breeding, etc. Heart rate (fH) may also be used as an indicator of metabolic rate (Butler, 1993). This method is based on the relationship between rate of oxygen consumption (VO₂) and fH, as described by Fick’s convection equation for the cardiovascular system:

\[ \dot{V}_O_2 = f_H \times V_S(C_aO_2-C_VO_2), \]  

where Vₜ is cardiac stroke volume, CₐO₂ is the oxygen content of arterial blood and CₜO₂ is the oxygen content of mixed venous blood. If Vₜ(CₐO₂–CₜO₂), the oxygen pulse (sO₂ pulse), remains constant or varies systematically, there is a linear relationship between VO₂ and fH. Clearly, the usefulness of the fH method for estimating FMR depends on the relationship between VO₂ and fH being similar under different conditions.
Trillmich, unpublished data). The transmitters were implanted for 14–81 days (M. Wikelski and F. Thom, 2000). On top of this is the cost of reproduction. Females 'shrink' (reduction in body length as well as in body mass), and those that 'shrink' the most survive the longest (Wikelski and Thom, 2000). Thus, there are many potential applications for the fth method in this species, which occupies an unusual niche for a lizard, in order to determine the energy costs of specific behaviours.

Materials and methods

This study was performed on seven marine iguanas Amblyrhynchus cristatus Bell at the Darwin Research Station, Santa Cruz Island (SC iguanas), and on four iguanas on board the vessel Quest anchored off the Island of Santa Fé, Galapagos Islands, Ecuador (SF iguanas). The iguanas were captured by noosing or by hand and held in captivity for no longer than 48 h before being used. The body mass (mean ± s.d.) of the SC animals was 1.39±0.31 kg (see Table 2 for individual values), while that of the SF animals was 1.35±0.55 kg. Heart rate data loggers were implanted into the abdominal cavity of the iguanas while they were anaesthetised with a mixture of Isoflurane (Abbott Laboratories, USA) and air. Upon exposure to the mixture, the iguanas usually stopped breathing for several minutes. However, once they started to inhale the Isoflurane, they immediately became deeply anaesthetised. They were then positioned upside down between two foam pads. The skin and underlying muscles were opened along a 3.5–4 cm long incision, which was approximately 2 mm off the ventral midline, in order to avoid a small vein.

The sterilised loggers were inserted with one electrode close to the heart and the other laying along the side of the HRDL. The body of the HRDL was fixed in place with two sutures of surgical silk (#2, Dexon, Germany) through the body wall. The logger incorporated a low-power radio frequency transmitter which emitted a short pulse on each QRS wave of the electrocardiogram (ECG). Detection of this signal by a radio receiver indicated when the electrodes were in the correct position. The muscle layer and skin were individually closed together with dissolvable surgical suture (#1, Dexon, Germany) and an antibiotic/antifungal spray (Chloromycetin, Parke Davis, USA) was used on the wound after surgery. The animal was then taken off Isoflurane and woke within 5 min. The iguanas were left for at least 24 h before they were used in an experiment.

To determine whether iguanas suffered from post-surgical stress after the implantation of data loggers, we took a blood sample from the tail vein of four implanted females approximately 24 h after surgery and of six control females that had not undergone surgery. Plasma corticosterone levels were determined using a standard radioactive immuno-assay procedure (Romero and Wikelski, 2000). There was no difference in the levels of corticosterone between the two groups (implanted, 6.3±1.8 ng ml–1; control, 5.4±1.4 ng ml–1; means ± s.d., t-test, P=0.39). Thus, we conclude that iguanas do not suffer post-surgical trauma that would be indicated by an increased corticosterone level compared to that of controls. None of the animals showed signs of infection or discomfort and all data loggers were removed 3 days after implantation. All the animals survived the surgical procedures and four of the SC animals were seen 9 months later at the location where they had been caught and released.
The animals were studied either in the early morning or early afternoon when their body temperatures were at approximately 27 °C or 36 °C, respectively. When required, the use of a refrigerator or an infrared lamp enabled us to maintain the animals at these temperatures. Body temperature was determined by a thermocouple placed 3–4 cm into the cloaca. Once body temperature had been maintained close to the required value for at least an hour, the animal was fitted with a loop aerial on the top of its body. This enabled the transmitted heart beat signal from the implanted data logger to be detected by a radio receiver and the output from the receiver to be sent to a pre-amplifier (Isleworth, Electronics, England, model A101) and the signal appropriately filtered.

A transparent mask constructed from a plastic water bottle was placed over the head of the animal and held in place with a rubber collar around the neck. An airtight seal between the collar and the skin of the iguana was achieved with a layer of quick-setting, non-toxic polyether material (Impregum, ESPE Dental AG, Germany). The mask was fitted with inlet and outlet tubes through which air was drawn at a rate of 2.6 l min–1 STPD by a pump (Reciprotor, Dental AG, Germany). The mask was fitted with inlet and gas analyser were collected at 1 kHz (Powerlab 800, Denmark, model 506R) on the outlet side. The air flow rate was set and monitored by a mass flow meter and controller (Sierra, models 840L and 902C). A subsample of the air leaving the pump was passed through a drying column (Drierite, Hammond) and analysed for the fractional content of O₂ and CO₂ by a gas analyser (ADInstruments, model ML205). The gas analyser was calibrated with room air and was accurate to 0.01 % for both gases. Outputs from the ECG pre-amplifier and gas analyser were collected at 1 kHz (Powerlab 800, ADInstruments) and displayed on a computer using Chart software (ADInstruments) as heart rate and rate of oxygen consumption. Rate of oxygen consumption was determined from the airflow through the mask and the difference between inert and excurrent fractional concentrations of dry air following consideration of respiratory quotient (RQ)-related errors (see Appendix in Frappell et al., 1992).

After instrumentation, the iguanas were placed on a variable-speed treadmill (1.2 m long and 0.5 m wide) and allowed to settle for at least 30 min, when f_H and V̇O₂ had reached steady (pre-exercise) values. They were then run at the maximum speed that they could comfortably maintain for a few minutes (maximum exercise). Although this included bursts of locomotion, the animals were not run to exhaustion. When an iguana no longer wanted to run, the treadmill was stopped and recordings continued for approximately 60 min during the recovery phase (see Gleeson, 1980, for recovery times of V̇O₂ after exhaustive exercise in marine iguanas). Rate of oxygen consumption and f_H data were obtained from each animal during the pre-exercise period, at maximum exercise (one datum point at each) and at four approximately equally spaced points during recovery. Data were averaged over 30–60 s. At the Darwin Station, each iguana was run, in random order, at body temperatures of 27 °C and 36 °C. On board the Quest, the animals were run only at a body temperature of 36 °C and values of f_H and V̇O₂ were recorded only during the pre-exercise period and at maximum exercise. All values of V̇O₂ are at standard temperature and pressure, dry (STPD).

Least-squares regressions were used to determine the relationships between f_H and V̇O₂, for individuals and for the group data at the two different temperatures for the SC animals. Regression equations were compared using an analysis of variance (ANOVA) general linear model (GLM; Zar, 1984) and, after testing for normality (Kolomogorov–Smirnov test), a Student’s t-test was used to compare the significance of any difference between the means of two populations. When more than two means were compared, a repeated-measures ANOVA was used with two grouping factors (location and level of exercise). Post-hoc modified t-tests with Bonferroni corrections were used to test for differences between the various factors.

### Table 1. Mass-specific rate of oxygen consumption (sV̇O₂), heart rate (f_H) and mass-specific oxygen pulse (sO₂ pulse) of marine iguanas during pre-exercise and maximum exercise at 27 °C and 36 °C

<table>
<thead>
<tr>
<th>Body temperature T_b</th>
<th>Santa Cruz animals</th>
<th>Santa Fé animals</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>27 °C</td>
<td>36 °C</td>
</tr>
<tr>
<td></td>
<td>Pre-exercise</td>
<td>Maximum exercise</td>
</tr>
<tr>
<td>sV̇O₂ (ml g⁻¹ h⁻¹)</td>
<td>0.09±0.02</td>
<td>0.47±0.07</td>
</tr>
<tr>
<td>f_H (beats min⁻¹)</td>
<td>32.3±4.8</td>
<td>60.4±4.2</td>
</tr>
<tr>
<td>sO₂ pulse (µl g⁻¹ beat⁻¹)</td>
<td>0.047±0.010</td>
<td>0.130±0.018</td>
</tr>
<tr>
<td>sV̇O₂ (ml g⁻¹ h⁻¹)</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>f_H (beats min⁻¹)</td>
<td>–</td>
<td>–</td>
</tr>
<tr>
<td>sO₂ pulse (µl g⁻¹ beat⁻¹)</td>
<td>–</td>
<td>–</td>
</tr>
</tbody>
</table>

Values are means ± S.D.

N=7 marine iguanas from Santa Cruz Island, Galapagos, N=4 for iguanas from Santa Fé Island, Galapagos.

* Denotes a significant difference between comparable variables at 27 °C and 36 °C.

† Denotes a significant difference between pre-exercise and maximum exercise at a given temperature.
Two means were considered to be significantly different when P<0.05 and are quoted at the level at which they were found to be significant. All mean values are given ± S.D.

Results

The mean values of \( fH \), mass-specific \( V\dot{O}_2 \) (s\( V\dot{O}_2 \)) and mass-specific oxygen pulse (s\( O_2 \) pulse, see equation 1) for animals during the pre-exercise period and at maximum levels of exercise at the two different body temperatures (\( T_b \)) are given in Table 1. In all animals, both \( fH \) and s\( V\dot{O}_2 \) exhibit significant increases over their pre-exercise values at maximum levels of exercise. For the SC animals at 27 °C, s\( V\dot{O}_2 \) increased 5.2-fold, whereas there was only a 1.9-fold increase in \( fH \). This means that there was a 2.8-fold increase in s\( O_2 \) pulse. The comparable value for maximum s\( V\dot{O}_2 \) of 2.8 at 27 °C and 36 °C, which is equivalent to a Q10 of 1.5. Mass-specific oxygen pulses during the pre-exercise period were not significantly different at 27 °C and 36 °C (\( P=0.11 \)) whereas s\( O_2 \) pulse during maximum exercise at 27 °C was significantly (21%) greater than that at 36 °C (\( P=0.02 \)). There was no significant difference between the values obtained from the SC and SF animals at 36 °C during the pre-exercise period and at maximum exercise for \( fH \), s\( V\dot{O}_2 \) and s\( O_2 \) pulse.

Heart rate and s\( V\dot{O}_2 \) were well correlated in each individual SC iguana (Table 2) and the relationships were well described by a linear function. Analysis of covariance (ANCOVA) was used to compare the values of the intercepts (\( a \)) and slopes (\( b \)) of the individual regressions within each group (i.e. at 27 °C and at 36 °C). While there was no significant difference between the slopes, there were significant differences between the intercepts. Thus, the intercepts were regarded as a random sample from a distribution of intercept values and a random-effects model was adopted (see Green et al., 2001). The group regression equations derived in the present study are:

\[ s\dot{V}_O_2 = (0.013±0.0009)fH - 0.361±0.048 \]  

for animals at 27 °C (\( N=7, r^2=0.86, P=0.018 \)) and

\[ s\dot{V}_O_2 = (0.011±0.0006)fH - 0.561±0.058 \]  

for the same animals at 36 °C (\( N=7, r^2=0.91, P=0.015 \)), where

\[ s\dot{V}_O_2 = a + fH \times b. \]

\( N \)= number of data points for each regression, \( a \)= intercept, \( b \)= slope of the regression (regression coefficient), \( r^2 \)= coefficient of determination, \( S_b \)= standard error of \( b \), \( S_a \)= standard error of \( a \), \( S_{yx} \)= standard error of estimate, \( \bar{X} \)= mean value of \( fH \) (heart rate).

The pooled and group regressions for the data at each temperature are also given.

### Table 2. Individual regression equation variables for mass-specific rate of oxygen consumption (s\( V\dot{O}_2 \)) against heart rate (\( fH \)) for seven marine iguanas from Santa Cruz Island, Galapagos, at 27 °C and 36 °C

<table>
<thead>
<tr>
<th>Iguana number</th>
<th>Mass (kg)</th>
<th>( N )</th>
<th>Variable</th>
<th>( a )</th>
<th>( b )</th>
<th>( r^2 )</th>
<th>( S_b )</th>
<th>( S_a )</th>
<th>( S_{yx} )</th>
<th>( \bar{X} )</th>
<th>( P )</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>Iguanas at 27 °C</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ig1</td>
<td>1.35</td>
<td>6</td>
<td></td>
<td>-0.5644</td>
<td>0.0175</td>
<td>0.8131</td>
<td>0.0042</td>
<td>0.2038</td>
<td>0.0965</td>
<td>47.667</td>
<td>0.0014</td>
</tr>
<tr>
<td>Ig2</td>
<td>1.73</td>
<td>6</td>
<td></td>
<td>-0.1479</td>
<td>0.0090</td>
<td>0.9600</td>
<td>0.0009</td>
<td>0.0399</td>
<td>0.0249</td>
<td>42.167</td>
<td>0.0143</td>
</tr>
<tr>
<td>Ig3</td>
<td>1.15</td>
<td>6</td>
<td></td>
<td>-0.3824</td>
<td>0.0136</td>
<td>0.9931</td>
<td>0.0006</td>
<td>0.0263</td>
<td>0.0138</td>
<td>45.333</td>
<td>0.0004</td>
</tr>
<tr>
<td>Ig4</td>
<td>1.18</td>
<td>6</td>
<td></td>
<td>-0.2945</td>
<td>0.0122</td>
<td>0.9552</td>
<td>0.0013</td>
<td>0.0658</td>
<td>0.0351</td>
<td>48.667</td>
<td>0.0022</td>
</tr>
<tr>
<td>Ig5</td>
<td>1.38</td>
<td>6</td>
<td></td>
<td>-0.5175</td>
<td>0.0142</td>
<td>0.8672</td>
<td>0.0028</td>
<td>0.1563</td>
<td>0.0546</td>
<td>55.667</td>
<td>&gt;0.0001</td>
</tr>
<tr>
<td>Ig6</td>
<td>1.90</td>
<td>6</td>
<td></td>
<td>-0.2883</td>
<td>0.0116</td>
<td>0.8389</td>
<td>0.0026</td>
<td>0.1128</td>
<td>0.0542</td>
<td>43.333</td>
<td>&gt;0.0001</td>
</tr>
<tr>
<td>Ig7</td>
<td>1.05</td>
<td>6</td>
<td></td>
<td>-0.4526</td>
<td>0.0145</td>
<td>0.8930</td>
<td>0.0025</td>
<td>0.1302</td>
<td>0.0624</td>
<td>51.000</td>
<td>0.0029</td>
</tr>
<tr>
<td>Pooled regression</td>
<td>42</td>
<td></td>
<td>-0.2983</td>
<td>0.0117</td>
<td>0.7945</td>
<td>0.0009</td>
<td>0.0459</td>
<td>0.0651</td>
<td>47.690</td>
<td>&gt;0.0001</td>
<td></td>
</tr>
<tr>
<td>Group regression</td>
<td>7</td>
<td></td>
<td>-0.3610</td>
<td>0.0130</td>
<td>0.8598</td>
<td>0.0009</td>
<td>0.0480</td>
<td>0.0571</td>
<td>47.690</td>
<td>0.0180</td>
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<td><strong>Iguanas at 36 °C</strong></td>
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<td></td>
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<tr>
<td>Ig1</td>
<td>1.35</td>
<td>6</td>
<td></td>
<td>-0.5908</td>
<td>0.0117</td>
<td>0.9397</td>
<td>0.0015</td>
<td>0.1277</td>
<td>0.0622</td>
<td>84.167</td>
<td>0.0140</td>
</tr>
<tr>
<td>Ig2</td>
<td>1.73</td>
<td>5</td>
<td></td>
<td>-0.3777</td>
<td>0.0093</td>
<td>0.8979</td>
<td>0.0018</td>
<td>0.1493</td>
<td>0.0841</td>
<td>80.000</td>
<td>0.0006</td>
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<td>6</td>
<td></td>
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<td>0.0110</td>
<td>0.9680</td>
<td>0.0010</td>
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<tr>
<td>Ig4</td>
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<td>6</td>
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<td>0.9240</td>
<td>0.0020</td>
<td>0.1791</td>
<td>0.0664</td>
<td>89.333</td>
<td>0.0008</td>
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<tr>
<td>Ig5</td>
<td>1.38</td>
<td>6</td>
<td></td>
<td>-0.6607</td>
<td>0.0127</td>
<td>0.9742</td>
<td>0.0010</td>
<td>0.0885</td>
<td>0.0331</td>
<td>84.500</td>
<td>&gt;0.0001</td>
</tr>
<tr>
<td>Ig6</td>
<td>1.90</td>
<td>6</td>
<td></td>
<td>-0.5712</td>
<td>0.0112</td>
<td>0.9906</td>
<td>0.0005</td>
<td>0.0432</td>
<td>0.0174</td>
<td>78.167</td>
<td>0.0103</td>
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<td>Ig7</td>
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<td>6</td>
<td></td>
<td>-0.5549</td>
<td>0.0099</td>
<td>0.7633</td>
<td>0.0028</td>
<td>0.2499</td>
<td>0.1073</td>
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<td>0.0045</td>
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<td>0.0108</td>
<td>0.8608</td>
<td>0.0007</td>
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<td>0.0737</td>
<td>84.146</td>
<td>&gt;0.0001</td>
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<tr>
<td>Group regression</td>
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<td></td>
<td>-0.5606</td>
<td>0.0111</td>
<td>0.9060</td>
<td>0.0006</td>
<td>0.0577</td>
<td>0.0639</td>
<td>84.146</td>
<td>0.0150</td>
<td></td>
</tr>
</tbody>
</table>

The form of the equation is: \( s\dot{V}_O_2 = a + fH \times b. \)
Heart rate and oxygen consumption in marine iguanas

The relationship between mass-specific rate of oxygen consumption ($\dot{V}_{\text{O}_2}$) and heart rate ($f_H$) for seven marine iguanas from Santa Cruz Island, Galapagos, at 27 °C (open circles) and 36 °C (filled circles). The group regression equations are: $\dot{V}_{\text{O}_2}=0.013f_H-0.361$, $r^2=0.86$, and $\dot{V}_{\text{O}_2}=0.011f_H-0.561$, $r^2=0.91$, respectively.

$s\dot{V}_{\text{O}_2}$ is in ml g$^{-1}$ h$^{-1}$ and $f_H$ is in beats min$^{-1}$. These regression lines with their individual data points are illustrated in Fig. 2. The slopes of these lines are not significantly different from each other ($P=0.10$), but the intercepts are ($P=0.003$).

The intercept is a random factor, so if one of the above equations is to be used to estimate $s\dot{V}_{\text{O}_2}$ from an average value of $f_H$ measured in the field, the usual method for estimating the standard deviation ($\sigma$) of an estimate using regression equations (see equation 17.28 in Zar, 1984) has to be modified, as indicated in equation 11 of Green et al. (2001):

$$\sigma = \sqrt{d^2\left[\frac{1}{n_1} + \frac{1}{n_3}\right] + e^2\left[\frac{1}{n_2} + \frac{1}{n_4}\right] + \frac{(X_i - \bar{X})^2}{\sum x^2}}.$$  (4)

where $d^2$ is the error associated with the variation between the intercepts of the individual regression lines for the calibration (SC) iguanas, $n_1$ is the number of iguanas used in the calibration process, $n_3$ is the number of iguanas from which the field value of heart rate was obtained, $e^2$ is the error associated with the scatter around the regression line (residual mean square), $n_2$ is the total number of data points in the regression, $n_4$ is the number of data points from which the field value of heart rate was obtained, $\bar{X}$ is the mean value of all the heart rates used in the regression, $X_i$ is the average value of heart rate from the field and $\sum x^2$ is the sum of squares (SS $x$) of heart rate values used in the regression. If the values of $n_3$ and $n_4$ for the data obtained at 36 °C are set to 4, which represents the number of animals and of data points, respectively, from the SF iguanas, then equation 4 can be used to produce the 95% prediction intervals for the regression under these conditions (Fig. 3). Also in Fig. 3 are the values (mean ± s.d.) of $f_H$ and $\dot{V}_{\text{O}_2}$ for the four SF animals during the pre-exercise period and at maximum exercise, and it can be seen that they fall within the 95% prediction intervals of the regression line.

**Discussion**

In order to be able to use $f_H$ for the estimation of $\dot{V}_{\text{O}_2}$ in the field, it is important that the calibrations are performed under conditions that are representative of those in the natural environment. Fig. 1 shows mean daily variation in $T_b$ from animals in the field during two consecutive summers and the two values of temperature that we used in the present experiments were chosen on the basis of these data. Iguanas, like many other species of lizards, often use relatively short bursts of locomotion. For example, most (>95%) marine iguanas forage in intertidal areas and make repeated short forays during which they run to particular foraging sites, take a few bites of algae, and run back to safe places to escape huge waves (Wikelski and Trillmich, 1994). Similarly, iguanas walk in short bouts from coastal resting areas towards foraging sites. Each walking bout consists of approximately 20–40 fast steps, with interspersed resting pauses (seconds to minutes; Wikelski and Hau, 1995). Likewise, iguana males engage in relatively fast head-bob walking bouts during territorial activities, again with intermittent resting phases. During the mating season, females are constantly harassed by satellite males and have to run away and struggle away from males several times every hour (Wikelski et al., 1996, 2001; Wikelski and Bäurle, 1996). Nesting females engage in bouts of intense digging activities lasting several minutes at a time. Even during diving bouts,
marine iguanas are only active for a short time while grazing under water for an average of 2–5 min. Animals then resurface and remain floating largely motionless before diving again or swimming back to shore (Wikelski and Trillmich, 1994; Drent et al., 1999). Thus, the inclusion of data during the recovery period after activity is important if the energy cost of a particular behaviour is to be determined in the field (Scholnick and Gleeson, 2000).

Perhaps because of their propensity for short bursts of locomotion, we did not find it easy to persuade all the animals to walk/run at speeds below the maximum speed they could maintain for a few minutes. Nonetheless, we were successful in achieving this with three animals at both temperatures and there was no significant difference between the slopes of the regression lines of data obtained from animals during the pre-exercise period and when walking/running at different speeds, and data obtained during the recovery period (P=0.67 at 27 °C and 0.07 at 36 °C, Fig. 4). Thus our experimental procedures simulated as closely as possible what is known for marine iguanas exercising in the wild and we are confident that the regression lines given in Fig. 2 represent both exercise at different levels and recovery from maximum exercise.

The \( \dot{V}_{O_2} \) data that we obtained are similar to those obtained by other workers studying the Galapagos marine iguana (Bennett et al., 1975, who electrically stimulated the animals in order to obtain activity; Bartholomew and Vleck, 1979; Gleeson, 1979, 1980), with the exception of pre-exercise \( \dot{V}_{O_2} \) at 27 °C, where our mean value is approximately twofold greater than the ‘resting’ values obtained by the above workers. On the other hand, our mean value for pre-exercise \( f_H \) at 27 °C is within the range given by Bartholomew and Lasiewski (1965), but our mean value for pre-exercise \( f_H \) at 36 °C is approximately 75 % of that reported by the latter authors while the iguanas were being heated and cooled. As far as we can determine, there are no values in the literature for \( f_H \) of marine iguanas during exercise.

It would appear from the present study that it should be possible to use \( f_H \) as an indicator of \( \dot{V}_{O_2} \) for iguanas in the field, as between 86 and 91 % of the variation in the latter could be explained by the fitted regressions from the calibration experiments. The utility of the \( f_H \) method for the estimation of \( \dot{V}_{O_2} \) in the marine iguana was further supported by the fact that the mean values of \( \dot{V}_{O_2} \) from four animals from a population different from that involved in producing the calibration equations were within the 95 % prediction intervals of the regression. However, the effect of temperature is to vary the intercept of the relationship between the two variables, rather than to extend a single regression line (see Fig. 2).

It is clear from the field data that have been obtained so far (M. Wikelski and A. J. Woakes, unpublished data) that temperature can change by between 6–12 °C or so within 1–3 h, particularly when the animals are foraging so, during such periods estimations of \( \dot{V}_{O_2} \) from \( f_H \) will have to involve adjustments to equations (2) and (3) based on the \( Q_{10} \) values determined from the data from the SC animals (Table 1). A

\[
\dot{V}_{O_2} = 0.0113 f_H - 0.2983 Q_{10} (\text{m}L g^{-1} h^{-1})
\]

Fig. 4. The relationship between mass-specific rate of oxygen consumption and heart rate for three marine iguanas from Santa Cruz, Galapagos at 27 °C (open symbols) and 36 °C (filled symbols). The squares represent data obtained from animals during the pre-exercise period and while walking/running at different speeds, while the circles represent data obtained from the animals during recovery from the preceding exercise (see text for further details). The lines represent the least-squares regressions through all of the data points. At 27 °C, \( \dot{V}_{O_2} = 0.011 f_H - 0.240, r^2 = 0.76 \). At 36 °C, \( \dot{V}_{O_2} = 0.011 f_H - 0.572, r^2 = 0.92 \).

Fig. 5. The relationships between mass-specific rate of oxygen consumption, heart rate and body temperature for marine iguanas (N=7). Data are from Fig. 2. The mesh is described by the equation: \( \dot{V}_{O_2} = 0.0113 f_H - 0.2983 Q_{10} (T_e - 27)^{10} \) (see text for further details).
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References


convenient way of incorporating temperature as an influence on sVO2, is to include Q10 in the regression. There are linear relationships between logVO2 and Tb for resting and active Sauromalus hispidus (an iguanid) and the marine iguana between 25 and 35°C (Bennett, 1972; Bennett et al., 1975) and between logfH and Tb for resting and active S. hispidus between the same temperatures (Bennett, 1972). Thus, it is assumed that there are also linear relationships between logfH and Tb for resting and active marine iguanas between 27 and 36°C. Given that there is no difference between the slopes of the pooled regression equations (Table 2), the relationship between the two lines can be ascribed to a Q10 effect, where the Q10 can be determined from the intercepts. In the present case Q10=1.93, which is similar to the Q10 values derived from the pre-exercise and maximum fH values in Table 1. If the following equation:

sVO2 = 0.0113fH − 0.2983Q10(Tb−27)10.

The standard error of the estimate can be determined from equation 17.28 in Zar (1984).

An interesting aspect of the present data is the fact that the increase in sVO2 in response to an increase in Tb is the result of an increase in fH, with no significant change in sO2 pulse. However, during exercise at both temperatures, the increases in fH are insufficient to provide all of the additional O2 required and there are significant increases in the sO2 pulses. Consequently, the situation arises (as illustrated in Fig. 2) whereby an fH value of around 60 beats min−1 is related to an sVO2 value of approximately 0.4 ml g−1 h−1 at 27°C, when the animal is exercising maximally, and to an sVO2 value of approximately 0.1 ml g−1 h−1 at 36°C during the pre-exercise period. This means, of course, that the sO2 pulse is fourfold greater during the former than during the latter. It is apparent from equations 1–4 and 6–9 and Fig. 9 of Bennett (1972) that a similar phenomenon occurs in S. hispidus and in Varanus gouldii, when activity is the result of electrical stimulation, although in the latter species, the values of fH during ‘exercise’, at 27°C and while at ‘rest’ at 36°C do not actually overlap. On the basis of a study on Iguana iguana and Varanus exanthematicus at 35°C, it would seem that the major contribution to the increase in sO2 pulse during exercise is a twofold increase in CaO2–CVO2 (Glesson et al., 1980).

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