Cardiovascular responses to graded activity in the lizards *Varanus* and *Iguana*

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Gleeson, Todd T., Gordon S. Mitchell, and Albert F. Bennett. *Cardiovascular responses to graded activity in the lizards Varanus and Iguana.* Am. J. Physiol. 239 (Regulatory Integrative Comp. Physiol. 8): R174-R179, 1980.—Respiratory gas exchange and blood oxygen content were measured in two lizard species at rest and during treadmill activity at low speeds. These data were used to evaluate the changes in cardiac output and oxygen extraction from the blood during activity. The high aerobic scope (1.07 ml O₂-g⁻¹-h⁻¹) of *Varanus* allows a wider range of running speeds that can be sustained aerobically than can *Iguana* with its low aerobic scope (0.65 ml O₂-g⁻¹-h⁻¹).

Both *Varanus* and *Iguana* increase their cardiac output (Q̇) and oxygen extraction in response to activity. As these lizards increase their running speeds to the maximum speed which is sustained for ≥20 min (0.5 km/h, *Iguana*: 1.2 km/h, *Varanus*), heart rate and stroke volume change in a manner which affords *Varanus* a greater factorial scope in cardiac output than *Iguana* (3× vs. 1.7×) despite equal maximum rates of Q̇ (20.5 ml·g⁻¹·h⁻¹). The greater oxygen content of arterial blood in *Varanus* permits a greater oxygen extraction from the blood than *Iguana* (6.1 ± 0.4 vol% vs. 3.8 ± 0.5 vol%) while running at speeds that elicit maximum oxygen consumption. The cardiovascular responses to activity in these lizards are similar to each other and to other vertebrates. The larger aerobic scope of *Varanus* appears due to a quantitative increase in the oxygen content of arterial blood relative to *Iguana* and in the contribution of stroke volume to increasing the factorial scope of cardiac output in *Varanus.*

*Varanus exanthematicus; Iguana iguana; oxygen consumption; cardiac output; arteriovenous difference; stroke volume; heart*

**THE PHYSIOLOGICAL BASIS for increasing oxygen delivery to match the oxygen demand of muscular contraction during periods of activity and elevated whole animal oxygen consumption has previously been studied in mammals (2, 4, 10, 17). Increased oxygen delivery has been shown to involve changes in respiratory gas exchange, cardiac output, and oxygen extraction from the blood. Study of these parameters in lizards has been limited to two species at rest as a function of different body temperatures (18, 23). Activity, however, places a much greater demand on the oxygen delivery system than does a change in body temperature of resting animals. Comparative studies of this type are interesting in view of the low oxygen carrying capacity of reptilian blood (14), the incompletely divided saurian ventricle (22), and the limited range of activity that many lizards can sustain (6).

In this study, the adjustments of the oxygen delivery system to activity were studied in two lizard species during unrestrained running over a range of speeds. Respiratory gas exchange (V₀₂ and V_CO₂), heart rate, and oxygen content of arterial and mixed venous blood were measured in green iguanas (*Iguana iguana*) and savannah monitors (*Varanus exanthematicus*) during rest and treadmill running. *Varanus* are highly active predators and are noted for their large aerobic scope (3, 5, 24). *Iguana*, typical of many other lizards in the family Iguanidae, possess a limited aerobic scope (12, 13, 18) in keeping with their sedentary arboreal existence (12). Both species were run at 35°C, the preferred body temperature of these lizards (12, 24). These measurements were used to calculate the rate of whole-animal oxygen consumption, cardiac output, stroke volume, and oxygen extraction from the blood. These parameters were utilized to study the relationship between oxygen delivery and oxygen demand during steady-state activity. These measurements also provide data that can be used to understand the physiological basis for the large aerobic scope possessed by varanid lizards relative to lizards of other families. Related studies of blood gas and acid-base regulation in *Iguana* and *Varanus* during treadmill running have been studied (unpublished research).

**METHODS**

**Animal care.** Four savannah monitors, *Varanus exanthematicus*, of mean mass 1,025 g (815-1,141 g) and four green iguanas, *Iguana iguana*, of mean mass 709 g (600-816 g) were used in this study. Savannah monitors were fed mice ad lib; iguanas were fed lettuce and dog food daily. All animals were purchased from licensed commercial animal dealers and were in good health. Lizards were housed in large cages containing photothermal gradients on a 12:12 photoperiod.

**Surgical preparation.** Animals were cooled to room temperature and anesthetized with halothane (Fluothane), 1–3% in air. A fluted polyethylene cannula (PE-50 tapered to PE-20) was inserted 1.5–2.5 cm into the external carotid or hyomandibular artery (right side, *Iguana*; left side, *Varanus*). A second cannula of similar design was inserted into the jugular vein of the same side and passed down to the sinus venosus of the heart to...
ensure sampling of mixed venous blood. Postmortem inspection confirmed cannula placements. Both cannulas were flushed with heparinized saline (50–100 U/ml) and sealed with stainless-steel plugs. Lizards were allowed 24–48 h to recover before experimentation.

Experimental design. Lizards were placed in a temperature cabinet and allowed to equilibrate to 35°C for 2–3 h before experimentation. Animals were fitted with a cloacal thermistor and a clear lightweight plastic mask and were then placed on a motor-driven treadmill. A vacuum line connected to the mask drew air from the mask at a rate of 1.8–2.6 l/min. This airflow was pumped through Drierite (anhydrous CaSO₄), silica gel, and a calibrated Brooks rotameter. A portion of this flow (≤25%) was then passed through a Beckman LB2 infrared carbon dioxide analyzer and an Applied Electrochemistry 39A oxygen analyzer connected in series. Continuous analysis of gas content in the expired airflow allowed calculation of oxygen consumption and carbon dioxide production in a manner previously described (8). The arterial cannula was connected to a Statham pressure transducer to monitor pulse pressure, which was amplified and recorded on a Beckman type RS dynograph. Heart rates were calculated from the pulse pressure recordings.

Lizards rested quietly on the treadmill until their heart rate, \( V_{O₂} \), and \( V_{CO₂} \) had returned to resting rates (25–45 min). The treadmill was then activated and the lizards began running at the desired speed. At running speeds below those that elicited \( V_{O₂ \text{max}} \), lizards were able to sustain activity for prolonged periods. Most experiments were terminated at the discretion of the experimenter after 20–45 min. At higher running speeds, animals tended to fatigue, and runs were correspondingly shorter. Each lizard was run at only one speed per trial, one to two trials per day, with at least 3 h rest at 35°C between runs. Blood samples were drawn from the lizards just before running and again near the end of each running session.

Blood sampling and analysis. Approximately 300 μl of blood was drawn from each cannula and temporarily stored in a heparinized syringe. Samples for blood analysis (30 μl arterial, 125 μl venous) were then drawn anaerobically and immediately stored on ice. The first volume of blood was then returned to the animal and the cannula flushed with heparinized saline. Sample analysis was usually begun within 5 min, although storage on ice for as long as 45 min had no effect on blood gas tensions or concentrations. Arterial blood gas pressure (\( P_{A\text{o}_2} \), and \( P_{ACO₂} \)) and blood pH were analyzed at 35°C with a Radiometer Copenhagen BMS3 Mk3 blood microsystem. Arterial and mixed venous blood oxygen contents (\( Ca-V_{O₂} \)) were analyzed in 100 μl subsamples by the technique of Tucker (19). A few analyses were sampled by the method of Roughton and Scholander (15). All blood gas volumes reported have been corrected to STP and are expressed as volume % (ml oxygen/100 ml blood). Arterial and mixed venous samples (25 μl) were mixed with 50 μl 0.6 N HClO₄ and refrigerated. Acid supernatants were later analyzed for lactate with enzymatic test kits (Boehringer-Mannheim) on a Beckman model 25 spectrophotometer. Since no consistent differences between arterial and mixed venous lactate concentrations were observed, data were combined for analysis. Net lactate accumulation in the blood during activity was calculated from the difference in the blood lactate concentration before and at the end of a run.

Data are reported as mean ± SE. Differences between species were tested using a Student’s \( t \) test; differences between rest and activity within one species were tested using a paired \( t \) test. All tests were two-tailed, and \( P \leq 0.05 \) was required for significance.

RESULTS

Oxygen consumption. The metabolic response to treadmill running at 35°C is shown for both \( I. \) iguana and \( V. \) exanthematicus in Fig. 1. Activity increases the rate of oxygen consumption in both lizard species. The \( V_{O₂ \text{max}} \) of Iguana was 0.83 ± 0.08 ml \( O₂ \cdot g⁻¹ \cdot h⁻¹ \). Maximum running speed that iguanas sustained for ≥20 min with respiratory quotients (\( R \), where \( R = \frac{V_{CO₂}}{V_{O₂}} \)) of 1.0 or less averaged 0.5 km/h. In contrast, the greater \( V_{O₂ \text{max}} \) of Varanus (1.26 ± 0.08 ml \( O₂ \cdot g⁻¹ \cdot h⁻¹ \); \( P = 0.008 \)) provides a greater range of running speeds (up to 1.2 km/h) which it can sustain using aerobic metabolism alone.

Lactate production. Net lactate accumulation is reported as a function of the maximum sustainable running speed for each species in Table 1. Lactate accumulation in the blood is not a linear function with time at the
lower running speeds, but generally occurs only during the first few minutes of exercise (unpublished observations). Running at faster speeds resulted in the greatest lactate accumulations, suggesting that anaerobic metabolism supplements aerobic energy production.

Blood oxygen content and oxygen extraction. The oxygen content of arterial blood remained relatively constant at all levels of activity in both species ($P > 0.11$; Fig. 2). Arterial oxygen content in I. iguana averaged $5.55 \pm 0.29$ vol% whereas that of V. exanthematicus was significantly higher ($P = 0.008$), averaging $7.50 \pm 0.36$ vol%. Oxygen content of mixed venous blood decreased as running speed increased in both species (Fig. 2). In a similar manner for both species, mixed venous oxygen content declined from 3-4 vol% to about 1.8 vol% at running speeds that elicited $V_{O_2 \text{max}}$. Oxygen extraction from the blood, calculated as the difference between arterial and mixed venous blood oxygen contents, is shown in Fig. 2A for both species. Varanus oxygen extraction increased ($P = 0.004$) from $2.6 \pm 0.3$ vol% at rest to $6.1 \pm 0.4$ vol% during maximum sustained activity. Oxygen extraction in Iguana increased as activity increased ($P = 0.02$), changing from $1.8 \pm 0.2$ vol% at rest to $3.8 \pm 0.5$ vol% at maximum sustainable speeds.

Cardiac function. The cardiac outputs of resting and active lizards were calculated according to the Fick principle: $Q = \frac{V_{O_2}}{C_a - V_a}$, where $Q$ is cardiac output in ml blood·g$^{-1}$·h$^{-1}$, $V_{O_2}$ is oxygen consumption in ml O$_2$·g$^{-1}$·h$^{-1}$ (Fig. 1), and $C_a - V_a$ is oxygen extraction in ml O$_2$/ml blood (Fig. 2A). Calculation of cardiac output in this manner can underestimate true cardiac output if a right-to-left intraventricular shunt of blood occurs during measurements. The preferred term for this factor is systemic cardiac output (22). Cardiac output of Varanus increased in a linear fashion from $6.7 \pm 1.3$ ml·g$^{-1}$·h$^{-1}$ at rest to $20.5 \pm 0.9$ ml·g$^{-1}$·h$^{-1}$ when running at their maximum sustainable speed (Fig. 3A), a threefold increase ($P = 0.002$). Three of four iguanas increased $Q$ in response to increased running speed, from mean resting rates of $12.1 \pm 1.3$ ml·g$^{-1}$·h$^{-1}$ to $20.6 \pm 3$ ml·g$^{-1}$·h$^{-1}$ at maximum sustainable running speeds. The high variability in response between individuals makes this significant only at the $P = 0.10$ level (paired $t$ test).

Heart rate doubled as activity increased (Fig. 3B). Heart rate response was similar in both species, increasing from resting rates of approximately 50 beats/min to maximum rates of 105-110 beats/min. This doubling of heart rate is highly significant ($P < 0.001$ for both species) and was the major component in increasing $Q$ during activity.

Stroke volume was calculated by dividing heart rate into the cardiac output (ml blood·g$^{-1}$·min$^{-1}$/beats·min$^{-1}$ = ml blood·g$^{-1}$·beat$^{-1}$). All four varanids demonstrated a 30% increase in stroke volume ($P = 0.033$), changing from $0.0023 \pm 0.0003$ ml·g$^{-1}$·beat$^{-1}$ (2.5 ± 0.3 ml/beat) to $0.0031 \pm 0.0002$ ml·g$^{-1}$·beat$^{-1}$ (3.2 ± 0.3 ml/beat) at running speeds that elicited their $V_{O_2 \text{max}}$ (Fig. 3C). In contrast, the stroke volume in three of four

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**Fig. 2.** Blood oxygen contents and extraction in Varanus and Iguana as a function of activity. A: oxygen extraction (a-v difference) as a function of treadmill running in Varanus and Iguana. B: oxygen contents of arterial and mixed venous blood in Varanus and Iguana. R, resting; 100% maximum sustainable running speed = 0.5 km/h, Iguana; 1.3 km/h, Varanus. Triangles, Iguana; closed circles, Varanus; vertical lines, ±1 SD.

**Fig. 3.** Cardiac function in Varanus and Iguana as a function of maximum sustainable running speed. A: cardiac output. B: heart rate. C: changes in stroke volume of the heart in Varanus and Iguana. Symbols as in Fig. 2.
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iguanas declined slightly during the same conditions. Mean stroke volume at rest \( [0.0041 \pm 0.0007 \text{ ml.g}^{-1}\cdot\text{beat}^{-1}] \) decreased by 20% \( [0.0032 \pm 0.0005 \text{ ml.g}^{-1}\cdot\text{beat}^{-1}] \) at maximum sustainable running speeds.

DISCUSSION

The different capacities of these lizard species to sustain vigorous activity is reflected in their different aerobic scopes and activity levels under natural conditions. The savannah monitor, a predatory carnivore, sustained activity twice as vigorous as that which could be maintained by the more sedentary arboreal green iguana. Varanus utilizes its large aerobic scope to support this activity: lactate production during submaximal runs was quite low (Table 1). The absolute contribution of anaerobic metabolism to total energy production cannot be quantified from these data, as they do not represent the total amount of lactate produced during activity. The large lactate accumulation in the blood during high speed nonsustainable running, however, suggests that supplementary anaerobic metabolism makes a significant contribution during exhaustive work loads. *I. iguana* appears to partition aerobic and anaerobic metabolism in much the same way during activity. *Iguana*’s small aerobic scope, however, reduces the range of speeds that it can sustain.

The metabolic rates of lizards resting quietly on the treadmill were higher than standard or minimum metabolic rates for these species. True resting \( V_{O2} \) is approximately 50% lower for both lizard species (3, 18, 23, 24). Minimum cardiac output and other parameters of oxygen delivery, therefore, are also slightly lower than in these preactive animals (18, 23).

Evaluation of the cardiovascular changes that occur within the range of aerobically supported activity provides clues as to the physiological basis of the differential aerobic scopes of varanid and iguanid lizards. The components of oxygen delivery are compared for *Varanus* and *Iguana* at equal running speeds in Fig. 4A. The metabolic cost of walking at 0.5-0.6 km/h is similar for both lizards. The manner by which the two lizard species match oxygen delivery to oxygen demand, however, is markedly different. *Iguana* utilizes both its \( Q_{max} \) and maximum arteriovenous (a-v) difference at this level of oxygen consumption. Relative to *Iguana*, *Varanus* provides the same oxygen delivery with a lower \( Q \) but a greater oxygen extraction from the blood. This emphasis on a-v difference at low-level activity in *Varanus* represents recruitment of 75% of the available increase in a-v difference, but only 52% of the scope in cardiac output. Greater increases in varanid cardiac output are reserved for greater rates of oxygen consumption.

The greater \( V_{O2max} \) of *Varanus* relative to *Iguana* is due to the greater scope in both cardiac output and oxygen extraction by *Varanus* (Fig. 5A). Both species extract oxygen from arterial blood down to an average of less than 2 vol% as it passes through the peripheral tissues. The difference in the \( Ca-Vo_2 \) response to activity is thus a reflection of greater arterial oxygen content in *Varanus* (Fig. 2). This difference is maintained despite a greater oxygen tension in *Iguana* blood (90-100 Torr) compared to *Varanus* (80-90 Torr) both at rest and during activity (11). The high \( CaO_2 \) of varanid blood relative to iguana blood is in part due to the higher hematocrit of varanid blood (29-33%, *Varanus*; 24-26%, *Iguana*). Hematocrit varies widely in *Iguana* (18, 25) and this fact likely accounts for the variability in *Iguana* \( CaO_2 \) reported in other studies (14, 18, 21, 25). The a-v differences reported for *Iguana* are in good agreement with previous studies (1, 18).

Increments in cardiac output during activity function to increase the rate of oxygen delivery in both lizards. *Iguana* increase \( Q \) approximately twofold during activity. \( Q_{max} \) is reached at intermediate levels of sustainable activity. Further increases in \( Q \) in *Iguana* can apparently be maintained for only brief periods of time, as during exhaustive running at nonsustainable speeds (Fig. 3A). The factorial scope in cardiac output is greater in *Varanus* than in *Iguana* (3x vs. 1.7x, Fig. 3A). Starting from lower resting rates of \( Q \) in *Varanus*, cardiac output

![Image 4](https://via.placeholder.com/150)

**FIG. 4.** Comparison of mean cardiac output and mean oxygen extraction in *Iguana* and *Varanus* walking at 0.5-0.6 km/h. This is maximum sustainable speed for *Iguana*, but a submaximal speed for *Varanus*. Area enclosed within each rectangle is product of \( Q \) and a-v difference, and is proportional to \( Vo_2 \) reported in parentheses (ml \( O_2 \cdot g^{-1} \cdot h^{-1} \)). *Iguana*, broken lines; *Varanus*, solid lines.

![Image 5](https://via.placeholder.com/150)

**FIG. 5.** Comparison of mean cardiac output and mean oxygen extraction at rest and at 100% maximum sustainable running speed for *Varanus* and *Iguana*. Resting values are shaded. Symbols as in Fig. 4.
increases linearly to \( Q_{\text{max}} \) values equal to that of Iguana. Analysis of the components of cardiac output, heart rate, and stroke volume, indicates that the twofold increase in heart rate (Fig. 3C) is responsible for virtually all the increase in cardiac output of Iguana; changes in stroke volume being statistically insignificant (\( P = 0.33 \)). Heart rate increment in Varanus accounts for approximately 80% of the increase in \( Q \) during strenuous activity, whereas a 50% increase in stroke volume contributes 20%.

The ratio \( Q/V_{O_2} \), the blood convection requirement, is compared for these two lizard species in Table 2. The ratio \( Q/V_{O_2} \) represents an index of work done by the heart to provide adequate circulation at a given metabolic rate. During both rest and activity, the iguanid heart must pump considerably more blood to achieve equivalent levels of oxygen delivery. This difference is a consequence of the removal of a smaller amount of oxygen per unit volume of blood pumped through peripheral tissues. In a pattern consistent with other vertebrates, both lizards demonstrate a decreased blood convection requirement as \( V_{O_2} \) increases. Inasmuch as \( Q/V_{O_2} = 1/Ca-V_{O_2} \), this simply reiterates the fact that oxygen extraction increases as \( V_{O_2} \) increases.

Lizard ventricles are not completely separated by a septum, unlike mammalian ventricles. Separation of oxygenated and deoxygenated blood within the lizard ventricle depends largely on the flow patterns within the ventricle. The possibility of both right-to-left and left-to-right shunts exists in lizard ventricles (22), but the extent to which this actually occurs is not clear. Iguanas did not demonstrate any shunting in one study (21) while 50 and 75% of iguanas studied shunted right to left in two other studies (1, 18). Both right-to-left shunting (7) and no shunting (11, 23) have been reported for resting savannah monitors. Changes in stroke volume during activity might be expected to alter the flow pattern through the lizard ventricle, which could conceivably affect any shunting of oxygenated and deoxygenated blood that might be occurring. The occurrence of blood shunting cannot be determined from the data collected in the present study. The constancy of arterial oxygen tension in both species (unpublished research) at all heart rates and stroke volumes, however, suggests that vigorous activity does not substantially alter blood mixing characteristics in the ventricle.

The relative importance of increasing heart rate, stroke volume, or oxygen extraction to meet the demands of increased oxygen consumption can be evaluated by determining their relative contributions to the increment in oxygen delivery during activity. Some animals might emphasize changes in cardiac output (heart rate or stroke volume) while the cardiovascular systems of other vertebrates may be better suited for increasing oxygen extraction selectively. The pattern of cardiovascular support of increased oxygen demand during exercise for several animals is summarized in Table 2. The cardiovascular response to vigorous activity is similar in all these vertebrates. Most appear to rely equally on \( Q \) and oxygen extraction during maximal activity. The similarity in increasing oxygen delivery is surprising in view of the differences in circulatory patterns, aerobic scope, and cardiac morphology of fish, lizards, and mammals. The role that stroke volume plays in increasing cardiac output of vertebrates appears to be less conservative. In trout it plays a major part in increasing oxygen delivery, but in iguanas and possums it can actually reduce \( Q \). The role of stroke volume plays during exercise in man is less clear. Both large and small changes in stroke volume have been reported in exercising man depending on whether resting stroke volume is measured in the standing (22) or supine

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**TABLE 2. Cardiovascular contributions to increased oxygen delivery**

<table>
<thead>
<tr>
<th>Species, mass, kg</th>
<th>Activity Level, km/h</th>
<th>( V_{O_2}, \text{ml} \cdot \text{g}^{-1} \cdot \text{h}^{-1} )</th>
<th>( Q, \text{ml} \cdot \text{g}^{-1} \cdot \text{h}^{-1} )</th>
<th>( Q/V_{O_2}, \text{ml blood/ ml } O_2 )</th>
<th>( Ca-V_{O_2}, \text{vol}% )</th>
<th>% Contribution to Metabolic Increment</th>
<th>Ref. No.</th>
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<td>1.06</td>
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<td>3.3</td>
<td>11.6, 31.2, 57.1</td>
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<td>(0.9-1.5)*</td>
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<td>0.091</td>
<td>0.7</td>
<td>18.7</td>
<td>5.4</td>
<td>11.5, 39.7, 51.2</td>
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<td>Iguana (0.7-1.0)</td>
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<td>35.0</td>
<td>2.6</td>
<td>33.2, 20.2, 46.6</td>
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<td>37.2, 30.4, 43.4</td>
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* Weight range.
subject (18, 22). In Table 2, resting man is considered in the standing position as this best represents the preexercise condition of man and the other animals to which it is compared. In terrestrial vertebrates for which data are available, excluding man, the contribution that increments in stroke volume make to maximal oxygen delivery appears small.

The data suggest that the larger aerobic scope of Varanus relative to Iguana and other lizards is not due to any qualitative change in the way that monitor lizards increase oxygen delivery during activity. It appears that most vertebrates increase oxygen delivery in a similar manner. The larger aerobic scope of Varanus appears due to a quantitative increase in the oxygen content of arterial blood relative to Iguana, and in the contribution that stroke volume makes in increasing the expansibility of cardiac output in Varanus.

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