OXYGEN TRANSPORT BY THE CIRCULATORY SYSTEM OF THE GREEN IGUANA (*IGUANA IGUANA*) AT DIFFERENT BODY TEMPERATURES

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INTRODUCTION

Since the early investigations of Cowles & Bogert (1944), it has become established that many lizards when active under natural conditions have mean body temperatures that are several degrees higher than air temperature in the shade and are relatively constant (Brattstrom, 1965). This difference between the mean (or eccritic) body temperature and air temperature is maintained primarily by absorption of heat from the environment since lizards cannot heat themselves more than a few degrees by metabolic heat production alone (Bartholomew & Tucker, 1963, 1964). Both behavioural and physiological mechanisms influence the absorption of environmental heat. When they are below their eccritic temperature, lizards tend to move into the sun or flatten on warm substrates (Bogert, 1949; Norris, 1953; Pearson, 1954; Saint-Girons & Saint-Girons, 1956). Changes in skin colour can alter the rate at which solar radiation is absorbed (Atsatt, 1939; Norris, 1958), and heat transport from the skin to the core of the body can be altered by changes in the circulatory system (Bartholomew & Tucker, 1963, 1964). However, lizards are not always able to attain their eccritic temperatures during cool seasons, at night or during periods of overcast skies and confinement in burrows. It is interesting to investigate how an animal that is found active and abroad at only a narrow range of body temperatures maintains physiological co-ordination over the wide range of body temperatures it may experience.

The relation of the cardiovascular system to temperature is particularly interesting, for this system transports all of the oxygen required to meet the energy demands of lizards. Oxygen transport by the cardiovascular system is described by the equation

\[ \text{oxygen consumption} = \text{heart rate} \times \text{stroke volume} \times \Delta V \text{ difference.} \]

The last factor is the difference in oxygen content of arterial (A) blood from the dorsal aorta and of mixed venous (V) blood. Stroke volume may be calculated if the other quantities in the equation are measured. Of these, only oxygen consumption and heart rate have been measured simultaneously in lizards (Dawson & Bartholomew, 1958; Dawson, 1960; Dawson & Templeton, 1963; Bartholomew & Tucker, 1963, 1964; Bartholomew, Tucker & Lee, 1965; Hudson & Bertram, 1964; Moberly, 1964). This study investigates the effects of temperature and of activity on oxygen consumption, heart rate, stroke volume and \( \Delta V \) difference in the green iguana (*Iguana iguana*).

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METHODS

Experimental animals

Iguanas from Columbia, S.A., were obtained through commercial dealers in Florida. They were housed indoors in a cage approximately 1.8 m. wide, 2.7 m. long and 2.1 m. high. Branches were arranged in the cage so the lizards could climb off the floor and bask beneath four 250 W. spotlights. Air temperature varied between 28 and 32°C, and humidity between 30 and 70%. A time-clock provided a 12 hr. light–dark cycle.

The lizards were fed with lettuce, bananas and canned dog food. Drinking water was continuously available. About half the lizards ate voraciously, gained weight and lived indefinitely. The others did not eat well or were subject to infections of the mouth and feet. For economy the lizards that did not eat or were suffering from infections were used preferentially for experiments requiring sacrifice of the animal. These ailing lizards were never emaciated or moribund when used for experiments, and several lizards in excellent condition were used as well. There were no obvious differences in results that could be attributed to the initial condition of the lizard.

The iguanas used in these experiments weighed between 510 and 1900 g. (mean = 1050 g.). Most individuals were docile and easy to handle.

Natural history

Although the iguana is widely distributed in the lowlands of tropical America, little has been published on its behaviour and thermal relations in nature. Swanson (1950) describes iguanas as arboreal, spending much of their time in high trees, often over a water-course. Iguanas appear to be heliothermic. Bogert (1959) mentions that the body temperatures of Mexican iguanas were 10 to 15°C above air temperature during the day. Hirth (1963) found that the body temperatures of sixteen iguanas in Costa Rica averaged 36.2°C (range 33–38°C) during the day when the mean air temperature was 30°C.

Oxygen consumption and heart rate

The procedures used in this study made it necessary to measure oxygen consumption without restricting access to the lizard’s body. This was accomplished by designing an air-tight neoprene rubber mask that covered only the mouth, nostrils and eyes (Pl. 1, fig. 1). A base for the mask was made of neoprene foam rubber strips 2 mm. thick and 5 mm. wide glued to the lizard’s head with contact cement. The mask was glued to this base with neoprene cement and could be removed quickly with solvent. Two rubber tubes entered the posterior part of the mask and opened on either side at the posterior corners of the mouth. The mask was tested for leaks after application by applying air pressure while the lizard’s head was immersed in water. It was invariably air-tight.

Air passed through a flow-meter, the mask, Drierite and Ascarite, and a Beckman G2 recording oxygen analyser. Air flow varied between 250 and 600 ml./min., depending on oxygen consumption. The oxygen content of air leaving the mask was always greater than 20% with one exception when it dropped to 18.5%. The mean pressure in the mask never exceeded 3 cm. of water above atmospheric.
The lizard was tied to a wooden jig in normal supine posture with legs free to move. Heart rate was counted from electrocardiograms. The leads were inserted subdermally at the base of the right hind leg and each foreleg. Body temperature was recorded ± 0.2°C. with a polyethylene-sheathed 30 gauge copper-constantan thermocouple inserted at least 6 cm. into the cloaca. The thermocouple and electrocardiographic leads were clipped to the jig and the animal with wires and tubes attached was placed in a constant-temperature cabinet. This cabinet was a large commercial refrigerator equipped with a fan, heater and thermostat that regulated the inside temperature to ± 0.2°C. All experiments were carried out at body temperatures within 1 °C. of 20, 30 and 38°C. Stimulation to activity was accomplished by attaching an induction coil to the electrocardiograph leads and giving repeated shocks. The lizards responded by struggling violently.

**Anatomy and cannulation techniques**

The lizard heart consists of right and left atria and a ventricle that is partially divided into dorsal and ventral chambers by a septum. The base of the ventricle communicates with the atria and three great arteries: the right and left systemic arches and the pulmonary artery. The ventricular septum is incomplete at the ventricular base. The right systemic arch curves dorsally and posteriorly along the right side of the vertebral column and gives off several vessels that are the only significant blood supply for the head and body anterior to the apex of the heart. The left systematic arch curves dorsally and posteriorly along the left side of the spine and gives off only the small ductus caroticus that connects with the left carotid artery. The right and left systemic arches join symmetrically just posterior to the heart and form the dorsal aorta. In this study, I have followed the nomenclature of Oelrich (1956) for arteries and Mahendra (1942) for veins.

The cannulation technique was similar to that of Popovic & Popovic (1960). Cannulas were made from polyethylene tubing (PE50) drawn out to a fine taper. A side opening was made 2–3 mm. back from the bevelled tip. The outside diameter of the tip was 0.3–0.4 mm.

Lizards were anaesthetized with an intraperitoneal injection of 300–500 mg./kg. tricaine (M.S. 222—Sandoz). An incision was made on the ventral side of the neck to the right or left of the mid-line, and on the dorsal surface of the thigh. Cannulas were tied into blood vessels after ligating the vessel distally. Each cannula was then externalized by slipping it into a hypodermic needle inserted through the skin and muscle into the incision, and withdrawing the needle. The incision was closed with sutures and sealed with methyl 2-cyanoacrylate monomer adhesive (supplied through the courtesy of Ethicon, Inc.). The exits of the cannulas through the skin also were sealed with adhesive.

After cannulation, iguanas were allowed to recover at least 12 hr. before any measurements were made. Recovery from the tricaine anaesthesia was complete after 30–60 min. Measurements continued for up to 5 days. All cannulas usually remained open during this time.

Three cannulas were placed in each lizard. They sampled blood from the right common jugular vein or sinus venosus, the right or left systemic arch, and the dorsal aorta. At the termination of each experiment, the iguana was dissected and the exact
locations of the cannulas were noted. The vessels in which the cannulas were inserted and the source of blood samples are shown in Table 1.

With the exception of the common jugular vein, the vessels ligated in the neck are small and supply or drain only superficial tissues of the head. The right and left common jugulars are connected by a sinus in the skull so that ligating one does not block venous return from the head.

<table>
<thead>
<tr>
<th>Insertion</th>
<th>Blood sampled</th>
</tr>
</thead>
<tbody>
<tr>
<td>Right tracheal vein</td>
<td>Usually right common jugular vein, occasionally sinus venosus</td>
</tr>
<tr>
<td>Right hyomandibular artery</td>
<td>Right systemic arch</td>
</tr>
<tr>
<td>Left hyomandibular artery</td>
<td>Usually right systemic arch, occasionally left systemic arch via ductus caroticus</td>
</tr>
<tr>
<td>Left common jugular vein</td>
<td>Sinus venosus</td>
</tr>
<tr>
<td>Femoral artery</td>
<td>Dorsal aorta</td>
</tr>
</tbody>
</table>

**Table 1. Insertion of cannulas and blood sampled**

Blood samples were drawn with a micrometer syringe attached by a four-way valve to three polyethylene tubes (PE100), each of which terminated in a glass capillary tube approximately 11 cm. long. The capillary tubes could be attached directly to the cannulas protruding from the lizard. Since polyethylene is permeable to oxygen, the glass capillary tubes were necessary to prevent contamination of the blood samples with atmospheric oxygen. Blood could be drawn almost simultaneously through all three cannulas by switching the micrometer syringe rapidly from one to another. The syringe and tubing were filled with heparinized saline.

When sampling blood, about 150 μl. of blood were drawn up into each polyethylene tube, the terminal 75 μl. remaining in the glass capillary tubes. Mixing of blood and heparinized saline was prevented by an air bubble. The cannulas were clamped off and disconnected, and 45 μl. of blood were transferred from each glass capillary tube to Roughton–Scholander blood pipettes (Roughton & Scholander, 1943). The pipettes were stored vertically at 3° C. after bringing the blood menisci to the scribed marks and sealing the tips with parafilm. Blood transfer to a pipette took less than a minute. Meanwhile, the other blood samples in their glass capillary tubes were rotated gently to prevent settling of the red cells. After all samples had been transferred, the capillary tubes were reattached to the cannulas and the unused blood was returned to the lizard.

Although there was some differential movement of plasma and blood cells through the cannulas and other tubing used in the sampling process, the haematocrit of blood decreased by less than 3% of the measured value during sampling. This loss is insignificant in the present study.

A mammalian haemoglobin solution that was 30% oxygenated was used to check the blood sampling and storage procedure for contamination by atmospheric oxygen. No measurable contamination occurred in haemoglobin stored for up to 3 hr. The oxygen content of lizard blood was always determined within 1 hr. of the time the blood was drawn.
Blood analysis

Oxygen content was determined on 39·3 µl. of blood by the method of Roughton & Scholander (1943). Oxygen content values could be repeated ± 0·1 ml. O₂/100 ml. blood.

Haematocrit was determined by filling a 1 × 75 mm. glass tube with blood and centrifuging for 30 min. at 1200 g. The lengths of the blood samples and packed red cells were measured to 0·1 mm. with vernier calipers.

Oxygen capacity was determined by equilibrating 150 µl. of blood with humidified air in a spherical 17 ml. tonometer rotated at 30 r.p.m. for 30 min. Duplicate oxygen content measurements were made. Deoxygenated blood placed in the tonometer reached 98% of maximum oxygen content in 10 min.

pH was determined with a Beckman micro blood pH assembly (no. 46850) and model 160 Physiological Gas Analyser. One end of the electrode chamber was connected to a 1 ml. syringe. The other end was connected by polyethylene tubing to a cannula protruding from the lizard. Blood was drawn into the electrode chamber, displacing heparinized saline solution. After a 3 min. equilibration period, pH was recorded. The blood was then returned to the lizard. The electrode assembly was immersed in a water-bath at the temperature of the lizard and was standardized with buffer prior to each pH measurement. pH determinations were accurate to ± 0·02 units.

Heart weight

Hearts including contained blood were excised and weighed after trimming off the sinus venosus and the great arteries where they left the ventricle. Ventricles were weighed after trimming off the atria, cutting open the ventricle, and washing out the blood.

RESULTS

Oxygen consumption and heart rate

Oxygen consumption and heart rate of nine lizards with a mean weight of 1054 g. (range 507–1897 g.) were measured at body temperatures (T_b) of approximately 20, 30 and 38°C. The animals were exposed to each temperature for at least 5 hr. They rested quietly if they were not disturbed. The blood vessels of seven of the lizards had been cannulated. There was no difference between the resting oxygen consumption and heart rates of cannulated and non-cannulated lizards. Measurements of resting oxygen consumption and heart rate in other intact iguanas (Moberly, 1964, and personal communication) are within the range of values reported here.

The relation between resting oxygen consumption and body temperature is linear when plotted semilogarithmically (Text-fig. 1). The equation of the eye-fitted line is

\[ \log \text{ml. O}_2 \,(\text{g. hr.})^{-1} = 0.0360 \, T_B + (7.850 - 10). \]

The slope of the line corresponds to a Q₁₀ of 2.29.

Resting heart rate also has a linear relation to body temperature when plotted semilogarithmically (Text-fig. 2). The equation of the eye-fitted line is

\[ \log \text{beats/min.} = 0.034 \, T_B + 0.68. \]

The slope of the line corresponds to a Q₁₀ of 2.19.
On a few occasions cannulated iguanas were stimulated to struggle while oxygen consumption, heart rate and oxygen content of blood were measured. Moberly (1964 and personal communication), using the same methods described here, has measured

Text-fig. 1. Relation of oxygen consumption to body temperature in the iguana. The upper line is for lizards stimulated to activity (data from Moberly, 1964 and personal communication). The lower line is for resting lizards. ○, Vertical lines and numbers indicate means, ranges and individuals respectively. O, Δ, Indicate oxygen consumption of the two iguanas in which oxygen transport measurements during activity were made (SV-5, SV-7).

Text-fig. 2. Relation of heart rate to body temperature in the iguana. Lines and symbols as in Fig. 2.
Circulatory system of green iguana

Oxygen consumption and heart rate in struggling, non-cannulated iguanas. My data and curves calculated from Moberly's data are shown in Text-figs. 1 and 2. The oxygen consumption and heart rates of struggling cannulated lizards were usually below those of non-cannulated lizards.

Haematocrit values and oxygen capacity

Haematocrit measurements on blood obtained by heart puncture or from newly cannulated lizards had a mean value of 30-6 ml. red cells/100 ml. blood ($s_m = 1.53$, $N = 13$). After blood loss, haematocrit values fell as low as nineteen before fatalities occurred. The highest haematocrit value observed was 42-8.

In eight lizards haematocrit and oxygen capacity were measured simultaneously. The mean ratio of oxygen capacity to haematocrit was 27.5 ml. $O_2$/100 ml. red cells ($s_m = 1.35$). After correcting for dissolved oxygen (Sendroy, Dillon & Van Slyke, 1934), this value would correspond to 19.0 g. haemoglobin/100 ml. red cells if one assumes 1.34 ml. $O_2$/g. haemoglobin. The oxygen capacity calculated from the mean haematocrit is 8.4 ml. $O_2$/100 ml. blood.

Blood pH

Blood pH of eight resting lizards varied with body temperature. Between 20 and 38°C, the least squares equation fitted to the data has the equation

$$pH = 7.83 - 0.017T_B$$

(standard error of estimate = 0.14, $N = 15$). The pH values of arterial and venous blood did not differ significantly.

Percentage saturation of arterial blood

The percentage saturation of arterial blood may differ in the two systemic arches of the iguana. The lizards used in this study can be divided into two groups: those in which both systemic arches carried blood equally saturated with oxygen and those in which blood from the left arch was less saturated with oxygen than that from the right arch. No case was observed where the right arch consistently carried blood containing less oxygen than the left arch.

Blood was sampled simultaneously from the right or left systemic arch and dorsal aorta in ten lizards at body temperatures of 20, 30 and 38°C. Not all lizards were exposed to all three temperatures. The percentage saturation values of blood from the right arch formed a single population, irrespective of temperature, with a mean value of 72% ($s_m = 4.1$, $N = 18$).

In five of the ten lizards, there was no consistent difference in the percentage saturation of blood from the right systemic arch and the dorsal aorta. In the other five, blood from the dorsal aorta was consistently less saturated with oxygen than blood from the right arch (three lizards) or more saturated with oxygen than blood from the left arch (two lizards). This indicates that in these five lizards, more venous blood entered the left systemic arch than the right. If one assumes that both arches contribute equal quantities of blood to the dorsal aorta, the left arch in these lizards must have been carrying blood only 49% saturated with oxygen. There was no relation between the distribution of venous blood in the systemic arches and body temperature or activity.
Stroke volume and AV difference

Heart rate, oxygen consumption, and oxygen content of blood from the dorsal aorta and the sinus venosus were measured simultaneously at different body temperatures in four resting lizards. (The sinus venosus contracts with each heart beat, and the blood obtained from it is assumed to be mixed venous blood.) Stroke volume was calculated from these data by the Fick principle. Stroke volume decreased as temperature increased (Table 2). The mean stroke volume changed from 1.9 ml./kg. at a body temperature of 20°C to 0.97 ml./kg. at a body temperature of 38°C. The extreme values of stroke volume were 2.5 and 0.38 ml./kg.

Mean values of AV difference increased in resting lizards as body temperature increased, changing from 1.9 ml. O$_2$/100 ml. blood at 20°C to 4.1 ml. O$_2$/100 ml. blood at 38°C. (Table 2).

### Table 2. Stroke volume, AV difference, heart rate and cardiac output in resting iguanas

<table>
<thead>
<tr>
<th>Experiment</th>
<th>$T_B$ (°C.)</th>
<th>Mean stroke volume (ml./kg.)</th>
<th>Mean AV difference (ml. O$_2$/100 ml. blood)</th>
<th>Mean heart rate (beats/min.)</th>
<th>Cardiac output (ml./kg.)</th>
<th>Number of determinations</th>
</tr>
</thead>
<tbody>
<tr>
<td>SV-4</td>
<td>20</td>
<td>2.5</td>
<td>1.7</td>
<td>22.5</td>
<td>56.2</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>1.4</td>
<td>2.6</td>
<td>44.7</td>
<td>62.6</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>38</td>
<td>1.1</td>
<td>2.0</td>
<td>92.4</td>
<td>104</td>
<td>2</td>
</tr>
<tr>
<td>SV-5</td>
<td>20</td>
<td>1.0</td>
<td>2.4</td>
<td>22.6</td>
<td>22.6</td>
<td>4</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>1.2</td>
<td>3.2</td>
<td>30.5</td>
<td>36.6</td>
<td>1</td>
</tr>
<tr>
<td></td>
<td>38</td>
<td>0.38</td>
<td>5.7</td>
<td>107</td>
<td>40.6</td>
<td>2</td>
</tr>
<tr>
<td>SV-6</td>
<td>38</td>
<td>0.70</td>
<td>6.5</td>
<td>85.5</td>
<td>59.8</td>
<td>2</td>
</tr>
<tr>
<td>SV-7</td>
<td>20</td>
<td>2.1</td>
<td>1.6</td>
<td>19.5</td>
<td>41.0</td>
<td>2</td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>1.9</td>
<td>1.8</td>
<td>39.5</td>
<td>75.0</td>
<td>2</td>
</tr>
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<td></td>
<td>38</td>
<td>1.7</td>
<td>2.3</td>
<td>83.2</td>
<td>142</td>
<td>4</td>
</tr>
<tr>
<td>Means</td>
<td>20</td>
<td>1.9</td>
<td>1.9</td>
<td>21.5</td>
<td>39.9</td>
<td></td>
</tr>
<tr>
<td></td>
<td>30</td>
<td>1.5</td>
<td>2.5</td>
<td>38.2</td>
<td>58.1</td>
<td></td>
</tr>
<tr>
<td></td>
<td>38</td>
<td>0.97</td>
<td>4.1</td>
<td>92.0</td>
<td>86.1</td>
<td></td>
</tr>
</tbody>
</table>

### Table 3. Oxygen transport at rest* and during activity in the iguana

<table>
<thead>
<tr>
<th>$T_B$ (°C.)</th>
<th>Expt. SV-5</th>
<th>Expt. SV-7</th>
</tr>
</thead>
<tbody>
<tr>
<td>Rest</td>
<td>20</td>
<td>20</td>
</tr>
<tr>
<td>Active</td>
<td>24.4</td>
<td>29.4</td>
</tr>
<tr>
<td>AV difference (ml. O$_2$/100 ml. blood)</td>
<td>32.7</td>
<td>52.4</td>
</tr>
<tr>
<td>Rest</td>
<td>2.8</td>
<td>1.6</td>
</tr>
<tr>
<td>Active</td>
<td>8.5</td>
<td>2.2</td>
</tr>
<tr>
<td>O$_2$ consumption (ml. O$_2$ (g. hr.)$^{-1}$)</td>
<td>3.8</td>
<td>3.4</td>
</tr>
<tr>
<td>Rest</td>
<td>0.0219</td>
<td>0.0379</td>
</tr>
<tr>
<td>Active</td>
<td>0.0586</td>
<td>0.141</td>
</tr>
<tr>
<td>Stroke volume (ml./kg.)</td>
<td>3</td>
<td>5.6</td>
</tr>
<tr>
<td>Rest</td>
<td>2.1</td>
<td>1.0</td>
</tr>
<tr>
<td>Active</td>
<td>3.2</td>
<td>1.6</td>
</tr>
<tr>
<td>No. of determinations</td>
<td>2</td>
<td>2</td>
</tr>
</tbody>
</table>

* Resting measurements were made immediately prior to activity.
Increases in AV difference were accomplished by a decrease in the oxygen content of venous blood rather than an increase in the oxygen content of arterial blood. Lizards survived venous oxygen contents as low as 1 ml. \(O_2/100\) ml. blood, but three animals, stimulated to activity or exposed to temperatures of 38° C., died shortly after venous oxygen content fell to 0.7, 0.6 and 0.3 ml. \(O_2/100\) ml. blood (14, 7.1 and 2.9% saturated, respectively). The percentage saturations of blood from the dorsal aortas of these three animals, measured at the same times as the venous values, were 68, 74 and 87% respectively.

Measurements were made on two lizards stimulated to activity. Stroke volume did not change consistently with activity but AV difference and heart rate always increased (Table 3).

Heart volume

The volume of the iguana heart is more than adequate to contain the largest observed values of stroke volume. Of fifteen hearts, the five that held the most congealed blood contained between 3.5 and 6.6 g. of blood per kg. body weight. These values were determined by subtracting the weights of the empty atria and ventricle from the total weight of the heart.

DISCUSSION

Oxygen transport and oxygen consumption at rest

One function of the vertebrate cardiovascular system is transport of oxygen from the lungs to the tissues. The amount of oxygen transported is equal to the oxygen consumed and is the product of three factors: heart rate, stroke volume and AV difference. If oxygen consumption increases by a factor \(K\), then each of these three quantities must change by factors whose product is \(K\).

The oxygen consumption of resting lizards increases as body temperature increases, and one or more of the three factors in the oxygen transport equation must change accordingly. In the resting iguana oxygen consumption increases by a factor of 4.4 as body temperature changes from 20 to 38° C. This increase is accompanied by a decrease in stroke volume by a factor of 0.5, but heart rate and AV difference increase by factors of 4.1 and 2.2 respectively (Text-fig. 3).

Both the oxygen consumption and heart rates of resting iguanas at 30° C. are above the range of values observed in other lizards. Bartholomew & Tucker (1964) summarized the existing data on oxygen consumption of resting lizards at a body temperature of 30° C. with the equation

\[
\text{ml. } O_2 \text{ (g. hr.)}^{-1} = 0.82W^{-0.38} (W \text{ in g.})
\]

This equation predicts an oxygen consumption of 0.058 ml. \(O_2\) (g. hr.)\(^{-1}\) for 1054 g. iguanas. The observed oxygen consumption was 0.085 ml. \(O_2\) (g. hr.)\(^{-1}\), 47% above the predicted value.

Heart rates in other lizards comparable in size to the iguanas used in this study have been measured only among the varanids. The equation heart beats/min. = 87.1\(W^{-0.156}\) for several Australian species of \(Varanus\) (Bartholomew & Tucker, 1964) predicts a resting heart rate of 29.6 beats/min. for a 1054 g. lizard at 30°. The observed heart rate of the iguana under these conditions is 50.1 beats/min., 69% above the predicted value for \(Varanus\).
Moberly's mean values for oxygen consumption and heart rates of resting iguanas at 30°C are comparable to those given here (1964 and personal communication).

Complete information on oxygen transport in other resting lizards is lacking, but simultaneous measurements of heart rate and oxygen consumption in several species permit the computation of oxygen pulse. Oxygen pulse is the oxygen consumed per heart beat per g. body weight and is the product of $AV$ difference and stroke volume per g. body weight. In all of the lizards for which data are available, oxygen pulse at rest at a temperature of 30°C is remarkably constant, lying between $3.0 \times 10^{-8}$ and $4.8 \times 10^{-5}$ ml. O_2 (beat g.)^{-1}. These data are from lizards of four families covering a size range from 0.25 g. to 4.4 kg. (see Bartholomew & Tucker, 1963, for summary; also Bartholomew & Tucker, 1964; Bartholomew, Tucker & Lee, 1965; Hudson & Bertram, 1964; Moberly, 1964; this study) Furthermore, Bartholomew & Tucker (1964) found an insignificant difference in exponents relating heart rate and oxygen consumption at rest to body weight in varanids 'indicating that oxygen pulse is independent of size in these lizards.

The constancy of oxygen pulse in resting lizards at 30°C suggests that the factors of oxygen pulse (stroke volume per g. body weight and $AV$ difference) are also independent of body weight. If one assumes that the stroke volume of 1.5 ml./kg. measured at 30°C in the resting iguana applies to all lizards, $AV$ differences between 2.0 and 3.2 ml. O_2/100 ml. blood can be calculated from the oxygen pulse values given above. This range includes the value of 2.5 measured in the iguana and could be readily accommodated by the known oxygen capacities of lizard bloods (Dawson & Poulson, 1962). Thus, no inconsistencies arise if the iguana is used as a model for oxygen transport in other lizards.

Text-fig. 3. Changes in heart rate, stroke volume and $AV$ difference accompanying the increase in oxygen consumption as the body temperature of a resting iguana changes from 20 to 38°C. Oxygen consumption is represented as a volume since it is the product of the three dimensions of each solid. The figures in parentheses are the factors by which oxygen consumption and each dimension change as body temperature increases. Solids are drawn to scale.
Oxygen transport and oxygen consumption during activity

The oxygen consumption of lizards depends not only on body temperature but also on activity level. It is interesting to consider how heart rate, stroke volume and AV difference change to accommodate increased oxygen consumption during activity at a given body temperature.

In the two iguanas for which measurements during activity are available, both heart rate and AV difference invariably increased with activity at all temperatures. However, stroke volume decreased with activity in one animal, but increased in the other (Table 3).

Although complete information on oxygen transport in other lizards during activity is lacking, the data for the iguana suggest the changes that occur. There are measurements of oxygen pulse during activity in three lizards other than the iguana: Amphibolurus barbatus (Bartholomew & Tucker, 1963), Varanus spp. (Bartholomew & Tucker, 1964) and Tiliqua scincoides (Bartholomew, Tucker & Lee, 1965). If one assumes that the resting levels of stroke volume measured in the iguana are valid for these lizards during activity, AV difference can be calculated from oxygen pulse.

Alternatively, the maximum AV difference that a lizard could attain can be estimated from the oxygen capacity of its blood, the percentage saturation of arterial blood and the lowest oxygen content of mixed venous blood that is not fatal. Oxygen capacity of blood from a variety of lizards has been measured (Dawson & Poulson, 1962). The mean percentage saturation of arterial blood in iguanas was about 70, and the minimum non-fatal oxygen content of mixed venous blood was 1 ml. O₂/100 ml. blood. If the maximum values for AV difference for lizards calculated from these data are much smaller than those calculated from oxygen pulse during activity, then percentage saturation of arterial blood, stroke volume, or both must increase with activity.

Table 4. Comparison of maximum values for AV difference in active lizards calculated from oxygen pulse and from oxygen capacity of the blood. See text for explanation

<table>
<thead>
<tr>
<th>Species</th>
<th>Temperature (°C)</th>
<th>Estimated stroke volume (ml./kg.)</th>
<th>Maximum oxygen pulse during activity (ml. O₂/g. best)⁻¹</th>
<th>Oxygen capacity (ml. O₂/100 ml. blood)</th>
<th>Max. AV difference calculated from oxygen pulse (ml. O₂/100 ml. blood)</th>
<th>Max. AV difference calculated from oxygen capacity (ml. O₂/100 ml. blood)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Amphibolurus barbatus</td>
<td>20</td>
<td>1.9</td>
<td>12.2 x 10⁻⁴</td>
<td>10.2*</td>
<td>6.4</td>
<td>6.1</td>
</tr>
<tr>
<td>Tiliqua scincoides</td>
<td>40</td>
<td>1.0</td>
<td>5.4 x 10⁻⁵</td>
<td>12.6†</td>
<td>5.4</td>
<td>7.8</td>
</tr>
<tr>
<td>Varanus</td>
<td>40</td>
<td>1.0</td>
<td>10.7 x 10⁻⁵</td>
<td>12.7‡</td>
<td>10.7</td>
<td>7.9</td>
</tr>
</tbody>
</table>

† Estimated from Eumeces: Dawson & Poulson (1962).
‡ Calculated from Varanus: Nair (1955).

Values for these two estimates of AV difference during activity are shown in Table 4. In both Amphibolurus and Tiliqua, AV differences estimated from oxygen capacity are greater than or close to those estimated from oxygen pulse. These lizards could meet the oxygen demands of activity with a stroke volume no greater than that observed in...
the resting iguana. However, the $AV$ difference estimated from oxygen capacity for *Varanus* is 26% less than that estimated from oxygen pulse. Thus, varanids during activity must have a larger stroke volume than the resting iguana or arterial blood that is more than 70% saturated with oxygen. In connexion with the latter possibility, it is interesting to note that varanids have unusually well developed lungs for lizards (Bellairs, 1957).

**Comparisons with mammals**

The resting oxygen consumption at 38°C of the iguanas used in this study approaches basal mammalian rates more closely than those of most other lizards, being about one-third as much. Other 1 kg. lizards at a body temperature of 37°C consume approximately one-sixth as much oxygen as mammals of the same size under basal conditions. This fraction was calculated from the expression $0.35W^{-0.11}$ (W/kg.), which is the ratio of the equations relating oxygen consumption to body weight in mammals and lizards (Morrison, Ryser & Dawe, 1959; Bartholomew & Tucker, 1964; assuming a $Q_{10}$ of 2).

The stroke volume, heart rate, cardiac output and $AV$ difference of resting iguanas at 38°C also may be compared with those of mammals under basal conditions. Mean stroke volumes up to 2.5 ml./kg. were obtained for the resting iguana. This value exceeds the stroke volumes of small mammals (0.5–1 ml./kg.; Spector, 1956; Popovic & Kent, 1964). It is possible that some of the high stroke volume determinations in the iguana were errors resulting from incomplete mixing of venous blood in the sinus venosus or from profound differences in oxygen content of the right and left systemic arches. However, even assuming that oxygen content of mixed venous blood is 0, stroke volumes of 1.9 ml./kg. can be calculated for some lizards that had equally oxygenated blood in the systemic arches. It must be concluded that iguanas may have stroke volumes of over 2 ml./kg.

The mean heart rate of resting iguanas at 38°C is roughly one-third that of small mammals (Altman & Dittmer, 1964). Cardiac output (ml. (min.kg.)$^{-1}$) is roughly one-half that of small mammals (Spector, 1956; Popovic & Kent, 1964; Table 2). $AV$ difference values for iguanas and small mammals are about the same, since the cardiac output and oxygen consumption of iguanas are roughly the same fraction of mammalian values.

In homeotherms increased oxygen demands result primarily from activity, but in poikilotherms they result from increases in body temperature as well. Increases in oxygen transport associated with changes in body temperature in the resting iguana take place by different mechanisms from the increases accompanying activity in mammals. In the resting iguana oxygen transport increases by a factor of 4.4 as body temperature changes from 20 to 38°C. This increase is accompanied by a decrease in stroke volume but heart rate and $AV$ difference both increase. In contrast, increases in oxygen transport during activity in men and dogs are accompanied by an increase in stroke volume as well as in heart rate and $AV$ difference (Astrand, Cuddy, Saltin & Sternberg, 1964; Cerretelli *et al.* 1964).

**Oxygen capacity and haemoglobin content**

Compared to other lizards and snakes, the iguana has blood with both a low oxygen capacity (8.4 ml.O$_2$/100 ml. blood) and a low haemoglobin content/100 ml.
Circulatory system of green iguana

red cells (19 g.). Other lizards and snakes have blood with oxygen capacities between 6 and 16 ml.O_2/100 ml. blood (Dawson & Poulson, 1962) and haemoglobin contents of 26–31 g./100 ml. red cells (Dill, Edwards, Bock & Talbot, 1935; Edwards & Dill, 1935; Dittmer, 1961).

Circulation in the lizard heart

The functional anatomy of the lizard heart and great arteries has been a subject of interest and controversy for many years. There are two basic problems: (1) how much mixing of pulmonary and venous blood occurs in the partially divided ventricle? (2) what is the distribution of pulmonary and venous blood in the three great arteries leaving the ventricle? Various views on these questions are summarized by Khalil & Zaki (1964), White (1959), Foxon, Griffith & Price (1956) and Mathur (1944).

Some of the disagreement may result from the different methods that have been used to investigate circulation through the heart. In living lizards, the problem has been approached by using radiography to follow radio-opaque liquids as they pass through the heart and by comparing the oxygen contents of blood samples drawn by puncturing various vessels and heart chambers. These techniques involve opening the chest cavity and pericardium. They prevent normal respiration and the shape of the heart changes markedly when it is removed from the tough pericardium. The permanent cannulation technique used in this study avoids these objections.

The results of this study may be compared with those of Khalil & Zaki (1964) and White (1959) who have measured the oxygen content of blood drawn by direct puncture from the various vessels and heart chambers. These authors do not agree. Khalil & Zaki, using the lizards Agama stellio and Varanus griseus, found that venous and pulmonary blood mixed in the ventricle, since blood from the pulmonary artery contained significantly more oxygen than blood from the sinus venosus. In Varanus, blood from the pulmonary vein contained more oxygen than blood from the right systemic arch, again indicating mixing of venous and pulmonary blood. Khalil & Zaki did not compare oxygen contents of blood from the right and left systemic arches of lizards, but in the snake Zamensis diadema, the left arch carried blood with a lower oxygen content than the right arch. This situation also was observed in a tortoise and crocodile.

White (1959), using the iguana, found no appreciable mixing of venous and pulmonary blood in the heart. Blood from the right atrium and pulmonary artery had approximately the same oxygen content, and there was no difference in oxygen contents of blood from the right and left systemic arteries and the pulmonary vein (63 % saturated). Similar observations were made on the snake Coluber constrictor.

My observations on the iguana are partly in agreement both with those of Khalil & Zaki and with those of White. In half the lizards that I investigated the two systemic arches carried blood with equal oxygen contents, the mean percentage saturation being 72. Judging from White's data, both arches were probably carrying only pulmonary blood. In the other iguanas, the mean percentage saturation of blood in the left arch was less than in the right, indicating that venous blood may mix with pulmonary blood and preferentially enter the left arch.

In those lizards where mixing occurs, about one-half of the blood entering the left arch may be venous. If one assumes that both arches contribute equal quantities of
blood to the dorsal aorta, then the mean percentage saturation in the left arch must have been 49% (see Results). The mean oxygen capacity of iguana blood is 8.4 ml. O₂/100 ml. blood and the mean AV difference at 30°C is 2.5 ml. O₂/100 ml. blood. Calculations based on these figures and the percentage saturation of blood in the right and left arches and dorsal aorta indicate that 56% of the blood entering the left arch is venous and 44% has the same oxygen content as blood from the right arch. If pulmonary blood has a higher oxygen content than the blood in the right arch, the pulmonary contribution to the left arch would be even lower. The fact that large quantities of venous blood can be directed into one arch but not the other suggests that sharp boundaries exist between arterial and venous blood during the cardiac cycle.

Since the left systemic arch is found in all lizards, is almost as large as the right arch (Khalil & Zaki, 1964; Mathur, 1944; Mahendra, 1942) with which it joins symmetrically to form the dorsal aorta, and since there may be a distinct separation of blood flow between it and the right arch, it seems likely that the left arch has some specific function. Ewer (1950) has suggested that the lungs of lizards cannot accommodate the entire cardiac output, and the left arch shunts some venous blood back to the systemic circulation. Meanwhile, the right arch maintains a supply of well-oxygenated blood to the head and anterior body. However, White's observations and my own in which the two systemic arches carried equally oxygenated blood do not support this view.

A possible role of the left arch in lizards may concern thermoregulation as well as respiration. Bartholomew & Tucker (1963, 1964) have shown that some lizards can control the rate of heat transport by the circulatory system. This ability supplements their behavioural thermoregulation. In *Amphibolurus barbatus*, increases in heart rate and presumably cardiac output accompany increased heat transport. The anatomical arrangement of the lizard heart and great vessels may be a device for greatly increasing cardiac output for heat transport by allowing large quantities of venous blood to bypass the lungs and enter the left systemic arch. At the same time, a well-oxygenated supply of blood could be maintained to the brain and major sense organs via the right systemic arch.

There are two lines of argument that support this hypothesis besides the known function of the lizard circulatory system in the control of heat transport. First, the anatomy of the lizard heart suggests that the lungs have a high resistance to blood flow, and bypassing them could substantially reduce the energy requirements of increased cardiac output. The openings of the pulmonary and systemic arteries are in a single ventricular chamber and are separated only by a muscular ridge of the ventricle wall. It is questionable whether large pressure gradients could exist across this ridge. Hence, blood may enter the systemic and pulmonary arteries at about the same pressure and flow to pressures near 0 in the right and left atria. Accordingly, if blood flow is to be equally divided between pulmonary and systemic circulation, the resistance of the lungs should approximate the peripheral resistance of the total body.

The second line of argument deals with data on the oxygen contents of blood in the two systemic arches. The hypothesis predicts that a lizard being heated to its ecctic temperature would have a high cardiac output, and the oxygen content of blood in the left systemic arch would be less than that in the right. During cooling, the difference in oxygen contents of blood from the two systemic arches would be
Circulatory system of green iguana

reduced or non-existent. White's measurements and my own demonstrate that blood from the left systemic arch of the iguana may indeed have an oxygen content that is equal to or less than that of blood from the right arch, but not vice versa. Thus, the distribution of venous blood in the systemic arches of the iguana is not inconsistent with the hypothesis. Whether this distribution is related to heating and cooling conditions remains to be investigated.

SUMMARY
1. Oxygen consumption, stroke volume, heart rate and the difference in oxygen contents of arterial and venous blood (AV difference) were measured in the resting iguana at body temperatures of 20, 30 and 38°C. Oxygen consumption increased by a factor of 4.4 as temperature changed from 20 to 38°C. This increase was accomplished by a decrease in stroke volume by a factor of 0.5, and increases in heart rate and AV difference by factors of 4.1 and 2.2, respectively.
2. During activity increases in oxygen consumption at a given temperature were accompanied by increases in heart rate and AV difference, but stroke volume did not change consistently.
3. The percentage saturation of arterial blood with oxygen in the iguana may differ in the right and left systemic arches. In some lizards, both arches carried equally saturated blood, but in others the left arch carried blood containing less oxygen than the right arch.
4. An hypothesis is presented concerning the function of the double systemic arches and incompletely divided ventricles of lizards. These structures may be a device for permitting increased cardiac output associated with thermoregulation to bypass the lungs while maintaining a supply of well-oxygenated blood to the head.
5. Data on oxygen capacity, percentage saturation of blood with oxygen, haematocrit and pH of iguana blood are included in this study.

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REFERENCES


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**EXPLANATION OF PLATE**

Fig. 1. Iguana fitted with a neoprene mask for oxygen-consumption measurements. Electrocardiographic leads and two cannulas can be seen in the neck and shoulder region.
VANCE A. TUCKER

(Facing p. 92)