PULMONARY OXYGEN TRANSPORT
DURING ACTIVITY IN LIZARDS

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Abstract. Oxygen consumption ($\dot{M}_{O_2}$), effective alveolar ventilation ($\dot{V}$eff), arterial and alveolar P_{O_2} (Pa_{O_2}, PA_{O_2}) and the alveolar-arterial P_{O_2} difference [$(A–a)P_{O_2}$] were determined in the lizards *Varanus exanthematicus* and *Iguana iguana* at rest and during treadmill exercise at 35 °C. In both species, $\dot{V}$eff increased more rapidly than $\dot{M}_{O_2}$ giving rise to an increased PA_{O_2}. In contrast, Pa_{O_2} remained unchanged through the highest levels of $\dot{M}_{O_2}$ attained. As a result, the $(A–a)P_{O_2}$ increased with increasing $\dot{M}_{O_2}$.

We suggest that the observed increase in $(A–a)P_{O_2}$ may be due to a rather low pulmonary oxygen diffusing capacity ($D_{L_{O_2}}$) and limited capacity to increase $D_{L_{O_2}}$ during exercise. Arterial desaturation was prevented by a compensatory hyperventilation, thus enhancing the gradient for alveolar-capillary gas exchange. These results indicate that both lizard species increase pulmonary oxygen transport sufficiently so that it is not a limiting factor to aerobic scope under the conditions of this study.

Gas exchange	Reptiles
Iguana iguana	Treadmill exercise
Pulmonary diffusion limitation	*Varanus exanthematicus*

The primary function of the pulmonary system is to ensure normal levels of oxygen and carbon dioxide in the arterial blood. In order to fulfil this role during periods of increased oxygen consumption: (1) pulmonary ventilation must be adjusted in order to maintain the levels of intrapulmonary P_{O_2} and P_{CO_2} and (2) the capacity for gas exchange between the lungs and blood must be sufficient to establish systemic arterial gas tensions which approximate the partial pressures in the pulmonary gas.

Little is known about pulmonary gas exchange during activity in reptiles. However, the relatively simple lung structures of many reptilian lungs (*cf.* Wood and Lenfant, 1976) suggest that pulmonary gas exchange may be an inefficient process, and that pulmonary oxygen transport may even be a limiting factor in

the aerobic scope of some reptiles. Thus, it is of interest to investigate the adequacy of pulmonary gas exchange during periods of increased whole body oxygen consumption in reptilian species which differ in lung structure and aerobic scope.

We have recently conducted experiments on cardiovascular responses (Gleeson et al., 1980) and acid–base balance (Mitchell et al., 1980) in two lizard species exercised on a treadmill. In this paper, we will present additional data from these same animals which relate to pulmonary gas exchange during activity.

The two lizard species used in this study are from different families, and differ substantially in their physiological and morphological characteristics. Varanus exanthematicus is a highly active predator with a relatively large aerobic scope (Bartholomew and Tucker, 1964; Bennett, 1972; Wood et al., 1978; Gleeson et al., 1980). In contrast to most other lizards, Varanus has well developed alveolar lungs (Wolf, 1933; Mertens, 1942; Kirshfeld, 1970; Perry and Duncker, 1978). The second species studied, Iguana iguana, is a sedentary arboreal animal with a lower aerobic scope (Tucker, 1966; Moberly, 1968a,b; Gleeson et al., 1980) and a poorly developed lung (Milani, 1894; Wolf, 1933; Perry and Duncker, 1978).

The specific objectives of this study were to determine whether pulmonary oxygen transport may in fact limit the aerobic scope of either species, and to compare the efficiency of gas exchange in Varanus with that in Iguana.

Methods

Four savannah monitors (Varanus exanthematicus; mean body size 1.02 kg) and six green iguanas (Iguana iguana; mean body mass 0.80 kg) were used in this study. Under halothane anesthesia, a catheter was placed in the external carotid artery and exteriorized on the back of the neck. A second catheter was inserted into the ipsilateral jugular vein and passed down to the sinus venosus of the heart in order to sample mixed venous blood and determine cardiac output (see Gleeson et al., 1980). Following surgery, one day was allowed for recovery before experiments commenced.

MEASUREMENTS

The rates of oxygen consumption ($\dot{M}_{O_2}$) and carbon dioxide production ($\dot{M}_{CO_2}$) were determined as described previously (Gleeson et al., 1980; Mitchell et al., 1980). Gas was drawn at a known rate from a loose fitting plastic mask, dried and then analyzed with oxygen (Applied Electrochemistry, model S3A) and carbon dioxide analyzers (Beckman, model LB-2). Values of $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ are expressed in ml O_2 (STPD) $\cdot$ kg^{-1} $\cdot$ h^{-1}.

Blood samples (0.3 ml) drawn from the arterial cannula were stored anaerobically on ice until analyzed (within 5 min) for P_{O_2} and P_{CO_2} with a micro blood gas

analyzer (Radiometer; models BMS 3 Mk II and PHM 73) maintained at 35 °C. The electrodes were calibrated before and after every measurement: the P_{CO_2} electrode with gases from a mixing pump (Radiometer, model GMA2), and the P_{O_2} electrode with air equilibrated water (35 °C). The values of P_{CO_2} were corrected to the rectal temperature of the animals using the correction factors for human blood (Bradley *et al.*, 1956) although body temperature seldom deviated from 35 °C by more than 1 °C. Values of P_{O_2} were not corrected for differences in temperature since it does not appear that the correction factors determined for mammalian blood are applicable to lizards and, to our knowledge, similar correction factors have not yet been reported for reptilian blood. A portion of each blood sample was also used to determine hematocrit.

EXPERIMENTAL PROTOCOL

After equilibration at 35 °C for several hours, an animal was fitted with the metabolic mask, catheter extensions, and a cloacal thermistor probe. It was then placed on a thermostatically controlled treadmill and covered with a cloth until $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ remained stable for more than 20 min. Resting measurements were made followed by an experimental run between 0.5 and 2.0 km·h^{-1} in *Varanus* and 0.2 and 1.0 km·h^{-1} in *Iguana*. Blood samples were drawn during a run when it became clear that $\dot{M}_{O_2}$ and $\dot{M}_{CO_2}$ had reached steady values at lower running speeds, or when it appeared that exhaustion was at hand at the higher running speeds. Animals were allowed a minimum of four hours to recover before the next trial. Seldom were more than two trials run on the same animal in a given day.

CALCULATIONS

The effective alveolar ventilation ($\dot{V}$eff) was calculated from Pa_{CO_2} and $\dot{M}_{CO_2}$ using the equation:

$$\dot{V}eff = R \cdot T \cdot \dot{M}_{CO_2} \cdot (Pa_{CO_2})^{-1} \tag{1}$$

where R is the gas constant [2.785 ml·Torr·(ml STPD·K)$^{-1}$] and T is the absolute temperature (°K). Values of $\dot{V}$eff are reported in ml (BTPS)·g^{-1}·h^{-1}.

The ideal alveolar P_{O_2} (PA_{O_2}) was calculated according to the alveolar gas equation (cf. Otis, 1964):

$$PA_{O_2} = PI_{O_2} - [1 - (1-R.E.) \cdot FI_{O_2}] \cdot \frac{PA_{CO_2}}{R.E.} \tag{2}$$

where R.E. in this case is the respiratory exchange ratio ($\dot{M}_{CO_2} \cdot \dot{M}_{O_2}^{-1}$) and PA_{CO_2} is the ideal alveolar P_{CO_2}, taken to be the same as Pa_{CO_2}. The principal

assumptions in this equation are (1) steady-state for gas exchange and (2) complete equilibration of CO_2 between lung and blood so that alveolar P_{CO_2} = arterial P_{CO_2}. From the calculated value of PA_{O_2}, the alveolar-arterial P_{O_2} difference, $(A-a)P_{O_2}$, was determined.

STATISTICAL ANALYSIS

Statistical comparisons between mean data groups were made using Student's t-test. Individual measurements of Pa_{O_2}, PA_{O_2} and $(A-a)P_{O_2}$ were expressed as a difference from the average resting value in a given animal. Significant correlations of these variables and $\dot{V}eff \cdot \dot{M}_{O_2}^{-1}$ with $\dot{M}_{O_2}$ were established by standard least squares regression and a two-tailed t-test.

Results

RESTING VALUES

The values of measured and calculated variables in resting animals are summarized in table 1. Both *Varanus* and *Iguana* maintain levels of Pa_{O_2} at about 90 Torr; however, PA_{O_2} is substantially higher in both species giving rise to alveolar-arterial P_{O_2} differences of 14 and 19 Torr respectively. There were no significant differences $(P > 0.10)$ between the mean values of $\dot{M}_{O_2}$, $\dot{V}eff \cdot \dot{M}_{O_2}^{-1}$, Pa_{O_2}, PA_{O_2}, $(A-a)P_{O_2}$ or hematocrit between these species at rest.

RESPONSES DURING ACTIVITY

From the mean resting value of $0.19\ ml \cdot g^{-1} \cdot h^{-1}$, $\dot{M}_{O_2}$ increased progressively with running speed in *Varanus* until a maximum value was reached between 1.0 and

TABLE 1

Values of measured and calculated variables in resting *Varanus* and *Iguana* at 35 °C

Variables	Units	*Varanus*	*Iguana*
$\dot{M}_{O_2}$	ml O_2 (STPD) $\cdot g^{-1} \cdot h^{-1}$	0.19 ± 0.03	0.18 ± 0.01
$\dot{M}_{CO_2}$	ml CO_2 (STPD) $\cdot g^{-1} \cdot h^{-1}$	0.13 ± 0.02	0.13 ± 0.01
R.E.		0.67 ± 0.04	0.71 ± 0.04
$\dot{V}eff/\dot{M}_{O_2}$		18.1 ± 1.2	19.3 ± 1.5
Pa_{O_2}	Torr	91 ± 4	90 ± 3
PA_{O_2}	Torr	104 ± 3	108 ± 4
$(A-a)P_{O_2}$	Torr	13.6 ± 1.7	18.6 ± 4.9
Hct	Volume %	25 ± 2	26 ± 2
Body wt.	kg	1.02 ± 0.04	0.80 ± 0.05

Mean values ± 1.0 S.E.M. from 4 *Varanus* and 6 *Iguana*.
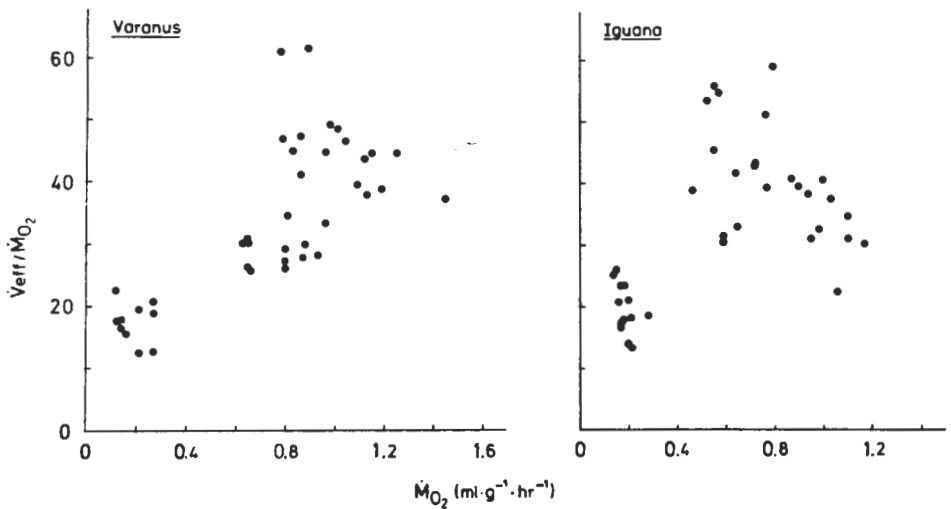
Fig. 1. The air convection requirement ($\dot{V}eff/\dot{M}_{O_2}$) as a function of oxygen consumption ($\dot{M}_{O_2}$) in *Varanus* (n = 4) and *Iguana* (n = 6) exercised on a treadmill at 35 °C.

1.5 km $\cdot$ h^{-1}. Maximum $\dot{M}_{O_2}$ averaged 6.5 times the resting value. In *Iguana*, $\dot{M}_{O_2}$ reached a maximum value between 0.2 and 0.5 km $\cdot$ h^{-1}. The average maximum value of $\dot{M}_{O_2}$ was 5 times the resting value of 0.18 ml $\cdot$ g^{-1} $\cdot$ h^{-1}. Additional details on the metabolic responses to activity in *Varanus* and *Iguana* can be found in Gleeson *et al.* (1980) and Mitchell *et al.* (1980).

The air convection requirement ($\dot{V}eff \cdot \dot{M}_{O_2}{}^{-1}$) is presented as a function of $\dot{M}_{O_2}$ in fig. 1. In both *Varanus* (P < 0.001) and *Iguana* (P < 0.001), this ratio increased with increasing $\dot{M}_{O_2}$ giving rise to increased levels of PA_{O_2} (fig. 2; P < 0.001).
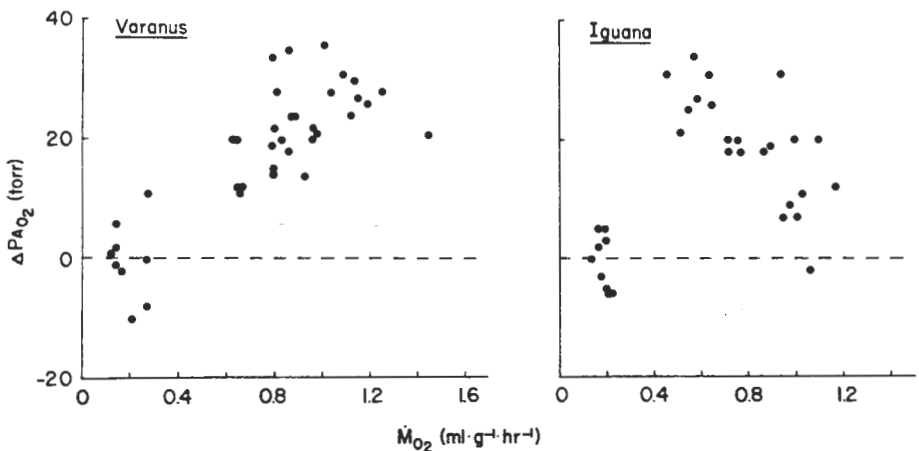

Fig. 2. The change in ideal alveolar P_{O_2} from the mean resting value in the same animal (ΔPA_{O_2}) as a function of oxygen consumption ($\dot{M}_{O_2}$) in *Varanus* and *Iguana* exercised on a treadmill at 35 °C. The horizontal dotted lines indicate no change.
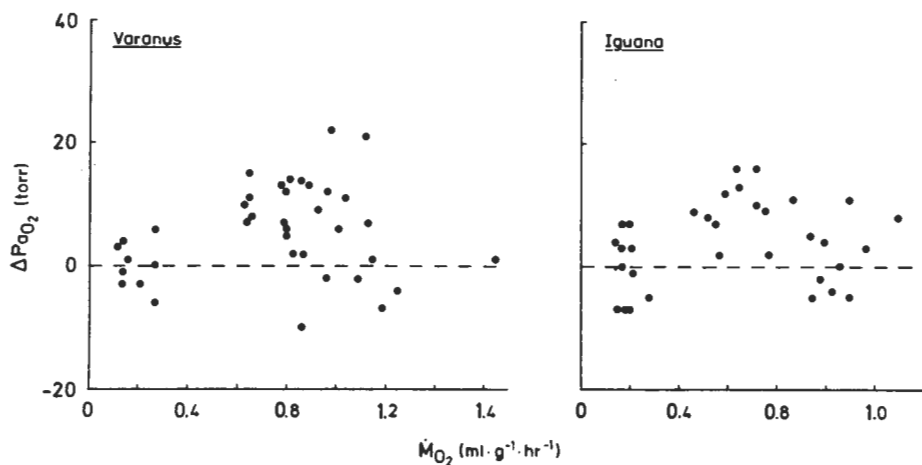
Fig. 3. The change in arterial P_{O_2} from the mean resting value in the same animal (ΔPa_{O_2}) as a function of oxygen consumption ($\dot{M}_{O_2}$) in *Varanus* and *Iguana* exercised on a treadmill at 35 °C. The dotted line at $\Delta Pa_{O_2} = 0$ indicates no change.

Arterial P_{O_2} apparently rose to a small extent with $\dot{M}_{O_2}$ in both species (fig. 3), but the changes were small and not statistically significant ($P > 0.05$). The rising level of PA_{O_2} with a relatively constant Pa_{O_2} resulted in an increasing $(A-a)P_{O_2}$ (*Varanus*, $P < 0.001$; *Iguana*, $P < 0.01$) as shown in fig. 4. In *Varanus*, the level of $(A-a)P_{O_2}$ remained relatively unchanged until $\dot{M}_{O_2}$ increased above $0.6 \, \text{ml} \cdot \text{g}^{-1} \cdot \text{h}^{-1}$. The variation in $(A-a)P_{O_2}$ was greater in *Iguana*, but it appeared to increase at all elevated levels of $\dot{M}_{O_2}$ observed.
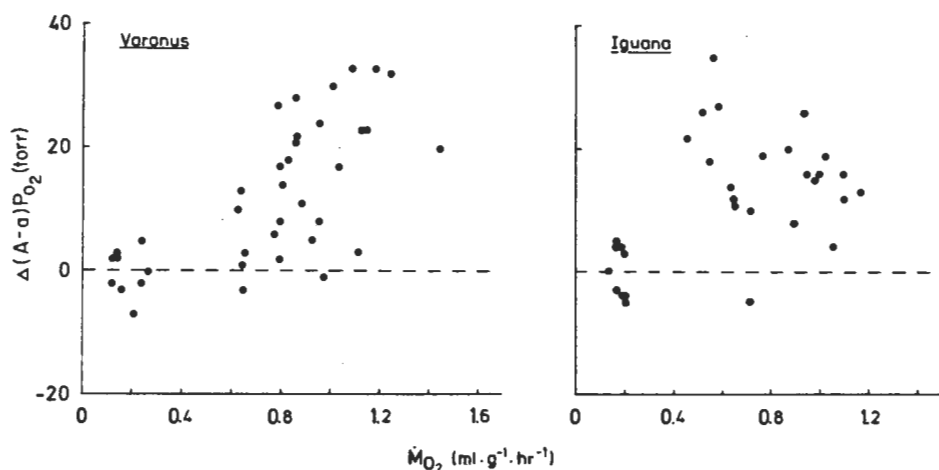

Fig. 4. The change in the alveolar-arterial P_{O_2} difference from the mean resting value in the same animal ($\Delta(A-a)P_{O_2}$) as a function of oxygen consumption ($\dot{M}_{O_2}$) in *Varanus* and *Iguana* exercised on a treadmill at 35 °C. The horizontal dotted lines indicate no change.

Discussion

CRITIQUE OF METHODS

Increasing whole body oxygen consumption via treadmill exercise may not be strictly comparable to the natural circumstances in which these animals increase $\dot{M}_{O_2}$, particularly in the arboreal *Iguana*. Accordingly, it is premature to extend the findings of this study to all circumstances in which these animals are active. Additional factors to consider include: dynamic as opposed to steady-state exercise, exercise at different body temperatures, and postural changes which may affect gas exchange.

One technical aspect to consider which could have given rise to erroneous measurements of Pa_{O_2} and, thus, $(A-a)P_{O_2}$ is that corrections for differences between the temperature at which Pa_{O_2} was measured and the animal's body temperature were not made. However, we feel it is unlikely that the findings would be significantly altered by such a correction since: (1) the animal's body temperature seldom deviated from 35 °C by more than 1 °C in either direction, (2) there were no detectable directional trends in body temperature with increasing exercise intensity and (3) relatively large changes in temperature have very little effect on the P_{O_2} of 90% saturated blood in either *Iguana* (Wood and Moberly, 1970) or *Varanus* (Wood *et al.*, 1977).

PULMONARY OXYGEN TRANSPORT

The ability to maintain adequate pulmonary oxygen transport during periods of activity and increased oxygen consumption depends on both a mechanism of increasing pulmonary ventilation according to demand and efficient pulmonary gas exchange. In order to maintain the level of PA_{O_2} and thus the gradient for pulmonary oxygen exchange, alveolar ventilation must increase in direct proportion to $\dot{M}_{O_2}$ multiplied by a term which reflects changes in the respiratory exchange ratio (R.E. $= \dot{M}_{CO_2} \cdot \dot{M}_{O_2}^{-1}$). The basis for this relationship can be seen by combining equations 1 and 2:

$$\dot{V}eff = \frac{R \cdot T \cdot \dot{M}_{O_2}}{PI_{O_2} - PA_{O_2}} \cdot [1 - (1-R.E.) \cdot FI_{O_2}] \tag{3}$$

Equation (3) is the alveolar ventilation equation derived from O_2 rather than CO_2 (*cf*. Otis, 1964). Since R.E. increases with activity in both lizard species (Mitchell *et al.*, 1980), the air convection requirement could actually decrease slightly and the level of PA_{O_2} would still be maintained at or above the resting value. The large increase in the air convection requirement observed (fig. 1) assures that the level of PA_{O_2} is in fact substantially elevated during activity and the gradient for pulmonary oxygen transport is thus enhanced.

Efficient gas exchange between the lungs and blood during periods of increased $\dot{M}_{O_2}$ is dependent on three primary factors: (1) minimal presence of cardiopulmonary blood shunts, (2) homogeneous distribution of ventilation with respect to perfusion and (3) a pulmonary oxygen diffusing capacity which is adequate to fully oxygenate the blood within its contact time at the gas exchange surfaces. The possibility that oxygen delivery to the tissues is limited by a severe deficiency with regard to any of these factors is ruled out by the observation that Pa_{O_2} was maintained through the maximal levels of $\dot{M}_{O_2}$ attained by either species (fig. 3). Thus, both *Varanus* and *Iguana* increase pulmonary oxygen transport sufficiently so that it does not limit aerobic scope under the conditions of this study. The factors which ultimately limit the ability to increase $\dot{M}_{O_2}$ further in these species must be in the cardiovascular system or the tissues themselves.

Whereas the capacity to increase pulmonary oxygen transport equals or exceeds the aerobic scope in both *Varanus* and *Iguana*, it appears that the hyperventilation and enhanced alveolar-pulmonary capillary O_2-gradient are necessary to prevent a degree of arterial desaturation when $\dot{M}_{O_2}$ increases. This is evidenced by the distinct rise in alveolar P_{O_2} which is not reflected in the arterial P_{O_2} (figs. 2 and 3), suggesting that one or more of the primary factors involved in gas exchange between the lungs and blood was relatively inefficacious.

The level of $(A-a)P_{O_2}$ is an index of the efficacy in lung-blood oxygen transport. Both *Varanus* and *Iguana* have a large $(A-a)P_{O_2}$ at rest (14 and 19 Torr respectively; table 1) which increases with increasing $\dot{M}_{O_2}$ during activity (fig. 4). The values of $(A-a)P_{O_2}$ in these lizards contrast with those in healthy young men where the level of $(A-a)P_{O_2}$ is generally between 5 and 10 Torr at rest (*cf.* Rahn and Farhi, 1964; Whipp and Wasserman, 1969) and then decreases with increasing $\dot{M}_{O_2}$ during moderate exercise (Whipp and Wasserman, 1969).

The establishment of large positive alveolar-arterial P_{O_2} differences at rest in both *Varanus* and *Iguana* can be accounted for in large part by the presence of cardiopulmonary blood shunts. Right to left cardiac shunts ranging between 16 (Berger and Heisler, 1977) and 30 percent (Heisler, N., personal communication) of the systemic cardiac output occur in resting *Varanus exanthematicus*. A shunt of 20% would be expected to decrease the saturation of hemoglobin in the arterial blood from approximately 100% to about 90% since end pulmonary capillary blood is expected to be near 100% saturation and the mixed venous blood nearly 50% saturated (Wood *et al.*, 1977; Gleeson *et al.*, 1980). The decline in blood saturation would be accompanied by a substantial drop in P_{O_2} due to the almost flat slope of the O_2 dissociation curve in this region (Wood *et al.*, 1977; Wood and Moberly, 1970); thus, one expects a corresponding increase in the alveolar-arterial P_{O_2} difference. Literature reports also indicate that right-left shunts exist in resting *Iguana iguana* (Tucker, 1966; Baker and White, 1970), although these reports do not allow quantification of the shunt.

In principle, a persistent cardiopulmonary shunt during treadmill exercise could also account for an increasing value of $(A-a)P_{O_2}$ since the O_2 content of mixed venous

blood declines (Gleeson *et al.*, 1980). However, a constant or increasing shunt would result in decreasing levels of Pa_{O_2} and arterial oxygen content which cannot be rectified by an elevation of alveolar P_{O_2} (*cf.* West and Wagner, 1977). Thus, the finding that both Pa_{O_2} and Ca_{O_2} are constant or elevated during activity suggests that the magnitude of the cardiopulmonary shunt is decreasing, and that other mechanisms cause the increase in $(A-a)P_{O_2}$.

Alternative mechanisms for an increase in $(A-a)P_{O_2}$ at increased $\dot{M}_{O_2}$ are: (1) inhomogeneity with respect to the matching of ventilation and perfusion in various regions of the lungs and (2) a gas exchange limitation with respect to the pulmonary oxygen diffusing capacity (DL_{O_2}). Little is known about the matching of ventilation and perfusion within reptilian lungs. However, in animals with unicameral or paucicameral lungs such as *Iguana*, the classical concepts of $\dot{V}A/\dot{Q}$ variation between lung compartments are difficult to apply. Discrete compartments varying in gas composition could be defined in functional terms only, and would arise solely as a result of incomplete gas mixing in the lung air space (stratification). In *Varanus* on the other hand, the lungs are multicameral, and the possibility of discrete compartments which vary in gas composition is more likely.

The existence of a functional mismatch between ventilation and perfusion at rest which persists during activity would result in both decreased Pa_{O_2} and increased $(A-a)P_{O_2}$ since $C\bar{v}_{O_2}$ declines. The decrease in Pa_{O_2} may have been prevented in both *Varanus* and *Iguana* by the alveolar hyperventilation, giving rise to elevated levels of PA_{O_2} and $(A-a)P_{O_2}$ with no apparent change in Pa_{O_2} from its resting control value. Such a mechanism would contrast with that in man where the matching of ventilation with perfusion is improved during exercise resulting in a decreased $(A-a)P_{O_2}$.

We suggest that the most likely mechanism of increased $(A-a)P_{O_2}$ with increased $\dot{M}_{O_2}$ in both *Varanus* and *Iguana* is a low value of DL_{O_2} and limited capacity to increase DL_{O_2} during exercise. Such a diffusion limitation may be associated with either the diffusional characteristics of the alveolar-capillary membrane itself, the diffusion and chemical combination in blood, or both. In several species of lizard, the alveolar surface area was found to be approximately 1% of that in a mammal of comparable size (Tenney and Remmers, 1963; Tenney and Tenney, 1970). Since the resting and active levels of $\dot{M}_{O_2}$ in lizards are generally about 10% of the values in mammals of equal size (Bennett, 1978), the limited alveolar surface area may be insufficient to sustain the levels of pulmonary oxygen transport attained during activity without a compensatory hyperventilation. The observation that $(A-a)P_{O_2}$ apparently increased at lower levels of $\dot{M}_{O_2}$ in *Iguana* than in *Varanus* is consistent with this hypothesis since *Varanus* has a rather well developed lung structure in comparison with *Iguana* (Milani, 1894; Wolf, 1933; Mertens, 1942; Kirshfeld, 1970; Perry and Duncker, 1978) and, presumably, a greater alveolar-capillary surface area. On the other hand, the large size of red blood cells in lizards (*cf.* Saint Girons, 1970) may suggest that the diffusive resistance is quite substantial once oxygen enters the blood, and this factor may be involved in reducing DL_{O_2}.

Unfortunately, there have been no reports concerning the magnitude of DL_{CO} or DL_{O_2} in lizards to our knowledge. Such measurements would be of considerable interest in assessing the validity of the hypothesis that pulmonary oxygen transport is diffusion limited in active lizards.

In conclusion, during periods of increased oxygen consumption in lizards, the capacity to increase pulmonary oxygen transport does not limit aerobic scope under the conditions of these experiments. However, substantial differences develop between the partial pressure of oxygen in the pulmonary gas and the systemic arterial oxygen tension. Firm conclusions concerning the cause of these alveolar-arterial P_{O_2} gradients must await quantification of the variables which characterize pulmonary gas exchange (*e.g.* DL_{CO} or DL_{O_2}, shunt, degree of stratification and unevenness of ventilation/perfusion ratios). Nevertheless, it does not seem likely that the rise in $(A-a)P_{O_2}$ during activity is due exclusively to either cardiopulmonary shunts or inadequate matching of ventilation with respect of perfusion in regions of the lung; the rise may be due, at least in part, to a low DL_{O_2} and limited capacity to increase DL_{O_2} during exercise.

Acknowledgements

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