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VENTILATION, GAS EXCHANGE, AND AEROBIC SCOPE IN A SMALL MONITOR LIZARD, *VARANUS GILLENI*¹

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Standard rates of O₂ consumption ($\dot{V}O_2$) in the dark of *Varanus gilleni* (mean mass = 30 g) were measured at 25, 31, 34, and 37 C. At 37 C, the mean value (195 ml O₂ STPD kg⁻¹ h⁻¹) was 22% lower than that predicted by a regression equation for lizards as a group (Bennett and Dawson 1976). Despite appearing to be asleep, three- to fourfold elevations in standard $\dot{V}O_2$ were seen in lizards with lightweight, transparent respiratory masks. $\dot{V}O_2$ was also measured during treadmill exercise at speeds from 5 to 15 m min⁻¹ and during bouts of maximal exercise. *Varanus gilleni* has the highest factorial aerobic scope (27.5) of any lizard examined to date. The cost of transport in *V. gilleni* is relatively high and may relate to short limb length. Pulmonary ventilation and gas exchange ($\dot{V}E$, $\dot{V}O_2$, $\dot{V}CO_2$) were simultaneously measured at 25 C, during warming from 25 to 35 C, and again after several hours at 35 C. Air-convection requirements for CO₂ and O₂ were independent of temperature. The patterns of lung ventilation suggest that arterial PCO₂ and pH are constant with rising temperature, behavior that is common to that in large varanids and in contrast to that in other reptiles.

INTRODUCTION

Lizards of the family Varanidae are generally considered to exceed the capabilities of lizards of other families in the ability to sustain intense aerobic exercise. The varanid characteristics of high hematocrit and efficient O₂ uptake from lung gas to blood and from blood to tissues correlate with their high aerobic scopes for exercise (Bennett 1973; Gleeson 1981). However, data for these generalizations come exclusively from a few large species (~1 kg; see Gleeson 1981). Currently, it is not known whether these functional capabilities are shared by the smaller members of the family.

The relationships of body size to standard oxygen consumption ($\dot{V}O_2$) and to $\dot{V}O_2$ during maximal exertion in varanids is not clear. There are several reports of elevated

standard $\dot{V}O_2$ in larger varanids (Bartholomew and Tucker 1964; Wood et al. 1978), but other measurements of standard $\dot{V}O_2$ of large varanids fall on the regression of body mass and $\dot{V}O_2$ of lizards as a group (Bennett 1972; Gleeson 1980).

Lung ventilation in large varanids responds to changes in body temperature in a different way than has been reported for lizards of other families: the ratio of minute volume ($\dot{V}E$) to $\dot{V}O_2$ is independent of temperature (Wood, Glass, and Johansen 1977; Wood et al. 1981). This pattern achieves a relatively constant O₂ extraction efficiency over a range of temperature as well as a relatively constant lung PO₂. It has been suggested that the relatively constant lung PO₂ serves to support O₂ delivery to tissues during activity (Wood et al. 1977). These patterns of ventilation may also produce a relatively constant relationship between lung PCO₂ and body temperature. The constant lung PCO₂ is reflected in temperature-independent arterial PCO₂ and hence in relatively constant arterial pH despite temperature changes (Wood et al. 1981).

The present study was done to see whether some of the physiological features of large varanids are shared by one of the smallest members of the family. The lizard we studied, the pigmy mulga monitor (*Varanus gilleni*) is small (<0.1 kg), secretive, and thigmothermic (i.e., it obtains heat

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from warm substrates) (Pianka 1969). This arboreal species is found under the bark of trees in the deserts of central Australia. It preys principally on large arthropods and small arboreal gekkos. Although field-active body temperatures have not been reported for this species, varanids of similar ecology and body size have body temperatures while active of 37–38 C (Pianka 1969). We measured standard $\dot{V}O_2$, $\dot{V}O_2$ during treadmill and maximal exercise, respiratory exchange ratios, and patterns of pulmonary ventilation at different body temperatures.

MATERIAL AND METHODS

For 30 days prior to the study in spring 1981, four *Varanus gilleni* of mass 20–40 g (held in captivity for 1 yr) were kept in large glass terraria under 12L:12D photoperiods. A 2,000-w photoflood lamp placed above one end of each terrarium provided light and heat during photophase. Lizards thermoregulated freely at a body temperature (T_b) of ~ 37 C. At night T_b dropped to ambient temperature, ~ 25 C. All lizards were fed a diet of mealworms, crickets, and small lizards; water was continuously available.

STANDARD METABOLISM

Standard rates of $\dot{V}O_2$ (standard metabolic rate [SMR]) were measured in the dark, during apparent sleeping behavior in the first half of normal scotophase. The lizards were not fed for 2–3 days before a trial. The lizards were placed unrestrained in respiratory chambers 3–4 h before a trial. SMRs were also measured in lizards treated identically except for being fitted with a lightweight, airtight plastic mask fitted with inflow and outflow lines. We used an open-circuit respirometry system. Dried, CO_2 -free air was drawn through either the respirometry cylinders (8 cm diam. \times 20 cm length) or the mask of lizards placed into the cylinders. The flow then passed to a pump, a Brooks Rotameter flowmeter calibrated against a Brooks Thermal Mass Flowmeter, and to the analysis cell of an Applied Electrochemistry O_2 analyzer equipped with dual sensors. Reference flow was also dry and CO_2 free. $\dot{V}O_2$ was calculated according to the equations of Withers (1977). The entire analysis system was located in a constant-temperature room

maintained at either 25, 31, 34, or 36–37 C. We weighed the lizards and took their cloacal temperature immediately after each trial. Rates of oxygen consumption reported represent the means of values obtained every 5 min for 2–3 h. The lizards appeared to be asleep during the entire 2–3-h period.

EXERCISE METABOLISM

The lizards were fasted 2–3 days before exercise on the treadmill. At the onset of fasting, plastic collars for the attachment of respiratory masks were glued on to the necks with silicone sealant. Lizards were then placed in a temperature-controlled cabinet at 35–37 C under the previously established photoperiod. On the day of measurement of $\dot{V}O_2$ during exercise, clear plastic masks (snap-cap vials) were placed over the head and sealed to the collar. Air was drawn through the masks by the lizards for the remainder of the day. Flexible latex tubing was attached to the mask for routing of incurrent and excurrent air. The tubes were positioned above and in front of the exercising lizards so that the combined weight of the tubing and mask did not interfere with locomotion.

The lizards were run on a treadmill in a 37 C room. All measures of $\dot{V}O_2$ for exercising lizards were obtained during the first half of photophase during a 3-day period. $\dot{V}O_2$ was measured with the same open-circuit system described for the standard metabolic rate (SMR) measurements.

Each day several treadmill speeds were used for each lizard, the slowest speed being used first. Steady $\dot{V}O_2$ values were typically obtained after 3–10 min of running. These steady-state values were then recorded at 30-s intervals for the next 4–14 min. If steady-state values were achieved at the slower speed, then treadmill speeds were increased gradually to the next desired level. Steady-state values were recorded as before. Cloacal temperatures of the lizards were measured on cessation of exercise. Lizards cooperated if treadmill speeds were not changed rapidly and if speeds were set at sustainable levels. Occasionally, a lizard could not be coaxed into walking even at low speed; these trials were discontinued for the day. We feel that we were unable to coax the lizards into attaining their maxi-

imum aerobically sustainable speed since we could never fatigue individual lizards. Their refusal to walk with increased velocity was due to their behavioral disposition and not to exhaustion. In an attempt to elicit $\dot{V}O_{2\max}$, we agitated the lizards by prodding and grabbing them repeatedly. $\dot{V}O_{2\max}$ was obtained within the first couple of minutes.

VENTILATION MEASUREMENTS

We simultaneously measured gas exchange ($\dot{V}O_2$, $\dot{V}CO_2$) and ventilation frequency (f) and tidal volume (V_T) in lizards fitted with masks and placed in a whole-body plethysmograph. A description of this system can be found in Bickler (1981). The lizards were fitted with the collars to the masks 2–3 days prior to a trial. Before an experiment, the lizards were placed in the plethysmograph and allowed 2–3 h to settle. During this time the T_b of the lizard (monitored via a fine thermocouple in the cloaca) was maintained at 25 C by adjusting the temperature of the plethysmograph water jacket. Ventilation and gas exchange were then measured for 1 h at 25 C, during warming to 37 C (duration of warming = ~2 h), and 2–3 h after 37 C had been reached. We have not corrected tidal volume and gas exchange values for the differences in body mass among our specimens.

RESULTS

STANDARD METABOLISM

Standard $\dot{V}O_2$ at different body temperatures is summarized in table 1. There were no consistent differences in $\dot{V}O_2$ between lizards of different mass when these data

were expressed on a mass-specific basis. The mean \pm SE Q_{10} for standard $\dot{V}O_2$ between 25 and 37 C was 1.97 ± 0.11 . $\dot{V}O_2$'s from lizards with masks were three to four times greater than those in lizards without masks. Behaviorally, the masked lizards seemed to be asleep, but their bodies were not as limp as those of the unrestrained lizards.

EXERCISE METABOLISM

Overall, the regression equation relating speed to $\dot{V}O_2$ was $\dot{V}O_2 \text{ ml kg}^{-1} \text{ h}^{-1} = 3,144 + 64 \text{ m min}^{-1} (r = .28; n = 20)$. When data for individual lizards were analyzed separately, however, velocity was significantly related to running speed (fig. 1). The most complete data set, that for a 37-g male, was described by the equation $\dot{V}O_2 \text{ ml kg}^{-1} \text{ h}^{-1} = 1,990 + 111 \text{ m min}^{-1} (r = .97; n = 8)$.

$\dot{V}O_{2\max}$ for *Varanus gilleni* was 5.4 liters $O_2 \text{ kg}^{-1} \text{ h}^{-1}$. Table 2 contains a summary of standard and activity metabolism for *V. gilleni*, other varanids, and the iguanid *Dipsosaurus dorsalis*. *Varanus gilleni* has the highest weight-corrected aerobic capacity ($\dot{V}O_{2\max \text{ corr}}$; factorial aerobic scope) of any lizard studied to date.

VENTILATION

Minute ventilation ($\dot{V}E$) increased with temperature. This was due to augmentation in both ventilatory rate and tidal volume (fig. 2). Minute ventilation increased uniformly with temperature up to 37 C, and little or no further changes in ventilation were noted after 3–4 h at the final temperature. Thus, steady-state patterns were reached almost immediately, and no transient changes were seen with warming. Corresponding air-convection require-

TABLE 1

MEAN \pm SE STANDARD OXYGEN CONSUMPTION ($\dot{V}O_2$;
ml O_2 STPD/[kg \cdot h]) IN *Varanus gilleni* MEASURED
AT CONSTANT TEMPERATURES

BODY TEMPERATURE (°C)	MEAN \pm SE $\dot{V}O_2$ (N) OF LIZARDS	
	Masked	Unrestrained
25–27	372 \pm 48 (4)	101 \pm 18 (6)
31.0	...	126 \pm 6.6 (3)
34.0	...	154 \pm 19.4 (2)
36–37	619 \pm 36 (5)	195 \pm 11.4 (5)

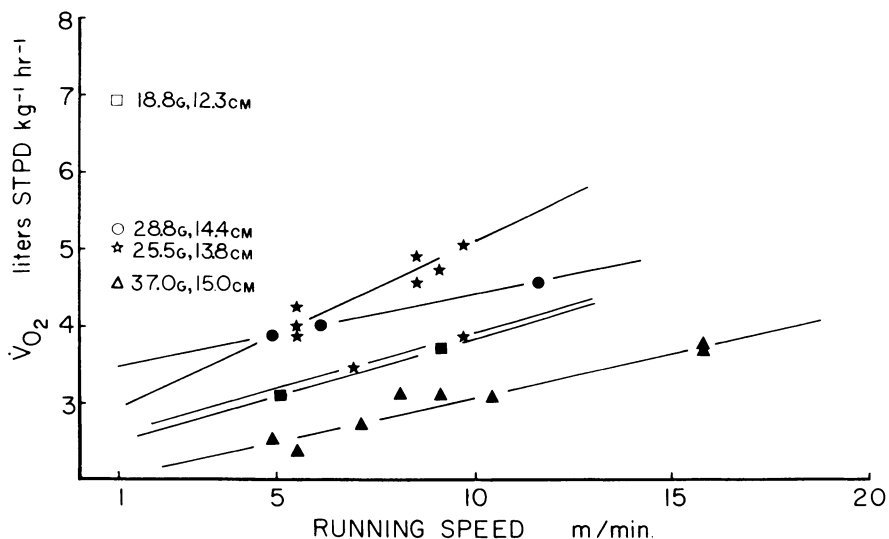


FIG. 1.—Relationship of weight-specific $\dot{V}O_2$ to running speed in individual *Varanus gilleni* (solid symbols). The lower line of stars represents the 25.5-g lizard at a later date. See Results for overall regression formula. Open symbols show $\dot{V}O_{2max}$ produced by prodding the lizards to maximal activity; weight and snout-vent length are indicated next to these symbols.

ments ($\dot{V}E/\dot{V}O_2$) are shown in figure 3. These ratios were independent of temperature (analysis of covariance with F -test = $P < .001$). After reaching 37 C little or no further changes in air-convection requirements were seen over the next several hours.

Hence, ventilation is quickly matched to gas exchange, and no time-dependent thermal acclimation of the respiratory system occurs within this range of temperatures and for these rates of temperature change. Mean \pm SE pulmonary respiratory ex-

TABLE 2

SUMMARY OF OXYGEN CONSUMPTION ($\dot{V}O_2$), FACTORIAL AEROBIC SCOPE (STANDARD METABOLIC RATE [SMR]/MAXIMUM $\dot{V}O_2$ [$\dot{V}O_{2max}$]), AND WEIGHT-CORRECTED $\dot{V}O_{2max}$ ($\dot{V}O_{2max\ corr}$) IN VARANIDS AND *Dipsosaurus dorsalis*

Species	Mass (g)	T_b (°C)	SMR (ml O ₂ /[g · h])	$\dot{V}O_{2max}$ (ml O ₂ /[g · h])	Factorial Aerobic Scope	$\dot{V}O_{2max\ corr}$ ^a (ml O ₂ /[g · h])	Reference
Varanidae:							
<i>Varanus gilleni</i>	27.5	37	.195	5.4	27.7	12.14	Present study
<i>V. salvator</i>	505	35	.144	1.10	7.6	4.90	Gleeson 1981
<i>V. gouldii</i>	674	35	.10	.76	7.6	3.63	Bennett 1972
<i>V. exanthematicus</i>	1025	35	.189	1.26	6.7	6.65	Gleeson et al. 1980
		35	3.39 $W^{-0.049}$			8.2	Wood et al. 1978
Iquanidae:							
<i>D. dorsalis</i>	51.3	40		2.00	15.4	5.75	John-Alder and Bennett 1981
	35.2	40	.13	2.27	17.5 ^b	5.53	Bennett and Dawson 1972

^a $\dot{V}O_{2max\ corr}$ was calculated as $\dot{V}O_{2max} \cdot (g^{0.76} \cdot h)^{-1}$.
^b Shocked electrically.

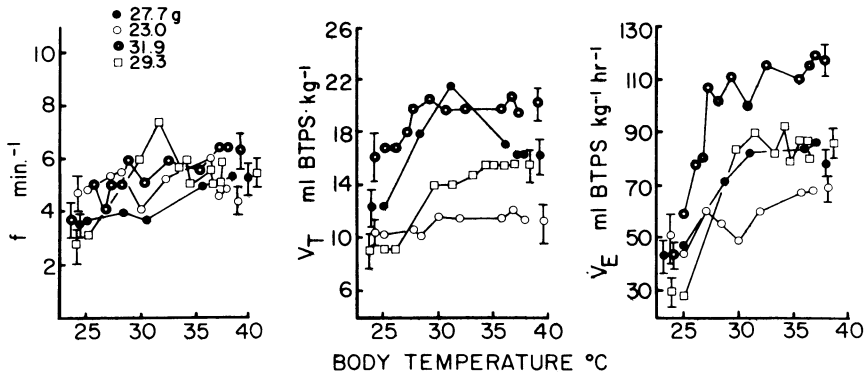


FIG. 2.—Ventilatory parameters from individual *Varanus gilleni* at 25 C during warming to 37 C and after 2-3 h at 37 C. Vertical bars denote SE.

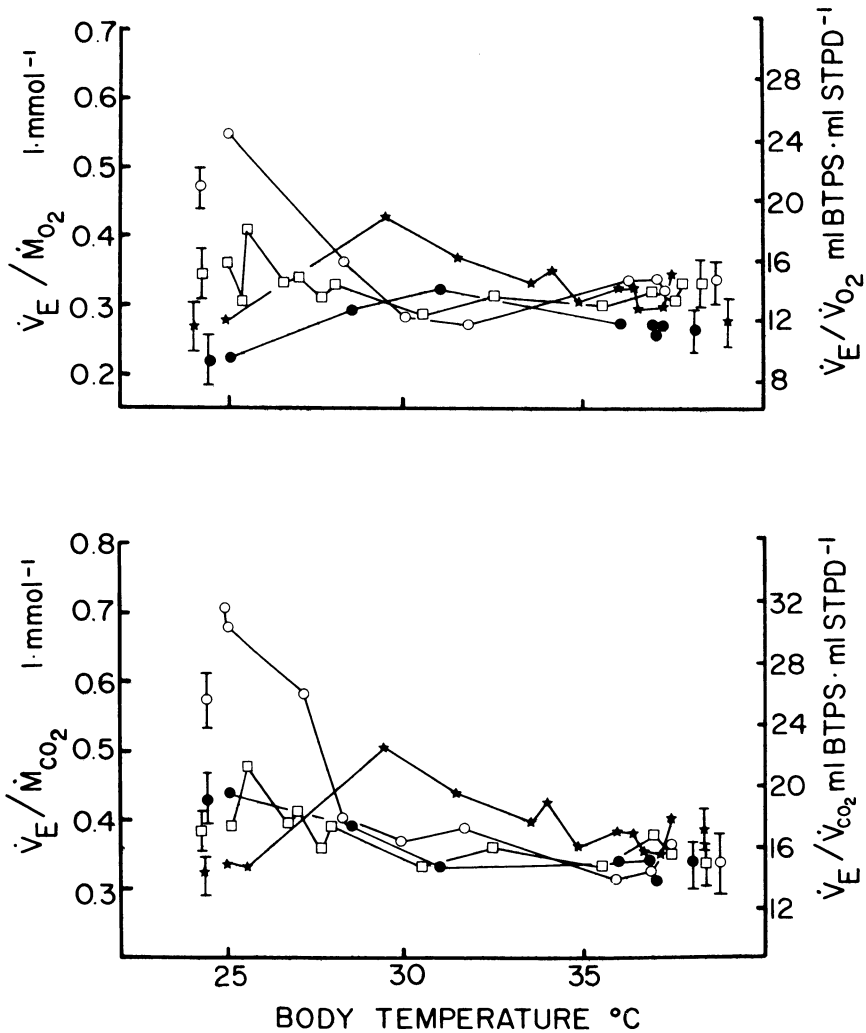


FIG. 3.—Air-convection requirements for *Varanus gilleni* at 25 C during warming to 37 C and after 2-3 h at 37 C. Vertical bars denote SE.

change ratios (RE; $\dot{V}CO_2/\dot{V}O_2$) were 0.75 \pm 0.03 at 25 C and 0.72 \pm 0.05 at 37 C. No significant transient values in RE were seen during or after the warming from 25 to 35 C (analysis of covariance with *F*-test for *P* < .05).

DISCUSSION

STANDARD METABOLISM

Our values for standard $\dot{V}O_2$ at 37 C are 22% lower (194 ml kg⁻¹ h⁻¹ vs. 237) than values predicted for lizard $\dot{V}O_2$ at 37 C ($\log \text{cm}^2 \text{O}_2 \text{g}^{-1} \text{h}^{-1} = \log 0.424 - 18 \log \text{g}$) from Bennett and Dawson (1976). This regression is for lizards as a group. However, our values fall within the 95% confidence limits for that regression. Our values for SMR are somewhat lower than those for some other varanids previously studied (see Bartholomew and Tucker 1964; Louw, Young, and Bligh 1976; Gleeson, Mitchell, and Bennett 1980; Gleeson, 1981; and table 3).

In contrast to Bennett (1972), we noted substantial differences between the $\dot{V}O_2$'s of unrestrained and masked lizards. Our values for masked lizards at 37 C are approximately three times those of controls and are near mean values predicted by the regression equation given by Wood et al. (1978). Wood's lizards were confined in cylinders and may not have been relaxed. At present, whether these differences in SMR between *Varanus exanthematicus* and unmasked *V. gilleni* are due to behavioral state or true differences in physiology is problematic.

ACTIVITY METABOLISM

Varanus gilleni exhibits one of the highest factorial aerobic scopes of any vertebrate studied to date, owing, in part, to its relatively low standard $\dot{V}O_2$. Therefore, we do not believe that standard $\dot{V}O_2$ bears any direct causal relationship to maximal aerobic capacity in lizards. Another striking example is that of the iguanid *Dipsosaurus dorsalis*. Its SMR is comparable to that of other iguanids, yet it greatly exceeds other family members in its aerobic capacity (table 3). At the other end of the spectrum is *Physignathus lesueri* (Agamidae; mean mass = 549 g) with a similar resting metabolic rate (Wilson 1974) but less than one-

half the $\dot{V}O_{2\text{max}}$ of the similarly sized *Amblyrhynchus cristatus* (Iguanidae; mean mass = 580 g [Gleeson 1979]).

Gleeson (1979) presented the following equation for predicting the net cost of transport for lizards: ml O₂ = 3.77 mass^{-0.25}. The predicted value for *V. gilleni* (mean mass = 27.5 g) is 1.65 ml O₂ g⁻¹ km⁻¹. Using velocities close to those for which $\dot{V}O_2$ was measured for each lizard (0.3 km h⁻¹, 5 m min⁻¹), we performed the conventional technique for obtaining the cost of transport for each lizard by subtracting the y-intercept value of $\dot{V}O_2$ from the $\dot{V}O_2$ at 0.3 km h⁻¹, then divided that value by 0.3 km to obtain the net cost of transport at that speed (John-Alder and Bennett 1981). The approximate mean net cost of transport for *V. gilleni* is 2.9 ml O₂ g⁻¹ h, a value 75% higher than that predicted (Gleeson 1979). *Varanus gilleni* has rather short limbs (20% shorter in front and 40% shorter in rear than *Dipsosaurus dorsalis* of similar mass), and this may increase the cost of transport.

The largest *V. gilleni* (37.5 g) ran for many minutes with no signs of fatigue at 1.0 km/h, a speed greater than the 0.8 km/h maximum aerobically sustained speed of *D. dorsalis*. We could not accurately determine the maximum speed continuously sustained by aerobic metabolism in *V. gilleni*.

Large home ranges and pursuit and excavation of vertebrate prey are ecological features common to large *Varanus* (Aufenberg 1978; Green and King 1978). *Varanus gilleni*, in contrast, eats gekkos and insects and is arboreal, secretive, and thigmothermic (Pianka 1969). The intense male-combat behavior of *V. gilleni* (Murphy and Mitchell 1974) seems to be the only factor in this species' behavioral repertoire that may require high aerobic capacity.

PULMONARY VENTILATION

Our values for air-convection requirements ($\dot{V}E/\dot{V}O_2$) in *V. gilleni* are only ~35% of those in *V. exanthematicus* (table 3). This difference results from roughly comparable mass-specific ventilation values and much greater mass-specific metabolic rates in *V. gilleni*. While *f* has no apparent correlation with body mass, *V_T* scales with mass to the 0.85 power at 37 C (Bennett

TABLE 3

COMPARISON OF VENTILATORY PARAMETERS FROM VARANID LIZARDS

Species	Mass (g)	Temperature (°C)	f (min ⁻¹)	V_T (ml/kg)	\dot{V}_E (ml/kg·min)	\dot{V}_E/\dot{V}_{O_2} (ml BTFS/ml STPD)	Reference
<i>Varanus exanthematicus</i>	NS	25	2.5	20.5 ± 4.9 ^a	34.8	39.5	Wood et al. 1977
<i>V. gouldii</i>	674	35	3.0	24.3 ± 4.3 ^a	73.8	38.1 ± 2.6 ^a	Bennett 1973
<i>V. gilleni</i> ^b	30	25	6.2	6.3	23.3	25.3	Present study
		35	20.0	8.5	100.5	53.9	
		25	3.7	12.2 ± 1.0 ^a	45.5 ± 4.1 ^a	14.4 ± 3.8 ^a	
		35	5.5	15.7 ± 1.3 ^a	85.0 ± 3.9 ^a	13.4 ± 3.0 ^a	

NOTE.—NS = not specified.

^a Means ± SE.^b Collected from lizards fitted with lightweight respiratory masks. Changes in ventilatory and gas-exchange parameters for these *V. gilleni* during warming are shown in figs. 2 and 3.

1973). Our tidal volume estimates for *V. gilleni* fall within the 95% confidence limits of Bennett's (1973) regression. The oxygen extraction efficiency (EO_2) was 68.6% at 25 C and 63.8% at 35 C as calculated by the expression $EO_2 = (\dot{V}O_2/\dot{V}E) (100\%/C_{I}O_2)$, where $C_{I}O_2$ is the concentration of O_2 in inspired air (Dejours 1981). In light of the spectacular aerobic capacity of *V. gilleni*, measurements of O_2 extraction during activity would be of interest.

The $\dot{V}A/\dot{V}O_2$ ($\dot{V}A$ = alveolar minute ventilation) value for *V. exanthematicus* from Wood et al. (1977) is 45.8 at 25 C and 38.1 ml BTPS ml⁻¹ at 35 C, implying that arterial PCO_2 was 17.1 torr at 25 C and 21.8 torr at 35 C, as calculated from the gas equation and assuming a $\dot{V}CO_2/\dot{V}O_2$ of 0.80.

Values for arterial PCO_2 calculated in this way for *V. gilleni* at 25 and 37 are 43.8 and 42.0 torr. Our temperature-independent $\dot{V}E/\dot{V}CO_2$ values are consistent with the nearly constant arterial PCO_2 and pH values that have been reported for *V. exanthematicus* (Wood et al. 1977, 1981). Constant blood PCO_2 with rising temperature means that the total CO_2 content of the blood decreases with rising temperature. Changes in the respiratory exchange ratio were not seen, however. This suggests that changes in the total CO_2 content of the various body-fluid compartments, if they indeed occur, must involve exchanges between compartments rather than net changes in total CO_2 content between the animal and environment via the respiratory system.

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