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Patterns of Gas Exchange and Extended Non-Ventilatory Periods in Small Goannas (Squamata: Varanidae)

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ABSTRACT. Standard metabolic rate and evaporative water loss were measured for three species of small goanna (*Varanus caudolineatus*, *V. brevicauda* and *V. eremius*). Four general patterns of gas exchange are associated with often extended periods of no gas exchange, which presumably are non-ventilatory periods. Extended periods of no gas exchange continued for as long as 137 min at 14°C, 37 min at 20°C and 28 min at 25°C. These extended non-ventilatory periods have two important implications. First, when measuring Vo_{2std}, it is important to recognize these non-ventilatory periods and not include them in the period for determining standard metabolic rate or else ensure that any non-ventilatory periods are accompanied by an "oxygen deficit payback" period. Second, the extended non-ventilatory period enables the partitioning of cutaneous and respiratory standard evaporative water loss. Pulmonary evaporative water loss, expressed as a percentage of total evaporative water loss, was found to be very low: 4.7%, 2.4% and 5.9% at 14, 20 and 25°C, respectively. COMP BIOCHEM PHYSIOL 118A;4:1411–1417, 1997. © 1997 Elsevier Science Inc.

KEY WORDS. *Varanus*, goanna, gas exchange, ventilation, non-ventilatory period, evaporative water loss, metabolism, lizard

INTRODUCTION

Short arrhythmic breathing patterns have frequently been reported for terrestrial reptiles (2,8,9,12,14,20). There are typically two types of arrhythmic breathing patterns: breath holding interrupted by a series of breaths (8,10,12) or a single breath followed by a relatively short breath hold (1,20,28). Breath-holding duration generally decreases with increased body temperature (T_b) (2,11,17). During breath holds, the partial pressure of oxygen (Po_2) in the lungs decreases at a highly variable rate, whereas the partial pressure of carbon dioxide (Pco_2) increases but always at a lower rate, such that the gas exchange rate (R_E) for the lung declines progressively as the ventilatory pause is extended (1,3,7,14,16,18,22). Shelton *et al.* (23), in summarizing the literature for ventilation patterns of varanid lizards, reported that their breathing pattern is a continuous rhythm, even for several species at rest, and they attributed this to the higher aerobic metabolism of varanids. This is in contrast with the general arrhythmic breathing pattern described for most reptiles. Earlier investigations of the standard metabolic rate (Vo_{2std}) for goannas indicated no non-ventilatory periods at about their preferred T_b (24–26). Given this, the presence of significant non-ventilatory periods might not be considered when measuring Vo_{2std} for goannas.

During experiments measuring the Vo_{2std} of small goanna, *Varanus caudolineatus*, at 25°C (25), we occasionally observed long periods (10–45 min) of very low or negligible Vo_2, which was contrary to our expectations based on Shelton *et al.* (23). We thought that these periods were prolonged non-ventilatory bouts. The objectives of this study were to confirm the presence of these long non-ventilatory periods and to quantitatively describe the duration and frequency of these periods for three species of small goanna (*V. caudolineatus*, *V. brevicauda* and *V. eremius*). The presence of non-ventilatory periods also provided the opportunity to partition total evaporative water loss (TEWL) into cutaneous evaporative water loss (CEWL) and pulmonary evaporative water loss (PEWL).

MATERIALS AND METHODS

Five *V. caudolineatus* and five *V. brevicauda*, which had been held in captivity for over 6 months, were studied during August and September 1994 and three *V. brevicauda* and nine *V. eremius* captured in October were studied in late October and early November 1994; all lizards were in good

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health when studied. *V. caudolineatus*, *V. brevicauda* and *V. eremius* were examined at 25°C; subsequently, the *V. caudolineatus* were examined at 14 and 20°C and *V. brevicauda* at 20°C. Individual lizards were only studied once at each particular temperature. All varanids were maintained in indoor aquaria with incandescent lighting as the heat source for 12 hr/day. They were fed cockroaches, mealworms and small mice, with an occasional mineral and vitamin supplement. Water was available at all times.

Oxygen consumption (Vo_2; ml/g/hr), carbon dioxide production (Vco_2; ml/g/hr) and TEWL (mg/g/hr) were measured using a flow-through respirometry system. All goannas, after being fasted for at least 60 hr (no feces were voided after this period), were weighed and then placed inside a plastic mesh cage located in an opaque plastic cylinder (260 × 35 mm diameter for *V. eremius* and 170 × 27 mm diameter for *V. caudolineatus* and *V. brevicauda*). The plastic mesh cage inside the cylindrical chamber kept the lizard in an extended position, with the head directed toward the chamber air outlet. This ensured that the goannas could not curl up in the tube or have a significant portion of their skin against the sides of the cylinder (thereby reducing the skin surface exposed to the air flow). The respiratory chamber was placed in a controlled temperature room at 14, 20 or 25°C (±1.0°C). Dried and preheated compressed air (water content ≈2.5 g H_2O/m^3) flowed through the chamber at 50 ml/min for *V. caudolineatus* and *V. brevicauda* and 100 ml/min for *V. eremius* (controlled by a Brooks, Hatfield, PA, thermal mass-flow controller) to provide an excurrent O_2 content of approximately 20.7%. The higher air-flow rate for *V. eremius* was used to ensure a similar reduction in O_2 and increase in water vapor content in excurrent air to those recorded for the two smaller species.

Vaisala (Helsinki, Finland) humidity/temperature probes (HMP 35B) were placed in the air flow immediately before and after the chamber. The two probes were monitored by a Vaisala Humidity Data Processor (HMI 36) microprocessor that recorded temperature and water content of incurrent and excurrent air. After the excurrent humidity probe, a Drierite column removed water vapor from the excurrent air before it passed through one channel of a paramagnetic oxygen analyzer (Servomex 184A, Sussex, UK) and a carbon dioxide analyzer (Hereus-Leybold Binos, Hanau, Germany). The O_2 analyzer was calibrated with room air daily and occasionally with zero using pure nitrogen. The carbon dioxide analyzer was occasionally calibrated using a ethanol burner to obtain an RQ of 0.67. A PC microcomputer recorded the analog output of the oxygen analyzer (difference in O_2 content between ambient and excurrent air) and the carbon dioxide analyzer, via a Thurlby (Huntingdon, UK) digital volt-meter with a RS232 interface. Air temperature and humidity were monitored via an RS232 connection between the data processor and the PC. A baseline for Vo_2, Vco_2 and EWL were obtained upon the removal of the goanna from the chamber. The Vo_2, Vco_2 (STPD) and EWL were computed every 10 sec, for a 4- to 8-hr period commencing between 0000 and 0400 hr and continuing to approximately 0800 hr. Vo_{2std} and standard carbon dioxide production (Vco_{2std}) were calculated using equations modified from Withers (27). EWL was calculated from the difference between the water content of the incurrent and excurrent air flow through the chamber and the air-flow rate.

The occurrence and duration of non-ventilatory periods was inferred from instantaneous metabolic data, calculated using a washout correction (4). It was presumed that periods of no measurable Vo_2 or Vco_2 indicated non-ventilatory periods, although we have not directly confirmed the absence of breathing. Although the washout characteristics of the respirometry system were not adequate to allow the unequivocal detection of individual breaths from either the Vo_2, Vco_2 or EWL traces, individual or groups of breaths were often apparent, especially for the EWL trace, except during the periods of presumed non-ventilation. We therefore presume throughout this study that the extended periods of no Vo_2 and Vco_2, and reduced EWL, correspond to non-ventilatory periods.

When a non-ventilatory period immediately preceded or followed a period of rhythmic breathing and the EWL of the ventilatory and non-ventilatory periods could be consecutively measured, it was presumed that the EWL during the non-ventilatory period represented CEWL, and that the PEWL was the difference (i.e., PEWL = TEWL − CEWL).

Values reported throughout are mean ± SE. Repeated-measures ANOVA was used to determine differences between measured parameters at different T_b for a single species (29) and ANOVA was used to determine differences between species at 25°C.

RESULTS

The metabolic rate (MR) and EWL of the goannas reached standard levels during measurement, from 0000 to 0800 hr (Table 1). For some goannas, the Vo_2 and Vco_2 declined to a stable value during the entire experiment, or for some parts of the experiment, and this was interpreted as the Vo_{2std}. However, for some goannas during part of the experiment, there were short (1–2 min) to long (5–60 min) periods of non-detectable gas exchange (Vo_2 and Vco_2 ≈0), particularly at the lower temperatures. A similar pattern was observed for EWL, except that it declined to what was presumed to be CEWL. An example is given in Fig. 1. These periods of insignificant gas exchange and low EWL are presumed to reflect periods of no gas exchange (i.e., non-ventilatory periods). The initial rate of CO_2 elimination after a period of increased ventilation was lower than that of O_2 consumption, but the increased level of expired CO_2 lasted longer than the increase in O_2 consumption, even after instantaneous correction (Fig. 2). These gas exchange patterns can be differentiated from periods of elevated Vo_2, Vco_2 and EWL presumed to be caused by activity or move-

TABLE 1. Standard V_{O_2} and V_{CO_2} for *V. caudolineatus, V. brevicauda* and *V. eremius* at 14, 20 and 25°C

T_b (°C)	Mass (g)	V_{O_2} (ml/g/hr)	V_{CO_2} (ml/g/hr)	EWL (ml/g/hr)	RQ	*n*
			V. caudolineatus			
14	16.3 ± 1.38	0.013 ± 0.0016	0.008 ± 0.0011	0.065 ± 0.023	0.67	5
20	18.4 ± 1.63	0.028 ± 0.0034	0.025 ± 0.0032	0.117 ± 0.020	0.89	5
25	15.1 ± 1.62	0.041 ± 0.0038	0.036 ± 0.0016	0.317 ± 0.074	0.88	5
			V. brevicauda			
20	16.2 ± 1.54	0.031 ± 0.0025	0.026 ± 0.0017	0.407 ± 0.194	0.84	5
25	16.5 ± 1.10	0.049 ± 0.0034	0.039 ± 0.0041	0.319 ± 0.073	0.79	8
			V. eremius			
25	42.6 ± 6.51	0.059 ± 0.0034	0.048 ± 0.0028	0.241 ± 0.037	0.82	9

Values are mean ± SE and the sample size (*n*) for each temperature.

ment by the goannas while in the respiratory chamber, as the V_{O_2} starts at the normal standard rate and then declines toward zero during the non-ventilatory period and is followed by an increase in V_{O_2}. In contrast, the elevated V_{O_2} values associated with activity are not normally preceded by V_{O_2} values close to zero.

The number, duration and other properties of the non-ventilatory periods varied considerably, even within species and with temperature; in fact, not all individuals even showed non-ventilatory periods (Table 2). Although these data suggest that the length of the non-ventilatory period, the number of non-ventilatory periods and the maximum duration of non-ventilatory periods decrease as the T_b increases from 14 to 25°C, these differences were not statistically significant for *V. caudolineatus*. The longest non-ventilatory period recorded for each species is shown in Table 2. There were no significant differences among the species at 25°C with respect to length of the non-ventilatory period, number of non-ventilatory periods per hour or the mean length of the non-ventilatory period per hour. There was no significant relationship between the mean duration and frequency of non-ventilatory periods at either 14, 20 or 25°C for any of these three species (Table 2).

We distinguished four basic patterns of V_{O_2} for these small goannas (Fig. 3A–D), although these four patterns represent different points on a broad continuum in patterns. A common pattern (P_1) was the maintenance of a stable V_{O_2} (i.e., $V_{O_{2std}}$), associated with a presumably continuous

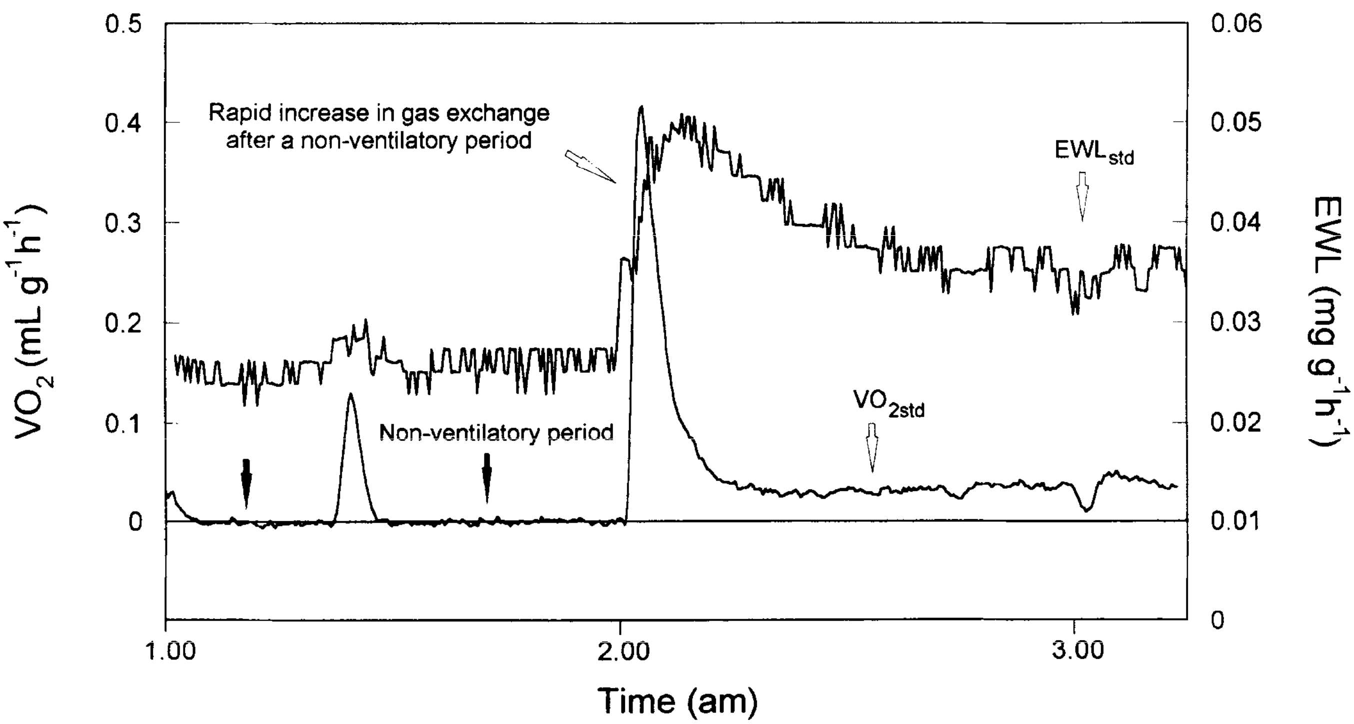

FIG. 1. Standard metabolic and evaporative water loss rates for a 14.4-g *V. caudolineatus* at 20°C showing presumed non-ventilatory periods (of pattern 1) compared with the standard metabolic rate.

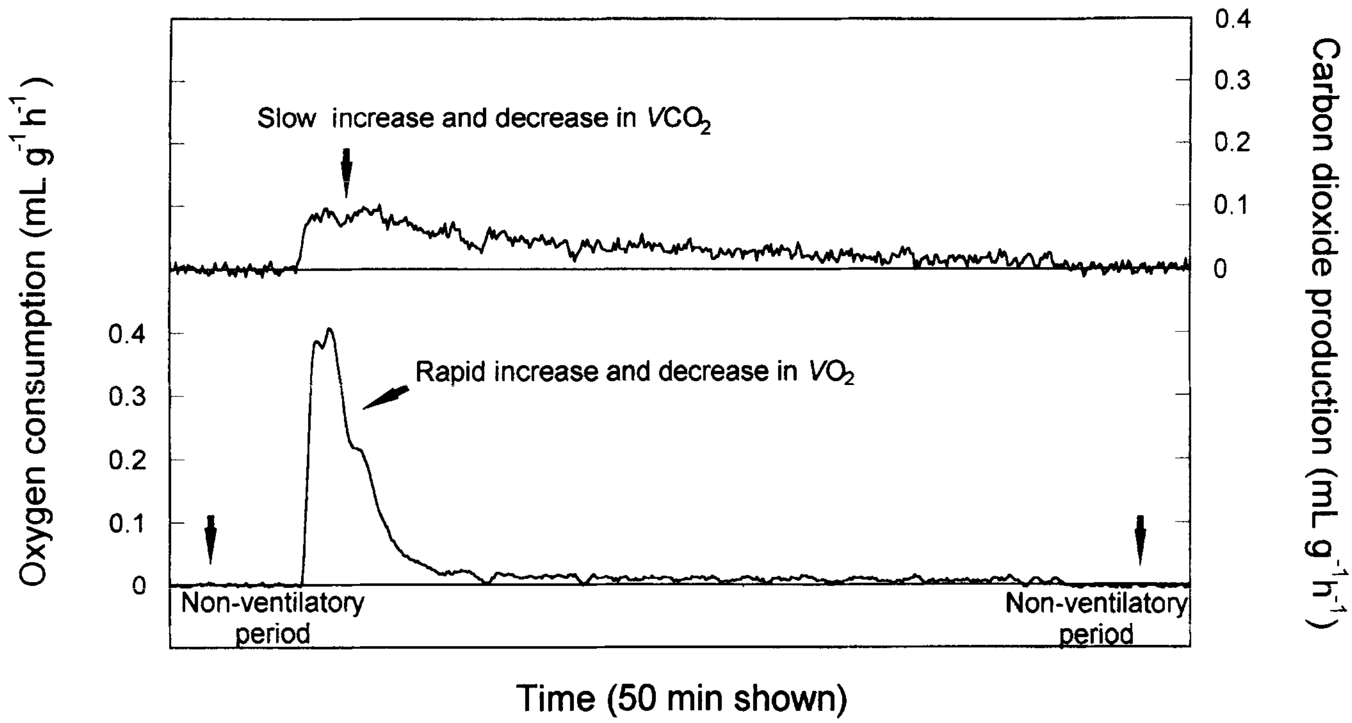

FIG. 2. Varying rates of oxygen consumption and carbon dioxide production for a *V. caudolineatus* at 14°C.

and rhythmical breathing pattern, which was followed by a non-ventilatory period with no measurable Vo_2 and then a subsequent increase in Vo_2 (Fig. 3a). In each of the 12 examples of pattern P_1 where a Vo_{2std} could be accurately measured, the average Vo_2 over a total cycle of a non-ventilatory period followed by the subsequent increase in Vo_2 was slightly, but significantly, higher (0.0034 ml/g/h, paired *t*-test = 2.46, *df* = 11) than the Vo_{2std} immediately before or after this period, indicating that the Vo_2 "peak" after the non-ventilatory period accounted for slightly more O_2 consumption than was conserved by the Vo_2 "trough" of the non-ventilatory period. Pattern P_1 was common (1 of 5 at 14°C; 3 of 10 at 20°C; 9 of 22 at 25°C). A second pattern (P_2) consisted of extended non-ventilatory periods followed by rapid increases in O_2 consumption (Fig. 3b), frequently with no stable period of Vo_2 at about the expected Vo_{2std}. This pattern was infrequently seen (2 of 5 at 14°C; 1 of 10 at 20°C; 0 of 22 at 25°C). A third Vo_{2std} pattern (P_3) consisted of a series of short non-ventilatory periods where Vo_2 transiently fell to zero and then was followed by a rapid increase in Vo_2 (Fig. 3c). This pattern was also infrequently seen (0 of 5 at 14°C; 1 of 10 at 20°C; 2 of 22 at 25°C). The fourth Vo_{2std} pattern (P_4) showed a series of brief non-ventilatory periods that were seldom of sufficient duration

TABLE 2. Duration of non-ventilatory period at 14, 20, and 25°C for *V. caudolineatus, V. brevicauda* and *V. eremius*

T_b (°C)	Mass (g)	Proportion of goannas that showed non-ventilatory period	Non-ventilatory periods* (min/hr)	Number of non-ventilatory periods* (r)	Mean longest non-ventilatory periods* (min)	Longest non-ventilatory period (min)
			V. caudolineatus			
14	16.3 ± 1.38	5/5	23.64 ± 9.48	2.03 ± 0.86	61.0 ± 27.9	137.3
20	18.4 ± 1.63	5/5	15.73 ± 4.90	2.58 ± 0.91	16.8 ± 5.94	36.8
25	15.1 ± 1.62	5/5	10.31 ± 3.44	2.03 ± 0.71	10.2 ± 2.16	14.3
			V. brevicauda			
20	16.2 ± 1.54	4/5	14.86 ± 5.45	3.66 ± 2.45	15.2 ± 4.78	29.5
25	16.5 ± 1.10	6/8	8.63 ± 2.51	2.85 ± 0.59	7.3 ± 1.92	17.5
			V. eremius			
25	42.6 ± 6.51	6/9	4.28 ± 1.36	1.45 ± 0.38	6.7 ± 2.75	27.7

*Values are means ± SE for the duration of non-ventilatory periods.

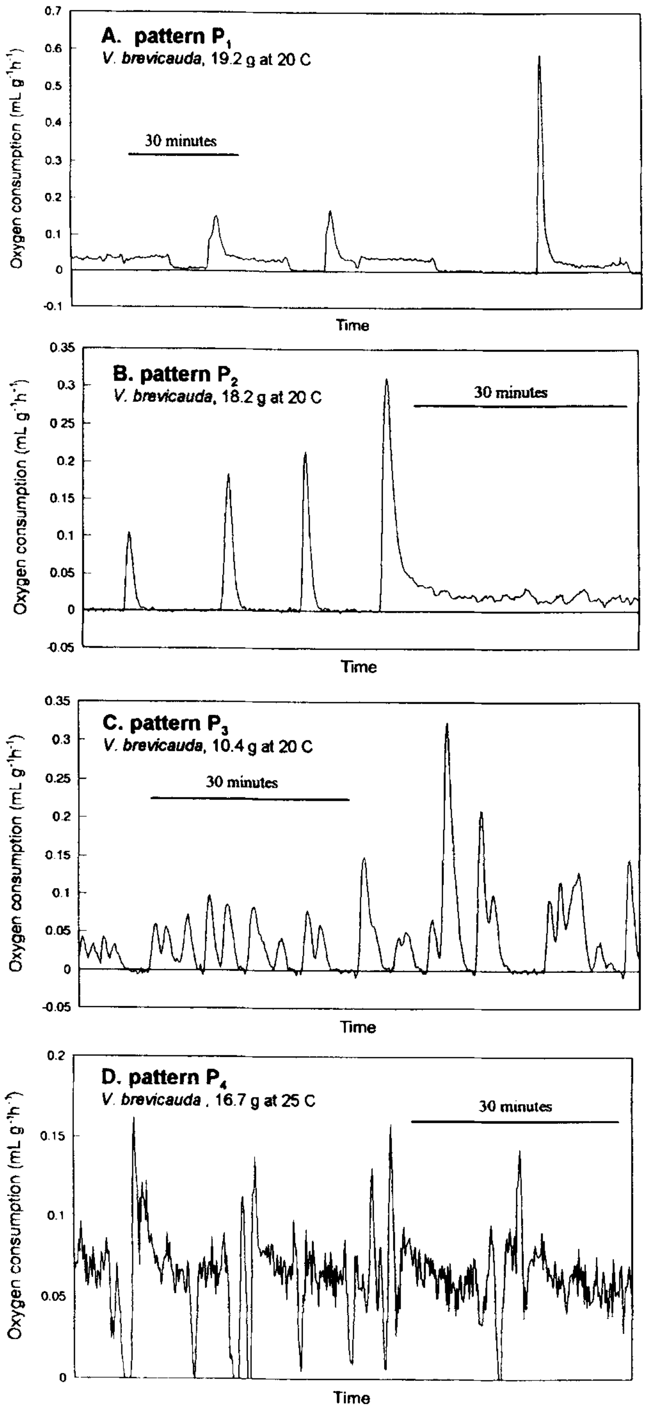

FIG. 3. Four patterns of VO_2 for *V. brevicauda* when non-ventilatory periods are evident.

to reach zero VO_2; these non-ventilatory periods were not always followed by a compensatory period of increased VO_2 (Fig. 3d). This pattern was equally common with P_1 (2 of 5 at 14°C; 2 of 10 at 20°C; 9 of 22 at 25°C). The oscillations of VO_2 in pattern P_4 sometimes gradually decreased to a brief non-ventilatory period before VO_2 rose again to repeat the pattern. More than one pattern was often observed for a goanna during the measurement period, although P_1 was seldom associated with the other patterns. For some experiments, it was not possible to determine a dominant pattern.

During a non-ventilatory period, it was presumed that there was no pulmonary water loss and that it was therefore possible, at least for VO_{2std} pattern P_1, to calculate pulmonary water loss as the difference between the TEWL and the CEWL during a non-ventilatory period. Nineteen examples were recorded where the duration of the non-ventilatory periods was sufficient for the complete washout of pulmonary evaporative water to enable the measurement CEWL. The calculated PEWL was very low, ranging from 1.0 to 10.0% of TEWL for the temperature range of 14–25°C (Table 3). Sample sizes for individual species displaying P_1 at a range of temperatures were too small to test for a temperature effect.

DISCUSSION

Reptiles, in contrast to birds and mammals, typically have an arrhythmic breathing pattern consisting of gas exchange periods (with one or more consecutive breaths) interspersed with non-ventilatory periods of a variable duration [e.g., (9,10,13,19,23)]. This arrhythmic ventilation presumably reflects the relatively low metabolic demand of reptiles and the mechanics of pulmonary gas exchange (19). It appears mechanically (or energetically) expedient to intersperse normal gas exchange periods of regularly spaced breaths with variable-duration non-ventilatory periods to match total pulmonary ventilation with metabolic demand, in preference to altering tidal volume or the period between breaths (19). Hence, terrestrial reptiles breathe relatively frequently and single or multiple lung ventilations alternate with short-duration non-ventilatory periods. For example, the small dragon *Ctenophorus nuchalis* (30 g) has short non-ventilatory periods (about 18 sec duration) interspersed with longer ventilatory periods (about 80 sec) at a T_b of 37°C but considerably longer non-ventilatory periods (100 sec) and slightly shorter ventilatory periods (50 sec) at a lower T_b of 18°C with a concomitantly lower metabolic demand (10).

We found that small goannas can also have a markedly arrhythmic gas exchange pattern, often with very extended periods of non-ventilation (15–30 min), at least under standard conditions at low temperatures. Their arrhythmic gas exchange was readily observed during many VO_{2std} measurements as periods of no measurable VO_2 that were often immediately followed by a rapid increase in VO_2 (Fig. 3a–c). An inspection of raw data from earlier VO_{2std} experiments for other goannas (24–26) indicates that this characteristic arrhythmic breathing pattern and a compensatory increase in VO_2 after non-ventilatory periods were not evident in larger species at 25 or 35°C. Beck and Lowe (5) similarly report that *Heloderma horridum* and *H. suspectum* can have extended non-ventilatory periods ranging from 15 to 90 min

TABLE 3. Standard cutaneous ($CEWL_{std}$) and pulmonary ($PEWL_{std}$) water loss values pooled for *V. caudolineatus* (n = 10), *V. brevicauda* (n = 5) and *V. eremius* (n = 4) at 14, 20 and 25°C

	14°C (n = 3)	20°C (n = 6)	25°C (n = 10)
$PEWL_{std}$ (mg/g/hr)	0.0017 ± 0.0001	0.0035 ± 00053	0.012 ± 0.002
$CEWL_{std}$ (mg/g/hr)	0.038 ± 0.0089	0.157 ± 0.0332	0.21 ± 0.0260
$TEWL_{std}$ (mg/g/hr)	0.039 ± 0.0089	0.161 ± 0.0332	0.225 ± 0.0253
% $PEWL_{std}$	4.7 ± 1.0	2.4 ± 0.4	5.9 ± 1.1
PEWL/SMR (mg/ml O_2)	0.15 ± 0.015	0.16 ± 0.028	0.25 ± 0.033
SMR (ml O_2/g/hr)	0.0114 ± 0.001	0.0219 ± 0.0021	0.046 ± 0.003

Values are means ± SE. SMR, standard metabolic rate.

but did not indicate if non-ventilation was followed by a rapid increase in V_{O_2}.

Long non-ventilatory periods are characteristic of semi-aquatic and aquatic reptiles (23), where non-ventilatory periods may account for 10–40% of the total time and may exceed 1 hr duration (13). For example, Courtice (8) reported that the eastern water dragon (*Physignathus lesueurii*) often showed non-ventilatory periods, a useful adaptation for a semi-aquatic reptile, whereas Pough (21) indicated that the phenomenon is also evident in some sand-"diving" lizards.

Milsom (19) suggested an optimum combination of tidal volume and respiratory frequency achieves the ventilation required to sustain V_{O_2} and V_{CO_2}, and it is mechanically more efficient to intersperse optimally spaced breaths with ventilatory pauses when continuous breathing is not required to meet their metabolic demands. If this is applicable for the small goannas we studied, then it would be expected that the V_{O_2} for periods with arrhythmic breathing and extended non-ventilatory periods would have been lower than those periods of continuous rhythmical breathing. However, this was not the finding of this study. When no non-ventilatory periods were evident, the V_{O_2} pattern showed little variability over time and the $V_{O_{2std}}$ was readily calculated as a time-averaged mean. However, the mean MR for a set of non-ventilatory periods followed by the subsequent increase in V_{O_2} and ventilation for P_1 was slightly, but significantly, higher than the MR during a period of continuous rhythmical breathing and a stable V_{O_2} for *V. caudolineatus* and *V. brevicauda*.

The periodically undetectable levels of O_2 consumption and CO_2 production measured for these goannas suggests no or negligible respiratory or cutaneous gas exchange during this period. Although terrestrial reptiles rely primarily on pulmonary gas exchange, there is limited cutaneous CO_2 exchange in some reptiles (13), but apparently not in these goannas.

The V_{O_2} of goannas was higher immediately after a non-ventilatory period than the measured rate of V_{CO_2}, and there was a more rapid return of V_{O_2} to either $V_{O_{2std}}$ levels or a further non-ventilatory period compared with V_{CO_2} (Fig. 2). Courtice (8) suggested that long respiratory pauses result in a greater O_2 extraction from the blood while minimizing water loss and respiratory work, a view supported by the inverse relationship between ventilation frequency and the coefficient for O_2 extraction from lung air by reptiles (6). Courtice (8) reported for the water dragon (*P. lesueurii*) that the P_{O_2} of lung air decreased during the non-ventilatory periods, whereas there was a minimal change in P_{CO_2}. The almost unaltered lung P_{CO_2} was presumably the result of sequestration of CO_2 in the body's fluids during non-ventilatory periods [as occurs in some turtles; (2)]. This is consistent with Courtice's (8) suggestion that CO_2 is temporarily stored in body tissues during non-ventilatory periods before being transferred to the lungs to be blown off when ventilation commences or increases.

Implications of Extended Non-Ventilatory Periods

The occurrence of prolonged non-ventilatory periods in these small goannas may be a consequence of the low air convection required to sustain their standard V_{O_2} and optimal breathing mechanics. Although of interest in itself, these prolonged non-ventilatory periods have two significant consequences. The first is that $V_{O_{2std}}$ is often determined for a lizard by calculating the mean V_{O_2} value from the lowest series of consecutive values for flow-through respirometry during the quiescent period or as a time-averaged value for closed respirometry. If such metabolic measurements incorporate a substantial non-ventilatory period and not the subsequent compensatory increase in V_{O_2} that immediately follows the non-ventilatory period, then the calculated V_{O_2} will be lower than the actual $V_{O_{2std}}$. If the data include arrhythmic breathing patterns and non-ventilatory periods, then the mean value may be higher than the actual $V_{O_{2std}}$. $V_{O_{2std}}$ is therefore best measured during a period of continuous rhythmical breathing when $V_{O_{2std}}$ is stable. Second, it allows the partitioning of pulmonary and cutaneous water loss. Green (15) partitioned TEWL for *V. rosenbergi* into about 25% pulmonary and 75% cutaneous at a T_b of 30 and 38°C. Between 14 and 25°C, the PEWL that we calculated for *V. caudolineatus*, *V. brevicauda* and *V. eremius* were appreciably less, ranging from 1.0 to 10.0% of TEWL, with a mean of 4.6%. However, this marked discrepancy between the studies probably reflects the lower temperatures and the standard conditions of our present study, as well as variation in experimental technique (non-invasive partitioning in this study compared with placing a rubber diaphragm around the goanna's neck and measuring the EWL across the skin, excluding the head, and subtracting this from the TEWL).

All experimentation with goannas was done with the approval of the Animal Welfare Committee of the University of Western Australia and goannas were caught under a license issued by the Department of Conservation and Land Management.

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