Copeia, 1998(4), pp. 1054–1059

Standard Evaporative Water Loss and Metabolism of Juvenile *Varanus mertensi* (Squamata: Varanidae)

GRAHAM G. THOMPSON AND PHILIP C. WITHERS

Evaporative water loss (EWL) varies considerably both within and between reptile species (Dmi'el, 1985; Eynan and Dmi'el, 1993; Lahav and Dmi'el, 1996) and can also be affected by acclimation (Hillman et al., 1979; Kobayashi et al., 1983). EWL data are available for a wide variety of reptiles from various habitats (see review by Mautz, 1982) but are limited for goannas under controlled conditions (Warburg, 1965; Green, 1969; Thompson and Withers, 1997a).

For lizards, such as goannas, body water is lost by evaporation from the skin (including the eyes) and the respiratory passages and as a mixture of urine and feces (and in some species from nasal salt glands; Green, 1969; Saint Girons et al., 1981). The rate of cutaneous evaporative water loss (CEWL) is largely determined by the exposed surface area of the skin and eyes, the resistance of these surfaces to evaporation, and the difference in water vapor concentrations across the surfaces. The respiratory evaporative water loss (REWL) is determined mainly by the lung ventilation rate and body temperature but may be reduced by nasal countercurrent heat and water exchange (Mautz, 1980). Environmental conditions such as ambient temperature, relative humidity, and wind velocity also affect EWL (Thorpe and Kontogiannis, 1977; Mautz, 1980, 1982).

EWL is generally higher for mesic reptiles than arid species (Snyder, 1971; Dmi'el, 1972; Shoemaker and Nagy, 1977), and we would expect the EWL of a semiaquatic goanna to be higher than for comparable terrestrial species. However, there are no data for EWL of semiaquatic goannas under controlled conditions. The semiaquatic goanna *Varanus mertensi* has a much higher field water turnover (WTR) than predicted for lizards from arid and tropical zones (Christian et al., 1996), but it is not clear whether their high WTR is associated with a high cutaneous EWL, respiratory EWL, water excretion, or a combination thereof.

This study examines the standard EWL (EWL_{std}) and standard metabolic rate (VO_{2std}) for juvenile *V. mertensi.* The primary objectives were to measure total evaporative water loss and calculate resistance to water evaporation under standardized laboratory conditions ($TEWL_{std}$, r_{std}), and to partition $TEWL_{std}$ and r_{std} into its respiratory and cutaneous components. Thompson and Withers (1997a) report $TEWL_{std}$ and resistance to total water loss (r_{total}) for a number of terrestrial and arboreal Western Australian goannas and provide a useful comparison to $TEWL_{std}$ and r_{total} for *V. mertensi.*

MATERIALS AND METHODS

$TEWL_{std}$ was measured for 10 juvenile *V. mertensi* at mean air and body temperatures (T_b) of approximately 20 and 35 C. All goannas were tested between December and January, when four months old. These goannas had hatched in captivity (Aug. 1996) and were maintained in an outdoor cage under ambient photoperiod. Water for drinking and swimming was always available, and we presumed that all goannas were fully hydrated prior to the experiment. Goannas were fed raw meat with a vitamin supplement; they were rapidly increasing in body mass and in good health when studied.

VO_2 (mL g^{-1} h^{-1}) and TEWL (mg g^{-1} h^{-1}) were measured using a flow-through respirometry system. All goannas were weighed and then placed inside a plastic mesh cage in an opaque cylinder (33 mm dia) to keep the goanna in an elongated position, unable to curl up, and without the skin being pressed against the side of the cylinder (i.e., ensuring maximum skin surface exposure to the flow-through air current). A current of dried and preheated compressed air (water content = 2.5 g m^{-3}) was passed through the sealed cylinder at 209 mL min^{-1} (STPD, Brooks mass flow controller) to provide an excurrent O_2 content between 20.0% and 20.8%. The cylinder was in a controlled temperature room at 20 and 35 C ($\pm$ 0.5 C). A Vaisala Humidity Data Processor (HMI36) with two Vaisala humidity and temperature probes (HMP 35B) measured air temperature and water content of incurrent and excurrent air. A Drierite column removed water vapor from the excurrent air (after the humidity probe) before it passed through one channel of a paramagnetic O_2 analyzer (Servomex OA184). A PC microcomputer and a Qbasic computer program recorded the analog output of the O_2 analyzer (difference in O_2 content between ambient and excurrent air) via a Thurlby digital volt meter with a RS232 interface. Air temperature and humidity were monitored via a RS232

TABLE 1. MASS-SPECIFIC VALUES FOR STANDARD EVAPORATIVE WATER LOSS (EWL_{STD}), TOTAL RESISTANCE TO EVAPORATIVE WATER LOSS, AND STANDARD METABOLIC RATE (VO_{2STD}) for Juvenile *Varanus mertensi*. Values are mean ± SE (n = 10 except for total resistance to water loss at 20 C where n = 5).

T_b C	Mass (g)	$TEWL_{std}$ ($mg\ g^{-1}h^{-1}$)	r_{total} ($sec\ cm^{-1}$)	VO_{2std} ($mL\ g^{-1}h^{-1}$)	EWL_{std}/VO_{2std}
20	54.3 ± 2.75	0.52 ± 0.034	296 ± 30.3	0.032 ± 0.0018	16.2 ± 1.32
35	51.5 ± 2.36	1.95 ± 0.141	197 ± 21.9	0.154 ± 0.0076	12.7 ± 0.74
P from *t*-test	0.44	<0.01	<0.03	<0.01	<0.02

connection between the HMI36 Data Processor and the PC. The VO_{2std} was calculated using equations modified from Withers (1977). All goannas were placed in the chamber in late afternoon (1800–2000 h) after being taken from their pool between 1600 and 1700 h; they had been fasted for a period of at least 60 h prior to the experiment. The VO_2 (STPD) and TEWL were computed every 60 sec, for a period of approximately 7 h commencing at 0000 h, between 0000 and 0800 h, and all EWL_{std} and VO_{2std} values were calculated between 0500 and 0700 h.

The lizard's T_b was presumed to be equivalent to the temperature of excurrent air, which did not differ more than 0.5 C from incurrent air (T_a). $TEWL_{std}$ was calculated from the difference between the water content of incurrent and excurrent air flow through the chamber and the air flow rate. TEWL data from extended nonventilatory periods (at 20 C) and presumed activity periods were not used in the calculation of $TEWL_{std}$. Because REWL might have been a significant component of TEWL (Dawson et al., 1966; Green, 1969), incurrent air was passed through the chamber from the posterior end to the anterior end of the goanna to maintain a minimal relative humidity as air flowed over the goanna's skin. Data were discarded if the goanna urinated in the cylinder during the experiment; this was easily detected by a rapid and substantial increase in excurrent humidity that was sustained for more than 20 min. EWL_{std} and VO_{2std} were measured once for each goanna at each ambient temperature (T_a).

To account for variation in TEWL due to effects of skin surface area and ambient water vapour content, the total resistance to water loss (r_{total}) was estimated for goannas as follows:

$$r_{total}\ (sec\ cm^{-1}) = \frac{(AH*(100/RH))(1-(RH/100))}{(EWL*M/3.6)/(SA)},$$

where AH is absolute humidity of excurrent air (gm^{-3}), RH is relative humidity of excurrent air (%), M is body mass in g, EWL is in $mg\ g^{-1}\ h^{-1}$, and SA is skin surface area ($cm^2 = 12M^{0.67}$; M is body mass in g; Green, 1969). This r_{total} is the apparent total resistance of the goanna (including boundary layer resistance and respiratory water loss) and not skin resistance that requires partitioning the total TEWL into cutaneous and respiratory components. We partitioned TEWL into REWL and CEWL by presuming that periods of no measurable VO_2 reflected no pulmonary ventilation (see Thompson and Withers, 1997c). When a nonventilatory period was immediately preceded or followed by a period of rhythmic breathing and stable VO_2, such that the EWL during both the ventilatory and nonventilatory periods could be consecutively measured, we presumed that the nonventilatory period EWL represented cutaneous EWL (CEWL) and that REWL could be calculated by the difference (i.e., REWL = TEWL − CEWL). Unfortunately, nonventilatory periods only occurred at 20 C; none was recorded at 35 C.

Means are reported with ± 1 SE and sample size (n) throughout. Statistical significance was accepted when $P < 0.05$.

RESULTS

Mass-specific $TEWL_{std}$, r_{total}, and VO_{2std} for 10 individual juvenile *V. mertensi*, with a mean body mass of about 50 g, are summarized in Table 1. Metabolic rate increased significantly ($F_{1,18}$ = 244) from 0.032 $mL\ g^{-1}\ h^{-1}$ at 20 C to 0.154 mL $g^{-1}\ h^{-1}$ at 35 C. The juvenile goannas had a $TEWL_{std}$ that was significantly different ($F_{1,18}$ = 97) between 20 C (0.52 $mg\ g^{-1}\ h^{-1}$) and 35 C (1.95 $mg\ g^{-1}\ h^{-1}$), corresponding with a significant difference ($F_{1,13}$ = 7) in r_{total} of 296 and 197 $sec\ cm^{-1}$. There was a slight, but significant decrease in the "water economy" ratio ($TEWL_{std}/VO_2$) from 20 (16.2) to 35 C (12.7 mg/mL O_2). The Q_{10} was 2.69 for VO_{2std} and 2.29 for $TEWL_{std}$.

During nonventilatory periods at 20 C, CEWL was 0.50 (± SE 0.048, n = 6) $mg\ g^{-1}\ h^{-1}$, and so $REWL_{std}$ during ventilatory periods was calculated by the difference between $TEWL_{std}$ and $REWL_{std}$ to be 0.011 $mg\ g^{-1}\ h^{-1}$ (n = 6) or 2.2%

of $TEWL_{std}$. Boundary layer resistance of a goanna in the respirometry cylinder was calculated to be 4.5 sec cm^{-1} using equation (7) of Spotila and Berman (1976). Therefore, most of the total cutaneous resistance (200–300 sec cm^{-1}) was due to skin resistance per se.

It is apparent from the TEWL recording that there was a continual slight decrease over time. A regression equation for this "base line" of declining EWL over the period of 0000 h to approximately 0700 h was used to determine the mean rate of change in water loss (i.e., mg g^{-1} h^{-2}) possibly due to progressive drying of the skin. The rate of change in evaporative water loss for *V. mertensi* at 20 C [0.0051, (SE ± 0.0015) mg g^{-1} h^{-2}; compared with a $TEWL_{std}$ of 0.52 mg g^{-1} h^{-1}] and at 35 C [0.029, (SE ± 0.0057) mg g^{-1} h^{-2}; compared with 1.95 mg g^{-1} h^{-1}] differed significantly ($t_{10} = 4.11$, $P < 0.01$).

Discussion

The main objective of this study was to compare EWL for a semiaquatic, mesic-zone goanna and a similar-sized terrestrial and more arid-adapted goanna. It must be appreciated that considerable caution should be exercised in comparing EWL values between reptile species, particularly where different research protocols have been used. There is both an intra- and interspecific allometric effect, EWL values can vary dramatically with the research protocol used for measurement of EWL (e.g., Heatwole and Veron, 1977), and ambient relative humidity affects skin hydration and EWL. Nevertheless, we would expect that the mass-specific EWL_{std} would be higher for juvenile goannas than for adults because the surface area-to-mass ratio is higher for small goannas (Green, 1969; Foley and Spotila, 1978; Dunson and Bramham, 1981), if the skin of juveniles has the same resistance as adults. However, the common intraspecific slope for mass-specific EWL_{std} of adult goannas is about −0.05, with considerable variation among species, suggesting that small species have a higher cutaneous resistance to compensate for their higher surface area to volume ratio (Thompson and Withers, 1997a). Green (1969) also reports exposed corneal evaporation to be 64.9% of TEWL for a 15-g neonate *V. rosenbergi* compared with only 16.7% for adult specimens. We were unable to determine whether our goannas had their eyes open or closed in the chamber.

In many early studies, experimental protocols involved sealing lizards into a chamber with a desiccant for a known period of time at a given T_a, and the EWL was calculated from the total quantity of water absorbed by a desiccant. Data were thus time-averaged and could have included nonquiescent periods, and EWL would be affected by the size and shape of container influencing the humid boundary layer adjacent to the skin (Thorpe and Kontogiannis, 1977; Mautz, 1980; Eynan and Dmi'el, 1993). EWL data from such experiments would be expected to be higher than EWL_{std} values determined in this study by flow-through hygrometry during the quiescent phase. Even comparison of EWL_{std} values for *V. mertensi* and those reported by Thompson and Withers (1997a) is potentially difficult, despite the almost identical methodology, because of the necessary variation in air flow rate through different size chambers for the different size goannas (e.g., Warburg, 1965; Thorpe and Kontogiannis, 1977; Foley and Spotila, 1978). However, a similar water content of excurrent air for various species measured (Thompson and Withers, 1997a; this study) suggests that conditions in experimental chambers were approximately equivalent and enables cautious interspecific comparisons to be made.

A $TEWL_{std}$ of 1.95 mg g^{-1} h^{-1} for juvenile *V. mertensi* is significantly higher than values for adult varanids (Table 2, Fig. 1) as might be expected for a semiaquatic reptile. Warburg (1965) reports EWL for juvenile *V. gouldii* (80.2 g) as 0.18 and 0.81 mg g^{-1} h^{-1} in dry air (0–5% RH) at 25 and 35 C, respectively. These values, although higher than those reported for other similar-sized goannas by Thompson and Withers (1997a; possibly due to the different research protocols), are still lower than those for measured here for *V. mertensi.*

Water permeability increases when reptilian integument is hydrated (Lillywhite and Maderson, 1982). Hydration may cause the skin to swell and disrupt the water-proofing barrier resulting in increased permeability. The skin of *V. mertensi* would most likely have been more hydrated at the start of the experiment than for the terrestrial varanids measured by Thompson and Withers (1997a), but we doubt that this would result in measurement of lower resistance measurements. The *V. mertensi* were kept for 1–2 h in dry calico bags prior to being placed in the metabolic chamber. The rate of change in water loss measured during the experiment after at least 4 h of being placed in a dry air stream was only 0.0051 mg g^{-1} h^{-1} h^{-1} at 20 C and 0.029 mg g^{-1} h^{-1} h^{-1} at 35 C compared with $TEWL_{std}$ rates of 0.52 and 1.96 mg g^{-1} h^{-1}, respectively. To lower the $TEWL_{std}$ by 50% would require an additional 34–50 h of exposure to the dry air stream, if the change in EWL continued at the same rate.

TABLE 2. EVAPORATIVE WATER LOSS FOR GOANNAS AT 35 C AND THE RATIO OF EWL_{STD}/VO_{2STD} VALUES.

Species	Mass (g)	EWL ($mg\ g^{-1}\ h^{-1}$)	EWL ($mg\ cm^{-2}\ h^{-1}$)	n	VO_{2std} ($mL\ g^{-1}\ h^{-1}$)	EWL/VO_{2std}	r_{total} ($sec\ cm^{-1}$)
V. gilleni[a]	10	0.462	0.081	2	0.178	2.6	1,799
V. gilleni[b]			0.083+				
V. caudolineatus[a]	15	0.325	0.066	7	0.181	1.8	2,127
V. brevicauda[a]	15	0.557	0.114	5	0.156	3.6	1,253
V. eremius	42	0.474	0.136	9	0.175	2.7	1,036
V. acanthurus[b]	30*	0.600	0.181+	9			
V. acanthurus[a]	68	0.415	0.139	5	0.113	3.7	1,012
V. mertensi	51	1.950	0.597	10	0.154	12.7	197
V. tristis	94	0.212	0.079	4			1,317
V. gouldii[a]	292	0.409	0.222	14	0.122	3.3	711
V. gouldii gouldii[b]	1,000*	0.400	0.167+				
V. gouldii flavirufus[b]	1,000*	0.276	0.147+				
V. gouldii[c] dry‡	80.2	0.810	0.287	7			
V. panoptes[a]	2,411	0.249	0.271	8	0.108	2.3	535
V. rosenbergi[a]	1,487	0.448	0.416	5	0.138	3.2	332
V. rosenbergi[b]	1,000*	0.337	0.192+				

dry‡ RH 0–5%.
† Values are for cutaneous water loss only.
* Body mass estimated from figure 5 in Green (1969).
[a] Thompson and Withers (1997b).
[b] Green, 1969.
[c] Warburg, 1965.

Total resistance to water loss for juvenile *V. mertensi* (296 sec cm^{-1} at 20 C and 197 sec cm^{-1} at 35 C) was lower than that for all other terrestrial and arboreal goannas (see Table 2; Thompson and Withers, 1997a) under similar conditions. It is, however, much higher than the skin resistance of the semiaquatic American alligator (*Alligator mississippiensis*) at 55 sec cm^{-1} (Davis et al., 1980) but similar to that of the semiaquatic snake, *Nerodia sipedon* (308 sec cm^{-1}; Roberts and Lillywhite, 1980).

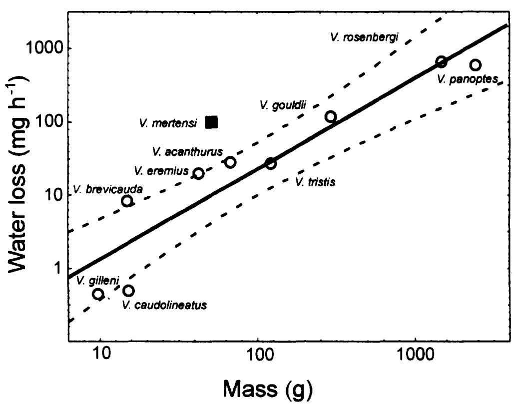

Fig. 1. Allometric comparison of evaporative water loss values for the semiaquatic *Varanus mertensi* with terrestrial goannas at 35 C; the mean for *V. mertensi* is shown by a filled square and for other goannas by open circles. The interspecific regression line for terrestrial species (with 95% confidence limits) is from Thompson and Withers (1997a).

Thompson and Withers (1997c), using a similar research protocol, report standard cutaneous water loss ($CEWL_{std}$) for the generally smaller adult *V. caudolineatus, V. brevicauda*, and *V. eremius* at 20 C as 0.157 mg g^{-1} h^{-1} and standard respiratory water loss ($REWL_{std}$) at 20 C to be 0.0035 mg g^{-1} h^{-1}. The $CEWL_{std}$ and $REWL_{std}$ measured for *V. mertensi*, 0.50 mL g^{-1} h^{-1} and 0.011 mg g^{-1} h^{-1}, indicate that both a higher cutaneous and respiratory water loss contribute to the higher TEWL of *V. mertensi*. The relative difference in CEWL (≈ 3.2 times) was similar to the difference in REWL (≈ 3.1 times). However, respiratory water loss is a small proportion of total water loss under standard conditions for both juvenile *V. mertensi* (2.2%) and adults of other small species (2.4%; Thompson and Withers, 1997c). This is much less than the 25% of TEWL attributed to respiratory water loss by Green (1969) for adult *V. rosenbergi* at 30 and 38 C in nonstandard conditions. However, this substantial difference between 2% and 25% is certainly due in part to the standard condition of our goannas (with a minimal VO_2 hence REWL) and probably also due to differences in body temperature and research protocol.

EWL generally increases as expected at higher T_b for most lizards (Warburg, 1965; Dmi'el, 1985; Withers, 1993), although there are exceptions (Eynan and Dmi'el, 1993). Goannas appear to be no different from most other squamates in their thermal sensitivity to EWL (Green, 1969; Thompson and Withers, 1997a). Thompson and Withers (1997a) report TEWL increases at higher T_b, with Q_{10} values ranging from 1.7–2.1 for *V. caudolineatus, V. brevicauda,* and *V. eremius.* The Q_{10} for TEWL of *V. mertensi* between 20 and 35 C was slightly higher at 2.29.

Resistance to total water loss is more constant with changes in T_b than is TEWL. Dmi'el (1985) reported that r_{skin} decreased at high T_b (35 C compared to 25 C) for the desert snake *Spalerosophis diadema* and was independent of body size. Withers (1993) reported that r_{total} for *Moloch horridus,* a slow moving, semiarid, terrestrial agamid decreased from 516–400 sec cm^{-1} then increased to 433 sec cm^{-1} at 15, 25, and 35 C, respectively. Thompson and Withers (1997a) reported that r_{total} was intraspecifically independent of both T_b and body mass for the arboreal *V. caudolineatus* and terrestrial *V. brevicauda* and *V. eremius,* as was suggested by Spotila and Berman (1976) and Roberston and Smith (1982) for some other species of lizards. For *V. mertensi,* r_{total} decreased with an increase in T_b (296 sec cm^{-1} at 20 C to 197 sec cm^{-1} at 35 C). The reason why r_{total} of *V. mertensi* (and some other lizards) decreases with increased T_b is not known.

A simple ratio that indicates the relative water economy of animals is EWL_{std}/VO_{2std}. For *V. mertensi* the EWL_{std}/VO_{2std} is 16.2 at 20 C and 12.7 mg H_2O/mL O_2 at 35 C. The value at 35 C is at least three times higher than that of any other goanna yet measured (Table 2). It is a high EWL rather than a low VO_{2std} that is the primary reason for the large difference in the water economy of *V. mertensi.*

Under standard laboratory conditions, the high EWL_{std} of the semiaquatic *V. mertensi* suggests that there are differences in physiological and anatomical skin properties, under ecologically relevant environmental conditions. There are at least three other semiaquatic Australian goannas (*V. semiremex, V. indicus,* and *V. mitchelli*) and a number of semiaquatic African and Asian monitors (e.g., *V. niloticus, V. salvator, V. karlschmidti*), but the extent to which physiological and anatomical parameters, such as increased skin permeability, are associated with a semiaquatic environment in species other than *V. mertensi* is unknown. The external morphological features associated with the use of a semiaquatic habitat, such as a laterally compressed tail and dorsal placement of the nostrils, appear to have coevolved a number of times in goannas (e.g., *V. mertensi* in Australia and *V. niloticus* in Africa). It will be interesting to determine whether the EWL and r_{total} values of other semiaquatic species of *Varanus* are comparable with those for *V. mertensi* and lower than for terrestrial goannas.

Acknowledgments

Varanus mertensi were hatched and kindly provided by S. Irwin of the Queensland Reptile and Fauna Park. The Western Australian Department of Conservation and Land Management licensed the collection of animals. Experiments were undertaken with the approval of the Animal Ethics and Experimentation Committee of the University of Western Australia.

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(GGT) CENTRE FOR ECOSYSTEM MANAGEMENT, EDITH COWAN UNIVERSITY, JOONDALUP DRIVE, JOONDALUP, WESTERN AUSTRALIA, 6027, AUSTRALIA; AND (PCW) ZOOLOGY DEPARTMENT, UNIVERSITY OF WESTERN AUSTRALIA, NEDLANDS, WESTERN AUSTRALIA, 6907, AUSTRALIA. E-mail: (GGT) G.Thompson@cowan.edu.au; (PCW) pwithers@cyllene.uwa.edu.au. Send reprint requests to GGT. Submitted: 8 Dec. 1997. Accepted: 27 May 1998. Section editor: R. G. Bowker.