

Evaporative water loss of Australian goannas (Squamata: Varanidae)

G.G. Thompson^{1,2}, P.C. Withers²

¹Edith Cowan University, Joondalup Drive, Joondalup, Western Australia, 6027
e-mail: G.Thompson@cowan.edu.au

²Zoology Department, University of Western Australia, Nedlands, Western Australia, 6907
e-mail: pwithers@uniwa.uwa.edu.au

Abstract. The common intra-specific mass exponent for the standard evaporative water loss was 0.86 for nine species of goanna (*V. gilleni*, *V. caudolineatus*, *V. brevicauda*, *V. eremius*, *V. acanthurus*, *V. tristis*, *V. gouldii*, *V. rosenbergi* and *V. panoptes*). The inter-specific mass exponent for evaporative water loss (EWL) was 0.95; $EWL (mg\ h^{-1}) = 2.149M^{0.95}$. The overall resistance to water loss was significantly lower inter-specifically for larger species than smaller species; however, there was no significant intra-specific relationship between resistance and body mass. The evaporative water loss of arboreal goannas (*V. caudolineatus*, *V. gilleni* and *V. tristis*) was less than that of terrestrial goannas (*V. brevicauda*, *V. eremius*, *V. acanthurus*, *V. gouldii*, *V. rosenbergi* and *V. panoptes*); this presumably reflects the exposure of these arboreal goannas to higher wind velocity and drier air. The more mesic *V. rosenbergi* had a higher evaporative water loss than the more arid species.

Introduction

Survival of squamates in semi-arid and arid environments is influenced by the availability of food and shelter, their capacity to regulate body temperature (T_b) within an optimal range, and their capacity to obtain and conserve water. For lizards such as goannas, most body water is lost by evaporation from the skin surface, the surface of the eyes, and the respiratory passages, and a lesser amount is lost as a mixture of urine and faeces (and in some species from nasal salt glands; Green, 1969). Cutaneous evaporative water loss (CEWL) is determined by the surface area of exposed skin, body shape and eye surfaces, and the resistance of these surfaces to evaporation; the respiratory evaporative water loss (REWL) is determined primarily by the respiratory ventilation rate. Environmental conditions such as ambient temperature, relative humidity and wind velocity, as well as activity level also affect evaporative water loss (Thorpe and Kontogiannis, 1977; Mautz, 1980, 1982). The skin surface area of lizards generally scales intra-specifically

to $\text{mass}^{0.67}$ (Claussen, 1967; Gans et al., 1968; Green, 1969; Peters, 1983), therefore cutaneous evaporative water loss (CEWL) would also be expected to scale with $\text{mass}^{0.67}$ (Dmi'el, 1985); this is similar to the inter-specific scaling of standard metabolic rate (SMR) for many squamates (Andrews and Pough, 1985).

Evaporative water loss (EWL) varies both within and between lizard species (Dawson et al., 1966; Claussen, 1967; Gans et al., 1968; Green, 1969; Mautz, 1980; Dmi'el, 1985; Eynan and Dmi'el, 1993) and can be affected by acclimation (Hillman et al., 1979; Kobayashi et al., 1983). EWL data are available for a wide range of reptiles from various habitats (see review by Mautz, 1982), but data for *Varanus* spp. under controlled conditions are limited to studies by Warburg (1965) and Green (1969). Both of these studies report EWL data for *V. gouldii*, and Green (1969) also provides data for *V. rosenbergi*, *V. acanthurus* and *V. gilleni*. However, Green's (1969) data are primarily at a T_b of 30°C, which is below the preferred T_b of these goannas.

This study had three objectives. Firstly, to measure standard evaporative water loss (EWL_{std}) near preferred T_b for a number of *Varanus* species. Secondly, to determine the intra-specific effect of body mass on evaporative water loss for various species of goannas and the inter-specific effect of mass on EWL. Finally, to determine the effect of temperature on EWL_{std} for various species of goannas.

Materials and methods

Evaporative water loss was measured for nine species of goanna: *V. gilleni* ($n = 2$ individuals), *V. caudolineatus* (7), *V. breviceauda* (9), *V. acanthurus* (5), *V. eremius* (9), *V. tristis* (4), *V. gouldii* (14), *V. rosenbergi* (5) and *V. panoptes* (8). Measurements were made at an air and body temperature of approximately 35°C. All goannas were tested in February or March 1994, except for all the *V. eremius* and four *V. breviceauda* which were measured in November 1994. In addition, five *V. caudolineatus* were also measured at 14, 20 and 25°C, five *V. breviceauda* were measured at 20 and 25°C, and all the *V. eremius* were also measured at 25°C, between September and November 1994.

The *V. gouldii* and *V. rosenbergi* were maintained in outdoor cages under normal photoperiod. The other smaller goannas were maintained in indoor cages with incandescent lighting as the heat source for 12 hours day^{-1} . The goannas measured at 14, 20 and 25°C were held in identical conditions except that their heat source was available for 7 hours day^{-1} . Water was available at all times and it was presumed that all goannas were fully hydrated prior to the experiment. *Varanus rosenbergi*, *V. panoptes*, *V. gouldii* and *V. tristis* were fed mice and raw meat, the smaller goannas were fed small mice, cockroaches and mealworms.

All goannas were placed inside a plastic mesh cage in opaque cylinders, with the size adjusted 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 = 2.49 g m^{-3}) was passed through the sealed cylinder at varying controlled flow rates (Brooks mass flow controller for rates less than 1000 ml min^{-1} , or a calibrated GAP flow meter for higher flows). The cylinders were placed in a controlled temperature room at 14, 20, 25 or 35°C ($\pm 0.5^\circ\text{C}$). Vaisala humidity and temperature probes (HMP 35B) were placed in the air flow immediately before and after the chamber containing the goanna. These two probes were connected to a Vaisala Humidity Data Processor (HMI 36) microprocessor that recorded air temperature and water content of incurrent and excurrent air. A microcomputer recorded temperature and relative humidity from the Humidity Data Processor every 10 seconds. All lizards were placed in the opaque chamber late in the afternoon (16:00–18:00 hours) after fasting for a period of at least 60 hours prior to the experiment. Data were recorded between 00:00 and 09:00 hours.

Body temperature (T_b) was presumed to be equivalent to the temperature of excurrent air, which did not differ more than 0.5°C from the incurrent air T_a . EWL_{std} was calculated from the difference between the water content of the incurrent and excurrent air flow through the chamber, and the air flow rate. Inflow air water content was the same for all experiments (2.49 g m^{-3}). To standardise the measurement of EWL_{std} as much as possible, flow rates were held constant at 2000 ml m^{-1} for goannas with a body mass greater than 400 g, 300 ml min^{-1} for goannas with a body mass between 200–400 g, 100 ml min^{-1} for goannas with a body mass between 30 and 200 g and the three small *V. eremius*, and 50 ml min^{-1} for goannas with a body mass less than 30 g; flow rates were chosen so that excurrent air had a relative humidity (RH) between 8–25%. These high air flow rates, in conjunction with data being recorded every 10 seconds, enabled the detection of increases in EWL due to presumed activity and decreases due to extended apnea. EWL data from extended apneic periods (at 14, 20 and 25°C) and periods of activity were not used in the calculation of EWL_{std} . As pulmonary evaporative water loss was likely to be a significant component of total water loss (Dawson et al., 1966; Green, 1969), incurrent air was passed through the cylinder from the posterior end to the anterior end of the goanna to maintain a minimal RH 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 increase in excurrent humidity that was sustained for more than 10 min. EWL_{std} was measured once for each goanna at each ambient temperature (T_a); it was calculated as the average of the lowest 100 consecutive recordings (i.e., over 16.67 min).

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

$$r_{\text{total}}(\text{s cm}^{-1}) = \frac{\Delta c}{\text{EWL}_{\text{std}}},$$

where Δc is the difference in absolute humidity ($\text{mg H}_2\text{O cm}^{-3}$) between the excurrent air and saturated air at body temperature, and EWL_{std} is the surface-area-specific evaporative

water loss ($\text{mg cm}^{-2} \text{ s}^{-1}$), calculated assuming the skin area skin surface area (cm^2) = $12M^{0.67}$, where M is body mass in grams (Green, 1969). This estimate of total resistance is an underestimate of the cutaneous resistance because of the unknown magnitude of the contribution of REWL to $\text{EWL}_{\text{total}}$.

The effects of body mass on EWL (and r_{total}) were examined using an allometric power relationship: $\text{EWL}_{\text{std}} (\text{mg H}_2\text{O h}^{-1}) = aM^b$, where M is body mass in grams, a is the mass coefficient and b is the mass exponent. Differences in allometry among species were first tested using ANCOVA (with the covariate of \log_{10} body mass). To further examine differences between species, we used ANOVA of the residuals from the pooled regression equation for all individual goannas, using Tukey's multiple comparison test. We considered the latter method ANOVA of residuals to be more appropriate than ANCOVA for analysing differences between species as there was a large variation in body mass between species. Means are reported with ± 1 standard error throughout. ANOVA and ANCOVA were calculated after Zar (1984).

Results

Mean mass-specific EWL_{std} and r_{total} values for the nine species of goannas are summarised in table 1. Values for one individual *V. brevicauda* at both 20 and 25°C were unusually and inexplicably high (see below) and have been deleted from all analyses. Increases in EWL_{std} rates during a measurement period were presumed to be associated with increased activity and metabolic rate. In some instances, there was an increase in EWL_{std} between 06:00 and 09:00 hours, presumably reflecting a circadian rhythm in metabolism and activity (goannas were kept in darkness during experiments).

It might be expected that closely-related species might have more similar mass exponents and intercepts, but we considered it premature to attempt to account for possible phylogenetic effects on either the intra- or inter-specific analysis of EWL_{std} or r_{total} , in the absence of a rooted phylogenetic tree for the genus (Baverstock et al., 1993).

Intra-specific allometry of EWL_{std} and r_{total}

There were significant differences in the intra-specific allometric slopes (table 2) for EWL_{std} between species ($F_{7,45} = 3.56$, $P < 0.05$; data for *V. gilleni* were not included because of the small sample size). A Tukey's multiple comparison test indicated that the intra-specific mass exponent of 2.1 for *V. acanthurus* was significantly different from that for *V. caudolineatus* (0.41), *V. brevicauda* (0.34), *V. eremius* (0.87), *V. tristis* (0.92), *V. gouldii* (0.82) and *V. panoptes* (0.89). The common (weighted) pooled within-species slope (b , Zar, 1984) was 0.86 for all species, excluding *V. gilleni* (too few values), and 0.84 for all species excluding *V. gilleni* and *V. acanthurus*.

Table 1. Mass-specific values for standard evaporative water loss (EWL_{std}) and resistance to water loss (r_{total}) for nine species of goannas at various temperatures. Values are means \pm 1 standard error with sample size (n).

	T_a (°C)	Mass (g)	EWL_{std} ($mg\ g^{-1}\ h^{-1}$)	r_{total} ($s\ cm^{-1}$)	n
<i>V. gilleni</i>	35	9.70	0.462	1799	2
<i>V. caudolineatus</i>	14	16.35 \pm 1.38	0.065 \pm 0.023	3545 \pm 1046	5
	20	18.36 \pm 1.63	0.117 \pm 0.020	2097 \pm 463	5
	25	15.07 \pm 1.62	0.317 \pm 0.074	2393 \pm 781	5
	35	15.30 \pm 2.32	0.325 \pm 0.041	2127 \pm 226	7
<i>V. brevicauda</i>	20	16.22 \pm 1.99	0.218 \pm 0.054	1216 \pm 219	4
	25	16.59 \pm 1.27	0.254 \pm 0.037	1394 \pm 189	7
	35	16.68 \pm 1.07	0.472 \pm 0.038	1253 \pm 84.1	9
<i>V. eremius</i>	25	42.62 \pm 6.51	0.242 \pm 0.037	1145 \pm 142	9
	35	42.46 \pm 6.59	0.474 \pm 0.050	1036 \pm 120	9
<i>V. acanthurus</i>	35	67.6 \pm 12.3	0.415 \pm 0.082	1012 \pm 243	5
<i>V. tristis</i>	35	94.2 \pm 48.3	0.212 \pm 0.035	1317 \pm 315	4
<i>V. gouldii</i>	35	292.4 \pm 60.8	0.409 \pm 0.036	711 \pm 47.6	14
<i>V. rosenbergi</i>	35	1487 \pm 236	0.448 \pm 0.058	332 \pm 58.4	5
<i>V. panoptes</i>	35	2411 \pm 450	0.249 \pm 0.032	535 \pm 74.6	8

Table 2. Relationship between $\log_{10} EWL_{std}$ ($mg\ h^{-1}$) with \log_{10} body mass at 35°C for eight species of varanids. Equations are of the form $\log_{10} EWL_{std} = a + b \log_{10} \text{mass}$. Values of a and b are \pm 1 standard error, the regression, F statistic, P value, coefficient of determination (r^2), mean body mass (g) and range in parentheses, are also given.

	a	b	r^2	n	F	P	Mass (g)
<i>V. caudolineatus</i>	0.172 \pm 0.3773	0.410 \pm 0.3233	0.24	7	1.60	0.26	15.30 (8.0-27.0)
<i>V. brevicauda</i>	0.469 \pm 0.4015	0.336 \pm 0.3360	0.13	9	1.04	0.34	16.68 (10.1-20.5)
<i>V. eremius</i>	-0.135 \pm 0.3445	0.868 \pm 0.2160	0.70	9	16.12	< 0.01	42.46 (15.2-68.3)
<i>V. acanthurus</i>	-2.453 \pm 0.1995	2.130 \pm 0.1103	0.99	5	372.75	< 0.01	67.6 (41.6-107.6)
<i>V. tristis</i>	-0.562 \pm 0.2397	0.924 \pm 0.1347	0.96	4	47.04	0.02	94.2 (9.2-212.5)
<i>V. gouldii</i>	-0.012 \pm 0.0982	0.820 \pm 0.0429	0.97	14	364.97	< 0.01	292.4 (18.0-680)
<i>V. rosenbergi</i>	-1.368 \pm 0.8536	1.320 \pm 0.2712	0.89	5	23.70	0.02	1487 (651-1978)
<i>V. panoptes</i>	-0.274 \pm 0.5990	0.893 \pm 0.1811	0.80	8	2411.0	< 0.01	2411 (434-4095)

There was no significant relationship between r_{total} and body mass for any of the species of goannas measured, except for *V. acanthurus* with r_{total} ($s\ cm^{-1}$) = 6184 (\pm 1083) - 2871 (\pm 599) \log_{10} mass ($F_{1,4} = 22.98$, $P < 0.05$).

Inter-specific allometry of EWL_{std} and r_{total}

Using the mean EWL_{std} and body mass values for the various species, the inter-specific allometric regression equation for EWL_{std} was: $\log_{10} EWL_{std} (mg\ h^{-1}) = -0.332 (\pm 0.115) + 0.950 (\pm 0.0536) \log_{10} M (F_{1,7} = 314, P < 0.001)$. Figure 1 shows this log-log relationship between mean EWL_{std} values and body mass. The allometric regression equation for r_{total} was: $r_{total} (s\ cm^{-1}) = 2285 (\pm 265) - 585 (\pm 124) \log_{10} M (F_{1,7} = 22.44, P < 0.001)$. It was not possible to account for the effects of both body mass and phylogeny at the subgenus level (*Varanus* and *Odatia*, Baverstock et al., 1993) because of the high correlation between body mass and subgenus (*Odatia* are the smaller species and *Varanus* are the larger species).

There were significant differences among species in both $\log_{10} EWL$ and r_{total} , independent of differences in body mass (ANCOVA, using \log_{10} body mass as a covariate: EWL_{std} ; $F_{7,52} = 5.94, P < 0.001$; r_{total} ; $F_{7,52} = 4.73, P < 0.001$ for all species except *V. gilleni*, or EWL_{std} ; $F_{6,48} = 8.55, P < 0.001$; r_{total} ; $F_{6,48} = 4.65, P < 0.001$ excluding the data for *V. gilleni* and *V. acanthurus*). The effect of mass was significant for both EWL_{std} and r_{total} .

Using ANOVA of the residuals from the regression equation of all individual goannas, a Tukey's multiple comparison test indicated significant differences in EWL_{std} values; *V. caudolineatus* < *V. rosenbergi*; *V. tristis* < *V. brevicauda*, *V. gouldii*, *V. rosenbergi* and *V. eremius*; and *V. panoptes* < *V. rosenbergi*. For r_{total} , *V. caudolineatus* values were significantly higher than the residuals for *V. brevicauda*, *V. acanthurus*, *V. gouldii*, *V. eremius* and *V. rosenbergi*. Comparison of the residuals for $\log_{10} EWL_{std}$ ($mg\ h^{-1}$) and r_{total} for the arboreal species (*V. caudolineatus*, *V. gilleni* and *V. tristis*) compared with those of the terrestrial species (*V. brevicauda*, *V. acanthurus*, *V. gouldii*, *V. rosenbergi*, *V. panoptes* and *V. eremius*) indicated significant differences for both EWL_{std} (ANOVA, $F_{1,61} = 16.41, P < 0.001$) and r_{total} ($F_{1,61} = 21.05, P < 0.001$), with the water loss being lower and resistance higher for the arboreal species.

Temperature effects on evaporative water loss and r_{total}

There was considerable variability in the regression equations that express the relationship between EWL_{std} with body mass and T_b (table 3), which appeared to be largely a function of the relatively high individual variability in EWL_{std} values for each of the three species assessed at the various T_b 's. Nevertheless, T_b was a highly significant predictor ($P < 0.001$) of mass-specific EWL_{std} for each species. In contrast, r_{total} was not significantly influenced by changes in T_b for any species. One *V. brevicauda* had appreciably higher EWL_{std} values at 20 and 25°C (1.16 and 0.78 $mg\ g^{-1}\ h^{-1}$, respectively) than any other small goanna; although there was no obvious reason for these exceptionally high values, they were deleted from all analyses.

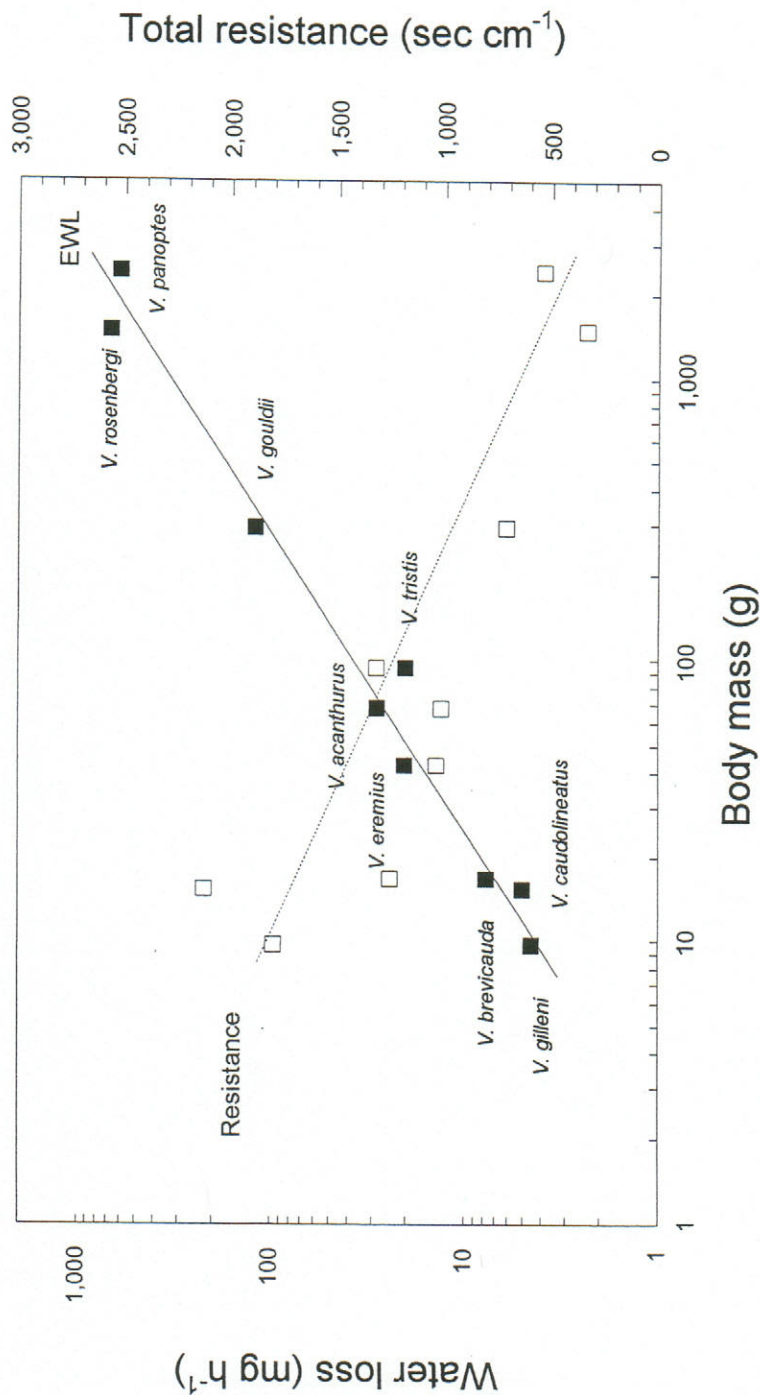


Figure 1. The inter-specific relationship for EWL₃₅ and resistance with body mass for nine species of goannas at 35°C. See text for regression equations. Closed squares are EWL and open squares are resistance.

Table 3. The relationship between EWL_{std} with body mass and T_b , for *V. caudolineatus*, *V. brevicauda* and *V. eremius*. Equations are of the form $\log_{10} EWL_{std} (mg h^{-1}) = a + b \log_{10} mass (g) + cT_b$ or $\log_{10} EWL_{std} (mg g^{-1} h^{-1}) = a + cT_b$. Values are $a \pm 1$ standard error, and $b \pm 1$ standard error from the regression equation, F statistics, P values, coefficient of determination (r^2) and T_b 's.

	a	b	c	r^2	F	P	T_b ($^{\circ}C$)
<i>V. caudolineatus</i>							
absolute EWL_{std}	-1.41 (± 0.654)	0.80 (± 0.492)	0.035 (± 0.0071)	0.56	12.26	<0.001	14, 20, 25, 35
mass-specific EWL_{std}	-1.67 (± 0.174)		0.036 (± 0.0067)	0.58	28.05	<0.001	
<i>V. brevicauda</i>							
absolute EWL_{std}	-0.02 (± 0.359)	-0.04 (± 0.284)	0.027 (± 0.0043)	0.70	2.46	0.113	20, 25, 35
mass-specific EWL_{std}	-1.25 (± 0.162)		0.026 (± 0.0056)	0.74	21.7	<0.001	
<i>V. eremius</i>							
absolute EWL_{std}	-1.22 (± 0.363)	0.87 (± 0.176)	0.031 (± 0.0076)	0.73	20.23	<0.001	25, 35
mass-specific EWL_{std}	-1.43 (± 0.228)		0.031 (± 0.0075)	0.72	16.95	<0.001	

Discussion

Considerable caution must be exercised when comparing the EWL values obtained in this study with values for goannas or other squamates from different studies, because of the substantial effect of the research protocol on the measurement of EWL. The EWL of lizards is most often expressed as mass-specific water loss ($\text{mg H}_2\text{O g}^{-1}\text{h}^{-1}$) or a skin-surface area-specific water loss ($\text{mg H}_2\text{O cm}^{-2}\text{h}^{-1}$) to compensate for body size effects. Environmental or experimental factors such as ambient humidity, temperature, and air velocity also influence the rate of evaporative water loss and make comparisons between different studies difficult (Robertson and Smith, 1982). In many early studies, the experimental protocol was to seal the lizard in a chamber for a known period of time at a given T_a , and EWL was calculated from the total quantity of water absorbed by a desiccant. Data were often collected during non-quiescent periods, and the size and shape of holding containers influenced the establishment of a humid boundary layer adjacent to the skin, thereby influencing EWL measurement (Warburg, 1965; Dawson et al., 1966; Claussen, 1967; Gans et al., 1968; Thorpe and Kontogiannis, 1977; Mautz, 1980; Eynan and Dmi'el, 1993). Evaporative water loss data from these experiments would generally be expected to be higher than EWL_{std} values determined by flow-through hygrometry during the quiescent phase, as in this study. Even comparison of EWL_{std} between the various species of goanna studied here is potentially difficult, despite the almost identical methodology, because of the necessary variation in air flow rate through the different chambers used (Warburg, 1965; Claussen, 1967; Thorpe and Kontogiannis, 1977). However, the similar water content of excurrent air for the various species suggests that the conditions in the experimental chambers for the different species were approximately equivalent, and enable cautious inter-specific comparisons to be made from the results. Spotila and Berman (1976) introduced the concept of skin resistance to water loss, but it was not possible in this study to partition pulmonary and cutaneous EWL; so, we have calculated a "total" resistance (somewhat analogous to skin surface area-specific EWL) to account for variation in skin surface area and the gradient in water vapour content.

Intra-specific allometry of EWL_{std}

The common (weighted) intra-specific slope (b) for EWL_{std} of 0.86 for varanids is surprisingly high, as it was expected that EWL_{std} would scale to approximately $\text{mass}^{0.67}$ since it is largely influenced by skin surface area, which scale with about $\text{mass}^{0.67}$ (Gans et al., 1968; Green, 1969; Dmi'el, 1985). However, the b values for individual species ranged widely from 0.3 to 2.1, reflecting the smaller sample size and more limited mass ranges. Had the sample sizes and mass ranges for each species been larger, there would have been less variability in these slopes.

Gans et al. (1968) reported that $\text{EWL}_{\text{total}}$ scaled with $\text{mass}^{0.6}$ for the snake *Elaphe climacophora*, and Dmi'el (1985) reported that cutaneous EWL scaled to $\text{mass}^{0.64}$ for

the desert snake *Spalerosophis diadema*; both slopes are close to the expected surface area dependent value of 0.67. However, Green (1969) reported that the intra-specific mass exponent for EWL at 30°C for *V. gouldii gouldii* was 0.82, which is the same as that measured for *V. gouldii* in this study at 35°C, although he reported a lower EWL mass exponent (0.70) for *V. g. flavirufus* (fig. 2). *Varanus rosenbergi* was found here to have a mass exponent of $1.32 (\pm 0.27)$, whereas Green (1969) reported a lower b value (0.77). Green's (1969) mass range for *V. rosenbergi* was larger than in this study, and this would improve estimation of the mass exponent. Green's (1969) mass exponent of 0.42 for *V. acanthurus* for the mass range of 2.7 to 62 g is much lower than that recorded for *V. acanthurus* in this study. However, he has included three goannas with a body mass less than 10 g in his sample, which would have reduced the slope of the mass exponent due to a significantly higher mass-specific EWL across the optical membrane for small individuals. Green (1969) reports optical evaporation to be 64.9% of total water loss for a 15 g *V. rosenbergi* compared with 16.7% for adult specimens.

Total resistance to water loss was not intra-specifically related to body mass for seven of the eight species measured, a finding similar to that of Dmi'el (1985) and Robertson and Smith (1982) for skin resistance.

Inter-specific allometry of EWL_{std}

Mautz's (1982a) regression equations for mass-specific EWL of a diverse range of mesic lizards ($4.436M^{-0.458}$) predicts a rate of $0.19 \text{ mg H}_2\text{O g}^{-1} \text{ h}^{-1}$ for a 1000 g mesic lizard, and a value of $0.09 \text{ mg g}^{-1} \text{ h}^{-1}$ for a semi-arid lizard ($2.754M^{-0.496}$), in the temperature range of 20–30°C. Using Green's (1969) Q_{10} value of 2.35 for EWL, and Mautz's (1982) predictive equation for EWL, a mesic 1000 g goanna would be predicted to have an EWL of approximately $0.45 \text{ mg H}_2\text{O g}^{-1} \text{ h}^{-1}$ at 35°C; similarly, a 292.4 g goanna would be expected to have an EWL of $0.77 \text{ mg H}_2\text{O g}^{-1} \text{ h}^{-1}$. Both of these predicted values for goannas are higher than those reported by Green (1969) for *V. gouldii* and *V. rosenbergi* (≈ 1000 g), and reported here for *V. gouldii* (≈ 292.4 g). Green's (1969) values for *V. gouldii* and *V. rosenbergi* at 30°C are similar to the EWL_{std} values measured here for these species at 35°C (fig. 2).

A comparison of the inter-specific allometric EWL slopes for a selection of lizards (from Mautz, 1982) with those of seven species of goannas suggests that EWL scales differently for goannas than other squamates, although Dawson et al. (1966), Gans et al. (1968) and Mautz (1980, 1982) report considerable inter-specific variability in EWL for lizards. Mautz (1982) reported EWL mass exponents for arid, semi-arid and mesic species of 0.75, 0.50 and 0.54, respectively, for the temperature range from 20–30°C, whereas we report an inter-specific mass exponent of 0.95 at 35°C. In addition to variation in skin resistance to water loss, respiratory EWL, habitat choice, acclimation, activity, temperature and experimental protocols may contribute to variation in measurements of total EWL among species of squamates. Therefore, until a more standardised procedure for measuring EWL, and partitioning CEWL and REWL, in squamates is established,

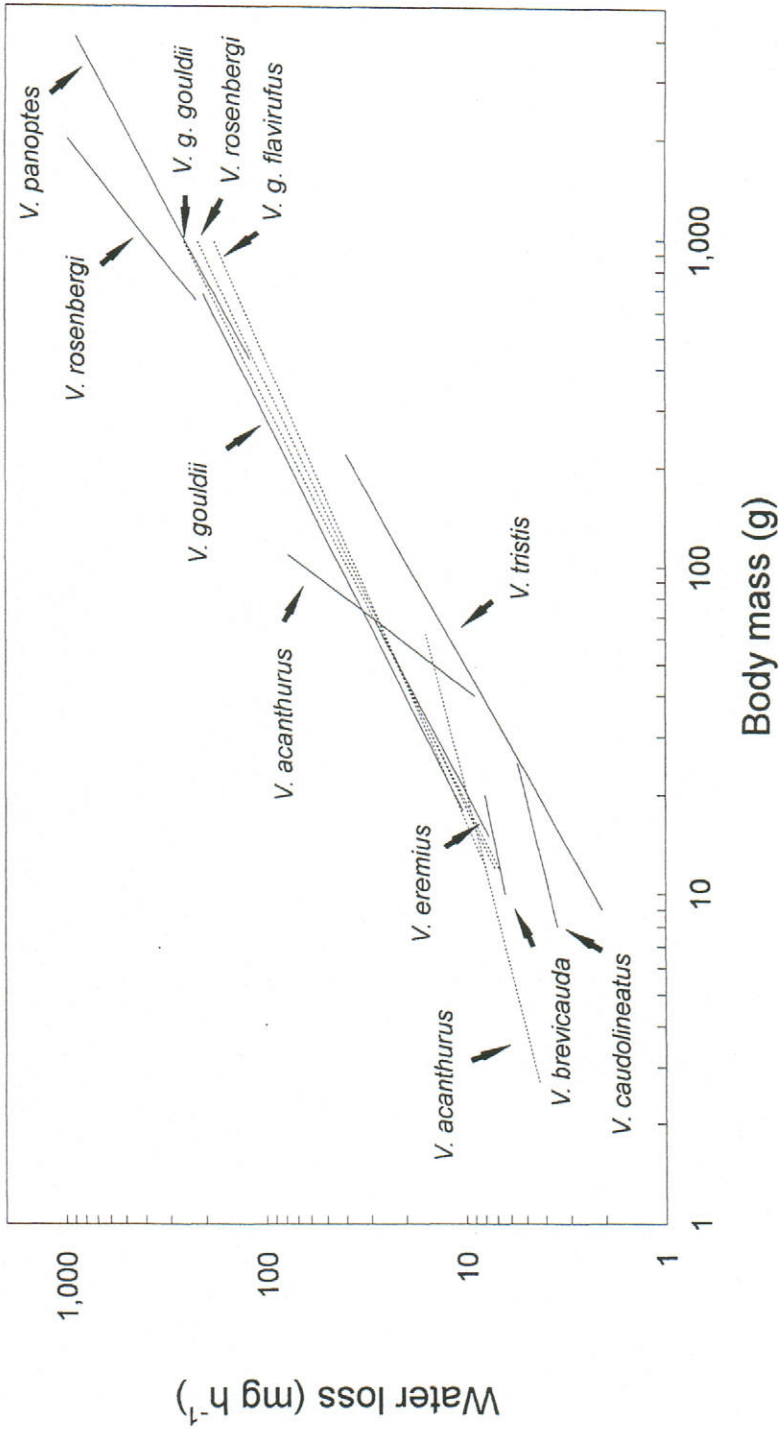


Figure 2. Intra-specific regression lines for EWL_{34} of goannas from this study at 35°C, compared with the regression lines for goannas from Green (1969) at 30°C. Green's (1969) data for *V. acanthurus*, *V. rosenbergi* and two subspecies of *V. gouldii* are represented by the dotted regression lines.

inter-specific comparisons and allometric analysis of EWL_{std} , CEWL and REWL will be difficult.

The inter-specific slope, calculated from the mean EWL_{std} values for each goanna species, of 0.95, is higher than what might have been expected if EWL was simply proportional to skin surface area (Gans et al., 1968), and is similar to the unusually high inter-specific SMR scaling exponent of 0.92 for goannas (Thompson et al., 1995). Inclusion of the lower EWL_{std} for the small, arboreal *V. caudolineatus*, *V. gilleni* and *V. tristis* would increase the scaling exponent, but not appreciably ($b = 0.92$ with these species excluded from the regression analysis). The surface area-to-mass ratio of the small goannas is higher than for the larger species, therefore it would be expected that small goannas would have a higher mass-specific EWL_{std} than large goannas. However, the higher total resistance to water loss of the smaller species results in these goannas having about the same mass-specific EWL as larger species (table 1).

The calculated r_{total} values for the goannas, although an underestimate of their actual skin resistance to water since these include REWL, appear to be in the upper range of those reported for squamates. Only the small diurnal xantusiid lizards (*Xantusia vigilis*, 2150–3310 s cm⁻¹; *Xantusia henshawi*, 1120–1510 s cm⁻¹) and *Klauberina riversiana* (1020–3080 s cm⁻¹; Mautz, 1980) have r_{total} values similar to those of the small goannas. Most other terrestrial reptiles seem to have lower values (e.g., 185 s cm⁻¹ for *Spalerosophis diadema*, a desert snake (Dmi'el, 1985), 196.4 s cm⁻¹ for *Anolis carolinensis* (Spotila and Berman, 1976), 190–320 s cm⁻¹ for *Lepidophyma smithii* (Mautz, 1980), 400–516 s cm⁻¹ for *Moloch horridus* (Withers, 1993)). The high resistance of small goannas to water loss is clearly a useful adaptation for widely-foraging, arboreal, predators that live in arid and semi-arid environments.

Effects of temperature on evaporative water loss

Total (or cutaneous) EWL generally increases with elevated T_b for lizards (Warburg, 1965; Dawson et al., 1966; Mautz, 1980; Dmi'el, 1985; Withers, 1993), although there are exceptions (Eynan and Dmi'el, 1993). Goannas appear to be no different from most other squamates (Green, 1969) as total EWL increases for small goannas with increased T_b , with Q_{10} values ranging from 1.7 to 2.1 for *V. caudolineatus*, *V. brevicauda* and *V. eremius*. In this study, r_{total} of goannas was found to be intra-specifically independent of both T_b and body mass, as has been reported by Spotila and Berman (1978) and Roberston and Smith (1982) for other lizards. In contrast, Dmi'el (1985) reported r_{total} decreased at high T_b for the desert snake *Spalerosophis diadema*, and CEWL increased or decreased with elevated T_b for some agamid lizards (Eynan and Dmi'el, 1993).

Ecological implications

The surface area-to-mass ratio for small goannas is higher than that for large goannas and it would therefore be expected that mass-specific EWL_{std} would also be signifi-

cantly higher in small goannas than in large goannas. However, the higher resistance to water loss in small goannas largely compensates for their proportionally higher skin surface area. Small goannas are therefore not required to make additional behavioural or physiological adjustments to conserve water compared with the larger species.

Although size and temperature have a major affect on absolute EWL, there were detectable differences in absolute EWL_{total} based on the habitat of the various species of goanna. As might be expected, we found that arboreal goannas have a significantly lower EWL_{std} and higher r_{total} than terrestrial species, a finding similar to that reported by Roberts (1989) for geckos. Basking in arboreal positions is likely to expose these goannas to a higher wind velocity than terrestrial species, and tree hollows are possibly not as humid a retreat as burrows underground. Consequentially, arboreal goannas could be exposed to greater desiccation than terrestrial species. The terrestrial *V. rosenbergi* has a higher EWL_{std} than most of the other similar-sized terrestrial goannas. This species is the only goanna of those measured here that is primarily found in mesic environments (all of the other species are from semi-arid or arid environments) and therefore it might be anticipated that *V. rosenbergi* would have a higher EWL and lower r_{total} (cf. Gans et al., 1968; Hillman et al., 1979; Dunson and Bramham, 1981; Mautz, 1982; Eynan and Dmi'el, 1993). These ecological interpretations are, however, made in the absence of any analysis of possible phylogenetic influences on EWL in goannas. The arboreal and the smaller goannas are all from the subgenus *Odatia* and the larger species from the subgenus *Varanus*. A proper phylogenetically based analysis of patterns of EWL in *Varanus* awaits further study of EWL in a wider range of species and a rooted phylogenetic tree for the family.

References

- Andrews, R.M., Pough, F.H. (1985): Metabolism of squamate reptiles: allometric and ecological relationships. *Physiol. Zool.* **58**: 214-231.
- Baverstock, P.R., King, D., King, M., Birrell, J., Krieg, M. (1993): The evolution of species of Varanidae: Microcomplement fixation analysis of serum albumins. *Aust. J. Zool.* **41**: 621-638.
- Claussen, D.L. (1967): Studies of water loss in two species of lizards. *Comp. Biochem. Physiol.* **20A**: 115-130.
- Dawson, W.R., Shoemaker, V. H., Licht, P. (1966): Evaporative water losses of some small Australian lizards. *Ecology* **47**: 589-594.
- Dmi'el, R. (1985): Effect of body size and temperature on skin resistance to water loss in a desert snake. *J. Therm. Biol.* **10**: 145-149.
- Dunson, W.A., Bramham, C.R. (1981): Evaporative water loss and oxygen consumption of three small lizards from the Florida Keys: *Sphaerodactylus cinereus*, *S. notatus*, and *Anolis sagrei*. *Physiol. Zool.* **54**: 253-259.
- Eynan, M., Dmi'el, R. (1993): Skin resistance to water loss in agamid lizards. *Oecologia* **95**: 290-294.
- Gans, C., Krakauer, T., Paganelli, C.V. (1968): Water loss in snake: interspecific and intraspecific variability. *Comp. Biochem. Physiol.* **27A**: 747-761.
- Green, B. (1969): Water and electrolyte balance in the sand goanna, *Varanus gouldii* (Gray), unpub. PhD thesis, University of Adelaide, Adelaide, South Australia.
- Hillman, S., Gorman, G.C., Thomas, R. (1979): Water loss in *Anolis* lizards: evidence for acclimation and intraspecific differences along a habitat gradient. *Comp. Biochem. Physiol.* **62A**: 491-494.

- James, C.D., Losos, J.B., King, D.R. (1992): Reproductive biology and diets of goannas (Reptilia: Varanidae) from Australia. *J. Herpetology*, **26**: 128-136.
- Korbayashi, D., Mautz, W.J., Nagy, K.A. (1983): Evaporative water loss: humidity acclimation in *Anolis carolinensis* lizards. *Copeia* **1983**: 701-704.
- Losos, J.B., Greene, H.W. (1988): Ecological and evolutionary implications of diet in monitor lizards. *Biol. J. Linnean Soc.* **35**: 379-407.
- Mautz, W.J. (1980): Factors influencing evaporative water loss in lizards. *Comp. Biochem. Physiol.* **67A**: 429-437.
- Mautz, W.J. (1982): Patterns of affect evaporative water loss. In: *Biology of the Reptilia*, 12, p. 443-481. Gans, C., Pough, F.H., Eds., London, Academic Press.
- Peters, R.H. (1983): *The Ecological Implications of Body Size*. Cambridge, Cambridge Univ. Press.
- Roberts, A. (1989): Morphological and physiological correlates of ecology. Unpub. Honours thesis, University of Western Australia, Perth, Western Australia.
- Robertson, S.L., Smith, E.N. (1982): Evaporative water loss in the spiny soft-shelled turtle *Trionyx spiniferus*. *Physiol. Zool.* **53**: 124-129.
- Spotila, J.R., Berman, E.N. (1976): Determination of skin resistance and the role of the skin in controlling water loss in amphibians and reptiles. *Comp. Biochem. Physiol.* **55A**: 407-411.
- Thompson, G.G., Heger, N.A., Heger, T.G., Withers, P.C. (1995): Standard metabolic rate of the largest Australian lizard, *Varanus giganteus*. *Comp. Biochem. Physiol.* **111A**: 603-608.
- Thorpe, G.S., Kontogiannis, J.E. (1977): Evaporative water loss in isolated populations of the coastal side-blotched lizard *Uta stansburiana hesperis*. *Comp. Biochem. Physiol.* **57A**: 133-137.
- Warburg, M.R. (1965): Studies on the environmental physiology of some Australian lizards from arid and semi-arid habitats. *Aust. J. Zool.* **13**: 563-575.
- Withers, P.C. (1993): Cutaneous water acquisition by the thorny devil (*Moloch horridus*: Agamidae). *J. Herpet.* **27**: 265-270.
- Zar, J.H. (1984): *Biostatistical Analysis*. London, Prentice Hall.

Received: July 1, 1995. Accepted: August 5, 1996.