

Chapter 8

Moulting, Size and Evaporative Water Loss Studies

8.1 Introduction

The rate of evaporative water loss in scorpions is dependent on a number of factors. Recently moulted scorpions have an increased permeability to evaporative water loss (Francke 1976, Toyé 1970) and incomplete moulting can result in the desiccation of young during their first moult (Sissom and Francke 1983). Size affects water loss. Early instars between moults lose more water than later instars because of their small size (Crawford and Wooten 1973, Hadley 1970b, Shorthouse 1971). The time of day can affect the rates of water loss which may be correlated with activity (Withers and Smith 1993).

The purpose of this study was:

1. to compare the rates of evaporative water loss of recently moulted and intermoult *Urodacus manicatus*.
2. to compare the rates of water loss of *U. manicatus* in the same state of hydration at night and during the day, and examine how water loss changes over time.
3. to examine the effect of size and sex on evaporative water loss in *U. manicatus*.
4. to determine the number of instars of *U. manicatus* and relate the instars to evaporative water loss.

8.2 Materials and Methods

The effect of moulting on evaporative water loss was investigated. Twelve sub adult and adult female *Urodacus manicatus* were collected on 4 March 1991 from Black Mountain NSW and maintained at 20°C for 2 days with water only. Over a period of two weeks 6 animals moulted at night, 5 successfully so with one found dead in the morning at a stage of incomplete ecdysis. Daily water loss measurements commenced the day after moulting at 30°C, 0% RH (Section 2.2). At the same time that the last animal moulted, measurements of water loss rates for the remaining 6 inter moult animals were commenced together. Covariate analysis was not chosen due to the small sample sizes and the narrow size range of the scorpions. Instead, the second day rates of water loss were expressed as permeability ($\text{mg H}_2\text{O cm}^{-2} \text{h}^{-1}$) and the permeabilities of the recently moulted and intermoult scorpions were compared with a Student's independent samples *t*-test. Condition of the cuticle was the grouping variable. Permeability was log transformed to achieve normality in the data.

To investigate any diurnal influences on evaporative water loss, two groups of adult females maintained as above were weighed after 6, 12, 24 and 48 hours at 30°C and 0% RH (Section 2.2). One group was placed into the desiccator at 12:00 h and the other at 18:00 h and mass-specific water loss was calculated. A one-way between-subjects MANOVA was performed on the four dependent variables associated with time interval of mass-specific water loss ($\text{mg H}_2\text{O g}^{-1} \text{h}^{-1}$) after placement in the desiccator (6, 12, 24 and 48 hours). The time of placement into the desiccator was the independent variable (12:00 or 18:00 h).

To investigate the relationship of evaporative water loss to sex and size, *Urodacus manicatus* of both sexes and from second instar to adult were collected on 4 March 1991 from Black Mountain NSW and maintained at 20°C for 2 days with water only. Daily water loss was measured over two days at 30°C and 0% RH (Section 2.2). Total water loss was calculated as $\text{mg H}_2\text{O h}^{-1}$ and surface area was calculated assuming $k = 12.47 \text{ cm}^2 \text{g}^{-1}$ (Section 2.2). Right hand (chela) and

fixed finger length (HFF), fourth tail segment length (FTL) and carapace width (CW) (Koch 1977) were measured to the nearest 0.1 mm with vernier callipers to determine the developmental stages.

The effect of sex on evaporative water loss was examined utilising the allometric relationship between evaporative water loss and body mass (Gunn 1935) and the relationship is presented as:

$$EWL = a m^b$$

where EWL is the rate of evaporative water loss ($\text{mg H}_2\text{O h}^{-1}$) and m is mass (g) with coefficient a and exponent b . The linear form of this model ($\log EWL = \log a + b \log m$) enables the comparison of means of EWL after adjustment for mass by the use of ANCOVA where mass is the covariate. A one-way between-subjects ANCOVA was performed on the second day rate of evaporative water loss as the dependent variable. Adjustment was made with the body mass as the covariate. Sex was the independent variable. Results of evaluation of assumptions of normality, homogeneity of variance-covariance matrices, linearity, and multicollinearity were satisfactory. Body mass was judged to be adequately reliable for covariance analysis (sex by mass interaction term non-significant, $F(1, 35) = 0.031, P > 0.05$). With the use of t -tests, the slopes of the logarithmic regressions for females and males were compared with 0.67 as predicted by surface area.

The theoretical approach reviewed by (Francke and Sissom 1984) was used to determine the number of moults from second instar to adult based on the structures HFF, CW and FTL. Growth in scorpions is typical of arthropods, the steps following a geometric progression which can be presented as:

$$\log A = \log Y + n \log P$$

where A is the dimension of the adult structure, Y is the dimension of the same structure in the young of known instar, P is the progression factor and n is the number moults separating the

young and the adult (Francke and Sissom 1984). The theoretical value of 1.26 for P was used which was not significantly different from the value determined for the scorpion *Vaejovis coahuilae* (Francke and Sissom 1984). By rearrangement and substitution of P, the above equation becomes:

$$n = 10 (\log A - \log Y).$$

The structures HFF, CW and FTL were measured in 25 female and 25 male second instars and 30 female and 15 male adults. The second instars were born in the laboratory so that their stadia were established. It was preferable to obtain measurements of first and second instar from the same individuals, but the survival of young diminished when first instars were temporarily removed from the mother and their unhardened cuticle made them susceptible to damage when handled. The females that had given birth in the laboratory were assumed to be adults however, (Francke and Sissom 1984) suggested that penultimate instars could be sexually mature. To ensure that only measurements of female adults were used, they were dissected and the presence of previous generation postpartum diverticulae as described by (Willmer 1967) was determined. The length of time spent in the penultimate instar was less than the gestation time of *U. manicatus*, therefore only final instars had such diverticulae. Males were also dissected for the presence of the paraxial organs, but there was no certainty as to whether they were all final instars because any previous sexual activity was unknown. The progression factor of 1.26 was used to predict the size ranges of HFF, FTL and CW from the morphometrics of the second instars.

An indirect method for calculating the number of instars used several body measures in cluster analysis. HFF, FTL and CW were measured for the 42 females and 47 males used in Section 8.3.1 above. The data were log transformed and standardised and then a Euclidean distance matrix for each sex was computed from the joined measures. Multidimensional scaling was used to cluster the data into two dimensions which were then visually analysed (SYSTAT for Windows: Statistics 1992).

8.3 Results

8.3.1 Effect of Moulting on Evaporative Water Loss

Moulting had the effect of increasing the permeability of *Urodacus manicatus*. The permeability of new untanned cuticle was $0.071 (\pm 0.010, n = 5)$ mg H₂O cm⁻² h⁻¹ compared to $0.048 (\pm 0.003, n = 6)$ mg H₂O cm⁻² h⁻¹ for normally tanned cuticle. The differences between the log transformed permeabilities were significant, $t(9) = -2.96, P < 0.05$.

8.3.2 Effect of Time of Day and Time on Evaporative Water Loss

The rate of water loss of *Urodacus manicatus* was dependent on the length of time of dehydration, but independent of the time of day (Table 8.1). The rate of water lost in the first six hours was $2.732 (\pm 0.300)$ mg H₂O g⁻¹ h⁻¹ during the photophase and $2.802 (\pm 0.246)$ mg H₂O g⁻¹ h⁻¹ during the scotophase. The equivalent rates decreased over the next 6 hours to $0.942 (\pm 0.203)$ mg H₂O g⁻¹ h⁻¹ during the day and $0.925 (\pm 0.184)$ mg H₂O g⁻¹ h⁻¹ during the night. The time of placement into the desiccator did not have a significant effect on the combined repeated measures, $F(4, 11) = 0.17, P > 0.05$. The rate of water loss was significantly different between time intervals from placement in the desiccator, $F(3, 12) = 32.54, P < 0.001$. Unevenly spaced polynomial contrasts that reflected the increasing time interval from the commencement of water loss indicated that the change in water loss rate was best described as linear, $F(2, 14) = 50.16, P < 0.001$, contributing 38.1% to the total sum of squares. The quadratic, $F(2, 14) = 38.08$, and cubic, $F(2, 14) = 37.63$, trends were also strong, contributing 34.6% and 27.5% respectively to the total sum of squares.

8.3.3 Effects of Body Size and Sex on Evaporative Water Loss

Female and male *Urodacus manicatus* from second instars to adults lost water at the same rate after adjustment by body mass, $F(1, 85) = 0.012, P > 0.05$. The logarithmic relationship between

female EWL and mass was: $\log \text{EWL} = -0.119 (\pm 0.033) + 0.890 (\pm 0.042) \log m$, $r^2 = 0.917$, $F(1, 40) = 441.61$, $P < 0.001$. The logarithmic relationship for males was: $\log \text{EWL} = -0.123 (\pm 0.048) + 0.876 (\pm 0.067) \log m$, $r^2 = 0.792$, $F(1, 45) = 171.47$, $P < 0.001$. The allometric relationships were thus

females: $\text{EWL (mg H}_2\text{O h}^{-1}) = 0.76 m^{0.890} \text{ (g)}$ and

males: $\text{EWL (mg H}_2\text{O h}^{-1}) = 0.75 m^{0.876} \text{ (g)}$.

The relationship for the combined sexes was: $\log \text{EWL} = -0.120 (\pm 0.029) + 0.884 (\pm 0.038) \log m$, $r^2 = 0.859$, $F(1, 87) = 528.36$, $P < 0.001$. The allometric relationship was thus

$\text{EWL (mg H}_2\text{O h}^{-1}) = 0.76 m^{0.884} \text{ (g)}$.

The combined slope (0.884) obtained in this study for *Urodacus manicatus* was significantly larger than 0.67, $t(89) = 5.63$, $P < 0.001$ and 0.75, $t(89) = 3.53$, $P < 0.001$. Examination of the plot of body mass against second day evaporative water loss rate on a logarithmic scale (Figure 8.1) suggested that linearity held for early instars, but not for older animals. Both females and males with masses greater than approximately 0.45 g had rates of evaporative water loss that did not correlate with body mass. Both females and males that had masses greater than 0.45 g were removed from the data set. The regression equation of mass and evaporative water loss for the combined sexes was then determined for animals weighing less than 0.45 g. The logarithmic relationship for the combined sexes was: $\log \text{EWL} = -0.379 (\pm 0.035) + 0.661 (\pm 0.034) \log m$, $r^2 = 0.894$, $F(1, 44) = 369.24$, $P < 0.001$. The allometric relationship was thus

$\text{EWL (mg H}_2\text{O h}^{-1}) = 0.42 m^{0.661} \text{ (g)}$.

The slope was not significantly different from 0.67, $t(44) = 0.27$, $P > 0.05$, but was significantly different from 0.75, $t(44) = 2.62$, $P < 0.05$.

8.3.4 Instars and Evaporative Water Loss

The calculated number of moults for second instars to attain adult size using the theoretical approach were similar for hand and fixed finger length, fourth tail segment length and carapace width (Table 8.2). The number of moults for females and males respectively were 4.9 and 4.9 for HFF, 4.8 and 4.8 for FTL and 4.4 and 4.1 for CW. The number of moults must be an integer, therefore rounding the averages off to 5 and with addition of the first instar, suggests the seventh instars of *Urodacus manicatus* for both sexes were mature adults. The predicted size ranges of HFF, FTL and CW for second instars to adults are presented in Table 8.3.

The predicted six instars (second instar to adult) did not appear as discrete clusters for either females Figure 8.2a or males Figure 8.2b when the measurements of HFF, FTL and CW were scaled into two dimensions using multidimensional scaling. Although some clumping seemed to be apparent, it was not possible to delineate the instars even with the theoretical number of six.

The instar at which water loss was not correlated with size was determined by plotting rate of evaporative water loss against HFF (Figure 8.3) and plotting the predicted instar size ranges for HFF obtained from Table 8.3. Female and male *Urodacus manicatus* exhibit greater variation in evaporative water loss during the sixth instar and into the seventh (adult) instar.

8.4 Discussion

Scorpions, like all arthropods, have a discontinuous growth with the periodic shedding of the exoskeleton after which the body then expands. Moulting results in the loss of the waxy layer of the cuticle which restricts evaporative water loss (Polis 1990). The new cuticle is without the waxy layer until the new cuticle hardens or "tans". Recently moulted *Urodacus manicatus* had permeabilities that were 1.48 times that of inter moult scorpions. This was similar to the findings of Toye (1970) in which recently moulted *Pandinus imperator* had permeabilities that were 1.77 times that of scorpions with hardened cuticles. The increase in permeability in *U. manicatus*, however, remained below that of most land arthropods by an order of magnitude (Edney 1977).

Thus, for a scorpion that was normally hydrated, the greater rate of water loss after moulting would not have a large impact on the animal's body water content. This suggests that the reason why moulting occurs in the burrow (Polis 1990), is not because water loss needs to be reduced, but because the burrow provides protection from predators (Polis 1981).

The time taken for complete tanning of the new cuticle is not certain. Le Berre (1979) found that moulting interrupted foraging behaviour 5 days before ecdysis and 4 days afterwards in *Buthus occitanus*. Similarly, *Mesoluthus eupeus* did not forage 4-5 days before moulting (Yusubov 1991). Second instars of *Aruroctonus phaeodactylus* did not begin to burrow in captivity until 45 days after moulting when the new cuticle had hardened, before which, they remained under surface shelters (Williams 1966).

This study has demonstrated that water loss in *Urodacus manicatus* was independent of the time of day, but dependent on the duration of the measurements especially over the first day.

Evaporative water loss in *Urodacus armatus* showed a daily fluctuation (Withers and Smith 1993); however, no details were provided as to when the measurements for day and night had commenced. The higher rates of water loss at night may have been measured at an earlier stage of dehydration than those during the day. Respiratory water loss is a small fraction of cuticular water loss at normal temperatures (Robertson et al. 1982). Increased activity and metabolic rate at night would raise respiratory water loss, but its contribution to an increase in total evaporative water loss for *U. armatus* may still be small.

The high initial rates of water loss of *Urodacus manicatus* were typical of scorpions (Crawford and Wooten 1973, Hadley 1970b) as well as other arthropods (Edney 1977, Loveridge 1968). Hadley (1970b) attributed this to water absorbed into the cuticle and water loosely bound to cuticular protein and lipid molecules. The rate of water loss of *Hadrurus arizonensis* dropped by more than 57% from the first hour to the sixth hour (Hadley 1970b). *Diplocentrus peloncillensis* dropped by 53% from 1.5 to 6 hours (Crawford and Wooten 1973). However, Loveridge (1968) suggested that the loss of hygroscopic water on the cuticle between 0 and 25% RH (29.5°C) was only a component of the initial high rates in insects and that a change in permeability did occur.

The allometry between rate of water loss and body mass in *Urodacus manicatus* changed during the sixth instar of both females and males. The increased variation in water loss was due to greater rates and not lower rates of water loss, because the allometric relationship for earlier instars defined the lower limit of water loss in the sixth and seventh instars (Figure 8.1). A slope of 0.66 for second day water loss at 30°C and 0% RH suggested that water loss in *U. manicatus* was determined by surface area.

Sixth and seventh instars lost water up to three times that predicted by the allometric relationship for earlier instars. The variation in the rate of water loss in sub adult and adult *Urodacus manicatus* may have reflected variation in their cuticular permeability to water. Variation in permeability may arise due to the abrasion of cuticular lipids that form the principle barrier to water flux thus increasing permeability. However, later instars of *U. manicatus* were not expected to have had increased cuticle permeabilities due to more abrasion than early instars because cuticle repair and the turnover of lipids is a continuous process in arthropods (Hall and Hadley 1982, Wigglesworth 1945). As well, age does not affect the permeability of arthropods (Loveridge 1968).

The variation in water loss rates of later instars may have been due to an increase in the variation of body shape or differing adaptational changes in cuticle permeability in response to different microhabitats within a population. Body shape in *Urodacus manicatus* changed dramatically depending on their nutritional status, degree of hydration and reproductive state. Scorpions that were well fed, well watered or in the last months of gestation had more rounded mesosomas. As such, they were expected to have had lower surface area to volume ratios and thus lower rates of water loss than animals of a more flattened appearance. If this phenomenon were to account for the variation in water loss in sixth instars and adults then those animals that had rates of water loss allometrically related to body mass were either well fed or more hydrated than those animals with higher rates of water loss. Reproductive status was discounted because gravid females were not included in this study. Water loss across the cuticle of the mesoabdomen may potentially increase by 2 to 3 times with the change in dorsal-ventral dimensions for an animal of given length and width. Similarly, for first instars of *Centruroides exilicauda*, their high body water content at birth gives them a more rounded shape which may help decrease transcuticular water loss by decreasing the surface area to volume ratio (Toolson 1985).

Variation in body shape, however, did not account for all the variation in rates of water loss in later instars. In chapter 7, it was established that gravid females (having the same appearance as well fed or hydrated non gravid scorpions) did not have lower rates of water loss compared to postpartum rates. Also, the assumption that earlier instars were better fed or more hydrated than later instars was not supported by general observations.

The variation in permeability may have then reflected variation in the microclimates within the Black Mountain population. In chapters 4, 5, 7 and 8, scorpions that were maintained for longer periods in captivity than in this study, had permeabilities that were greater than field-collected scorpions (Chapter 3) due to the higher water availability and smaller saturation deficit of the air in captivity. It was reasonable to assume then, that *Urodacus manicatus* that inhabited home sites that differed in microclimate differed in their cuticular permeabilities. If smaller instars competed less successfully for larger and better insulated home sites than larger instars, then they had to burrow under smaller shelters that were more xeric in their microclimate. If small scorpions were restricted in home site selection then they may be inhabiting more similar home sites to one another, thus accounting for the small variance in water loss rates. Although Smith (1966) stated that minimum rock area was not related to the developmental stage for *U. manicatus* at Black Mountain, Canberra, it was also stated that sampling was of the adult population, not of the immature stages. Smith (1966) also stated that there was a high rate in mortality of younger scorpions which occurred during dispersal when they were cannibalised upon entering an occupied home site. The competition for home sites in later instars would be more equitable resulting in the occupation of more mesic home sites as well as some animals occupying more xeric home sites. Therefore, those later instars that inhabited the more mesic home sites (such as those at the bases of trees, see Chapter 3) had greater cuticle permeabilities than otherwise. Also, the smaller the scorpion, the greater the rate of absolute water loss. As such, there may be more pressure on the smaller scorpions to restrict their rate of water loss as much as possible compared to larger scorpions.

Smith (1966) and Shorthouse and Maples (1982) obtained discrete clusters when plotting body measurements for *U. manicatus* and *U. yaschenkoi* respectively. Both authors claimed a total of six instars. Regardless of the method for plotting measurements, no discrete clumping was

apparent for *U. manicatus* in this study which could have been due to the small sample size. The instars of *Diplocentrus bigbendensis* did not cluster after plotting carapace length against chela length (Francke 1984). Application of the theoretical method from Francke and (Sissom 1984) to the data of Shorthouse and Marples (1982) confirms that *U. yaschenkoi* are adult in the sixth instar. When Francke and Sissom (1984) applied the method to the data of Smith (1966) for *U. manicatus*, seven instars were predicted, not six. This was confirmed with the data collected in this study using the theoretical method of Francke and Sissom (1984).

Sexual dimorphism among early instars as exhibited in *U. manicatus* appears to be unusual for scorpions, but common in subadults and adults. *Centruroides gracilis* carapace and chela lengths were the same until the penultimate moult. *Paruroctonus mesaensis* exhibited sexual dimorphism in mass only when mature, adult non gravid females being larger than mature males (Polis and Farley 1979b). Shorthouse and Marples (1982) as well found no sexual dimorphism in *U. yaschenkoi* pre-adult instars, but adult females were shorter than males.

The rate at which individuals lose evaporative water within a population depends on recent ecdysis, the amount of water absorbed into the cuticle, water availability and the size of the scorpion. Sub adults and adults are more variable in their rates of water loss than earlier instars, and this may reflect variability in home sites with respect to microclimate. However, all *Urodacus manicatus* and all species of scorpions have very low rates of evaporative water loss, compared to many other land arthropods. Therefore, changes in these rates within a species or the differences in rates between species may not be great enough to have any adaptive significance to the populations or to the species. In the final chapter, a discussion is presented that all species of scorpions are remarkably conservative in their physiological traits because their microhabitats do not reflect the broader habitat and the traits enable scorpions to exist in a wide variety of terrestrial habitats. Differences in the rates of water loss and metabolism are not necessarily adaptive, but perhaps epiphenomenal instead.

Table 8.1. Mass-specific rates of water loss ($\text{mg H}_2\text{O g}^{-1} \text{h}^{-1}$) (\pm SE) of two groups of adult females placed into the desiccator during the day and at night and measured at 30°C , 0% RH over the same time intervals (h). The rates over time were significantly different, $F(3, 12) = 32.54$, $P < 0.001$ and they did not significantly differ between the two groups, $F(4, 11) = 0.17$, $P > 0.05$.

Interval (h)	Rate of water loss ($\text{mg H}_2\text{O g}^{-1} \text{h}^{-1}$)	
	Photophase group	Scotophase group
6	2.732 ± 0.300	2.802 ± 0.246
12	0.942 ± 0.203	0.925 ± 0.184
24	0.945 ± 0.182	0.940 ± 0.174
48	0.896 ± 0.159	0.847 ± 0.153

Table 8.2. Predicted number of moults (n) for second instar (Y) female and male *Urodacus manicatus* to attain adult size (A). Values were derived for three morphological structures (cm) using the equation $n = 10 (\log A - \log Y)$ (Francke and Sissom 1984).

	Females			Males		
	Adult log A	Second instar log Y	n	Adult log A	Second instar log Y	n
HFF	1.060 ± 0.008	0.571 ± 0.009	4.9	0.995 ± 0.007	0.505 ± 0.008	4.9
FTL	0.596 ± 0.008	0.118 ± 0.010	4.8	0.594 ± 0.010	0.112 ± 0.009	4.8
CW	0.896 ± 0.008	0.454 ± 0.010	4.4	0.807 ± 0.007	0.400 ± 0.008	4.1

Table 8.3. Predicted size ranges for third to adult instars of female and male *Urodacus manicatus*, calculated from the observed size ranges of second instars with the progression factor of 1.26.

Instar	HFF (mm)	FTL (mm)	CW (mm)
<u>Female</u>			
Second	3.46 - 3.84	1.20 - 1.36	2.63 - 3.12
Third	4.36 - 4.84	1.51 - 1.71	3.33 - 3.93
Fourth	5.49 - 6.10	1.91 - 2.16	4.25 - 4.95
Fifth	6.92 - 7.68	2.40 - 2.72	5.36 - 6.24
Sixth	8.72 - 9.68	3.02 - 3.43	6.75 - 7.86
Seventh	10.99 - 12.20	3.81 - 4.32	8.51 - 9.91
<u>Male</u>			
Second	3.06 - 3.26	1.10 - 1.36	2.42 - 2.64
Third	3.86 - 4.11	1.39 - 1.71	3.05 - 3.33
Fourth	4.86 - 5.18	1.75 - 2.16	3.84 - 4.19
Fifth	6.12 - 6.52	2.20 - 2.72	4.84 - 5.28
Sixth	7.71 - 8.22	2.77 - 3.43	6.10 - 6.65
Seventh	9.72 - 10.35	3.49 - 4.32	7.69 - 8.38

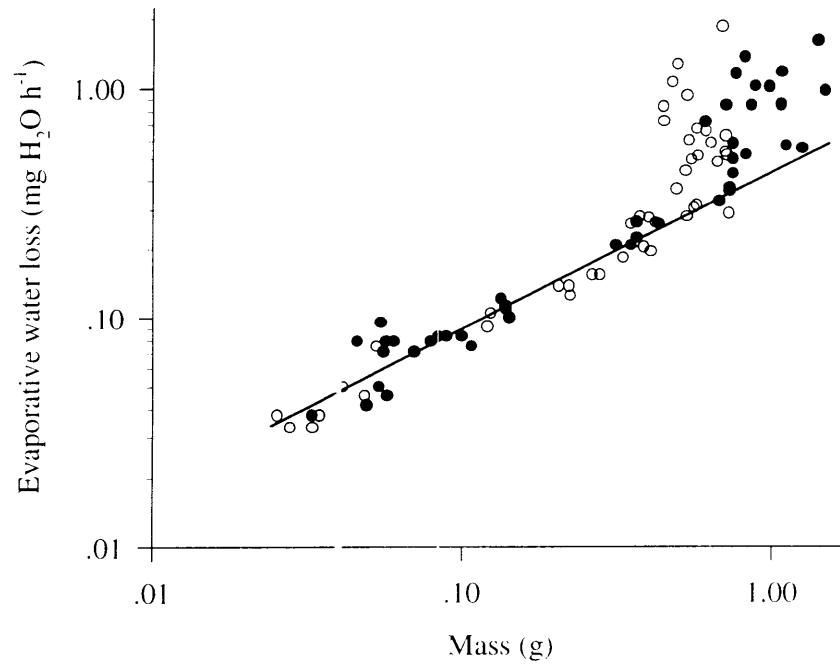


Figure 8.1. Relationship between wet body mass (g) and second day water loss rate ($\text{mg H}_2\text{O h}^{-1}$) measured at 30°C , 0% RH for female (closed circle) and male (open circle) *Urodacus manicatus*. Linear regression relationship is shown for animals less than 0.45 g ($r^2 = 0.928$, $P < 0.001$) and is presented in Table 8.6.

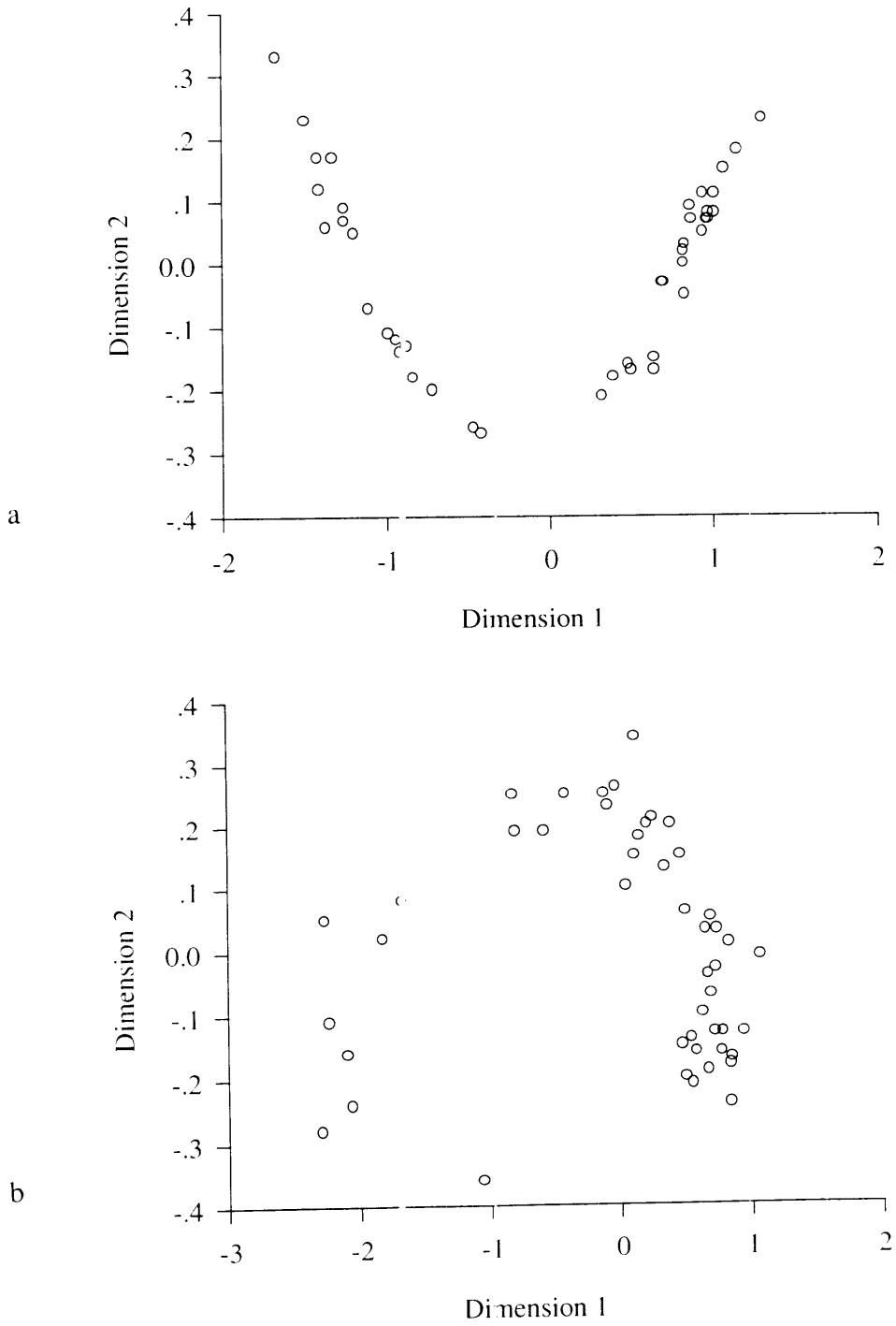


Figure 8.2. Distributions of (a) female and (b) male measurements of HHF, FTL and CW scaled into two dimensions using multidimensional scaling as a means of determining the number of instars from second instar to adult.

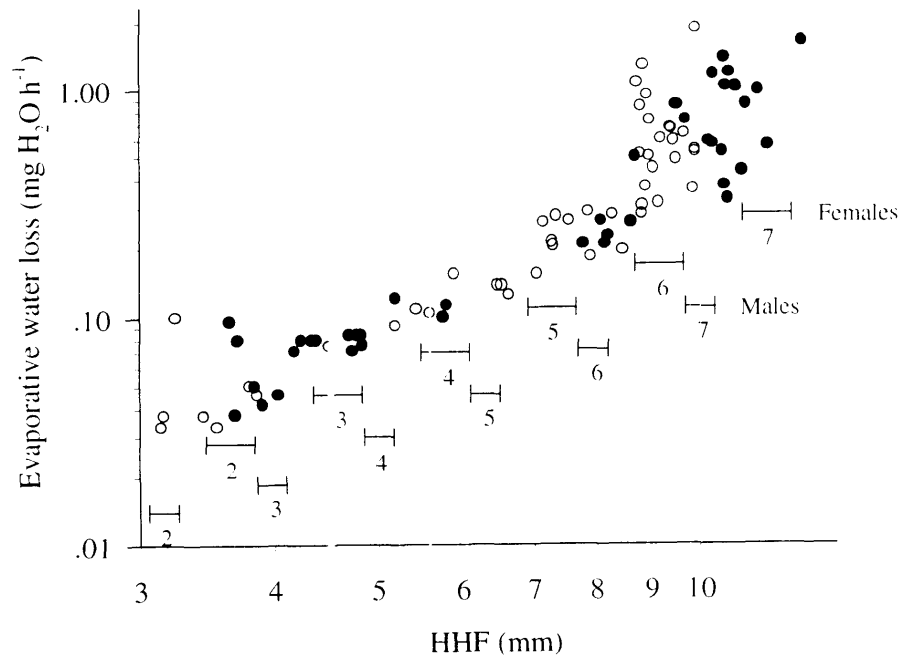


Figure 8.3. Relationship between length of right hand and fixed finger (HHF; mm) and second day rate of water loss (mg H₂O h⁻¹) measured at 30°C, 0% RH for females (closed circle) and males (open circle). The size ranges numbered 2 through 7 represent the theoretical limits from Table 8.7 for each instar of females and males. Deviation from linearity of water loss with size occurs during the sixth instar for females and the seventh instar for males.

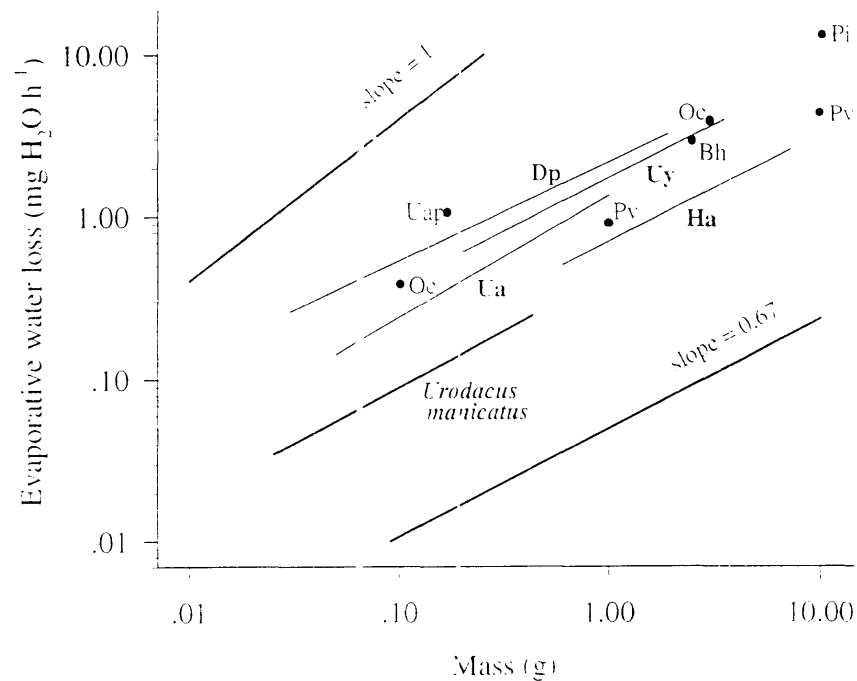


Figure 8.4. Allometric relationship for evaporative water loss of *Urodacus manicatus* compared with the allometric relationships and values of other species. The allometric relationships are: Ua, *Urodacus armatus* (Withers and Smith 1993); Uy, *Urodacus yaschenkoi* (Shorthouse 1971); Ha, *Hadrurus arizonensis* (Hadley 1970) and Dp, *Diplocentrus peloncillensis* (Crawford and Wooten 1973). Values for other species are: Op, *Opisthophthalmus capensis* early and late instars (Robertson et al. 1982); Uap, *Uroctonus apacheanus* (Toolson and Hadley 1977); Pv, *Parabuthus villosus* early and late instars (Robertson et al. 1982); Bh, *Buthus hottentotta* (Toye 1970); Pi, *Pandinus imperator* (Toye 1970). Conditions for water loss in *U. manicatus*, *U. armatus*, *D. peloncillensis*, *U. apacheanus*, *P. villosus* and *O. capensis* were 30°C, 0% RH. *U. yaschenkoi* was measured at 30°C, 30% RH. *H. arizonensis* was measured at 38°C, 0% RH, and *Buthus hottentotta* and *Pandinus imperator* were both measured at 25°C, 0% RH. The water log-mass graphs of (Hadley 1970) and (Crawford and Wooten 1973) were reanalysed logarithmically to obtain the allometric relationships.

Chapter 9

Final Discussion

Scorpions have remained remarkably conservative in their general morphology for 430 million years (Jeram 1990a, Vachon 1953). A physiological comparison of extant species suggests that their general physiology has also remained unchanged despite the large range of habitats in which scorpions occur. Vachon (1953) concluded that their survival in diverse habitats was due to their modification of the larger habitat along with their many capabilities and low demands.

In this thesis, it has been shown that the intraspecific conservatism of physiology in scorpions is reflected within *Urodacus manicatus*, the distribution of which covers regions that are diverse in their climates. By differentially modifying the larger, more perceptible habitat, *Urodacus manicatus*, as a species, can maintain similar microclimatic conditions during the warmer parts of the year throughout its range. This is analogous to the persistence of many species of scorpions in arid regions, which avoid the severe hot, dry desiccating conditions because of their subterranean habitats and nocturnalism (Hadley 1970a, Shorthouse 1971, Shorthouse and Marples 1980, Vachon 1953). It can be argued, therefore, that scorpions are not necessarily adapted to xeric environments (Vachon 1953), but instead have a suite of traits that enable them to live in a wide variety of habitats.

This thesis has shown that *Urodacus manicatus* is typical of most scorpions with regard to their physiology. For example, they have very low rates of evaporative water loss (Figure 8.4), low rates of metabolism (Figure 9.1), and can endure low haemolymph volumes (Chapters 3 and 5) relative to most other land arthropods. Low cuticular permeability in all scorpions may reflect the irregularity of water obtainability by scorpions and, thus, their need to conserve water. Because water is mostly obtained from prey, and feeding in scorpions is often irregular (even though prey may be abundant), water conservation may be related to foraging activity. Their low metabolic rates and large capacities for storing metabolic reserves enable scorpions to go extended periods without feeding. This was demonstrated for *U. manicatus* in chapter 6. However, there must exist a constraint on the maximum obtainable size of the hepatopancreas

after feeding that is determined by the elasticity of the intersegmental membrane. Since scorpions have a low energy expenditure resulting from their low metabolic rates and extended periods of inactivity, the hepatopancreas does not rapidly decrease in size between meals and thus, the animals cannot opportunistically forage and store more nutrients after a meal. Therefore, foraging activity can be independent of prey abundance and all scorpions, regardless of their habitat, will endure lengthy periods of little water uptake associated with prey. Some species, however, can supplement water uptake by readily drinking from free water sources (Hadley 1971) or obtaining moisture from sand (Gaffin et al. 1992).

An examination of the evolution and biogeography of the genus *Urodacus* further highlights the need for careful examination of the microclimate of a species. *Urodacus armatus* is a closely related species to *U. manicatus*, belonging to the same species group (Koch 1977). Its distribution is central and western and thus it occurs in semi-arid to arid habitats of Australia (Koch 1981). It constructs loosely or a tortuously spiralling burrows of depths up to 30 cm (Koch 1978). The population from which the scorpions in the study of Withers and Smith (1993) were collected constructed burrows in open ground with the entrances mostly in areas of bare soil. *Urodacus yaschenkoi* is the largest of these three species and is of a different species group. The distribution of *U. yaschenkoi* is regarded as being "central" (Koch 1981). It constructs burrows similar to *U. armatus*, but to a depth of 100 cm in sandy soil and are tortuously spiralled (Koch 1978, Shorthouse 1971, Shorthouse and Marples 1980). Both these species are typical of xeric-adapted scorpions.

The spiral burrows of *U. armatus* and *U. yaschenkoi* provide the scorpions with a mesic microclimate that is independent of the conditions at the surface. For example, below 40 cm, the burrow temperature of *U. yaschenkoi* remained more or less diurnally constant while soil temperatures at a depth of 5 cm rose above 40°C during the day (Shorthouse and Marples 1980). At 40 cm the temperature did not rise above 30°C in summer and in winter did not decrease below 15°C at a depth of 80 cm (Shorthouse 1971). For most of the year relative humidity was a constant 80% below 10 cm (Shorthouse and Marples 1980). Maximum summer burrow temperatures of *U. manicatus* were about 30°C at both the semi arid site (Dubbo) and the cool temperate site (Black Mountain).

The similarity of the burrow conditions of *Urodacus manicatus* and *Urodacus yaschenkoi* during summer may indicate that the selection of microclimate by these species is phylogenetic and reflects the evolution of the species in the genus. *Urodacus* ancestors inhabited subtropical environments that were once prevalent in Australia (Koch 1977). As the south-central regions became more arid, species remaining in the centre inhabited mesic refuges (*hoplurus*, *hartmeyeri* and *yaschenkoi* species-groups). Evolution of the deep spiral burrowing behaviour allowed *U. yaschenkoi* to spread into the arid regions (Koch 1978). The ancestral equivalent of the southern *armatus* group underwent speciation as the forests fragmented with the encroaching semi-arid environments (Koch 1977). Although changes in distributions had occurred since then, the ranges (particularly the eastern ranges with regards to *U. manicatus*) have been important as refugia from the prevailing arid conditions and sea intrusions and the ranges have also served as pathways for dispersal and radiation (Koch 1981). The distribution of *U. armatus* had extended from temperate into arid regions also by evolution of the spiral burrow which existed throughout its range, sometimes below rocks, but chiefly in open ground (Koch 1978). In essence then, *U. manicatus* had always had a cool-temperate distribution, whereas the distributions of *U. armatus* and *U. yaschenkoi* had become secondarily semi-arid and arid.

There exists a trend of larger *Urodacus* species inhabiting more arid habitats (Koch 1981). *U. yaschenkoi* adult females for example have chela of mean length 18.9 mm compared to 11.1 mm for *U. manicatus* (Koch 1977). This was attributed to the benefits of a larger size with regards to heat balance and water loss (Koch 1981). It is possible, though, that the size of *U. manicatus* is ecologically constrained because the use of ground cover as shelters for burrows confined the maximum size of the burrow which then places a limit on the maximum obtainable size of the inhabiting scorpion. Alternatively, a larger size may reduce the energy expenditure required for the construction of burrows to a depth where the microclimate is mesic and independent of the surface conditions. Most burrows, regardless of their complexity and length, are constructed within a day (Polis 1990), but to do so, deep burrowers must move 80 to 400 times their own body mass in soil or sand (Polis et al. 1986, Shorthouse and Marples 1980). This is energetically expensive for animals which spend most of their lives inactive. As a result, homing behaviour is well developed in those species that expend large amounts of energy in burrow construction (Polis 1990, Polis et al. 1986).

To investigate whether larger scorpions would have lower energetic costs than smaller scorpions, the effect of size on metabolic rate was determined. The oxygen consumption measurements of other species of scorpions were obtained from the literature and added to those of all female and male *Urodacus manicatus* collected from the field. Values were selected that were measured at temperatures closest to 30°C and were adjusted to 30°C assuming a Q_{10} of 2 as required. Overall $\dot{V}O_2$'s were calculated from mass-specific $\dot{V}O_2$'s for the largest specimens mentioned in each study. The logarithmic relationship of body mass and $\dot{V}O_2$ was:

$\log \dot{V}O_2 = 2.001 (\pm 0.039) + 0.753 (\pm 0.077) \log m$, $r^2 = 0.897$, $F(1, 11) = 96.02$, $P < 0.001$, $n = 13$). The allometric relationship was thus

$$\dot{V}O_2 (\mu\text{l O}_2 \text{ h}^{-1}) = 100.23 m^{0.753} (\text{g}).$$

The relationships between body mass and $\dot{V}O_2$ at 30°C for 12 species of scorpions including *Urodacus manicatus* are presented in Figure 9.1. The slope was not significantly different from either 0.75 or 0.67 (all $P > 0.05$), but was significantly different from 1.0 ($P < 0.01$). Since the scaling of mass to $\dot{V}O_2$ is less than 1.0 larger species of scorpion have a lower mass-specific metabolic rates than smaller ones. Thus, active energy expenditure during burrow construction is reduced in larger species.

In conclusion, the following physiological traits have assisted scorpions in occupying nearly all terrestrial habitats: low rates of evaporative water loss, low rates of metabolism, low costs of reproduction, efficient foraging behaviour and storage of nutrients, and the toleration of low haemolymph volume and concomitant high osmotic concentration. *Urodacus manicatus* regulates its physiology via behavioural means which can occur at two levels: (1) habitat selection and modification to obtain a conducive microhabitat for survival, and (2) selection of different parts of the microhabitat (temperature and humidity). The conservatism of these traits between species suggest that physiological responses to changes in the environment within a species should only be cautiously considered "adaptive" when in fact they may be epiphenomenal (Wells 1990).

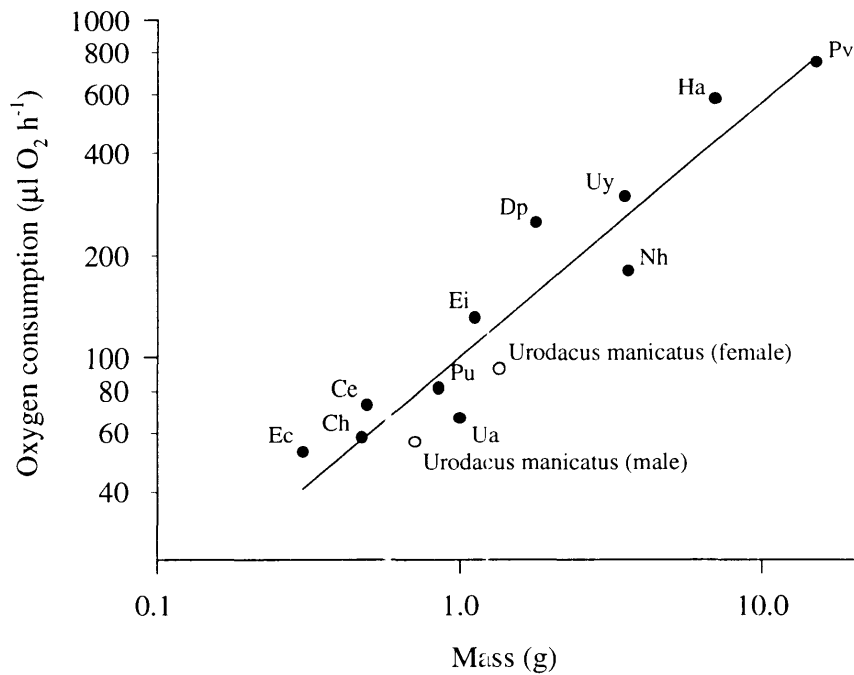


Figure 9.1. Allometric relationship for overall VO_2 ($\mu\text{l O}_2 \text{ h}^{-1}$) of female and male *Urodacus manicatus* (open symbols) and other species of scorpions (closed symbols) at 30°C . The other species are: Ua, *Urodacus armatus* (Withers and Smith 1993); Uy, *Urodacus yaschenkoii* (Shorthouse 1971); Ha, *Hadrurus arizonensis* (Hadley 1970); Dp, *Diplocentrus peloncillensis* (Crawford and Wooten 1973); Ch, *Centruroides hentzi* (Punzo 1991); Ce, *Centruroides exilicauda* (Hadley and Hill 1969); Pv, *Parabuthus villosus* (Robertson et al. 1982); Nh, *Nebo heirochonticus* (Dresco-Derout 1964); Ei, *Euscorpius italicus* (Dresco-Derout 1964); Ec, *Euscorpius carpathicus* (Dresco-Derout 1964); Pu, *Paruroctonus utahensis* (Riddle 1978). Measurements are based on largest mass mentioned in other studies and VO_2 's corrected to 30°C where required.

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