

WATER RELATIONS OF THE DESERT SCORPION, *HADRURUS ARIZONENSIS*

By NEIL F. HADLEY

*Department of Zoology, Arizona State University,
Tempe, Arizona 85281*

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INTRODUCTION

Water conservation is a prime concern for small arthropods which inhabit hot, dry environments. Scorpions, which are among the more successful desert inhabitants, rely on a combination of behavioural, morphological, and physiological adaptations to limit their water loss under stressful conditions. Cloudsley-Thompson (1956, 1961*a*, 1962) includes information on total water-loss rates for several Old World species; however, quantitative investigations of other aspects of the water relations of scorpions have not been conducted.

The present study was designed to provide more complete water-relations data for a single scorpion species, *Hadrurus arizonensis*. Areas of investigation included the effects of body size, desiccation, temperature, and relative humidity on water loss, breakdown of total transpiratory water loss into cutaneous and respiratory components, possible water uptake from the environment, and comparison of cuticular water loss in living versus dead scorpions.

MATERIALS AND METHODS

Scorpions were collected by ultraviolet light detection from South Mountain Desert Park, Phoenix, Arizona during May through October of 1968 and 1969. They were maintained in individual containers at 23 ± 1 °C and fed on crickets *ad lib*. To reduce water lost from faeces, all scorpions, unless otherwise stated, were starved for a minimum of 48 h prior to testing.

Water loss at various temperatures and relative humidities was determined using the closed, flow-through system described by Ahearn & Hadley (1969). Stated humidities were maintained by either silica gel or saturated salt solutions (Winston & Bates, 1960) and their accuracies were checked by an Atkins thermistor psychrometer (Atkins Technical Inc., Gainesville, Fla.) and humidity indicator papers (Humidial Co., Colton, Calif.). Temperatures were controlled to ± 0.5 °C by placing the system into a programmed refrigerator-incubator and monitoring the chamber containing the scorpions with a telethermometer. Weight changes were measured to 0.1 mg with a Mettler balance.

Oxygen consumption was measured with Warburg constant-volume respirometers (Umbreit, Burris & Stauffer, 1964; Hadley & Hill, 1969). For determinations of oxygen uptake at approximately 0% relative humidity, 10 g of CaCl₂ were placed into

each reaction flask and covered with a fine wire screen which supported the scorpion and separated it from the chemical. Volume displacement of the CaCl_2 was calculated from its weight and specific gravity.

Uptake of water from the substrate was investigated by placing scorpions on moist Dupont cellulose sponge strips ($10\frac{1}{2} \times 11 \times 2$ cm) which were contained in covered plastic boxes. Sponges were wetted 'dry' before the scorpion was placed on the surface. Using this procedure, the sponge surface remained moist throughout a 24 h period. Relative humidity within the chamber remained at 50-60%.

Cuticular water loss was determined by killing scorpions with cyanide vapours and sealing their book lungs with nail varnish. Water-loss rates in scorpions killed by cyanide were not significantly different ($P > 0.05$) than those killed by placement in pure nitrogen, indicating no apparent effect of cyanide on cuticular properties.

Additional techniques and/or modifications, plus statistical tests employed are included in the sections which follow.

RESULTS

The effect of size on water loss

Scorpions weighing between 0.5767 and 7.2441 g were tested over a 24 h period at 38 °C and in dry air (< 5% R.H.) to determine the relationship between body size and total water loss in living scorpions (Fig. 1). Water-loss rates decreased with increasing

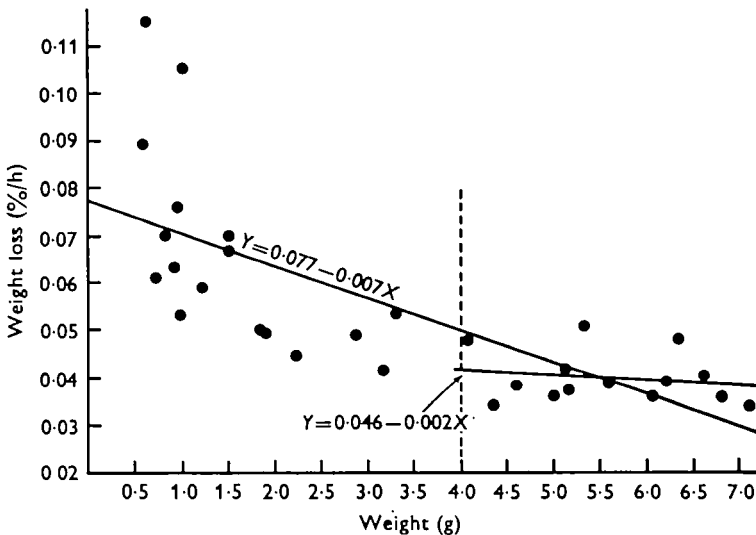


Fig. 1. The relationship between weight and total water loss at 38 °C and dry air. Regression equations are given for both the entire weight range sampled and for scorpions weighing above 4.0 g only.

body size of *Hadrurus*, with the highest and most variable rates occurring in early instars and sub-adults. Regression analysis produced a slope of 0.007 over the entire weight range ($P < 0.01$); however, no significant correlation between water loss and body size was observed for scorpions weighing over 4 g. Complete equations for both regression analyses are given in Fig. 1. On the basis of these results, to reduce any

error resulting from size variation, only scorpions larger than 4 g were used in the experimental treatments which follow.

Effect of temperature and saturation deficit on total water loss

Total water-loss rates for live scorpions in dry air and progressively higher temperatures are given in Table 1. Mean hourly rates were calculated from weight changes after 6 h exposure at each temperature. Rates at 12 and 24 h were also determined for scorpions tested from 25 °C up to 40 °C, and comparison with rates at shorter time intervals is discussed in a later section. All scorpions survived the temperatures employed, except 44 °C where approximately 25 % mortality occurred after 6 h. Data from dead scorpions are included in Table 1.

Table 1. *Effects of temperature and saturation deficit on total water loss in Hadrurus arizonensis*

N	Temperature (°C)	Sat. def. (mmHg)	% wt lost/h	% wt lost/h/mmHg × 10 ³
10	25	23·76	0·021 ± 0·001*	0·88
10	30	31·82	0·028 ± 0·002	0·87
10	35	42·18	0·035 ± 0·003	0·82
14	38	49·69	0·040 ± 0·002	0·80
25	40	55·32	0·137 ± 0·013	2·47
15	42	61·50	0·701 ± 0·068	11·39
14	44	68·26	1·302 ± 0·117	19·07

* Standard deviation.

Total water-loss rates showed a gradual increase up to a temperature of about 38 °C above which the rate increased steeply, especially at 42 °C and 44 °C. Accompanying this increased rate at higher temperatures was greater variation in individual water-loss values. When water loss was expressed in terms of % weight loss/h/mmHg saturation deficit (Beament, 1958), the trend was generally downward as temperatures increased to 38 °C. From 40 to 44 °C the rate increased sharply, indicating possible changes in cuticular permeability.

Components of total water loss in scorpions

Since total water loss was measured, other components must be examined before the above results can be accurately interpreted. Contributing factors to total water loss in *H. arizonensis* include cuticular transpiration, respiratory transpiration, defaecation and venom release. Starving the scorpions for 48 h before testing proved to be very effective in decreasing faecal production, and thus reduced faecal water loss to a minimum. Water loss associated with venom released by the scorpions striking at the containers was also negligible. Further experimentation, therefore, emphasized cuticular and respiratory components of total water loss.

The relationships between water loss, cuticular water loss, and oxygen consumption in dry air at progressively higher temperatures are shown in Fig. 2. The curve for total water loss was based on data given in Table 1. Values for cuticular water loss were obtained from dead scorpions whose book lungs were sealed. Hourly oxygen consumption rates represent means from 4 h runs, except at 42 °C and 44 °C where 2 h deter-

minations were conducted. Preliminary experiments on metabolic rate indicated that oxygen consumption did not vary with time of day, nor did values for males and females significantly differ if scorpions of similar weights were used (N. F. Hadley, unpublished data). Comparison of respiratory rates in dry air and 50–60% R.H. at 30 °C resulted in significantly higher ($P < 0.01$) metabolic rates at the higher relative humidity ($82.499 \pm 8.252 \mu\text{l O}_2/\text{g/h}$ vs. $63.240 \pm 7.411 \mu\text{l O}_2/\text{g/h}$). Comparison of the above values for dry-air determinations with those obtained from scorpions which had been desiccated ($\bar{x}_{16} = 17.68\%$ initial body weight) indicated no significant difference between means. Unusually high variation characterized metabolic rate values for desiccated individuals.

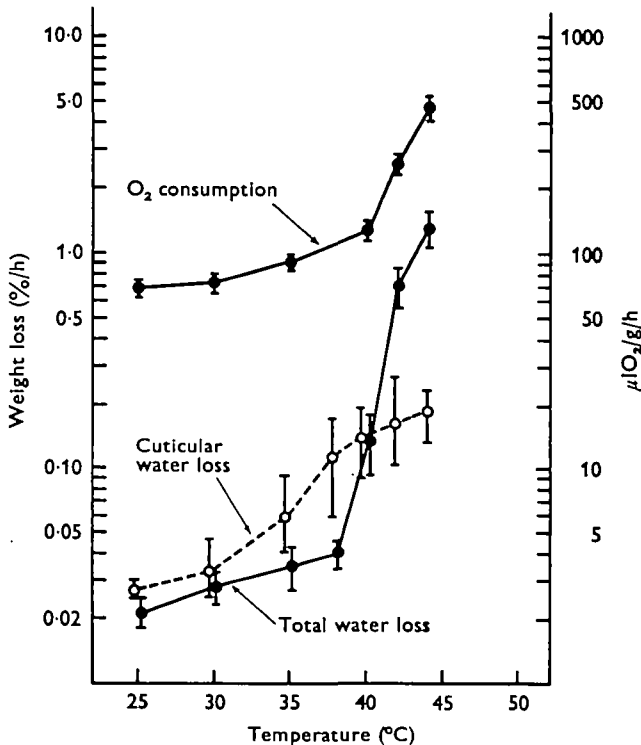


Fig. 2. The effect of temperature on total water loss (min. $n=10$), cuticular transpiration (min. $n=4$), and oxygen consumption (min. $n=15$) in dry air. Vertical lines represent 95% confidence limits.

Both for cuticular water loss and for oxygen consumption the curves show definite correlations with total water loss over various portions of the temperature range (Fig. 2). Between 25 and 35 °C mean values for cuticular and total water loss are not significantly different ($P > 0.05$), which suggests that virtually all water is lost through the cuticle at these temperatures. Above 38 °C cuticular water loss continues to increase with temperature, but at a rate well below that for total water loss. In contrast, oxygen consumption rates exhibit an abrupt increase as higher temperatures are encountered, and above 40 °C this curve closely parallels the curve for total water loss. Thus it appears that respiratory transpiration becomes the major pathway of water loss at high temperatures.

By expanding the temperature range at which cuticular water loss was determined and expressing values in units per saturation deficit to account for the increased drying power of air at higher temperatures, the contribution of cuticular transpiration to total water loss becomes clearer (Fig. 3). Two abrupt increases in the transpiration/temperature curve are evident. An initial break occurs at approximately 35–40 °C and represents a two-fold increase over the relatively constant transpiration rates observed between 25 and 35 °C. Above 40 °C no further breaks in the curve occur until 65–70 °C at which temperatures cuticular water loss rates exhibit another sharp increase.

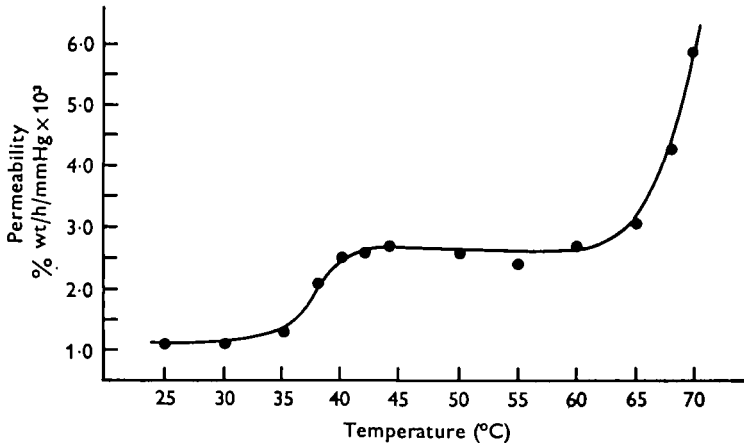


Fig. 3. The effect of temperature on the permeability of the cuticle of *H. arizonensis*. Dark circles represent mean water-loss values from a minimum of two scorpions. Air, not cuticle, temperatures were measured.

The rise in the cuticular transpiration curve at 35–40 °C, first plotted in Fig. 2, still remains when saturation deficit is considered (Fig. 3). This indicates that the cuticular permeability increases at these temperatures, although the increase is not readily apparent in terms of total water loss and may reflect a phenomenon occurring at these temperatures in dead scorpions only. The second break in the cuticular transpiration curve takes place at temperatures well beyond the normal biological range of this species, but may be important in terms of disruption of cuticular molecular organization. Cuticular water loss rates at 70 °C, however, are still less than the total water loss at 42–44 °C for live animals, which further emphasizes the role of respiratory water loss at near-lethal temperatures (> 40 °C).

Water loss in dead vs. living scorpions

Assuming that cuticular water-loss rates are the same in living and dead scorpions, quantitative contributions of respiratory transpiration at any given temperature could be determined by simply subtracting cuticular from total water loss. However, except for temperatures above 40 °C for *H. arizonensis*, cuticular water-loss values exceed those for total water loss. To test the assumption further, additional determinations of cuticular transpiration versus total water loss were conducted on a more abundant scorpion species, *Centruroides sculpturatus*. At 38 °C and in dry air, dead sealed *C. sculpturatus* ($n = 15$) lost over three times as much water as live specimens (0.377 ± 0.029 % wt/h vs.

0.120 ± 0.043 % wt/h) over a 24 h period. The difference between means was highly significant ($P < 0.01$). These results, plus the earlier findings on cuticular water loss in *Hadrurus arizonensis*, proved that rates of cuticular transpiration were greater in dead than in living scorpions. Subsequent experiments were therefore designed to indicate the degree and time course of increased cuticular permeability following death.

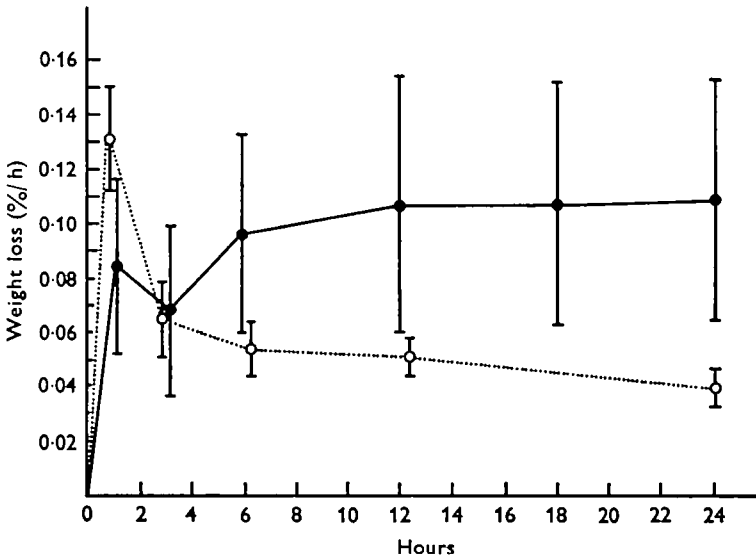


Fig. 4. Changes in water-loss rates with time in living scorpions (open circles) versus dead scorpions (dark circles) at 38 °C. in dry air. Vertical lines represent 95% confidence limits.

Water-loss rates at 38 °C in dry air from seven living and seven dead *H. arizonensis*, the latter with sealed book-lungs, are plotted in Fig. 4. At this temperature water-loss rates are sufficiently high to be detected over short intervals, yet cuticular transpiration still predominates. The system was modified to permit short-term weighings by removing the balance pan and extending a connecting rod and attached wire basket into the temperature chamber so that direct readings from individual scorpions could be made without disturbing the animals. Mean values are given for 1, 3, 6, 12, 18, and 24 h, but readings were made at half-hour intervals for the first 3 h and hourly up to 12 h for each scorpion.

Both living and dead scorpions exhibited high initial water-loss rates which then decreased between the first and third hours. After 3 h water-loss rates in living scorpions continued to decline, reaching their lowest level after 24 h of exposure. In contrast, rates for dead scorpions increased between the third and twelfth hour, levelling off at a rate well above that recorded during the first hour of exposure. Considerable individual variation in rates characterized dead animals, as is evident by the wide confidence limits. Nevertheless, mean differences between the two groups are highly significant ($P < 0.01$) at 6, 12, and 24 h, and provide a fairly accurate indication of times of changes in cuticular permeability following death.

Water loss in near-saturated air

Studies were also conducted in near-saturated atmospheres (98% R.H.) to determine the effect of relative humidity on total water loss and to establish whether this scorpion species was capable of absorbing atmospheric moisture under such conditions. A preliminary test of ten adult *H. arizonensis* placed at 30 °C in 98% R.H. for 24 h resulted in a mean water-loss rate of only 0.007 ± 0.002 % wt/h compared to the 0.028 ± 0.002 % wt/h observed for similar scorpions tested at 30 °C in dry air. This four-fold decrease from an already low water-loss rate was highly significant ($P < 0.01$); however, there was no evidence of water uptake by any of the individuals.

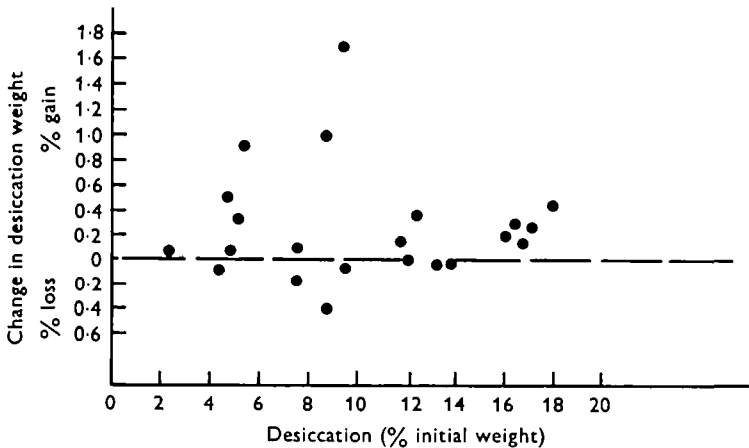


Fig. 5. Changes in desiccation weight of *H. arizonensis* after 24 h exposure to a moist sponge substrate (25 °C). Position of dark circles along horizontal axis indicates degree of dehydration of individual scorpions.

In a further attempt to demonstrate uptake of atmospheric water, twenty *H. arizonensis* were desiccated (mean desiccation = 12.74% initial weight; range = 8.00–17.57%) prior to 24 h exposure to 30 °C and 98% R.H. Mean water loss for the pre-desiccated scorpions was 0.004 ± 0.001 % wt/h. Although in this case means were not significant ($0.05 < P < 0.10$), this latter rate represents a further reduction in water loss when compared with the observed rate for hydrated individuals (0.007 ± 0.002). Nevertheless, no individual scorpion exhibited a gain in weight after the 24 h exposure. Nor did regression analysis indicate any correlation between the amount of desiccation and % weight lost; however, the extremely low rates recorded under these conditions may tend to obscure such a relationship which may normally exist at higher temperatures or higher saturation deficits.

Because *H. arizonensis* were unable to absorb water vapour from a subsaturated atmosphere, subsequent experiments were designed to demonstrate possible water uptake from a moist substrate. Twenty-two adults, which had lost between 4.67 and 18.00% of their initial weight ($\bar{x} = 11.21$ %), were placed on moistened sponge strips for 24 h at 25 °C. The gain or loss of weight for each individual was plotted against its amount of pre-desiccation (Fig. 5). All scorpions were air-dried briefly before weighing to reduce any error caused by adsorbed cuticular water. Fifteen scorpions exhibited

a net weight gain which ranged from 0.01 to 1.70% of their weight prior to exposure. Weight gain for the majority of individuals was less than 0.50%. Regression analysis failed to show a correlation between water uptake and extent of desiccation, nor was a relationship apparent between the amount of water uptake and body size.

Although many individuals demonstrated a limited ability to absorb water from moist substrates, the amounts were well below levels necessary to be important as a method for replenishing supplies of body water. It was concluded that water uptake from a subsaturated atmosphere or a moist substrate plays little or no role in the water economy of *H. arizonensis*, regardless of its hydration state.

DISCUSSION

The genus *Hadrurus* contains the largest North American scorpions, with adults occasionally exceeding 10.0 g. *H. arizonensis* occurs throughout much of the northern portion of the lower Sonoran Desert and is especially common in sandy creosote-bursage communities. This species occupies self-constructed burrows or burrows

Table 2. *Water loss in some desert arthropods*

Species	Temperature (°C.)	Water loss % body wt/hour	Source
Scorpions			
<i>Leiurus quinquestriatus</i>	33	0.030	Cloudsley-Thompson (1961a)
<i>Centruroides sculpturatus</i>	30	0.091	N. F. Hadley (unpublished)
<i>Diplocentrus</i> sp.	30	0.044	N. F. Hadley (unpublished)
<i>Hadrurus arizonensis</i>	30	0.028	Present Study
Tarantulas			
<i>Eurypelma</i> sp.	33	0.147	Cloudsley-Thompson (1967)
<i>Eurypelma californicum</i>	25*	0.45	Herreid (1969)
Solpugids			
<i>Galeodes arabs</i>	33	0.090	Cloudsley-Thompson (1961b)
Locusts			
<i>Locusta migratoria</i>	30	0.32	Loveridge (1967)
Tenebrionids			
<i>Eleodes armata</i>	30	0.245	Ahearn & Hadley (1969)
<i>Cryptoglossa verrucosa</i>	30	0.120	Ahearn & Hadley (1969)

* 25% relative humidity.

dug by small rodents or lizards, restricting its surface activities to nocturnal hours during which temperatures drop and humidities increase from extreme daytime levels. The micro-environment of *H. arizonensis* during a 24 h summer period depends on a complex of several interacting factors; however, typical daytime temperatures and humidities in burrows may range from 34 to 38 °C and from 50 to 65% R.H., while nocturnal surface conditions during the periods of activity might vary from 25 to 35 °C and from 60 to 80% R.H. (Hadley, 1970). Thus many of the test conditions employed in this water-loss study are seldom, if ever, encountered by this species in nature.

Accurate comparison of water-loss rates of different scorpion species as well as of other desert arthropods (Table 2) is difficult because of the variety of experimental techniques employed, large discrepancies in sample size used in compiling mean

values, and varying lengths of time which the animals were exposed to a given set of conditions. In addition, some of the values reported in Table 2 represent close approximations because of the difficulty in converting published values into % weight loss per hour. In spite of these limitations most of the values for closely related species are in general agreement. Among the scorpion species listed, *H. arizonensis* exhibits the smallest rate of water loss, losing only 0.028% of its body weight per hour in dry air at 30 °C. The higher rates observed for another scorpion, *Centruroides sculpturatus*, probably reflect differences in size rather than species differences in water-conserving ability. Water-loss rates of scorpions, as a group, are generally lower than for other desert arthropods, even after consideration of the size factor. Surprisingly, water-loss rates for the Tenebrionid beetle, *Eleodes armata*, which is sometimes found active on the surface during the hot, dry daytime hours, are approximately ten times greater than those recorded for the nocturnal *Hadrurus arizonensis*.

Cuticular and respiratory transpiration constitute the two major water-loss routes in *H. arizonensis*, the former predominating at lower temperatures and the latter at higher temperatures. Previous studies of water-loss in arthropods have stressed either changes in cuticular permeability with increased temperature and/or saturation deficit (Wigglesworth, 1945; Bursell, 1955; Mead-Briggs, 1956; Beament, 1959; Beament, Noble-Nesbitt & Watson, 1964) or spiracular control of respiratory evaporation (Mellanby, 1934; Bursell, 1957), so that relative contributions of the two pathways over the animal's normal temperature range remain somewhat speculative. Recently Loveridge (1968*a, b*) investigated both water-loss pathways for *Locusta* and found ventilation and water-loss to be closely interdependent. Between 42 and 45 °C the grasshoppers exhibited greatly increased transpiration with a concomitant increase in ventilation rates, a pattern similar to the relationship between transpiration and oxygen consumption in *H. arizonensis*.

The cuticular transpiration/temperature curve (Fig. 3) for *H. arizonensis* exhibits two breaks between 25 and 70 °C, the first occurring between 35 and 40 °C and the second between 65 and 70 °C. Both breaks indicate that a change in cuticular permeability has occurred; however, neither discontinuity is as sharply defined as those shown by Beament (1959) for membranes possessing a specific 'critical transition temperature'. Various arthropod species exhibit two-plateau transpiration/temperature curves over a similar temperature range (Bursell, 1955; Beament, 1959). In contrast, using a different experimental procedure, Cloudsley-Thompson (1956) reported only a single rapid increase in cuticle permeability beginning at approximately 65 °C for three Tunisian desert scorpions. The failure to demonstrate an abrupt discontinuity in the permeability curve of *H. arizonensis* may reflect the recording of air temperatures surrounding the scorpion rather than the actual cuticle temperature. Therefore these data do not necessarily signify the absence of an organized lipid water-proofing layer or layers.

Krishnan (1953) identified in scorpions the same fundamental cuticular layers which occur in insects and further stated that a primary chemical constituent of the epicuticle was lipid in nature. Thus there is strong evidence that lipids also play an important role in conferring certain impermeable qualities to the scorpion cuticle as has been shown for insects. Krishnan also points out, however, that the chemical composition of the basal layer of the epicuticle and the proteins which impregnate the endocuticle

during hardening are different from those described for insects, and provide the cuticle with special resistant properties. It has been shown that the reduction of hydrophilic properties of cuticular protein which occurs during the tanning process can supplement the role of lipids in reducing permeability (Wigglesworth, 1965). Further investigations are needed to determine whether these specific differences contribute to the extremely impermeable nature of the scorpion cuticle. Edney's (1957) statement, however, that cuticle hardness and appearance is not correlated with impermeability holds for scorpion species investigated so far by this author.

The relationship between water-loss in living versus dead scorpions (Fig. 4) suggests that restrictive mechanisms in the cuticle may supplement the effective physical barrier of the exoskeleton in controlling cuticular transpiration in these animals. The high initial water-loss rates, which characterized both groups, implicate the evaporation of adsorbed cuticular water, plus the loss of water loosely bound to cuticular protein and lipid molecules. Following the first hour, transpiration decreased with time throughout the 24 h period in living scorpions, while dead scorpions exhibited a slight drop followed by a further increase in cuticular permeability which culminated in fairly constant water-loss rates after 12 h that were significantly higher than those observed for total water-loss in living scorpions. Noble-Nesbitt (1969) reported greater water-loss in dead versus living firebrats and also loss-rate patterns for both groups between 0–12 and 12–24 h which were virtually identical to those observed for *H. arizonensis*. Higher water-loss rates in dead arthropods have also been reported for spiders by Davies & Edney (1952) who attributed the differences to an active secretion of water inward by epidermal cells in the living spiders, and for clover mites by Winston & Nelson (1965) who proposed an active retention of water by the cuticle. The data for *H. arizonensis* also strongly support the existence of some energy-requiring process(es) which increases cuticular impermeability. The same data do not rule out contributions due to spiracular control; however, respiratory activities at this temperature (38 °C) are still below the level where they greatly influence total water-loss.

Whereas a mechanism for active water retention by the cuticle is a strong possibility in *H. arizonensis*, there is no evidence of water uptake from either a near-saturated atmosphere or a moist substrate. A number of arthropods have been shown to possess this ability. The most recent list of these species is given by Noble-Nesbitt (1969) and impressive photographic evidence of this phenomenon is presented by Knülle & Spadafora (1969). However, of these arthropods, active water uptake in truly desert species has been reported only for desiccated nymphs and adult females of *Arenivaga* sp. (Edney, 1966). It appears that in the evolution of desert animals emphasis was placed on the development of mechanisms for conserving rather than regaining water. Thus desert species such as *H. arizonensis* rely on behavioural temperature regulation, an extremely impermeable cuticle which features possible active mechanisms for the retention of water, and very low metabolic rates to prevent them from incurring a severe negative water balance. Drinking may serve as a supplementary water source when bulk water is present (Hadley, in press); however, replenishment of lost body water is provided primarily by body fluids from captured prey, and for most desert species is the only water source necessary.

SUMMARY

1. Total water-loss rates for *Hadrurus arizonensis* (0.028% wt/h at 30 °C in dry air) are comparable to rates for Old World species and are well below rates for other desert arthropods under similar conditions.
2. Cuticular and respiratory transpiration constitute the two major avenues of water loss, cuticular water loss predominating at temperatures up to approximately 38 °C and respiratory transpiration predominating at temperatures above 40 °C.
3. The cuticular transpiration/temperature curve exhibits a two-plateau configuration with abrupt increases in cuticular permeability occurring between 35 and 40 °C and between 65 and 70 °C.
4. Cuticular water-loss values in dead scorpions exceed those of total water loss in living scorpions. The increased cuticular permeability after death is interpreted as evidence for the existence of an active cuticular water-retaining mechanism.
5. Water-loss rates are significantly reduced at lower saturation deficits; however, scorpions are unable to absorb significant quantities of water from near-saturated atmospheres or moist substrates, regardless of their hydration state.
6. The importance of water conserving versus water regaining mechanisms are discussed in relation to the total adaptations of these animals to hot, dry environments.

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