Hadley, N. F. 1974. Adaptational biology of desert scorpions. J. Arachnol. 2:11-23.

# ADAPTATIONAL BIOLOGY OF DESERT SCORPIONS

Neil F. Hadley

Zoology Department
Arizona State University
Tempe, Arizona 85281

## ABSTRACT

A conspicuous faunal element in hot dry desert regions worldwide, scorpions rely on a combination of behavioral, morphological and physiological adaptations in adjusting to harsh conditions found in these habitats. Foremost among behavioral adaptations are the exploitation of burrowing and nocturnal habits which provide a temporary escape from extreme daytime temperatures and desiccating air at the surface. Associated with these habits may be enlarged pedipalps used in digging and the presence of negative phototactic responses and orthokinetic avoidance of high temperatures. Still, lethal temperatures (45° to 47°C) of desert scorpions are higher than most other desert arthropods, and the presence of water-proofing wax layers which are perhaps supplemented by cuticular proteins provide scorpions with an impervious integument. Water loss rates approaching 0.01% of their body weight per hour (25°C) are the lowest reported for desert animals and are especially significant in view of their high surface area-volume ratio. Evidence suggests that restrictive mechanisms in the cuticle may supplement the effective physical barrier of the exoskeleton in controlling cuticular transpiration. Their extremely low metabolic rate not only results in a reduced respiratory component of total water loss, but extends the time that scorpions can remain inactive during particularly stressful periods. Water loss is further minimized by the excretion of nitrogenous wastes in the form of guanine and the production of extremely dry fecal pellets. Replenishment of lost body water is provided primarily by body fluids of captured prey, although drinking by some species can serve as a supplementary source when bulk water is available. No scorpion species has demonstrated water uptake from either a near-saturated atmosphere or a moist substrate, regardless of its hydration state. Scorpions are able to withstand considerable dehydration (30% to 40% of their body weight) and apparently tolerate the increased hemolymph osmotic pressures and ionic concentrations until body fluids can be replenished. The importance of water-conserving versus water-regaining mechanisms are discussed in relation to the total adaptations of these animals to hot dry environments.

## INTRODUCTION

Although scorpions are not restricted to desert regions, they usually comprise an important faunal element in these areas and are often among the few species that persist in extremely hot, dry habitats. It is not surprising, therefore, that this group has been the subject of numerous investigations concerning their ecological, physiological, and biochemical adaptations for withstanding the rigors of desert existence. The development of instrumentation and techniques for handling small samples and accurately measuring burrow microenvironments have stimulated much of this recent research. One tool of particular significance in this respect has been the use of ultraviolet light to detect scorpions in the field (Williams, 1968). This has permitted the collection of sufficient numbers for laboratory investigations of thermal and water relationships, and accurate observations of surface and burrowing activities without disturbing the scorpion in its natural environments as well as indicate areas requiring further investigation.

## BEHAVIORAL MECHANISMS

Scorpions can escape the high temperatures and extreme drying power of the surface air by burrowing or seeking some form of cover during daylight and restricting surface activities to nighttime hours. This combination is no doubt the most important adaptive mechanism for scorpions inhabiting desert areas.

**Burrowing**—The burrowing habit in scorpions is closely, but not completely, related to their taxonomic position. For example, most members of the family Buthidae do not burrow but instead inhabit scrapes beneath rocks, decaying vegetation, or surface litter. Exceptions are *Leiurus quinquestriatus* and *Parabuthus hunteri* which normally live in holes dug deeply into the ground (Cloudsley-Thompson, 1961, 1965). Species belonging to the families Scorpionidae (*Scorpio, Palamnaeus*), Vaejovidae (*Hadrurus, Vaejovis*), and Chactidae (*Euscorpius*) inhabitat deep burrows which they either dig themselves or which have been excavated by lizards or small rodents. Burrow depths approaching 75 cm have been reported for *Scorpio maurus* in the Sahara Desert (Cloudsley-Thompson, 1965) and between 60 to 90 cm for *Hadrurus arizonensis* in the Sonoran Desert by Stahnke (1945). Burrows of the latter are usually dug at or near the bases of vegetation where the ground is soft due to root penetration and soil texture is favorable for packing. Other factors such as temperature reduction resulting from shading and increased soil moisture may also be important in site selection. The majority of burrows I have observed were located where there was adequate drainage and the chances of inundation from flash flooding minimal.

Morphological modifications may accompany the burrowing habit. Large, bulky pedipalps often characterize species which dig deep burrows such as members of *Scorpio* and *Hadrurus*, while non-borrowing buthid species such as *Centruroides sculpturatus* possess slender, elongate pedipalps. There are exceptions to this general trend which may reflect the role of the pedipalps in prey capture, courtship behavior, and defensive display. For example, small slender pedipalps are found in two closely related burrowing species, *Vaejovis confusus* and *V. spinigerus* which often occur in association with populations of *C. sculpturatus*. Also many burrowing species such as *Anuroctonus phaiodactylus* apparently use chelicerae and walking legs more than pedipalps in burrow construction (Williams, 1966). A comprehensive study involving species from several families and emphasizing the evolutionary origin of the groups would shed much light on this possible eco-morphological relationship.

Avoidance of high temperatures by burrowing is readily apparent; however, recent studies indicate scorpions are also able to behaviorally regulate their temperature through vertical movements within the burrow (Hadley, 1970a). To monitor burrow microenvironment over a 24-hour period, two thermocouples were attached to large individuals of the genus *Hadrurus*, one placed above the dorsal surface, the other inserted beneath the metasomal surface. The scorpions were then allowed to enter burrows, pulling the thermocouples along with them. Results showed that the diurnal temperature fluctuation experienced by individual scorpions was largely dependent on the depth of penetration and subsequent movements inside the burrow. In one case, the scorpion was able to prevent temperatures from reaching lethal levels by simply retreating deeper into the burrow during early afternoon. Other individuals at depths of 40 cm or more experienced relatively minor fluctuations in temperature during the 24 hours.

Marked and often abrupt temperature changes were experienced by scorpions which moved out of the burrows onto the surface during the study (Fig. 1). Because of rapid

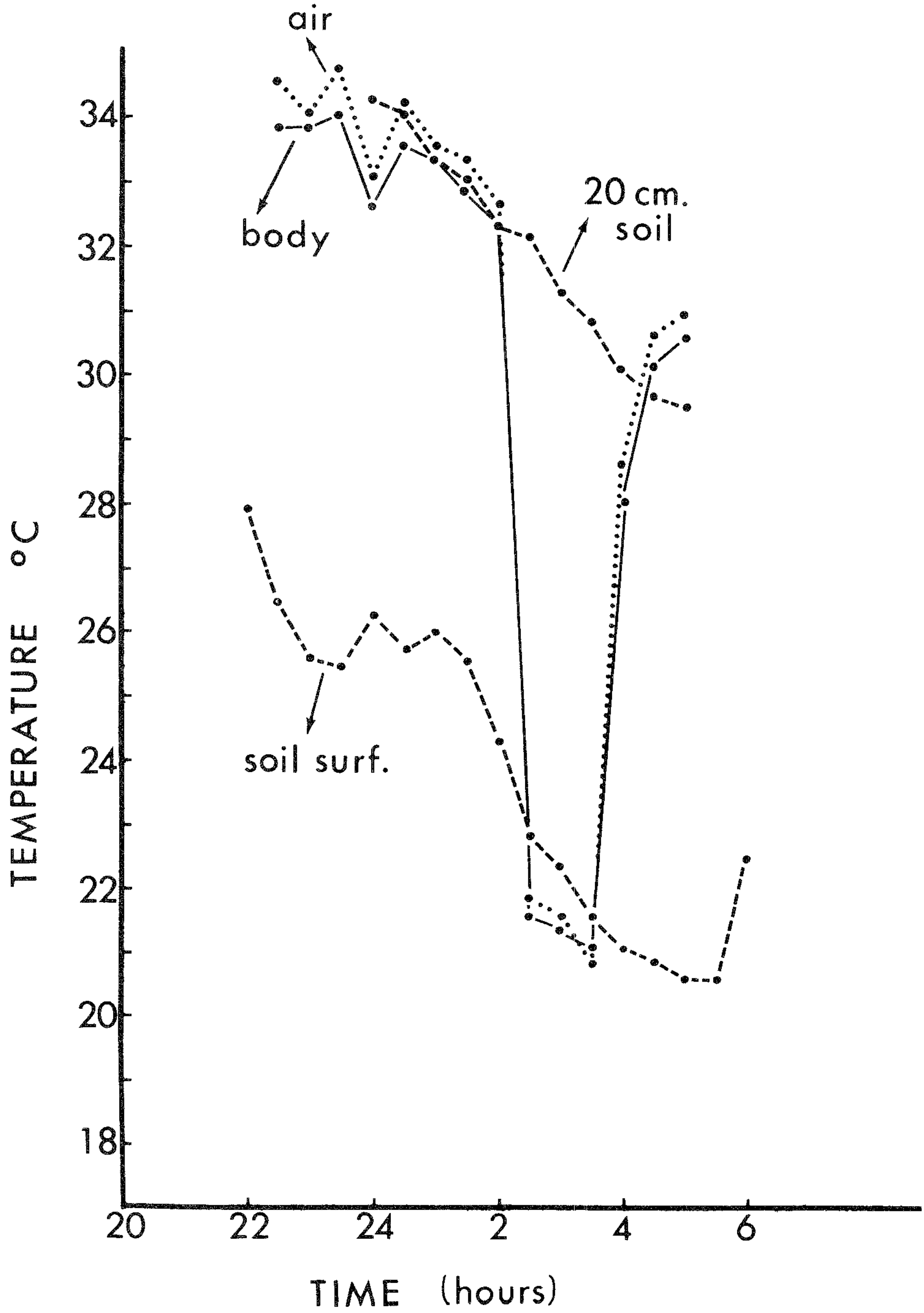

Fig. 1.—Temperature chances experienced by a scorpion moving from a burrow to the surface and returning to the burrow during the night. The scorpion carried both a thermocouple over its dorsal surface (air) and one inserted into the body cavity (body). Substrate and -20 cm soil temperatures are included for reference (Hadley, 1970a).

radiative cooling following sunset and the time lag in penetration of heat from the surface downward, the warmest region of the burrow in early evening was slightly beneath the surface with cooler temperatures above and below. Scorpions that remained in this region experienced temperatures 3° to 10°C higher than those recorded for individuals on the surface. Ultraviolet light detection in the early evening indicates that location at this depth is common in burrowing species. Since scorpions feed very effectively from this position, it is possible that they benefit from increased locomotor and digestive efficiences afforded by the warmer temperatures.

**Nocturnal Surface Activity**—The majority of scorpions are strictly nocturnal in their habits, particularly species inhabiting arid desert regions. The African scorpion, *Opisthophthalmus latimanus*, is found at the entrance to its burrow during daylight hours and exhibits a stilting behavior which is believed to reduce the heat load experienced at this location (Alexander and Ewer, 1958). Day-active species such as *Pandinus imperator* are usually restricted to subtropical forests where the heavy canopy and dense underbrush present light conditions quite similar to those of exposed habitats at night.

Night-active scorpions generally leave their burrow or shelter soon after sunset and occupy a stationary position on the surface or continue traveling over the substrate (Hadley and Williams, 1968). The time a scorpion remains on the surface varies between species, but generally surface occurrence is reduced as the evening progresses. Endogenous locomotor and oxygen consumption rhythms have been demonstrated in the laboratory for many species exhibiting the above behavior pattern. Diurnal activity rhythms of three Sudanese scorpions, *Buthotus minax, Leiurus quinquestriatus*, and *Pandinus exitialis* determined with an aktograph apparatus support observations that these scorpions exhibit strict nocturnal habits in nature (Cloudsley-Thompson, 1962b). Aktograph experiments on another nocturnal species, *Buthus hottentotta*, showed that 83.5% of its activity occurred during 18:00 to 21:00 hours, while the day-active species, *Pandinus imperator*, had 69.3% of its locomotory activity during the daytime (Toye, 1970).

Several scorpions also exhibit increased oxygen consumption rates during nighttime hours which persist for several days under conditions of constant temperature and darkness (Dresco-Derouet, 1961; Hadley and Hill, 1969). In the buthid scorpion, *Centruroides sculpturatus*, abrupt changes in illumination such as sunset initiate brief but large outbursts of respiratory activity which may signify movement onto the surface and subsequent locomotor activities.

Recent studies indicate that enzymatic and neurophysiological functions are correlated with the diurnal activity patterns exhibited by scorpions. Levels of muscle dehydrogenase activity in *Heterometrus fulvipes* are highest at times when this species exhibits increased locomotor activity and oxygen consumption (Rao and Govindappa, 1967). In a related study, Venkatachari and Dass (1968) found a positive correlation between spontaneous electrical activity of the ventral nerve cord and cholinesterase activity in the same species. These processes also show a regular circadean rhythm which coincides with the observed nocturnal activities of the scorpion in nature.

Most scorpions tested under laboratory conditions exhibit a positive response to high humidity but are negatively phototactic and avoid high temperatures orthokinetically (Cloudsley-Thompson, 1969). An exception is *Opisthophthalmus latimanus* which shows a striking photopositive response to directional light, but becomes photonegative at high temperatures (Alexander and Ewer, 1958). The sensory mechanisms responsible for these responses are poorly known. The distal-tarsal segments of the legs possess hair sensillae that are sensitive to humidity, while short, thin hairs distributed over the general body surface apparently function as thermal exteroceptors (Abushama, 1964). The initiation of behavioral responses to temperature by internal thermoreceptors has not been studied.

## TEMPERATURE TOLERANCE

Lethal temperature and water loss rates of scorpions indicate these arthropods are quite tolerant of hot, dry desert conditions and support the idea that ecological factors such as predator avoidance are as much responsible for their nocturnal surface activity as are physiological factors. Accurate comparisons are difficult owing to differences in experimental procedures; however, upper lethal temperatures for scorpions are generally several degrees above those of other desert arthropods. Upper lethal temperatures for two Sudanese scorpions, *Leiurus quinquestriatus* and *Buthotus minax*, after 24-hour exposure to relative humidities below 10% were 47° and 45°C, respectively (Cloudsley-Thompson, 1962a,b). For two North American species, *Hadrurus arizonensis* and *Centruroides sculpturatus*, $LD_{50}$'s were obtained at 45°C after a two-hour exposure at approximately 40-50% relative humidity during oxygen uptake determinations (Hadley, 1970b; Hadley and Hill, 1969). It is likely that scorpions exhibit greater temperature tolerance during summer months resulting from seasonal acclimatization. Cloudsley-Thompson reported an enhanced temperature resistance in *L. quinquestriatus* which had been preconditioned at higher temperatures for 24 hours. Comparative data on lethal temperatures of species from cooler, moister habitats are not available.

## WATER LOSS

Total water loss values for scorpions are given in Table 1. Comparisons between species are approximate at best because of the variety of experimental techniques employed, discrepancies in sample size used in compiling mean values, and differences in weight and hydration state of experimental animals. In spite of these limitations, water loss rates for scorpions, both Old and New World species, are comparable and generally lower than those for other desert arthropods (see Hadley, 1970b). The highest transpiration rates are found in *Pandinus imperator*, the black African scorpion which inhabits lowland rain forest zones. Significantly lower water loss rates characterize the remaining species which are either true desert forms or have geographical ranges which extend into arid regions. These data clearly indicate a relationship between scorpion transpiration rates

Table 1.—Water Loss in Scorpions. ([1] Mean of three newly molted individuals.)

| Species | Temperature °C | Rate of Water Loss $mg/cm^2/hr$ | Source |
|---|---|---|---|
| *Leiurus quinquestriatus* | 33 ± 2 | .021 | Cloudsley-Thompson 1961 |
| *Androctonus australis* | 19 ± 2 | .014 | Cloudsley-Thompson 1956 |
| *Buthotus minax* | 33 ± 2 | .037 | Cloudsley-Thompson 1962b |
| *Campsobuthus werneri* | 19 ± 2 | .010 | Cloudsley-Thompson 1962b |
| *Parabuthus hunteri* | 19 ± 2 | .030 | Cloudsley-Thompson 1962b |
| *Pandinus imperator* | 25 ± 1 | .233 | Toye 1970 |
| *Pandinus imperator* | 25 ± 1 | .413[1] | Toye 1970 |
| *Buthus hottentotta* | 25 ± 1 | .131 | Toye 1970 |
| *Centruroides sculpturatus* | 25 ± 1 | .131 | Hadley (unpublished) |
| *Hadrurus arizonensis* | 25 ± 1 | .029 | Hadley 1970b |
| *Paruroctonus mesaensis* | 25 ± 1 | .038 | Hill (unpublished) |

and distribution in terms of habitat dryness. However, no direct correlation is evident between the degree of nocturnalism shown by scorpions and their rate of water loss (Toye, 1970).

**Cuticular Transpiration**—The extremely low transpiration rates of scorpions can be attributed largely to the presence of an epicuticular wax layer or layers in their integument which provides an effective water-proofing barrier. Supplementing this lipid barrier may be either the tanned chitin-protein complex of the exocuticle or extensions of the lipid material into the underlying cuticular layers (Krishnan, 1953; Kurup, et al., 1969). I have been unable to correlate cuticular hardness and appearance with impermeability in scorpions examined to date, although individuals undergoing molting or recently molted generally exhibit significantly higher water loss rates than do intermolt individuals. Toye's (1970) results on *Pandinus imperator* support this observation (Table 1).

"Critical temperatures" can usually be demonstrated in arthropods with organized lipid water-proofing layers. These are temperatures at which the lipid molecules apparently lose their orientation causing a rapid and marked increase in cuticular transpiration. The cuticular temperature-transpiration curve for *Hadrurus arizonensis* indicates that the cuticle of this species does not exhibit abrupt changes in permeability until temperatures reach approximately 65°C, although a smaller break in the curve appears at 35° to 40°C (Fig. 2). Another desert species, *Scorpio maurus*, also exhibits a critical temperature at approximately 65°C (Cloudsley-Thompson, 1956). The ecological significance of this relationship is not readily apparent since lethal temperatures for both species lie between 45° and 50°C. However, since many arthropods species with higher transpiration rates have lower critical temperatures (35° to 40°C), the cuticular thermostability observed in scorpions may reflect the general impermeable nature of their integument.

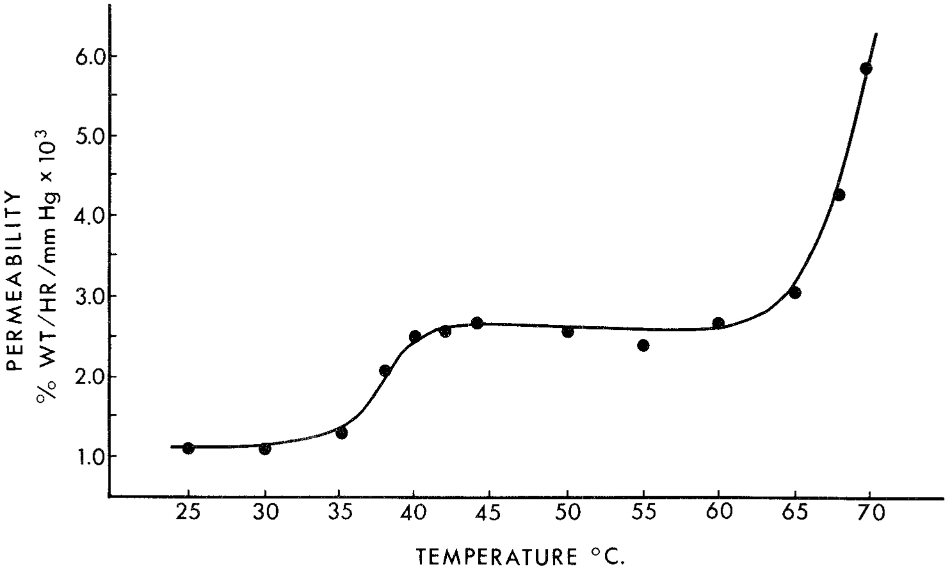

Fig. 2.—The effect of temperature on the permeability of the cuticle of *H. arizonensis*. Dark circles represent mean water-loss values from a minimum of two scorpions. Air, not cuticle, temperatures were measured (Hadley, 1970b).

The cuticular component of total water loss in scorpions can be demonstrated by killing the scorpion with cyanide vapors and sealing its book lungs with nail polish or some other water-proofing substance. However, when living versus dead scorpions are compared at low temperatures, transpiration rates for the latter often exceed water loss rates for living animals. This relationship over time is illustrated in Fig. 3 for *Hadrurus arizonensis* (Hadley, 1970b). In the same study, transpiration rates for dead sealed *Centruroides sculpturatus* were three times those for live specimens. Similar results have been observed for *Paruroctonus mesaensis* (Hill, unpublished). The apparent discrepancy between water loss rates reported for *Pandinus imperator* by Toye (1970) (0.233 mg/cm$^2$/hr) and Cloudsley-Thompson (1959) (1.25 mg/cm$^2$/hr) under similar temperature and humidity conditions may reflect the fact that the latter rate was obtained from a dead specimen. These data strongly suggest that some energy-requiring process(es) in the cuticle may supplement the physical barrier of the exoskeleton in controlling cuticular transpiration. Further research is necessary to determine if any of the mechanisms postulated for other arthropods which also exhibit this relationship can be applied to scorpions.

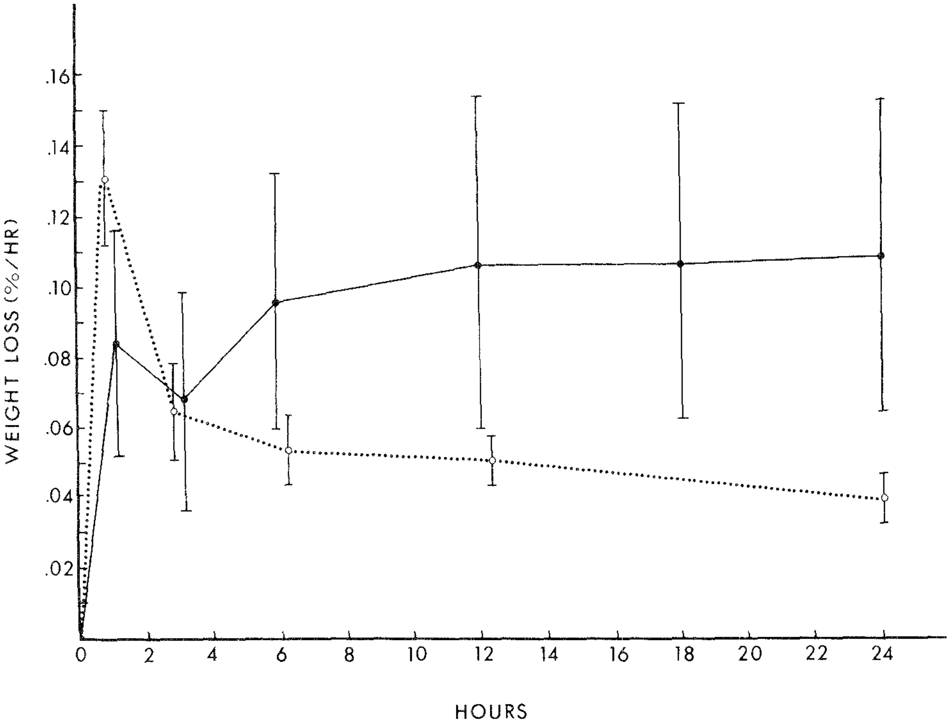

Fig. 3.–Changes in water-loss rates with time in living scorpions (open circles) versus dead scorpions (dark circles) at 38°C in dry air. Vertical lines represent 95% confidence limits (Hadley, 1970b).

**Respiratory Transpiration**–In spite of the impermeable integument, cuticular transpiration is responsible for much of the total water loss of scorpions over their normal temperature range. Metabolic rates of scorpions are very low (Sreenivasa Reddy, 1963; Dresco-Derouet, 1964; Hadley and Hill, 1969); individuals with only one of the eight book lungs functional continued to live and feed for six months following the operation (Millot and Paulian, 1943). Because of the low metabolic demands, respiratory evaporation can be almost negligible at low temperatures. However, increased ventilation rates at higher temperatures ($>40^\circ$C) may result in respiratory transpiration far surpassing cuticular transpiration, even though the latter also increases with temperature. Such is the case for *Hadrurus arizonensis*, the only species for which the relative contributions of the two water loss pathways over an extended temperature range have been determined (Hadley, 1970b). There is also some evidence of more stringent spiracular control in scorpions as they become dehydrated or when microclimatic conditions dictate water conservation.

Not only does the low metabolic rate reduce respiratory transpiration, it extends the time scorpions can remain inactive during particularly stressful periods of the year. It is well known that scorpions can go several weeks without food or water. During this time, glycogen which is stored in high concentrations in the liver and muscles serves as a nutrient reserve (Sinha and Kanungo, 1967). The glycogen is broken down into glucose and released into the blood so that even during extended starvation periods blood sugar levels remain fairly constant (Padmanabhanaidu, 1966).

**Excretory Water Loss**—The elimination of nitrogenous end-products and fecal material in a very dry state further reduces water loss in scorpions. In contrast to insects, the principle nitrogenous waste of scorpions appears to be the purine compound guanine, with uric acid second in importance (Table 2). Only in the Indian scorpion, *Palamnaeus bengalensis;* is this trend reversed. It is likely that the presence of uric acid in some species reflects dietary purines since scorpions feed principally on uricotelic insects; however, interspecific variation in nitrogenous end-products may reflect true differences in some cases (Horne, 1969). Horne also states that guanine rather than uric acid excretion might indicate more efficient water conservation for species in hot dry climates since guanine contains one more nitrogen atom than uric acid and is less soluble in water.

In addition to transpiration and water accompanying elimination of nitrogenous wastes and fecal material, trace amounts of water can be lost through venom release and a process called "washing" or "sponge bathing". The former probably represents a minor constituent of total water loss in laboratory determinations only because of scorpions striking at their containers. "Sponge bathing" refers to the use of exudate by scorpions to clean their pedipalps, chelicerae, telson, and first two pairs of walking legs (Williams, 1966; Kinzelbach, 1967). Williams reports that even though the fluid is exuded in large quantities in the preoral cavity, surface tension between the gnathobases and on the chelicerae prevents any extensive loss to the substrate. Because evaporation of the exudate would still be a factor, this cleaning behavior in nature is probably restricted to periods following fluid intake or times when water needs are not critical.

## RESISTANCE TO DESICCATION

One of the most widespread adaptations to desert environments is the ability of organisms to endure desiccation and recover unharmed (Hadley, 1972). Even if scorpions become inactive in burrows during unfavorable seasons or adjust their activity periods so that their surface occurrence coincides with times of reduced heat and high humidities, they are likely to encounter a water deficit. This is particularly true if there is an absence of insect prey to replenish body water needs. As indicated by the length of time they can go without food or water, scorpions obviously show an enhanced ability to survive

Table 2.–Nitrogenous Excretion in Scorpions. ●, major end-product; ⊕, present; ○, not detectable or present in trace amounts only.

| Species | Nitrogenous end-products | | | | Source |
|---|---|---|---|---|---|
| | Uric Acid | Guanine | Adenine | Hypoxanthine | |
| *Centruroides vittatus* | ⊕ | ● | ○ | ○ | Horne (1969) |
| *Centruroides marginaritatus* | ⊕ | ● | ○ | ○ | Horne (1969) |
| *Vaejovis mexicanus* | ○ | ● | ○ | ○ | Horne (1969) |
| *Heterometrus* sp. | ○ | ● | ○ | ○ | Horne (1969) |
| *Vaejovis* sp. | ○ | ● | ○ | ○ | Horne (1969) |
| *Heterometrus fulvipes* | ⊕ | ● | ○ | ○ | Rao & Gopalakrishnareddy (1962) |
| *Lycas tricarinatus* | ⊕ | ● | ○ | ○ | Rao & Gopalakrishnareddy (1962) |
| *Buthus tamulus* | ⊕ | ● | ○ | ⊕ | Rao & Gopalakrishnareddy (1962) |
| *Leiurus quinquestriatus* | ⊕ | ● | ○ | ○ | Haggag & Fouad (1965) |
| *Palamnaeus bengalensis* | ● | ○ | ⊕ | ⊕ | Kanungo, et al. (1962) |
| *Androctonus australis* | ○ | ● | ○ | ○ | Gregoire, et al. (1955) |
| *Androctonus amoreuxi* | ○ | ● | ○ | ○ | Gregoire, et al. (1955) |

desiccation. Depletion of body water levels approaching 30% of their initial weight have been observed for scorpion species in our laboratory, while Cloudsley-Thompson (1962b) reported a loss of approximately 40% body weight before death occurred in *Buthotus minax*. Unfortunately, information about the possible regulation of hemolymph concentration and composition during dehydration is lacking for scorpions. Preliminary results from a study in progress on *Hadrurus arizonensis* suggest that this species simply tolerates increased osmotic pressure and ion concentrations until lost body water can be replenished.

## WATER GAIN

Potential sources of water available to scorpions include fluids of captured prey, bulk surface water, atmospheric and substrate moisture, and metabolic water. Water contained in the juices of prey is the most important and the only source necessary for most species. The immobilized prey is subjected to both mechanical and external chemical digestion, with the resulting juices being drawn into the mouth by the pumping action of the pharynx. Water uptake by drinking is essential in some tropical species such as the Phillipine forest scorpion, *Palamnaeus longimanus*, which must replace water lost due to high transpiration rates (Schultze, 1927). Desert species will drink in the laboratory, especially when dehydrated, but have access to bulk water only infrequently in nature. An exception is the non-burrowing scorpion, *Centruroides sculpturatus*, which has been observed drinking from irrigation canals in the Salt River Valley, Arizona. The mean drinking rate for eight individuals was 10 mg/min. They were able to regain a mean of 70.8% of the weight they lost through desiccation; however, no correlation was evident between extent of desiccation and milligrams of water drunk (Hadley, 1971). Although *C. sculpturatus* is capable or rapid rehydration via drinking, it also survives well in xeric habitats where bulk water is absent and, therefore, like other desert species is not dependent upon this avenue of water gain.

In some desert species, water formed from the oxidation of foodstuffs is necessary for survival; however, its role in scorpions remains obscure since they usually obtain sufficient water with their food. Scorpions, like all arthropods, utilize metabolic water since it enters the total water pool, but its overall contribution to water balance is meager in comparison to the preformed water of the prey. There is good evidence that scorpions are very efficient in retaining metabolic water. Sinha and Kanungo (1962) reported that *Palamnaeus bengalensis* individuals starved for 12 days showed no change in the water content of liver and muscles. This observation also reflects the ability of scorpions to excrete dry fecal material and to decrease the amount of excreta produced with increased time of starvation.

The ability of arthropods to absorb atmospheric or substrate moisture has been the subject of much recent experimentation. This phenomenon has been observed in a number of different species, but is rare among truly desert forms. Scorpions appear to be no exception. It was thought that scorpions such as *Hadrurus arizonensis* which are abundant along desert coastal areas in Northern México might supplement their water intake by absorbing moisture from the near-saturated air or moist ground surface during the summer nights (Williams and Hadley, 1967). Laboratory experiments have failed to substantiate this hypothesis. Even highly desiccated individuals were unable to take up significant quantities of water from moist sponge strips (Fig. 4) and no individuals exhibited a weight increase after 24 hours exposure to 98% relative humidity (Hadley, 1970b). Water loss in the latter group, however, was only 1/7th the rate for hydrated individuals in dry air and 30°C (Table 1). Additional desert species must be investigated before the results obtained for *H. arizonensis* can be applied to scorpions as a group. Tropical species with more permeable integuments and high transpiration rates might provide some interesting contrasts to this general pattern.

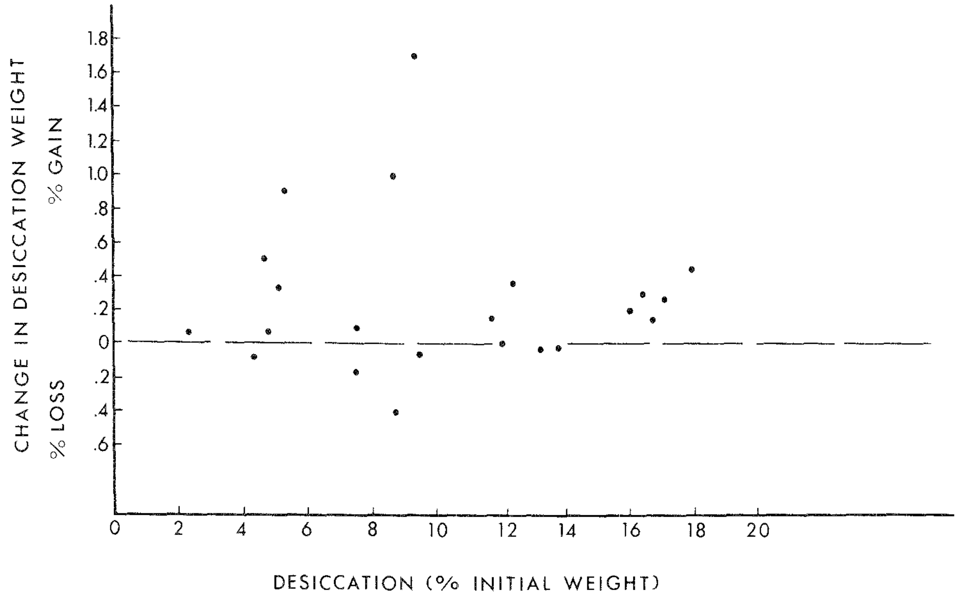

Fig. 4.–Changes in desiccation weight of *H. arizonensis* after 24 hour exposure to a moist sponge substrate (25°C). Position of dark circles along horizontal axis indicated degree of dehydration of individual scorpions (Hadley, 1970b).

## SUMMARY AND CONCLUSIONS

A combination of behavioral, morphological, and physiological adaptations enable scorpions to tolerate environmental stresses encountered in desert habitats. Paramount among these are the avoidance of climatic extremes by burrowing, nocturnal surface activity, increased heat resistance, an extremely impermeable cuticle with active mechanisms for water retention, a low metabolic rate, efficient elimination of excreta, and increased desiccation resistance. Mechanisms for conserving rather than regaining water are emphasized. The majority of adaptations exhibited by scorpions are not unique to these arachnids, but are highly developed and efficiently utilized.

## ACKNOWLEDGMENTS

I wish to express my gratitude to Stanley C. Williams for his helpful criticism of this manuscript and stimulating discussions which have contributed greatly to my understanding of scorpion ecology.

## LITERATURE CITED

Abushama, F. T. 1964. On the behaviour and sensory physiology of the scorpion *Leiurus quinquestriatus* (H. & E.). Anim. Behav. 12(1):140-153.

Alexander, A. J., and D. W. Ewer. 1958. Temperature adaptive behaviour in the scorpion, *Opisthophthalmus latimanus* Koch. J. Exptl. Biol. 35:349-359.

Cloudsley-Thompson, J. L. 1956. Studies in diurnal rhythms–VI. Bioclimatic observations in Tunisia and their significance in relation to the physiology of the fauna, especially woodlice, centipedes, scorpions and beetles. Ann. Mag. Nat. Hist., Ser. 12, 9:305-329.

Cloudsley-Thompson, J. L. 1959. Studies in diurnal rhythms–IX. The water-relations of some nocturnal tropical arthropods. Entomol. Exptl. Appl. 2:249-256.

Cloudsley-Thompson, J. L. 1961. Observations on the biology of the scorpion, *Leiurus quinquestriatus* (H. & E.), in the Sudan. Entomol. Monthly Mag. 97:153-155.

Cloudsley-Thompson, J. L. 1962a. Lethal temperature of some desert arthropods and the mechanism of heat death. Entomol. Exptl. Appl. 5:270-280.

Cloudsley-Thompson, J. L. 1962b. Some aspects of the physiology of *Buthotus minax* (Scorpiones: Buthidae) with remarks on other African scorpions. Entomol. Monthly Mag. 98:243-246.

Cloudsley-Thompson, J. L. 1965. The scorpion. Sci. J. 1:35-41.

Cloudsley-Thompson, J. L. 1969. The zoology of tropical Africa. W. W. Norton, New York. 355p.

Dresco-Derouet, L. 1961. Le metabolisme respiratoire des scorpions–I. Existence d'un rhythme nychemeral de la consommation d'oxygene. Bull. Mus. Hist. Nat. 32:533-557.

Dresco-Derouet, L. 1964. Le metabolisme respiratoire des scorpions–II. Mesures del l'intensite respiratoire chez quelques especes a differentes temperatures. Bull. Mus. Hist. Nat. 36:97-99.

Gregoire, J., J. Gregoire, and F. Miranda. 1955. Sur la presence de guanine et de faibles quantites d'agmatine dans les excreta de 2 especes de Scorpions (*Androctonus australis* (L.) et *Androctonus amoreeuxi* (Aud. et Sav.). C. R. Seances Soc. Biol. 149:1439-1444.

Hadley, N. F. 1970a. Micrometerorology and energy exchange in two desert arthropods. Ecology 51:434-444.

Hadley, N. F. 1970b. Water relations of the desert scorpion, *Hadrurus arizonesis*. J. Exptl. Biol. 53:547-558.

Hadley, N. F. 1971. Water uptake by drinking in the scorpion, *Centruroides sculpturatus* (Buthidae). Southwestern Nat. 15:495-505.

Hadley, N. F. 1972. Desert species and adaptation. Amer. Sci. 60(3):338-347.

Hadley, N. F., and R. D. Hill. 1969. Oxygen consumption of the scorpion *Centruroides sculpturatus*. Comp. Biochem. Physiol. 29:217-226.

Hadley, N. F., and S. C. Williams. 1968. Surface activities of some North American scorpions in relation to feeding. Ecology 49:726-734.

Haggag, G., and Y. Fouad. 1965. Nitrogenous excretion in arachnids. Nature 207:1003-1004.

Horne, F. R. 1969. Purine excretion in five scorpions, a uropygid and a centipede. Biol. Bull. 137:155-160.

Kanungo, M. S., S. C. Bohidar, and B. K. Patnaik. 1962. Excretion in the scorpion, *Palamnaeus bengalensis* C. Koch. Physiol. Zool. 35:201-203.

Kinzelbach, R. 1967. Waschen bei skorpionen. Natur und Mus. 97:9-16.

Krishnan, G. 1953. On the cuticle of the scorpion *Palamneus swammerdami*. Quart. J. Microscop. Sci. 94:11-21.

Kurup, P. A., S. Leelamma, P. L. Vijayammal, and N. R. Vijayalekshmi. 1969. Nature of cuticle of the scorpion, *Heterometrus scaber*. Indian J. Exptl. Biol. 7:27-28.

Millot, J., and R. Paulian. 1943. Valeur fonctionnelle des poumons des scorpions. Bull. Soc. Zool. France 68:97-98.

Padmanabhanaidu, B. 1966. Ionic composition of the blood and the blood volume of the scorpion, *Heterometrus fulvipes*. 17:157-166.

Rao, K. P., and T. Gopalakrishnareddy. 1962. Nitrogen excretion in arachnids. Comp. Biochem. Physiol. 7:175-178.

Rao, P. V., and S. Govindappa. 1967. Dehydrogenase activity and its diurnal variations in different muscles of the scorpion, *Heterometrus fulvipes*. Proc. Indian Acad. Sci., B, 66:243-249.

Schultze, W. 1927. Biology of the large Philippine forest scorpion. Philippine J. Sci. 32:375-389.

Sinha, R. C., and M. S. Kanungo. 1967. Effect of starvation on the scorpion *Palamnaeus bengalensis*. Physiol. Zool. 40:368-390.

Sreenivasa Reddy, R. P. 1963. Biology of scorpions with special reference to the pectines. Doctoral Thesis, Sri Venkateswara University.

Stahnke, H. L. 1945. Scorpions of the genus *Hadrurus* Thorell. Amer. Mus. Novitates 1298:1-9.

Toye, S. A. 1970. Some aspects of biology of two common species of Nigerian scorpions. J. Zool. London 162:1-9.

Venkatachari, S., and P. M. Dass. 1968. Choline esterase activity rhythm in the ventral nerve cord of scorpion. Life Sci. 7:617-621.

Williams, S. C. 1966. Burrowing activities of the scorpion *Anuroctonus phaeodactylus* (Wood) (Scorpionida:Vejovidae). California Acad. Sci. 34:419-428.

Williams, S. C. 1968. Methods of sampling scorpion populations. California Acad. Sci. 36:221-230.

Williams, S. C., and N. F. Hadley. 1967. Scorpions of the Puerto Penasco area (Cholla Bay), Sonora, Mexico, with description of *Vejovis baergi*, new species. California Acad. Sci. 35:103-116.