

## FEEDING AND EXCRETION IN THE SCORPION *PARUROCTONUS MESAENSIS*: WATER AND MATERIAL BALANCE

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### SUMMARY

Scorpions feed by a process involving the external grinding and digestion of prey, with the ingestion of only the soluble fraction. The water obtained from the prey represents the most important source of water intake for scorpions inhabiting arid regions, placing great importance on the animals' ability to utilize prey water effectively. The scorpion *Paruroctonus mesaensis* (Stahnke) was found to ingest a mean of 88% of the body water of selected prey. However, the scorpion loses 0.37 ml of its own body water per ml of prey water extracted, resulting in a net water gain of 0.51 ml water for every ml of prey water. Fluid uptake by the scorpion has been ascribed to a pharyngeal pumping mechanism. Direct measurements of the suction generated by the pharynx yielded a minimal estimate of its pumping capability of 130 mmHg.

The uptake and excretion of nitrogen and electrolytes by *Paruroctonus mesaensis* on a diet of *Tenebrio molitor* adults were also analysed. Almost all the potassium ingested was excreted, whereas most of the sodium and chloride were retained, possibly serving to expand haemolymph volume. Assuming a steady state for nitrogen, it was estimated that the net utilizable water obtained from prey, that is the water intake minus the excretory water necessitated by nitrogen excretion, was equivalent to about 35% of the initial prey water or 69% of the water ingested.

### INTRODUCTION

The maintenance of water balance plays a prominent role in the lives of many terrestrial animals. Studies of the water relations of many diverse animal groups have focused largely on adaptations for decreasing water loss. The arthropods excel at two approaches to water conservation, having the lowest transpiratory loss rates and excreta with the lowest water activities recorded (Edney, 1977). In general, the means of water intake have received much less attention. Important sources of water for terrestrial arthropods include free standing water, preformed water in food, and water produced by metabolism, with a few species being able to obtain net water from

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subsaturated atmospheres (Edney, 1977). In arid environments, in the absence of drinking water, dietary and metabolic sources become increasingly important. Scorpions, which are common inhabitants of such regions and which lack the ability to utilize water vapour, must rely on the water gained from their prey and their metabolism for most of the year (Hadley, 1974). Scorpions feed by a process involving external grinding with the ingestion of only a portion of their prey. Thus, not all the water and nutrients contained in the captured prey become available for utilization by this predator. There is also the potential for considerable evaporative losses during feeding, a situation exacerbated by the high temperatures, low humidities and strong winds frequent in desert regions. And, in addition to the water and energy acquired from each meal, the scorpion incurs a concomitant electrolyte load. In this study, the water, electrolyte and nitrogen intake through feeding and output by excretion have been evaluated in the scorpion *Paruroctonus mesaensis*.

The ingestion of prey fluids by spiders and scorpions is thought to be due to the actions of the muscular pharynx (Savory, 1964; Snodgrass, 1965). Consequently, the ability of the scorpion to assimilate prey water may be limited by the maximal suction pressure developed by this pump. This same mechanism is likely to account for the ability to take up soil water demonstrated for several spiders (Parry, 1954) and scorpions (Crawford & Wooten, 1973; Riddle, Crawford & Zeitone, 1976). Direct measurements of the suction pressures produced in the preoral cavity were made to assess the function of the pharyngeal pump.

#### MATERIALS AND METHODS

Adult specimens of *Paruroctonus mesaensis* were collected from sand dunes in the Coachella Valley of the Mojave Desert in Riverside County, California. The scorpions (2.5–3.5 g) were maintained in plastic vials at room temperature (21–24°C) and humidities (approximately 20–40%) and fed *Tenebrio molitor* larvae and *Periplaneta americana* nymphs.

#### *Water uptake during feeding*

A flow-through system was constructed to determine the water fluxes during feeding. Air, dried by passage through a dry ice vapour trap and anhydrous calcium sulphate (Drierite), was passed through a plastic feeding chamber at a flow rate of 0.5 l min<sup>-1</sup>, creating an average air velocity of 0.87 cm s<sup>-1</sup>. The water vapour gained during passage through the feeding chamber was then condensed in a collection tube immersed in an acetone-dry ice bath. The feeding chamber was maintained at 24–25°C in an incubator.

Adult crickets (*Acheta domesticus*) or nymphal cockroaches (*Periplaneta americana*), from 0.25–0.68 g fresh mass, to be used as prey were injected with about 70 nCi of tritiated water in 5 µl water. After a 3 h equilibration period, a 5 µl haemolymph sample was taken for the determination of the specific activity of tritium. Each prey item was then weighed and offered to a preweighed scorpion which had been allowed to acclimate to the feeding chamber for at least 2 h. During feeding the scorpion ingests the soluble portion of the prey and compacts the residue into small masses termed feeding pellets. Within 15 min of the scorpion discarding the

Feeding pellet, the air flow was stopped, the water vapour collection tube capped, and the scorpion and feeding pellets were weighed to the nearest 0.1 mg. A sample of the scorpion haemolymph was taken 2 h later for the determination of the specific activity of tritium. The feeding pellets were dried at 100 °C for the measurement of dry mass. The water vapour collection tube was rinsed twice with 10 ml of scintillation fluid for the measurement of the tritiated water collected. Tritium activity was measured by liquid scintillation counting (Beckman CPM-100) with a dioxane-naphthalene-PPO scintillation fluid using the external standard method for quench correction.

The initial prey body water was calculated from the live mass of the prey using the mean water content, determined by drying to constant mass, for crickets,  $72.0 \pm 1.4\%$  ( $\pm$ s.e.,  $N = 12$ ), and cockroaches,  $65.9 \pm 0.9\%$  ( $N = 5$ ). The prey water ingested by the scorpion during feeding was calculated from the specific activity of tritium in the haemolymph of the prey before feeding and the specific activity in the scorpion haemolymph after feeding, assuming the scorpion body water was equal to 70% of the fresh mass (the mean for laboratory-kept animals), by the formula:

$$W_{pi} = 0.70 M_{sf} (S_s/S_p), \quad (1)$$

where  $W_{pi}$  is the prey water ingested,  $M_{sf}$  is the live mass of the scorpion after feeding,  $S_s$  and  $S_p$  are the specific activities of tritium in the haemolymph of the scorpion and the prey, respectively, and the factor 0.70 has the units of  $\text{ml g}^{-1}$ . The prey water which is not obtained by the scorpion is the difference between the initial prey body water and the volume ingested by the scorpion. However, the scorpion invests part of its own body water in the feeding process, by exuding digestive fluids into the prey mass being ground. Thus, the net water uptake during feeding is the difference between the prey water ingested and the net scorpion body water which is either evaporated during feeding or left with the pellets, and can be calculated by the following equation:

$$W_{net} = (M_{sf} - M_{si}) - (M_{pd} - M_{fd}), \quad (2)$$

where  $M_{sf}$  and  $M_{si}$  are the final and initial live mass of the scorpion respectively,  $M_{pd}$  is the calculated dry mass of the prey, and  $M_{fd}$  is the dry mass of the feeding pellets produced.

The water which is not ingested by the scorpion is therefore composed of water both from the prey and the scorpion and has two components: the fraction evaporated during feeding and the liquid fraction left with the feeding pellets. Because several pellets may be produced sequentially from a single prey, the water left with the first pellets gradually evaporates to be collected as water vapour. Consequently, the precise measurement of the water content of the feeding pellets when discarded was not made. Although these considerations influence the relative proportion of loss in the two fractions, they should not affect the measurement of the prey water ingested or net water uptake.

#### *Electrolyte and nitrogen uptake and excretion*

The uptake and balance of electrolytes (Na, K and Cl) and nitrogen were evaluated in scorpions on a diet of adult *Tenebrio molitor* beetles. Scorpions were offered a weighed beetle every second day for 2 months. The feeding pellets, faeces and

urine were collected daily, dried and weighed. Uneaten beetles were discarded. Faeces and urine were distinguished visually by colour, white excrement being considered urine and dark excrement being considered faeces (Said, 1961; Yokota & Shoemaker, 1981). Electrolytes were extracted from samples with 0.1 N nitric acid. Sodium and potassium were analysed by flame photometry and chloride was determined with a chloridometer (Buchler-Cotlove). The nitrogen content of the feeding pellets was determined by the Dumas method with a nitrogen analyser (Coleman). The nitrogen content of the faeces and the urine was determined with a modified Kjeldahl method (Jaenicke, 1974) after dissolving the samples in 0.1 N sodium hydroxide.

#### *Water excretion*

To determine the water content of the excreta the posterior portion of the opisthosoma was enclosed in a small plastic vial by inserting the sting and last opisthosomal segment through a hole made in the cap and sealing this junction with wax. By attaching a tared minivial to the cap, the excreta were collected with negligible water losses. Five scorpions prepared in this manner were fed cockroach nymphs and the fresh excreta collected and weighed within 12 h of deposition. The excreta were then dried at room temperature in a vacuum desiccator with anhydrous calcium sulphate and reweighed.

#### *Pharyngeal pump activity*

The ability of *P. mesaensis* to develop suction pressures was initially investigated using a cotton wick probe and a mercury manometer in a system similar to that developed by Scholander, Hargens & Miller (1968) for measurements of tissue interstitial pressure. Scorpions were secured in either normal or inverted positions and the probe advanced into the preoral cavity with a micromanipulator. Later, a pressure transducer (Statham) was substituted for the mercury manometer, the entire system filled with water, and the suction pressure transients created by the pharynx recorded (Beckman Dynograph). A second type of probe consisting of open-ended, tapered polyethylene tubing was also used.

### RESULTS

#### *Water uptake during feeding*

Estimates of prey water ingestion, made using equation 1, indicate that a mean of 88 % of the original prey body water is ingested by the scorpion (Table 1). The use of equation 2 to estimate the net water uptake by the scorpion during feeding indicates that the scorpion realizes a net water gain equal to 51 % of the initial prey water. Therefore, water equal to 49 % of the prey body water is lost to the scorpion, either remaining with the feeding pellets or evaporating during feeding. The majority of the evaporative water loss occurred from scorpion body water (Table 2). This observation suggests that prey water is initially withdrawn and scorpion body water is added during feeding. A maximal estimate of the water content of the feeding pellets when discarded can be made if it is assumed that evaporative water losses before t

Table 1. *The efficiency of prey water ingestion by the scorpion Paruroctonus mesaensis*

Scorpion	Prey	Prey body H <sub>2</sub> O (ml)	Prey H <sub>2</sub> O ingested Prey body H <sub>2</sub> O	Net H <sub>2</sub> O uptake Prey body H <sub>2</sub> O
G3	Cricket	0.408	0.93	0.62
G5	Cockroach	0.166	0.84	0.45
G6	Cockroach	0.261	0.89	0.59
G7	Cockroach	0.235	0.86	0.34
G8	Cricket	0.451	—	0.56
Mean ± s.e.			0.88 ± 0.02	0.51 ± 0.05

rejection of each pellet are negligible. The average water content of the pellets estimated in this manner was about 79%. The complete feeding process, from prey capture to the rejection of the last pellet, averaged about 6 h.

The potential influx of tritiated water vapour across the cuticle and respiratory surfaces into the scorpion was ignored in these calculations. Previous studies had determined a mean unidirectional influx of water vapour of  $0.71 \pm 0.04 \mu\text{l H}_2\text{O g}^{-1} \text{h}^{-1}$  ( $\pm$ s.e.,  $N = 5$ ) at 90% relative humidity at 24°C (S. D. Yokota & K. Nagy, in preparation). In the present study, the average relative humidity during feeding would not have exceeded 6%, and most of the evaporative water loss originated from the unlabelled scorpion body water. Thus, the potential error from the influx of tritiated water vapour would be insignificant. In addition, respiratory and cuticular evaporative water losses for *P. mesaensis* are also insignificant over this period, at this temperature.

#### *Electrolyte and nitrogen uptake and excretion*

Adult *T. molitor* beetles contained 1.87 ml H<sub>2</sub>O, 89.4 mg nitrogen, 0.273 mmol potassium, 0.068 mmol sodium and 0.158 mmol chloride per gram dry mass. During the feeding experiment, scorpions were fed a mean of  $403 \pm 40$  mg dry mass of *T. molitor*. Since there was no significant correlation between the amount fed and the

Table 2. *Evaporative water loss (EWL) during feeding*

Scorpion	Evaporative H <sub>2</sub> O loss*	Scorpion EWL§
	Total H <sub>2</sub> O loss†	Prey EWL‡
G3	0.91	3.2
G5	0.93	2.1
G6	0.89	3.3
G7	0.92	1.2
G8	0.40	—
Mean ± s.e.	0.81 ± 0.10	2.4 ± 0.5

\* Calculated as the loss in the combined mass of scorpion and prey during feeding.

† Calculated as the EWL plus the water content of the feeding pellet.

‡ Prey EWL determined from the specific activity of <sup>3</sup>HHO in the prey haemolymph and the <sup>3</sup>HHO appearing in the water collection tube corrected for the efficiency of <sup>3</sup>HHO collection (78.4%).

§ Scorpion EWL calculated as the difference between total EWL and the prey EWL.

Table 3. *The electrolyte and nitrogen balance of Paruroctonus mesaensis on an adult Tenebrio diet*

	Fed ( $\mu\text{mol}$ )	Ingested $\times 100$ Fed	Excreted $\times 100$ Ingested	Urine $\times 100$ Total excreted
Sodium	27.0 $\pm$ 2.5	70.7 $\pm$ 3.3	11.7 $\pm$ 2.3	31.1 $\pm$ 7.0
Potassium	110 $\pm$ 11	41.6 $\pm$ 3.3	93.0 $\pm$ 5.6	27.3 $\pm$ 7.2
Chloride	62.3 $\pm$ 19.7	63.1 $\pm$ 2.3	31.4 $\pm$ 4.0	33.9 $\pm$ 7.4
Nitrogen	36.1 $\pm$ 3.6	60.8 $\pm$ 2.2	50.0 $\pm$ 4.8	30.7 $\pm$ 6.6

Data expressed as the means  $\pm$  s.e., ( $N = 10$ ).

fraction ingested, assimilated or excreted for any of the elements analysed, the data for uptake and excretion are presented as percentages (Table 3). *P. mesaensis* ingested about two-thirds of the sodium and chloride present in *T. molitor* but ingested a significantly lower fraction of the potassium ( $P < 0.001$ ). In addition, *P. mesaensis* excreted almost all the ingested potassium but retained most of the sodium and chloride (Table 3). The urine accounted for roughly one-third of the total sodium, potassium, chloride and nitrogen excreted, the faeces contributing the remainder. The sodium and chloride retained may have been incorporated by the volume expansion of the haemolymph which is composed predominantly of these two electrolytes (Padmanabhanaidu, 1966; Bowerman, 1977). The average amount of sodium retained was 17  $\mu\text{mol}$  which would be contained in about 60  $\mu\text{l}$  of haemolymph. The mean water intake of the scorpions during the 2-month feeding experiment was calculated to be 384  $\mu\text{l}$ , a volume quite adequate to allow for the isosmotic expansion of the haemolymph.

The scorpions ingested an average of 60.8% of the nitrogen in *T. molitor* and excreted about 50% of the nitrogen ingested (Table 3). The mean nitrogen contents of the three products of the scorpion were 9.55% of the dry mass of the feeding pellets, 27.0% of the faeces and 29.5% of the urine. The calculated assimilation efficiency of the ingested nitrogen was 52% and nitrogen incorporation, or retention, was equal to 49% of the nitrogen assimilated.

#### Water excretion

The range of water contents of the excreta collected with the encapsulation technique was 0.70–3.00 ml  $\text{H}_2\text{O g}^{-1}$  dry mass, equal to 42.9–75.0% water, with a mean of 1.75  $\pm$  0.20 ml  $\text{H}_2\text{O g}^{-1}$  dry mass ( $N = 10$ ). Urine and faecal material were not separated for these determinations.

#### Suction pressure of the pharyngeal pump

The use of the mercury manometer to measure pressure fluctuations provided quantitative information only about static pressures. The usual observations were that upon placement of the probe into the preoral cavity of the scorpion, a slight suction pressure of 2–7 mmHg was detected. This small pressure was attributed to the capillarity of the abundant fine hairs and the crevices of the preoral cavity. T

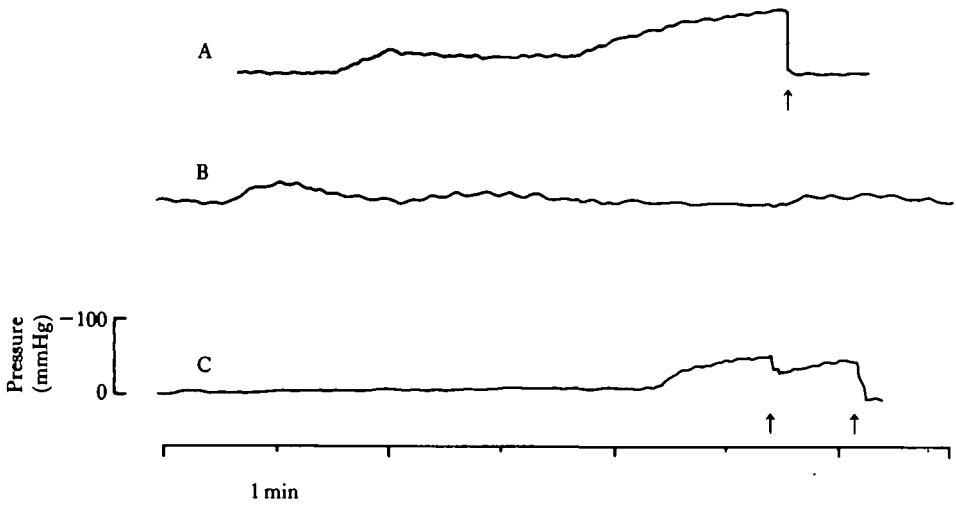


Fig. 1. Recordings of the suction pressures produced by the pharyngeal pump of *Paruroctonus mesaensis*. Each tracing begins at ambient pressure. Arrows mark disruption of water column by the entrance of air.

scorpion moved its mouthparts about the probe and initiated sucking soon thereafter. Typically, there appeared to be a period of small pressure fluctuations observed by the movement of small bubbles trapped in the wick of the probe and the meniscus of the manometer which was then followed by surges of greater magnitude, creating suction by a succession of pulses. Ultimately, air was drawn into the probe, either because of the failure of the wick to withstand the magnitude of the suction pressure or because of the release of the probe by the scorpion. The maximal suction pressures measured by this system were 120–130 mmHg.

The use of the pressure transducer to measure pressure changes had several advantages: accurate recordings of the pressures generated could be made and time resolution was vastly improved, allowing dynamic aspects to be studied. Tracings of examples of the recordings of suction pressure generation by *P. mesaensis* are shown in Fig. 1. Typically, large suction pressures were produced in successive surges. A surge of activity would create 20–50 mmHg of suction pressure which would be maintained for 0.5–2.0 min until the next surge of activity which would increase the total suction pressure in an additive fashion (Fig. 1A). Eventually, the water column would be disrupted by the entrance of air. Occasionally, the suction pressures would not be maintained but rather would decline until the next surge of pumping activity, giving the appearance of negative pressure cycles of 0.5–1.0 min duration (Fig. 1B). Infrequently, gradual and small increases in suction occurred over longer time periods of 2 min or more, and generally preceded periods of marked suction activity (Fig. 1C).

The achievement of large suction pressures appears to be due to the summation of smaller pulses. In every recording of the development of suction, pulses having a frequency of 0.2–0.3 pulses  $s^{-1}$  and a magnitude of 5–10 mmHg were observed (Fig. 1). In addition, smaller and more rapid fluctuations which were detected by the movement of bubbles trapped in the wick and not detected on the recordings were

observed, having a frequency of 1.5–1.8 pulses  $s^{-1}$ . Since the frequency of these small oscillations was consistent with the heartbeat frequency, it is considered probable that these small fluctuations represented the superposition of circulatory pressure on the pressure generated by the pharyngeal pump.

#### DISCUSSION

##### *Structure and function of the oral apparatus*

The oral apparatus of *P. mesaensis*, represented schematically in Fig. 2, is similar to descriptions of scorpion feeding organs given by Snodgrass (1965). Venkateswararao (1967) is the sole observer to note the presence of a unique grinding mill and to interpret the functions of the complex feeding organs. Most accounts agree that the pedipalps are used to capture and hold the prey with the sting being employed only to quell struggling. When the prey is subdued, it is brought within reach of the chelicerae which tear off small pieces and pass them posteriorly into the preoral cavity, where they are ground by a mill formed by the coxal endites of the first pair of walking legs. The endites, which have ridges of stiff setae on their opposing faces, slide across one another and reduce the larger prey fragments into fine particles. Simultaneously, the digestive secretions of the gnathocoxal glands present in both endites may aid in this process (Auber, 1960). The endite of the second pair of walking legs forms the lower plate of the preoral cavity and houses an elaborate canal system ramifying from a central midline canal, or gutter, and leading to the mouth. Venkateswararao (1967) suggests that fluid may flow passively down this gutter system to the mouth. In *P. mesaensis* at least, it is likely that the mouth connects the pharynx, whose function is discussed below, to this canal system which may serve to provide fluid contact with the masticated prey and to filter out the cuticular fragments.

A partly-digested mixture of solubilized prey tissues is ingested with the larger fragments, including most of the cuticle, being formed into compact feeding pellets and discarded. The efficiency of the grinding of the coxal endites is evidenced by the minute size of the cuticular fragments which make up the feeding pellets. When *P. mesaensis* was fed *T. molitor* larvae, the feeding pellets contained cuticular fragments

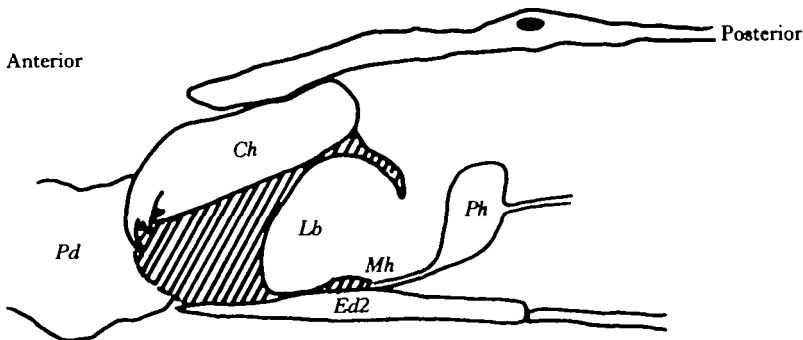


Fig. 2. Schematic drawing of a longitudinal section through the anterior of *Paruroctonus mesaensis*. Pd, base of pedipalp; Ch, chelicera; Lb, labrum; Mh, mouth; Ph, pharynx; Ed2, coxal endite of the second pair of walking legs; cross-hatched area depicts the preoral cavity.



Table 4. Size frequency and percentage area composition of cuticular fragments in feeding pellets of *Paruroctonus mesaensis* fed *Tenebrio molitor* larvae

	Mean linear dimensions ( $\mu\text{m}$ )						
	10	10-20	20-30	30-40	40-50	50-60	60
Frequency (%)	52.6	32.3	10.2	3.5	0.54	0.4	0.4
Area (%)*	14.8	36.2	25.8	15.7	3.5	4.0	—

\* Percent area composition was calculated by assuming the maximal linear mean dimension for each size category.  
*N* = 1897.

having a mean linear dimension of less than 10  $\mu\text{m}$  in the greatest frequency, with most of the total cuticular mass being made up of particles from 10-30  $\mu\text{m}$  (Table 4).

#### *Suction pressure of the pharyngeal pump*

Parry (1954) observed that several species of spiders were able to extract water from soil under considerable suction pressures. Using carborundum powder and applying suction to the interstitial water of the powder, Parry was able to demonstrate weight gain by spiders placed on substrates with suction pressures of 400 mmHg applied. Scorpions have also been demonstrated to possess the ability to take up water from wet soils (Crawford & Wooten, 1973; Riddle *et al.* 1976). In preliminary studies, *P. mesaensis* secured net water from moistened sand from its dune habitat containing 7% water by weight.

The magnitude of the suction generated by *P. mesaensis*, measured directly, reached 130 mmHg, which is considerably less than the suction pressures necessary to explain the uptake of soil water by spiders as shown by Parry (1954). However, the suction pressures measured in the present experiment should be considered as minimal estimates of the capability of the scorpion. It is quite likely that the probe-scorpion junction did not precisely duplicate the physical characteristics of the normal contact with the prey mass and therefore could not sustain the same magnitude of suction pressures. In addition, the necessary tubing imposed unnatural positions on the chelicerae and the base of the pedipalps, which normally completely enclose the preoral cavity. Upon occasion, the scorpions did press inward with the base of the pedipalps and the chelicerae on the preoral cavity, producing positive pressures. Similar movements were noted during normal feeding behaviour, suggesting that the scorpion may not only form the feeding pellets with these movements but also enhance the pressure gradient driving fluids into the mouth by exerting positive pressure on the prey mass being processed.

It seems likely that each suction pulse observed corresponded to a single pumping cycle by the muscular pharynx. This hypothesis requires that the fluid connection between the material in the preoral cavity and the pharynx be disrupted periodically to allow the pharynx to recycle. After an increase in suction pressure, which presumably requires the expansion of the pharynx, the connection with the preoral cavity must be obstructed to allow the pharynx to contract to its initial volume without

affecting the pressure generated in the preoral cavity. A simple sphincter, perhaps at the mouth, may provide this necessary function.

#### *Prey water uptake*

The method of feeding employed by scorpions results in the incomplete ingestion of the constituents of the prey. There is selective intake of soluble and easily digested components with the rejection of the great majority of refractory materials. Consequently, the scorpion ingests less water with a greater concentration of nutritive substances and defaecates smaller quantities of indigestible materials than animals which consume the entire prey. However, the overall utilization of prey energy by the scorpion is comparable to vertebrate predators feeding on the same prey (S. D. Yokota & K. Nagy, in preparation). One notable potential disadvantage to this process is that not all the prey water is available to the scorpion. Feeding water losses result from the inability to extract all water from the remains of the prey and from evaporation during feeding. Since *P. mesaensis* feeds in exposed positions in its sand dune habitat, evaporative water loss may be significant. Moreover, since prey body water is thought to represent the only water intake for much of the year (Hadley, 1974), the efficiency of prey water uptake may be crucial to the water balance of the scorpion in its natural environment. However, compensating for the lowered water intake is the consequence that lesser amounts of faecal material need be produced because less indigestible material refractory to digestion (i.e. chitin) is ingested. This would minimize faecal water expenditure.

To the author's knowledge, there are no similar reported data for the water intake of animals feeding in the selective manner of scorpions. An interesting result of the water flux analysis is that most of the water lost during feeding arose from scorpion body water. This result is consistent with observations of copious oral secretions during feeding (Stahnke, 1966). It would appear that the scorpion produces much greater quantities of digestive fluids than it eventually loses with the feeding pellets. It should be noted that both the isotopic and gravimetric techniques used in this study yield information only about the net movements of prey and scorpion water. Recirculation of the prey and scorpion body water inevitably occurs during the lengthy feeding period as the scorpion processes successive portions of the prey. In addition, the efficiency of water intake may be subject to environmental conditions. If one assumes that the ability of the scorpion to withdraw water from the food mass is constant, then the single variable affecting the efficiency of water uptake would be the magnitude of evaporation. Since fluids can frequently be seen in the preoral cavity during the feeding process, evaporation would appear to be a significant factor from this exposed surface. The magnitude of the evaporative losses would depend on the temperature, humidity, wind velocity, and the area and time of exposure. The handling time would be complicated by the size and nature of the prey.

#### *Excretory water*

Despite earlier generalizations that desert scorpions eliminate dry excreta (Hadley, 1974), *P. mesaensis* was never observed to excrete dry material. Fresh excreta appeared to have a paste-like consistency but with substantial water contents. Xanthine is the major nitrogenous excretory product of *P. mesaensis* and it possess

The low water solubility characteristic of purines (Yokota & Shoemaker, 1981). The excretory purines can be eliminated almost entirely in the solid state by the withdrawal of water from the primary urine in the hindgut. Therefore, additional water eliminated with the urine may be committed to the excretion of electrolytes and regulation of water balance, rather than necessitated by nitrogen excretion. The wide range of water contents found in the excreta of *P. mesaensis*, from 43–75 %, suggests that the scorpion may exert considerable control over the water content of the excreta, perhaps in response to its hydrational status.

#### *Electrolyte and nitrogen uptake and excretion*

The criterion used to distinguish faeces from urine (presumed products of the Malpighian tubules), that is colour, is arbitrary and tends to overestimate faecal contributions. It is quite likely that urine is continuously emptied into the gut and mixes with whatever chyme may be present. Therefore, excreta designated as faecal in this study probably represent a variable mixture of urine and faeces. The mixing of the two components may be reflected by the similarity of the nitrogen contents, being 27.0 and 29.5 % of the faeces and urine respectively. Moreover, whether the gut contents are segregated or not, the hindgut is likely to handle them identically with respect to water and electrolytes. The inability to separate faeces and urine reliably leads to an overestimate of faecal nitrogen excretion and consequently to an underestimate of the efficiency of nitrogen assimilation, calculated to be 50 % from the present data.

One can make estimates of the electrolyte concentrations of the ingested fluids, pellet fluid, faeces and urine using the measurements from the water flux experiments and the known mass and electrolyte content of the prey, pellets and excreta (Table 5). These calculations suggest that the ingested fluid is not representative of the whole body electrolyte concentrations of *T. molitor*, sodium and chloride being present in greater concentrations and potassium at lesser concentrations. The calculated ingestion efficiencies for each electrolyte reflect these differences, with the scorpion ingesting a significantly lower fraction of the prey potassium than sodium or chloride (Table 3). There appear to be two explanations for this differential uptake of the electrolytes.

Table 5. *Electrolyte content\* and estimated concentrations in ingested fluids, urine and faeces*

	Sodium		Potassium		Chloride	
	( $\mu\text{mol g}^{-1}$ )	( $\text{mmol l}^{-1}$ )	( $\mu\text{mol g}^{-1}$ )	( $\text{mmol l}^{-1}$ )	( $\mu\text{mol g}^{-1}$ )	( $\text{mmol l}^{-1}$ )
<i>Tenebrio</i> adult (whole body)	68	36	273	146	158	84
Feeding pellets§	61	26	478	205	170	73
Fluid ingested†	—	50	—	90	—	103
Faeces‡	53	30	1094	625	258	145
Urine‡	57	32	955	546	296	169

\* Data represent mean values from feeding experiment.

† Calculated from electrolytes ingested assuming a net uptake of 51 % of the prey  $\text{H}_2\text{O}$ .

‡ Calculated from the average water content of *Paruroctonus mesaensis* excreta, 1.75 ml  $\text{H}_2\text{O g}^{-1}$  dry mass.

§ Calculated assuming a water content of 70 %.

Table 6. *Calculations of the water and material balance for Paruroctonus mesaensis in steady state nitrogen balance and fed a 1 g cricket\**

	Prey	Ingested	Excreted†	Net gain
Dry weight (mg)	300	216	64	152
Nitrogen (mg)	30	18	18	0
Water (mg)	700	357	112	245

\*The calculations for this table were based on ingestion efficiencies for water, nitrogen and dry material of 51%, 60.8% and 72% respectively, a cricket water content of 70% of fresh mass and a nitrogen content of 10% of the dry mass.

†The nitrogen content of the excreta is assumed to be 28.5% of the dry mass. The water content of the excreta is assumed to be 1.75% ml H<sub>2</sub>O g<sup>-1</sup> dry mass.

One is the possible compartmentalization of potassium in intracellular pools which are more resistant to extraction by the digestive fluids of the scorpion. A more likely explanation is that the digestive fluids secreted by *P. mesaensis* have high concentrations of potassium. Mommsen (1978) has found that the oral digestive secretions of the spider *Tegenaria atrica* have potassium concentrations about nine times those found in the haemolymph. The salivary glands of several insects have also been found to secrete potassium enriched fluids (Maddrell, 1971).

*P. mesaensis* displays a marked ability to excrete potassium. Assuming that all potassium was excreted in solution, the calculated potassium concentrations in the urine and faeces are 6.1 and 6.9 times the concentration estimated for the ingested fluid, respectively (Table 5). The estimated potassium concentration of the excreta was about 600 mmol l<sup>-1</sup>, about 100 times the haemolymph potassium concentration (S. D. Yokota, in preparation). The calculated sodium and chloride concentrations of the excreta are more nearly equal to the calculated concentrations of the ingested fluid (Table 5). If the white excreta, or urine, were the product of the Malpighian tubules, these observations suggest that scorpion Malpighian tubules may function in a manner similar to that of some insects. Insect Malpighian tubules typically produce a secretion (urine) isosmotic to the haemolymph by the active transport of potassium into the lumen of the tubule (Maddrell, 1971). In view of the low potassium concentration of the haemolymph of *P. mesaensis* the existence of an active potassium pump seems likely. Thus far, there have been no studies relevant to this hypothesis in the arachnids.

#### *Prey water utilization*

It is possible to calculate the net utilizable water that *P. mesaensis* obtains from its prey from the present data. The following example is calculated for a 1 g prey containing 100 mg nitrogen and 2.33 ml H<sub>2</sub>O per gram dry mass, using the average water content of excreta, 1.75 ml H<sub>2</sub>O g<sup>-1</sup> dry mass, and assuming the scorpion to be in steady state with respect to nitrogen (Table 6). Since the scorpion has an ingestion efficiency of 60.8% for nitrogen (Table 3), 18 mg of the 30 mg of nitrogen in the prey is ingested. In the steady state, 64 mg dry mass of excreta is required to eliminate the nitrogen ingested. Using the average excreta water content, 112 µl of water is lost

excretion. Since the scorpion initially gains a net intake of 51 % of the prey water, or 357  $\mu\text{l}$  water, 245  $\mu\text{l}$  of water is the net gain, or utilizable water. The net utilizable water, that is the water ingested which is not committed to the elimination of nitrogenous wastes, is equal to 69 % of the water ingested and 35 % of the original prey water. The water content of the excreta produced will affect the magnitude of the utilizable water. The water content of the excreta varied over a four-fold range. Assuming the minimal observed excreta water content of 0.75 ml  $\text{H}_2\text{O g}^{-1}$  dry mass, the net utilizable water can be estimated as equal to 87 % of the ingested water and 44 % of the initial prey water. In summary, it appears that, although the scorpion only makes a net gain of about one-half of the water contained in its prey, it is able efficiently to retain the water it does obtain because excretory losses are small.

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