

LOW METABOLIC RATE IN SCORPIONS: IMPLICATIONS FOR POPULATION BIOMASS AND CANNIBALISM

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Summary

Scorpions are abundant in arid areas, where their population biomass may exceed that of vertebrates. Since scorpions are predators of small arthropods and feed infrequently across multi-year lifespans, a parsimonious explanation for their observed, anomalously high biomass may be a depressed metabolic rate (MR). We tested the hypothesis that scorpion MR is significantly depressed compared with that of other arthropods, and we also measured the temperature-dependence of the MR of scorpions to quantify the interaction between large seasonal variations in desert temperatures and MR and, thus, long-term metabolic expenditure. Scorpion MR increased markedly with temperature (mean $Q_{10}=2.97$) with considerable inter-individual variation. At 25 °C, the

MRs of scorpions from two genera were less than 24% of those of typical terrestrial arthropods (spiders, mites, solpugids and insects) of the same mass. It is likely, therefore, that the low MR of scorpions contributes to their high biomass in arid areas. The combination of high biomass and high production efficiency associated with low MR may also favor a density-dependent 'transgenerational energy storage' strategy, whereby juveniles are harvested by cannibalistic adults that may be closely related to their juvenile prey.

Key words: scorpion, metabolic rate, Q_{10} , population ecology, biomass.

Introduction

The natural history of scorpions is interestingly divergent from those of other arthropods that inhabit arid areas. Even taking into account a trend towards disproportionately high predator biomasses in arid areas (Chew, 1961), scorpions are 'extraordinarily abundant' (Polis and Yamashita, 1991). Polis and Yamashita (Polis and Yamashita, 1991) calculate that scorpion biomass, at over 50 kg ha⁻¹, exceeds that of all other arthropod taxa except ants and termites. Vertebrate biologists may be surprised to learn that in arid areas scorpion biomass exceeds that of all vertebrates combined, while making up approximately 7% of total arthropod biomass (Polis and Yamashita, 1991).

Ecologically, scorpions are characterized as 'equilibrium' species (Polis and Farley, 1980), with a stable *K*-selected (e.g. long-lived, low fecundity, efficient exploitation of resources; Keeton, 1976) standing population and density-dependent mortality. They are 'sit-and-wait' predators that feed on the surface only until a set amount of energy has been assimilated, thereafter returning to their burrow to minimize exposure to predation (a fixed-risk probability). Scorpions are therefore 'time minimizers' (Schoener, 1971; Polis, 1980), and their population dynamics is relatively insensitive to wide fluctuations in energy and water availability (Bradley, 1984; Polis and Farley, 1980; but see Polis and McCormick, 1987).

Yet stability does not equal success. What determines the outstanding success of scorpions in arid habitats? If we define the 'success' of a species as high biomass, the answer must reside in knowing how population biomass accumulates and dissipates. Given an overall energy flux rate through a given species, or 'guild' of ecologically similar species, total biomass is an inverse function of total metabolic rate (MR), other factors being constant. Low MR shunts more of the total energy flux of a species away from respiration, making it available for growth and reproduction. In broad terms, a lowered metabolic rate should increase production efficiency, thereby increasing population biomass for a given energy input, leading, in terms of our rather narrow definition, to 'success'.

Given that scorpion metabolic physiology is, therefore, central to the informed study of scorpion ecology, surprisingly few rigorous data are available. Polis and Yamashita (Polis and Yamashita, 1991) summarized the scattered measurements of scorpion MR in the literature and added some of their own. They reported MRs on a mass-specific basis across very different body mass ranges, concluding that scorpion MRs are 'an order of magnitude less than insects and slightly lower than spiders'. This conclusion contradicts Greenstone and Bennett (Greenstone and Bennett, 1980), who reported that the of MR

spiders is two-thirds of the value predicted for an insect of the same mass. Obviously, the ability to make accurate measurements of arthropod MR is a complicating factor here and in other studies. Traditional methods of MR measurement are long-term, integrative and lack objective indices of behavioral state, of which MR is an exquisitely sensitive function. With the advent of sensitive flow-through measurement technology for real-time measurement of both metabolic rate and activity (Lighton, 1991; for discussion, see also Lighton and Fielden, 1995), measurements can now be made that are accurate enough to separate the signal of genuine variation from the noise of instrumental technique. In this study, we used such techniques to determine whether the mass scaling allometry of the MR of scorpions differs from that of other arthropods.

Five species of scorpion from two New World genera were used to test the null hypothesis that scorpions exhibit MRs characteristic of other common terrestrial arthropods. In addition, we supplemented our measurements with measurements taken from the literature for four Old World scorpion species in four genera. Bearing in mind the probable importance to long-term survival of low metabolic rates during sustained periods of inactivity (winter) and the observed preference of foraging scorpions for moderate surface temperatures (Warburg and Polis, 1990), we also theorized that the temperature-sensitivity of the MR of scorpions was high, thus acting to depress the MR of scorpions at low temperatures. We therefore also tested the null hypothesis that scorpions exhibit a metabolic sensitivity to temperature similar to that of other common arthropods.

Materials and methods

Animals

Adult and juvenile scorpions of five species were collected in the Mojave Desert near Baker, CA, USA, during August and November, and in Henderson, NV, USA, during November (see Table 1 for species identification and their masses). In the laboratory, scorpions were housed individually in small containers with sand and fed weekly with 1–2 crickets of appropriate size. The sand was moistened periodically to maintain humidity. Ambient laboratory temperatures were 22–25 °C. Only those individuals that maintained body mass and apparent condition, but had not fed within the 24 h prior to an experiment, were used for measurements.

Respirometry

Flow-through analysis of CO₂ production was performed using a LiCor 6251 CO₂ analyzer connected to a computerized data-acquisition system (Sable Systems Datacan V; <http://www.sablesys.com>). Flow was maintained with a Tylan mass-flow valve and a Sable Systems MFC-1 controller at either 25 ml min⁻¹ for small scorpions or 100 ml min⁻¹ for the largest scorpions. The respirometer chamber incorporated an activity monitor consisting of two red LED (light-emitting diode)/photodetector pairs aligned across the long axis of the

chamber. The current outputs of the photodetectors, which varied with animal activity, were converted to a differential voltage that was monitored continuously by the data-acquisition system. The respirometer chamber was enclosed in a Peltier-effect constant-temperature cabinet controlled by the data-acquisition system over the range 15–30 °C with a precision of ±0.1 °C. By using a copper equilibration coil, incurrent air to the respirometer chambers was maintained at cabinet temperature. The cabinet was dark except for the red 650 nm glow of the activity monitor LEDs.

Our estimate of MR is dependent on assumptions about the respiratory substrate used by motionless scorpions. We assumed that lipid was the respiratory substrate because it is the only reasonable choice for long-term energy storage (see Withers, 1992). More specifically, the mean respiratory quotient of our scorpions (data not shown; acquired with Ametek S3-A oxygen analyzer) was 0.73, typical of lipid catabolism (see also Paul et al., 1989). In terms of MR measurement our choice of lipid as the respiratory substrate is actually conservative. Assuming a carbohydrate- or protein-based catabolism, the energy yield per unit CO₂ relative to lipid is reduced and results in a still lower estimate of MR. Our conclusions are not, therefore, biased by our assumption that lipids are the primary metabolic fuel reserves in scorpions.

Effects of body size on metabolic rate

Individuals were placed in the chambers and monitored overnight (total recording time 16–24 h) with the temperature set at 25 °C. Metabolic rate was calculated by identifying 60 min periods when the scorpion was motionless and selecting the lowest mean rate of CO₂ emission (\dot{V}_{CO_2}) over a 30 min interval within each period. Where more than one such 60-min period was found, their \dot{V}_{CO_2} values were averaged. Both \dot{V}_{CO_2} and metabolic rate were calculated from the equations in Lighton (Lighton, 1991) assuming aerobic catabolism of lipid.

Effects of temperature on metabolic rate

Individual scorpions were placed in chambers and exposed successively to 15, 20, 25, 30 and 35 °C with a minimum 1 h equilibration period between measurements at different temperatures. When the highest temperature was reached, the sequence was reversed. The up and down temperature-ramping procedure was continued until two or more 1 h recordings had been completed at each temperature. Metabolic rates were calculated as above by selecting the lowest mean CO₂ emission for each experimental temperature. Q₁₀, which is a measure of the temperature-sensitivity of MR, was calculated separately for each individual by computing the antilogarithm of the (slope × 10) of the regression of log(metabolic rate) *versus* temperature (see Lighton and Bartholomew, 1988).

Statistical analyses

Means are reported with sample sizes and standard deviations. Regressions were calculated by least squares using programs written by J.R.B.L. and validated against SYSTAT version 4 (Wilkinson, 1987). Axis transformation was used

Table 1. Metabolic rates and masses of New and Old World scorpions

Species	Family	Ecotype (locality)	Experiment	Stage*	Mass (g)	Metabolic rate (μ W)	Q ₁₀	
A								
<i>Hadrurus arizonensis</i>	Hadrurinae	Fossorial‡, xeric	M	Larval 3/4	2.250	508.6	–	
<i>Hadrurus arizonensis</i>	Hadrurinae	(Mojave)	M	Larval 3/4	1.450	162.4	–	
<i>Hadrurus arizonensis</i>	Hadrurinae		M	Adult male	8.900	1639	–	
<i>Hadrurus arizonensis</i>	Hadrurinae		M	Larval 2/3	1.500	364.3	–	
<i>Hadrurus arizonensis</i>	Hadrurinae		M	Adult female	9.000	1526	–	
<i>Paruroctonus luteolus</i>	Vaejovidae	Fossorial‡, xeric	M	Adult	0.120	40.22	–	
<i>Paruroctonus luteolus</i>	Vaejovidae	(Mojave)	M	Adult	0.136	30.99	–	
<i>Paruroctonus luteolus</i>	Vaejovidae		M	Adult	0.218	76.36	–	
<i>P. mesaensis</i>	Vaejovidae	Fossorial‡, xeric	M	Larval	0.164	30.69	–	
<i>P. mesaensis</i>	Vaejovidae	(Mojave)	M	Larval	0.412	110.4	–	
<i>P. mesaensis</i>	Vaejovidae		M	Adult female	2.380	623.4	–	
<i>P. mesaensis</i>	Vaejovidae		M, T	Larval	0.443	135.2	2.22	
<i>P. mesaensis</i>	Vaejovidae		M, T	Larval	0.393	143.8	3.06	
<i>P. mesaensis</i>	Vaejovidae		M, T	Larval	0.710	116.5	3.41	
<i>P. mesaensis</i>	Vaejovidae		T	Larval	0.541	–	3.69	
<i>P. mesaensis</i>	Vaejovidae		M, T	Larval	0.553	144.0	3.18	
<i>P. mesaensis</i>	Vaejovidae		M	Adult male	1.600	368.1	–	
<i>P. marksi</i>	Vaejovidae	Fossorial‡, xeric	M, T	Larval	0.567	129.1	3.27	
<i>P. becki</i>	Vaejovidae	(Mojave)	M, T	Larval	0.767	325.8	2.43	
<i>P. becki</i>	Vaejovidae		M, T	Larval	0.544	134.8	2.52	

Species	Family	Ecotype (locality)	Experiment	Mass (g)	Metabolic rate (μ W)	Q ₁₀	N
B							
<i>Opisthophthalmus flavescens</i> ¹	Scorpionidae	Fossorial‡, dunes, xeric (Namib)	M	5.260	1306	3.06	5
<i>Parabuthus villosus</i> ¹	Buthidae	Fossorial‡‡, xeric (Namib)	M	6.030	1687	2.50	8
<i>Pandinus imperator</i> ²	Scorpionidae	Fossorial‡, humid/tropical (African tropical forests)	M	15.00	2109	3.00	32
<i>Urodactylus armatus</i> ³	Scorpionidae	Fossorial, sandplain, mesic (W. Australia)	M	0.50	117.9	3.06	23

¹Bridges et al., 1997; ²Paul et al., 1989; ³Withers and Smith, 1993.

*3/4, 2/3 indicate developmental stage.

‡Shallow burrows; ‡‡burrows 30–50 cm deep.

Values in A are taken from the current study; values in B are calculated from values in the literature assuming a respiratory quotient of 0.72 (fat catabolism).

M, mass experiments; T, temperature experiments.

where known relationships are allometric rather than isometric (Bartholomew, 1977; Withers, 1992). Regressions were compared using analysis of covariance (ANCOVA), also using programs written by J.R.B.L. and validated as above.

Results

Effects of body size on metabolic rate

In the five species of scorpion we investigated, metabolic

rate ranged from 40.22 μ W at a body mass of 0.12 g, to 1639 μ W at a body mass of 9.0 g (Fig. 1). Analysis of covariance by species for the species represented by three or more individuals showed no species effect (ANCOVA: $F_{2,12}=0.579$, $P>0.4$). Pooling species by adult individuals only, resulting in one data point per species, produced a regression line that did not differ significantly (by ANCOVA) from that for our entire data set, including juveniles. Neither the inclusion of all species, therefore, nor the inclusion of juveniles

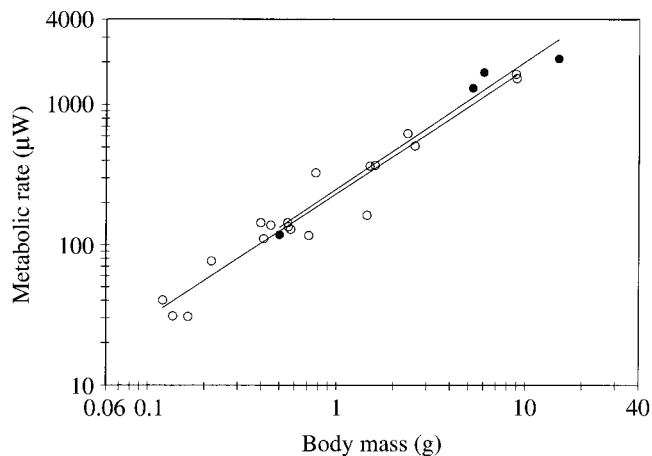


Fig. 1. Metabolic rate (MR in μW) versus body mass (M_b in g) for nine species of scorpion. Five species (open circles) are from this study (see Table 1); one (*Pandinus imperator*) is from Paul et al. (Paul et al., 1989), one (*Urodactus armatus*) is from Withers and Smith (Withers and Smith, 1993) and two (*Parabuthus villosus* and *Opisthophthalmus flavescens*) are from Bridges et al. (Bridges et al., 1997), and these are indicated by filled circles. The equation relating metabolic rate to body mass for all scorpions was $\text{MR} = 235M_b^{0.90}$, $r^2 = 0.953$, $F_{1,21} = 424$, $P < 0.0001$. The standard error of the slope was 0.044.

biased our results. Data were accordingly pooled across individuals and species rather than analyzed by species or age class. The allometric equation relating metabolic rate (MR) to body mass (M_b) for all measured scorpions in this study was:

$$\text{MR} = 231M_b^{0.885}, \quad (1)$$

where MR is in μW and M_b is in g ($r^2 = 0.937$, $F_{1,17} = 251$, $P < 0.0001$).

To increase the general applicability of our study, we supplemented our data set with measurements by other authors of four scorpion species (see Fig. 1 legend for species and citations). The addition of these species had almost no effect on our estimation of the mass allometry of MR. By ANCOVA, the two data sets differed neither in slope ($P > 0.4$) nor in intercept ($P > 0.4$) and were therefore combined. The allometric equation relating metabolic rate to body mass in the combined data set was:

$$\text{MR} = 235M_b^{0.90}, \quad (2)$$

where MR is in μW and M_b is in g ($r^2 = 0.953$, $F_{1,21} = 424$, $P < 0.0001$). The standard error of the mass scaling exponent was 0.044. The MR of scorpions was considerably lower than MR of most other arthropods of equivalent body mass (see Discussion).

Effects of temperature on metabolic rate

We tested the temperature-sensitivity of MR in three species: *Paruroctonus mesaensis*, *P. marksi* and *P. becki*. Metabolic rate, corrected for mass (by dividing by body mass raised to the value of the mass scaling exponent in equation 1), increased exponentially with temperature for all individuals

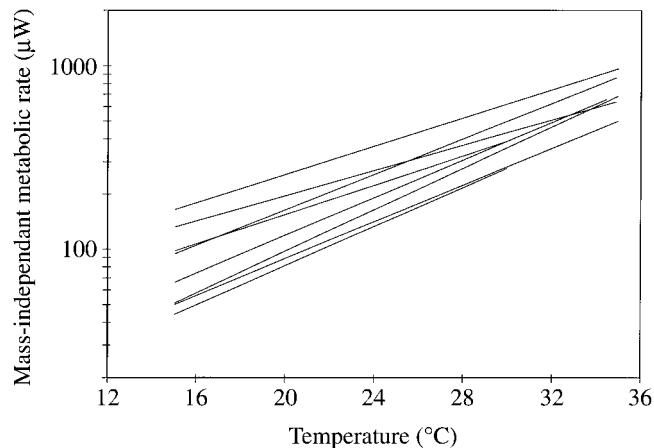


Fig. 2. The relationships between mass-independent metabolic rate and temperature for individual scorpions. Mass-independent metabolic rate was calculated by dividing metabolic rate by (body mass)^{0.885} (mass in g; see equation 1). These data were used to calculate values of the temperature coefficient, Q_{10} . Each line corresponds to an individual scorpion and is calculated from 5–15 individual measurements across the temperature range indicated. Individual r^2 values ranged from 0.93 to 0.99 (individual data points for each line are not shown; see Table 1 for masses and species). Mean Q_{10} was 2.97; see text for discussion.

tested (Fig. 2). The measured Q_{10} varied significantly among individuals (ANCOVA: $F_{7,22} = 3.40$, $P = 0.01$), and each individual showed a consistent and tightly determined temperature response, with typical r^2 values of $\log(\text{MR})$ versus temperature exceeding 0.93. The inter-individual variation did not allow us to combine Q_{10} data within species, so we could not compare Q_{10} among species. However, data for *P. mesaensis* ($N = 6$) did not differ from the overall mean value ($t = 0.47$, $P > 0.4$), suggesting no significant interspecific difference in temperature-sensitivity. The mean Q_{10} for all species was 2.97 ± 0.163 (mean \pm s.d., $N = 8$) with a range of 2.2–3.6.

Discussion

Metabolic rate relative to other arthropods

To test our null hypothesis that the MRs of scorpions are equivalent to those of other free-living arthropods, we compared our pooled scorpion metabolic scaling data (see Results and Fig. 1) with data derived from such arthropods. We used data from chelicerates (mites, Lighton and Duncan, 1995; ticks, Lighton and Fielden, 1995; solpugids, Lighton and Fielden, 1996; araneids, from data cited by Lighton and Fielden, 1995) and several hexapod orders (data cited by Lighton and Fielden, 1995). All the non-scorpion, non-tick data ('typical arthropods' in Fig. 3) formed a single line [ANCOVA: $P(\text{same slopes}) > 0.3$; $P(\text{same intercepts}) = 0.2$]. We then used ANCOVA to assess the null hypothesis that the mass scaling exponents of the 'typical arthropods', the scorpions and the ticks were equivalent. The shared mass scaling exponents

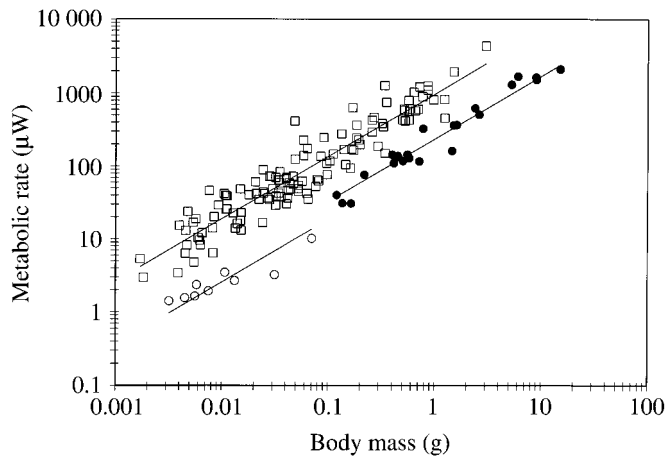


Fig. 3. Metabolic rate (MR in μW) versus body mass (M_b in g) for scorpions (filled circles), for ticks (open circles) and for five groups of typical arthropods (spiders, ants, beetles, solpugids and mites; open squares). Data for ticks, ants, spiders and beetles are taken from Lighton and Fielden (Lighton and Fielden, 1995), data for solpugids are taken from Lighton and Fielden (Lighton and Fielden, 1996) and data for mites are taken from Lighton and Duncan (Lighton and Duncan, 1995). See text for equations.

(=slopes) did not differ between these groups [ANCOVA: $P(\text{same slopes}) > 0.2$; shared mass scaling exponent = 0.856 ± 0.024 , mean \pm S.E.M.] Given that the three groups shared the same mass scaling exponent, we could test for differences in intercepts between the three groups and thus assess whether, for any given body mass, MR would differ between them. By ANCOVA, $P(\text{same intercepts})$ was negligible ($P < 10^{-6}$). The intercepts of the three groups were therefore entirely distinct.

The mass scaling equation for non-tick, non-scorpion arthropods was:

$$\text{MR} = 973M_b^{0.856}, \quad (3)$$

where MR is in μW and M_b is body mass in g at 25°C . The scorpion data formed a second, parallel line with a substantially lower intercept [24% of the general arthropod intercept; ANCOVA: $P(\text{same intercepts}) < 0.001$] and an identical slope [ANCOVA: $P(\text{same slope}) > 0.2$]. The mass scaling equation for this line was:

$$\text{MR} = 236M_b^{0.856}, \quad (4)$$

where the units are as in equation 3 (see Fig. 3). Ticks, as expected (Lighton and Fielden, 1995), form a third line with the same slope and a still lower intercept:

$$\text{MR} = 132M_b^{0.856}, \quad (5)$$

where the units are as in equation 3.

Scorpions, therefore, uniformly display MRs that are only 24% of those predicted for 'typical' (non-dormant) free-living hexapod or chelicerate arthropods of similar body mass. This test falsifies our null hypothesis that scorpions exhibit MRs typical of other free-living arthropods.

What do we mean by 'typical' arthropods in this context? Lighton and Fielden (Lighton and Fielden, 1995) examined

quantitatively several diverse hexapod orders and several aranaeid orders in the chelicerates and concluded that their MRs scaled identically as a function of body mass. This conclusion contradicted previous studies that claimed much lower MRs for aranaeid chelicerates than for hexapods (Anderson, 1970; Greenstone and Bennett, 1980). These and other earlier studies (e.g. Paul et al., 1989) used general metabolic scaling equations, especially those of Hemmingsen (Hemmingsen, 1960), as yardsticks against which to compare their data. These equations, as it turns out, overestimate MR when extrapolated to arthropod body masses. The study of Lighton and Fielden (Lighton and Fielden, 1995) supports the probability that, across diverse taxa of arthropods, the chronic energy flux required to sustain life processes, or to stem entropy, is a remarkably conservative function of body mass. The work of West et al. (West et al., 1997), modeling organismal design with fractal mathematics, suggests reasons for the common slope of these allometric relationships but, to date, there is no mechanistic explanation for the similarity of intercepts, a similarity that is as striking as it is unexpected.

To date, the only arthropod clade that demonstrably possesses an anomalously low MR is the ixodid ticks (13% of the typical arthropod MR; Lighton and Fielden, 1995). The acarine clade, from which they and argasid ticks have diverged, appears to be metabolically typical of other arthropods (Lighton and Duncan, 1995). Depressed MR in the ixodid branch appears to be an apomorphic character that facilitates long-term survival between blood meals, a period of fasting that may last several years (Needham and Teel, 1991), but its mechanism is, as yet, unknown.

Scorpions now join the tiny and exclusive group of arthropods known to possess routinely depressed MRs. We emphasize that the data in Table 1 and Figs 1 and 3 suggest that a depressed MR among scorpions is a general phenomenon, not restricted to particular families or niche-dwellers within the scorpion clade. The pooled data incorporate species from four families and include representatives from xeric, mesic and hygric habitats.

At less than 25% of typical arthropod MR, the metabolic rates of scorpions are not as dramatically reduced as those of ticks. Scorpions, however, are by no means as specialized as ticks. Scorpions earn an 'honest living' as sit-and-wait predators, not as opportunistic ectoparasites. They have a correspondingly greater investment than ticks in metabolic scope for activity, in prey-capture paraphernalia such as pincers and stings and thus, of necessity, in muscle tissues that may be metabolically expensive even when idle (Brody, 1945).

The mechanism of metabolic depression in scorpions is unknown. Hypotheses worth testing on scorpions in the light of the present study include unusually low plasma membrane permeability (P. W. Hochachka, personal communication), high mitochondrial efficiency (Hochachka and Somero, 1984; R. Suarez, personal communication), low mitochondrial volume density (R. Suarez, personal communication) and

perhaps an unusually high reliance on phosphagen storage (Hochachka and Somero, 1984) and high mitochondrial sensitivity to functional hypoxia and/or hypercapnia, possibly induced by ventilatory depression during inactivity.

Temperature effects on metabolism

The temperature-sensitivity of metabolic rate was relatively high at $Q_{10}=2.97$. Typical ectothermic heterotherms display Q_{10} values in the range 2.0–2.5 (Bartholomew, 1977; Withers, 1992). On average, scorpions experience a near-tripling of metabolic rate for a 10 °C increase in temperature (see also Bridges et al., 1997), but the precise extent of this increase varies widely among individuals. As a result of this inter-individual variability, which increased the variance of our measurements, the Q_{10} of our scorpions was not significantly higher than the upper end of the range for ectothermic heterotherms ($Q_{10}=2.5$, $t=-0.94$, $P=0.38$). Nevertheless, scorpion Q_{10} values are suggestively high, both in our hands and those of other investigators. A Mann–Whitney U -test comparison of Q_{10} values from this study with that of mean scorpion Q_{10} values available for scorpions from the literature (grouped literature mean $Q_{10}=2.91$) did not support a significant difference [$P(\text{same means})>0.20$; see Table 1 for values]. Scorpions will, therefore, maintain their roughly fourfold reduction in energy requirements relative to most other arthropods across a broad range of temperatures and across the inactive as well as the active seasons of the year. Our null hypothesis that these scorpions display a temperature-sensitivity of MR similar to that of typical arthropods is not falsified. However, research on the mechanisms of inter-individual variation in metabolic sensitivity to temperature in scorpions is warranted.

Ecological implications

Relative to most other arthropods, scorpions display a fourfold reduction in population-wide energy flux rates, with an accompanying increase in production efficiency (McCormick and Polis, 1990). The ecological implications of a low MR help to explain the anomalously high biomass of scorpion populations, as other authors have hypothesized (see Polis and Yamashita, 1991).

A low MR may also explain another peculiarity of scorpion natural history, their propensity for intraguild predation and, in many groups, cannibalism (Polis, 1981). In simple terms, for a given energy flux through a population, reducing the MR of that population increases its biomass, and with increased biomass comes an increase in population density if individual masses remain constant. As scorpion population density increases, the probability that the next arthropod encountered will be another scorpion also increases. The ranges of adult scorpions are limited, and the ranges of juveniles are even more constrained (Polis et al., 1985). Prey detection and localization in scorpions depend on relatively non-selective means (Brownell and Farley, 1979), and their diet is therefore catholic (McCormick and Polis, 1990). The use of a paralysing sting to subdue large or well-defended prey permits some departure

from classic trophic limitations on useable prey size, but for encounters between small and large scorpions, resistance by the small scorpion is futile (Polis, 1988) and it will be assimilated. In this context, it is interesting to note that Polis (Polis, 1981) describes *P. mesaensis* population dynamics as a 'grazer system' in which the smallest age classes, put out to pasture, as it were, harvest prey too small for adults and thus provide indirect access to a greater range of resources for the larger age classes (see also Polis, 1988; McCormick and Polis, 1990; Dong and Polis, 1992).

Clearly, a low MR increases the efficiency with which non-scorpion prey biomass becomes scorpion biomass. A low MR may also increase the efficiency with which intraguild predation, or cannibalism, which among scorpions might be called transgenerational energy storage, facilitates the dynamic reallocation of energy and food reserves within the scorpion population as a whole. Fox (Fox, 1975) points out that the increase in fitness from an individual cannibalistic encounter need not be large for the behavior to be maintained in some systems. Has low MR selected for cannibalism among scorpions? Or, does cannibalistic behavior (which is not universal among scorpions; McCormick and Polis, 1990) in some species select for low MRs? The comparative data (see Table 1; Fig. 1), which include both cannibalistic and non-cannibalistic (e.g. *Pandinus imperator*) species, suggest that the former hypothesis is more parsimonious. However, the sum of comprehensive metabolic measurements published in the literature is sparse, to say the least. When considering the relationship, if any, between low MR and cannibalism, the direction of the arrow of causality is still problematic.

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