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The Relative Importance of Respiratory Water Loss in Scorpions Is Correlated with Species Habitat Type and Activity Pattern

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ABSTRACT

Scorpions exhibit some of the lowest recorded water loss rates compared with those of other terrestrial arthropods of similar body size. Evaporative water loss (EWL) includes cuticular transpiration and respiratory water loss (RWL) from gas exchange surfaces, that is, book lung lamellae. Estimated fractions of cuticular and respiratory losses currently available from the literature show considerable variation, at least partly as a result of differences in methodology. This study reports RWL rates and their relative importance in scorpions from two families (Buthidae and Scorpionidae), including both xeric and mesic species (or subspecies). Two of the included Buthidae were surface-dwelling species, and another inhabits empty burrows of other terrestrial arthropods. This experimental design enabled correlating RWL importance with scorpion phylogeny, habitat type, and/or homing behavior. Buthidae species exhibited significantly lower EWL rates compared with those of Scorpionidae, whereas effects of habitat type and homing behavior were not significant. Resting RWL rates were not significantly affected by scorpion phylogeny, but rates for the xeric species (totaling ~10% of EWL rates at 30°C) were significantly lower compared with those of mesic species. These lower RWL values were correlated with significantly lower H₂O/CO₂ emission rates in xeric species. The experimental setup and ~24-h duration of each individual recording allowed estimating the effect of interspecific variation in activity on RWL proportions. The high respiratory losses in active hydrated *Scorpio maurus fuscus*, totaling 30% of EWL, suggest that behavioral discretion in this species is a more likely mechanism for body water conservation under stressful conditions when compared with the responses of other studied species.

Introduction

The highly impermeable integument of many terrestrial arthropods allows them to occupy some of the driest habitats on Earth despite their relatively small body size, which exacerbates body water conservation. Scorpions exhibit some of the lowest recorded water loss rates (WLRs) among all terrestrial arthropods (Hadley 1994). A relationship between WLR and habitat type is well established for arthropods in general and has also been suggested for scorpions (Hadley 1990, 1994). It has also been shown that phylogenetic constraints contribute considerably to interspecific variation in water-relations traits in scorpions (Gefen and Ar 2004, 2005).

Terrestrial arthropods lose body water to the surrounding dry environment through both cuticular and respiratory evaporation and in their excretions. Attempts to partition evaporative water loss (EWL) in scorpions have yielded a wide range of estimated cuticular and respiratory water loss (CWL and RWL, respectively) values. Differences in methodology (dead vs. live specimens) are possibly responsible for estimated respiratory losses in *Hadrurus arizonensis* (Uridae) at 25°–35°C, ranging from negligible (Hadley 1970) to more than 30% of total losses (Gefen et al. 2009). Within this range, values of 26%–33% of total water losses were reported in *Urodacus armatus* (Scorpionidae) at 20°–30°C (Withers and Smith 1993) and 15% for *Urodacus manicatus* at 20°C (Woodman 2008).

Metabolic rates (MRs) of scorpions are fourfold lower (Lighton et al. 2001), whereas WLRs of many scorpion species are an order of magnitude lower compared with those of other terrestrial arthropods of similar body size (Hadley 1994), suggesting that RWL could be considerable in scorpions. However, reported MRs in the literature were mostly measured in studies where the scorpions were confined to a small metabolic chamber and/or subjected to light conditions under which most scorpions remain inactive, whereas EWL rates have often been determined gravimetrically without distinguishing between periods of high or low MR (and RWL) between weight measurements (e.g., Warburg et al. 1980; Gefen and Ar 2004). Therefore, a concurrent measurement of gas exchange and EWL rates may provide a better estimate of the relative importance of RWL in scorpions. A study on free-roaming *H. arizonensis* using doubly labeled water showed that field MRs were two- to threefold higher than laboratory-measured resting values (King and Hadley 1979). Increased gas exchange rates during activity entail higher RWL rates. Thus, an experimental setup allowing scorpions to express their respective activity patterns under experimental conditions may also provide a better estimate of RWL importance in the field.

Regulation of gas exchange rates, and thus RWL, particularly

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under stressful conditions (see Riddle 1978; Gefen 2008), is more likely to have been the subject of selection in scorpions if respiratory losses were substantial. In insects, xeric species exhibit higher proportions of RWL compared with those of mesic species (Zachariassen 1996; Addo-Bediako et al. 2001). This study investigates RWL in scorpions, using a five-species (or subspecies; see “Methods”) experimental design that includes xeric and mesic representatives from two scorpion families, Buthidae and Scorpionidae. Scorpion phylogeny is still contentious (e.g., Prendini and Wheeler 2005), but it is widely accepted that scorpions of the Buthidae family are separated from all other non-Buthidae species, including Scorpionidae (Coddington et al. 2004).

Scorpionidae, like scorpions of most other families, are typically burrowers, whereas Buthidae are generally surface dwellers. However, included in this study is *Buthus occitanus* (Buthidae), which often inhabits empty burrows of other arthropods (Levy and Amitai 1980), including those of *Scorpio maurus palmatus* (Scorpionidae). This enables testing between alternative hypotheses of the effects of habitat type, phylogeny, and/or homing behavior (burrowing vs. surface dwelling) on the relative importance of RWL in scorpions. In addition, measuring MR and EWL of individual scorpions for more than 20 h, mostly in darkness and in large metabolic chambers that allow the scorpions free movement (Gefen et al. 2009), provides a better estimate of RWL across species differing in their activity patterns.

Methods

Choice of Species

The experimental design is a modification of that used previously by Gefen and Ar (2004, 2005). The geographic distribution of the included mesic species in Israel is limited to the Mediterranean zone (>350 mm annual rainfall) and extends to Lebanon, Syria, and Turkey, whereas the xeric species are distributed in arid zones in southern Israel, the Arabian Desert, and North Africa (Levy and Amitai 1980). Buthidae were represented by the mesic *Buthus judaicus*, the xeric *Leiurus quinquestriatus*, and the xeric burrow-inhabiting *Buthus occitanus*. Scorpionidae included the mesic *Scorpio maurus fuscus* and the xeric *Scorpio maurus palmatus*. *Scorpio maurus* is currently considered a monotypic genus, with 17 accepted subspecies, but high genetic divergence suggests a species complex (Froufe et al. 2008). Divergence between *S. m. fuscus* and *S. m. palmatus* is also supported by distinct geographic distribution, with a relatively narrow area of overlap near the Judea Mountains (Levy and Amitai 1980).

Scorpion Collection and Laboratory Maintenance

The mesic *S. m. fuscus* and *B. judaicus* were collected in June–September 2009 from pine woodlands near Migdal Ha'emek (32°40'N, 35°14'E), in the mesic lower Galilee (mean annual precipitation, ~540 mm), Israel. Mean maximum temperatures of 31°–33°C for June–September have been measured at the

nearby Kefar Yehoshua station over the past 20 yr (Israel Meteorological Service; <http://www.ims.gov.il/IMSEng/CLIMATE>). Xeric species were collected in October 2009 from areas of <100 mm mean annual precipitation in the Negev Desert, Israel. *Leiurus quinquestriatus* was collected near Yerucham (31°02'N, 34°51'E), whereas *B. occitanus* and *S. m. palmatus* were collected near Sede Boqer (30°52'N, 34°46'E; mean maximum October temperature in Sede Boqer, 27.2°C). The scorpions were placed in 500-mL plastic containers with soil from the collection site and were brought to the laboratory within 30 h of capture. In the laboratory, the scorpions were initially kept at room temperature (23°–25°C) for 48 h, and then they were placed in an incubator (Velp Scientifica, Milan) at 30.0° ± 0.5°C and a photoperiod of 22D : 2L for at least 2 wk before measurements began. Choice of photoperiod was based on the nocturnal behavior of most scorpions, characterized by retreating to their dark shelters (e.g., burrows, underneath rocks) during daytime. The scorpions were offered cockroaches twice a week throughout the measurement period and were measured at a random order.

CO₂ and Water Vapor Emission

During the 2-h daily light period, the scorpions were transferred to a plastic metabolic chamber (4.5 cm diameter × 13.5 cm length; volume, ~215 mL) equipped with a perforated stainless steel platform, which was placed horizontally in a controlled-temperature cabinet (Tritech Research, Los Angeles, CA) at 30.0° ± 0.2°C and an identical diurnal cycle. Dry CO₂-free air was supplied to the chamber at a rate of 100 mL min⁻¹, using FMA 2617A mass flow controllers (Omega Engineering, Stamford, CT). After 24 h, during which the scorpions acclimated to these experimental conditions, excurrent air was passed through a precalibrated LI-7000 CO₂/H₂O analyzer (LI-COR Biosciences, Lincoln, NE). The CO₂ detector was precalibrated by mixing CO₂-free dry air and 950 ± 2 ppm CO₂ in N₂ at various flow rates totaling 100 mL min⁻¹ through the analyzer. Calibration of the H₂O detector was carried out by injecting microliter amounts of water into a stream of CO₂-free dry air passing through the analyzer at 100 mL min⁻¹ and integrating the area under the resulting H₂O trace. Data were recorded every 5 s and analyzed using Expedata acquisition and analysis software (Sable Systems International, Las Vegas, NV). Determination of resting emission rates was typically based on basal traces recorded toward the end of each individual recording (Fig. 1), corresponding to >36 h from placing the scorpion in the metabolic chamber. Occasionally, when scorpions were active during that time, resting rates were determined using an earlier time period. Relative humidity in the metabolic chamber did not exceed 1.5% even when the scorpions were active.

Partitioning of EWL

Bouts of activity were used for calculation of RWL based on the increase in CO₂ and H₂O emission rates compared with resting values (assuming that elevated water loss during activity

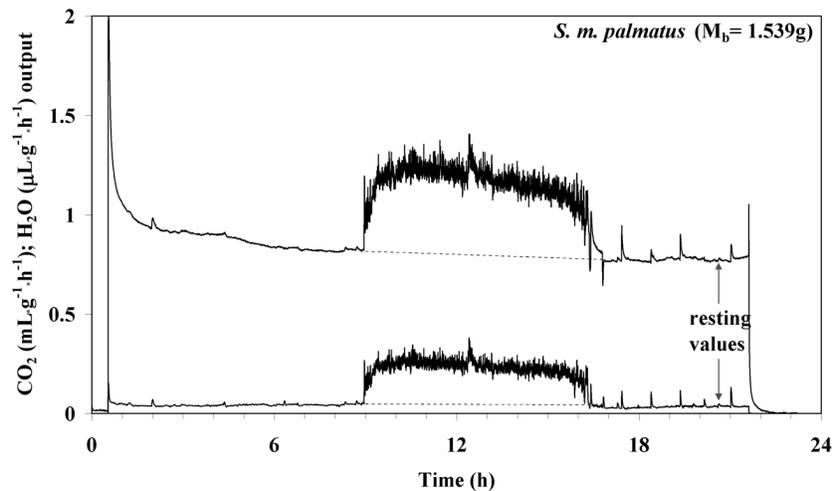


Figure 1. Example of CO₂ (bottom) and H₂O (top) emission traces from *Scorpio maurus palmatus* at 30°C. Note that rates are expressed in different units to fit scale. Rates during periods of activity (~9–16 h) were used for calculating H₂O/CO₂ emission ratio (by integrating areas above the dashed lines). A color version of this figure is available in the online edition of *Physiological and Biochemical Zoology*.

in the flow-through respirometry chamber results only from an increase in RWL at the constant experimental temperature). Integration of the CO₂ and H₂O output components resulting from activity bouts >45 min (see Fig. 1) was used to calculate the amount of water lost per unit of CO₂ emitted (Gefen et al. 2009). The H₂O/CO₂ emission ratios and resting CO₂ emission rates allowed calculation of resting RWL rates. Similarly, these ratios together with mean daily CO₂ emission rates (see below) yielded mean daily RWL rates during a 20-h cycle that typically included both resting periods and bouts of activity. If we assumed activity-independent CWL, this enabled calculation of the RWL proportions while accounting for varying levels of diel activities. The H₂O/CO₂ emission ratios were not calculated when long (>45 min) activity bouts were absent (see Fig. 2A) or when excretory water loss during defecation (see Fig. 3, arrow) was superimposed on an increased RWL signal during a single bout of activity.

Mean Daily CO₂ Emission

In order to reduce possible handling effects, only data recorded 2 h and onward after passing excurrent air through the analyzer were averaged for calculation of mean daily CO₂ output. The 2-h period was also required for a steady state signal from the metabolic chambers. Mean recording time for the total of 75 individual measurements was 20.5 h (± 1.1 h SD).

Statistics

Statistical analysis was carried out using STATISTICA 8.0 (StatSoft, Tulsa, OK). Between-species ANOVAs and ANCOVAs were followed by Tukey's HSD tests for post hoc comparisons of means of unequal sample sizes ($\alpha = 0.05$). Main effects (habitat type, family) were analyzed using two-way ANCOVA,

whereas one-way ANCOVA among xeric species was used to assess the effect of homing behavior, followed by Tukey's HSD tests. Body mass was used as a covariate for ANCOVA. Calculated RWL percentages were arcsine transformed before ANOVA. Log transforming the data did not improve normality, and therefore, raw data were used throughout the analyses.

Results

Body mass (mean \pm SE) and sample sizes for mixed-sex samples of the represented species are shown in Table 1. Female scorpions are larger than males, and therefore, calculated mean body mass is affected by the different sex ratios for the respective species. However, it has been shown that mass-specific gas exchange rates and WLRs are not significantly affected by gender (Terblanche et al. 2007; Gefen 2008).

Significant interspecific differences in resting MRs (as expressed by CO₂ emission rates) were found only between the xeric *Leiurus quinquestriatus* and *Scorpio maurus palmatus* (one-way ANCOVA, $F_{4,69} = 3.56$, $P = 0.01$; Table 1). Two-way ANCOVA suggested significant effect for habitat type ($F_{1,70} = 9.70$, $P < 0.01$) but not for scorpion family ($F_{1,70} = 0.06$, $P = 0.81$). However, the significant habitat type \times family interaction ($F_{1,70} = 6.64$, $P = 0.01$) explains the apparent inconsistent effect of scorpion family and habitat type resulting from between-species comparisons (Table 1). Furthermore, post hoc comparison did not support a significant difference in MR between xeric and mesic species (Tukey's HSD test, $P > 0.05$). In contrast, significantly higher EWL rates at 30°C were measured for Scorpionidae compared with Buthidae (two-way ANCOVA, $F_{1,70} = 23.10$, $P < 0.001$), with no significant effect of habitat type ($F_{1,70} = 0.11$, $P = 0.74$) or family \times habitat interaction ($F_{1,70} = 1.05$, $P = 0.31$). The consistent effect of scorpion family on EWL rates was mirrored in interspecific

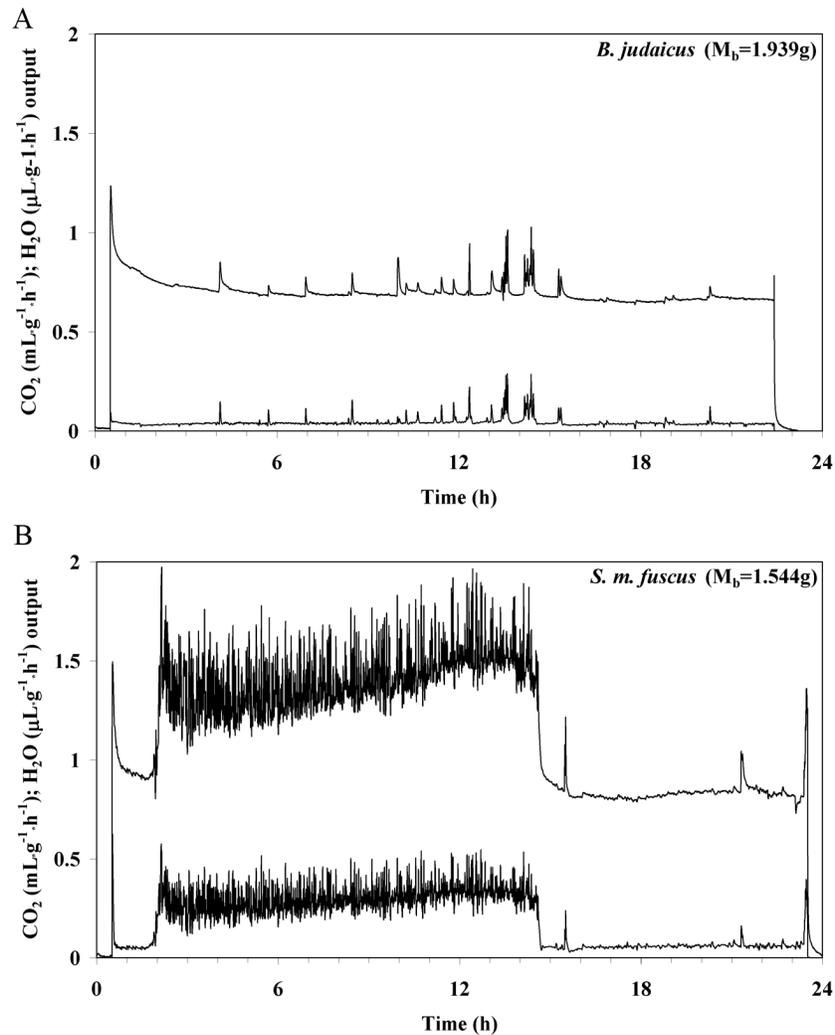


Figure 2. Typical CO₂ (bottom) and H₂O (top) emission traces from the sympatric mesic *Buthotus judaicus* (A) and *Scorpio maurus fuscus* (B) at 30°C. Note that rates are expressed in different units to fit scale. A color version of this figure is available in the online edition of *Physiological and Biochemical Zoology*.

comparisons (ANCOVA, $F_{4,69} = 5.94$, $P < 0.001$), where values for the two Scorpionidae were significantly higher than those recorded for *Buthotus judaicus* and *Buthus occitanus* (Tukey's HSD test, $P < 0.05$). Within Buthidae, no significant effect of homing behavior was observed when EWL rates of the surface-dwelling *L. quinquestriatus* and *B. judaicus* and the burrow-inhabiting *B. occitanus* were compared (ANCOVA, $F_{2,42} = 0.47$, $P = 0.63$).

Calculation of the amount of lost water associated with each unit of respiratory gas exchange yielded significantly lower values for xeric compared with mesic species (two-way ANOVA, $F_{1,51} = 9.59$, $P < 0.01$) and for Buthidae compared with Scorpionidae ($F_{1,51} = 6.02$, $P < 0.05$). No significant habitat type \times family interaction was observed ($F_{1,51} = 1.49$, $P = 0.23$). This is reflected in the lowest H₂O/CO₂ ratios calculated for the xeric buthids *L. quinquestriatus* and *B. occitanus* (ANOVA, $F_{4,50} = 6.66$, $P < 0.001$; Table 1). The H₂O/CO₂ emis-

sion ratio, resting MR, and resting EWL rates were used for calculating RWL and its relative importance in resting scorpions (see "Methods"). Scorpionidae and Buthidae did not differ in resting RWL levels (two-way ANCOVA, $F_{1,50} = 3.48$, $P = 0.07$), but significantly lower RWL rates were calculated for xeric compared with mesic species ($F_{1,50} = 22.43$, $P < 0.001$). There was no significant family \times habitat interaction on RWL rates ($F_{1,50} = 0.23$, $P = 0.63$). These values are also reflected in calculated RWL rates and their fractions from total losses, which ranged from 10.3% to 10.6% and from 14.1% to 16.8% in xeric and mesic species, respectively (Table 1).

Table 2 summarizes measured mean daily MR and calculated mean daily RWL rates and their relative importance when scorpions were relatively free to express their activity patterns over a >20-h measurement period. The lowest and highest levels of activity were observed for the two mesic species, with mean daily MR for *B. judaicus* on average 40% higher than resting

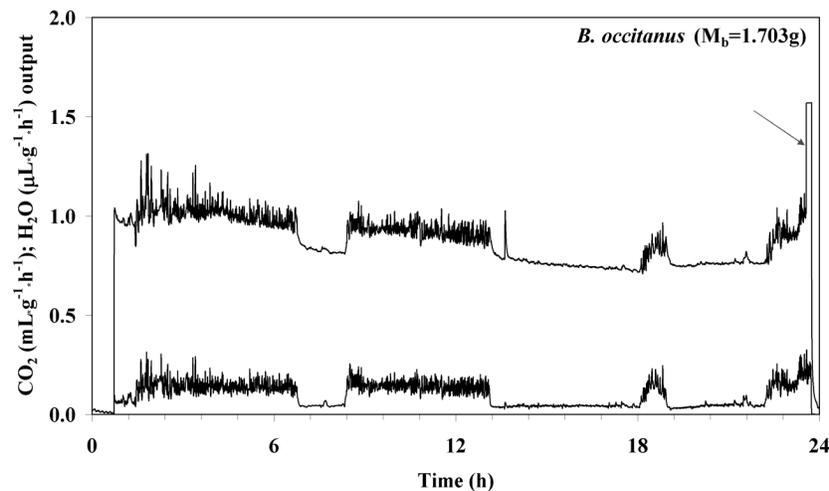


Figure 3. Typical CO_2 (bottom) and H_2O (top) emission traces from *Buthus occitanus* at 30°C . Note that rates are expressed in different units to fit scale. Elevated H_2O signal before final baselining (see arrow at ~ 24 h) corresponds to a defecation event. A color version of this figure is available in the online edition of *Physiological and Biochemical Zoology*.

values, whereas *S. m. fuscus* showed an almost threefold increase (Table 2). A total of nine activity bouts of 1 h or longer were recorded among only six active out of 15 *B. judaicus* individuals. Of these, only three lasted more than 3 h. In comparison, only one *S. m. fuscus* remained quiescent throughout the 24-h recording, and 10 out of the remaining 14 exhibited activity bouts of 12 h or longer (see Fig. 2). On average, all three xeric species exhibited mean daily MR 62%–67% higher than resting values. Despite the similar overall mean increase in MR resulting from activity, *B. occitanus* expressed a unique activity pattern (Fig. 3), as eight out of a total of 14 individuals exhibited two or three activity bouts of >1 h each. *Buthus occitanus* also stood out as the only studied species with no period of activity longer than 6 h, while every single individual was active for >1 h at least once during the ~ 20 -h measurement. The exceptional activity level of *S. m. fuscus* at 30°C was mirrored in significant family, habitat, and interaction effects ($P < 0.01$) on mean daily MR and on RWL rates. Similar to resting values, RWL rates were significantly lower in xeric species. However, the significant difference in the contribution of activity to daily MR in *B. judaicus* and *S. m. fuscus* was reflected in a twofold difference in mean daily RWL rates and in the relative importance of RWL in these two mesic species (Table 2; Fig. 2). RWL of the highly active *S. m. fuscus* totaled 30% of EWL at 30°C , whereas RWL proportions in the quiescent *B. judaicus* were not significantly higher than those of the xeric species (Table 2).

Discussion

Partitioning of EWL in insects into its respiratory and cuticular components has attracted considerable research attention (see Chown 2002), but relatively few studies have addressed this topic in scorpions. Moreover, the few available data from single-species studies have limited comparative value because differ-

ences in methodology (e.g., use of dead vs. live specimens, closed vs. open respirometry) resulted in substantially varied estimates, even within the same species. This comparative study is an attempt to describe a pattern of variation in RWL proportions that, like other water-relations traits, may correlate with selective pressures for desiccation resistance affecting various species in accordance with their habitat type, homing behavior, and phylogeny.

A significant family \times habitat interaction effect on resting MR (as expressed by CO_2 emission rates) indicates a lack of consistent effect of either main effect. In fact, the difference in MR between the xeric *Leiurus quinquestriatus* and *Scorpio maurus palmatus* was the only exception to previously reported lack of interspecific variation in scorpion MR (Lighton et al. 2001; Gefen and Ar 2004; but see Terblanche et al. 2007).

WLRs of scorpions in general have been reported to be lower than those of most other arthropods of similar body size sharing the same habitat (Hadley 1990, 1994). Within Scorpiones, interspecific variation in WLR was attributed to the EWL rate-habitat correlation typical for many terrestrial arthropods. More recently, WLRs of Buthidae were shown to be significantly lower than those of sympatric Scorpionidae, whereas no differences were found between xeric and mesic species within each family (Gefen and Ar 2004). The surface-dwelling existence of Buthidae means that scorpions of this family are less buffered from environmental extremes compared with burrowing species, which retreat to their shelters during periods of harsh climatic conditions. While the phylogenetic component of interspecific variation in WLR has already been highlighted, the experimental design employed by Gefen and Ar (2004) could not distinguish between phylogenetic effects and those of homing behavior. The inclusion of the burrow-inhabiting buthid *Buthus occitanus* in this study enabled testing the possible effect

Table 1: Mean (\pm SE; n in parentheses) resting rates of CO₂ emission ($\dot{M}CO_2$) and evaporative water loss (EWL), respiratory water and CO₂ emission ratios, respiratory water loss (RWL) rates, and calculated RWL fractions from total EWL

Species	Body Mass (g)	$\dot{M}CO_2$ ($\mu\text{L h}^{-1}$)	EWL Rate ($\mu\text{L h}^{-1}$)	H ₂ O/CO ₂ ratio ($\mu\text{L mL}^{-1}$)	RWL Rate ($\mu\text{L h}^{-1}$)	RWL (% of EWL)
<i>Buthotus judaicus</i> (Bu, me, sdw)	1.928 \pm .155 (15)	104.8 \pm 9.1 ^{AB} (15)	1.237 \pm .071 ^B (15)	1.93 \pm .16 ^{AB} (8)	.225 \pm .025 ^{AB} (8)	16.8 \pm 1.4 ^A (8)
<i>Leiurus quinquestriatus</i> (Bu, xe, sdw)	2.631 \pm .213 (17)	118.3 \pm 6.9 ^A (17)	1.444 \pm .110 ^{AB} (17)	1.27 \pm .08 ^B (12)	.156 \pm .019 ^B (12)	10.4 \pm .7 ^B (12)
<i>Buthus occitanus</i> (Bu, xe, bur)	1.614 \pm .130 (14)	93.6 \pm 4.6 ^{AB} (14)	1.217 \pm .083 ^B (14)	1.38 \pm .07 ^B (12)	.128 \pm .009 ^B (12)	10.6 \pm .7 ^{AB} (12)
<i>Scorpio maurus fuscus</i> (Sc, me, bur)	1.651 \pm .161 (15)	114.2 \pm 12.1 ^{AB} (15)	1.714 \pm .128 ^A (15)	2.11 \pm .19 ^A (13)	.259 \pm .038 ^A (13)	14.1 \pm 1.7 ^{AB} (13)
<i>Scorpio maurus palmatus</i> (Sc, xe, bur)	2.043 \pm .160 (14)	88.5 \pm 7.1 ^B (14)	1.671 \pm .121 ^A (14)	1.84 \pm .09 ^{AB} (10)	.159 \pm .018 ^B (10)	10.3 \pm .8 ^B (10)

Note. Values sharing a superscript are not significantly different (see "Methods" for details of statistical analyses). Bu, Buthidae; Sc, Scorpionidae; me, mesic; xe, xeric; sdw, surface dweller; bur, burrower.

Table 2: Mean daily rates of CO₂ emission ($\dot{M}CO_2$; mean \pm SE; *n* in parentheses), calculated increase compared with resting rates, respiratory water loss (RWL) rates, and their relative importance

Species	Body Mass (g)	$\dot{M}CO_2$ ($\mu L h^{-1}$)	$\dot{M}CO_2$ (% Increase vs. Resting Rates)	Mean Daily RWL Rate ($\mu L h^{-1}$)	RWL (% of EWL)
<i>Buthotus judaicus</i> (Bu, me, sdw)	1.928 \pm .155 (15)	152.9 \pm 25.1 ^B (15)	40.1 \pm 14.1 ^C (15)	.378 \pm .066 ^B (8)	24.6 \pm 2.5 ^{AB} (8)
<i>Leiurus quinquestriatus</i> (Bu, xc, sdw)	2.631 \pm .213 (17)	197.8 \pm 16.8 ^{ab} (17)	66.8 \pm 7.8 ^{AB} (17)	.274 \pm .036 ^B (12)	16.6 \pm .8 ^B (12)
<i>Buthus occitanus</i> (Bu, xc, bur)	1.614 \pm .130 (14)	149.5 \pm 10.9 ^B (14)	62.3 \pm 13.2 ^{ABC} (14)	.204 \pm .015 ^B (12)	15.8 \pm 1.0 ^B (12)
<i>Scorpio maurus fuscus</i> (Sc, me, bur)	1.651 \pm .161 (15)	284.9 \pm 28.9 ^A (15)	170.6 \pm 30.4 ^A (15)	.643 \pm .062 ^A (13)	29.6 \pm 2.1 ^A (13)
<i>Scorpio maurus palmatus</i> (Sc, xc, bur)	2.043 \pm .160 (14)	144.3 \pm 15.4 ^B (14)	62.6 \pm 11.7 ^{BC} (14)	.290 \pm .039 ^B (10)	17.0 \pm 1.6 ^B (10)

Note. Values sharing a superscript are not significantly different (see "Methods" for details of statistical analyses). Abbreviations as in Table 1.

of homing behavior among species of the same scorpion family. In addition to confirming the findings of Gefen and Ar (2004), using direct EWL measurements instead of gravimetric methods, results here show similar EWL rates for burrow-inhabiting and surface-dwelling Buthidae (Table 1). This suggests that the observed interspecific variation in EWL possibly reflects a phylogenetic constraint rather than a result of relaxed selection for desiccation resistance to which burrowing species are subjected in their buffered microclimate.

The significant effect of habitat type on RWL is reflected in the interspecific variation in both calculated rates and their relative importance (percent of total EWL) for resting scorpions (Table 1). Lower respiratory losses in xeric species disagree with reported RWL proportions in insects (Zachariassen 1996; Addo-Bediako et al. 2001). Addo-Bediako et al. (2001) argued that lower WLRs of xeric insects coupled with gas exchange rates similar to those of mesic species mean that RWL constitutes smaller proportions of EWL in the latter. Results in this study do not indicate lower MRs or EWL rates for xeric species (see also Gefen and Ar 2004). Still, the relative importance of RWL at rest was significantly lower in xeric species compared with mesic species from the same families (Table 1). Both phylogenetic affiliation and habitat type were correlated with the amount of water loss associated with gas exchange, which resulted in the lowest recorded H_2O/CO_2 emission ratios for xeric buthids. A ratio of $1.50 \pm 0.17 \mu L H_2O mL CO_2^{-1}$ was recently reported for the xeric *Hadrurus arizonensis* at 30°C (Gefen et al. 2009). This value is not significantly higher (ANCOVA, $F_{1,26} = 0.49$, $P = 0.49$) than the lowest ratio reported in this study for *L. quinquestriatus* (Table 1), which may support an adaptive role for reduced H_2O/CO_2 emission ratio in xeric species.

If we assume constant vapor pressure gradient between gas exchange surfaces and ambient environment at a given temperature, RWL could be reduced by increasing the associated PCO_2 gradient, thus increasing CO_2 washout through the book lung spiracles (Barnhart and McMahon 1987). Interestingly, hemolymph PCO_2 of 28.9 ± 2.2 Torr was reported for *L. quinquestriatus* at 28°C, in comparison with 19.5 and 17.7 Torr for the mesic *B. judaicus* and *S. m. fuscus*, respectively (Dejours and Ar 1992). Hemolymph PCO_2 of 19.7 ± 2.9 Torr was measured for the tropical species *Pandinus imperator* (Scorpionidae) at 25°C (Paul et al. 1994). These values are higher than values reported for other terrestrial arthropods at rest (Paul et al. 1994; Harrison 2001) and may represent an adaptive mechanism to reduce RWL in scorpions in general and xeric species in particular. Moreover, a significant increase in hemolymph PCO_2 values was recorded following 3-wk desiccation of *L. quinquestriatus* at 28°C (Dejours and Ar 1991), suggesting that tighter regulation of book lung spiracle opening could further improve H_2O/CO_2 washout ratios.

Data on the relative importance of RWL in terrestrial arthropods largely originate from studies concerned with the adaptive nature of discontinuous gas exchange as a mechanism for conserving body water in insects (see Quinlan and Gibbs 2006). As the increase in RWL with activity and increased met-

abolic demands is well established, most studies have focused on RWL during rest and its significance to evolved gas exchange patterns (reviewed in Chown 2002). However, results here demonstrate that laboratory-measured resting values may not only significantly underestimate respiratory losses of scorpions in the field but also overlook interspecific variation in activity and therefore the extent to which various species may modulate their RWL behaviorally under stressful conditions. In contrast with the comparable levels of diel activity among xeric species at 30°C, the mesic *B. judaicus* and *S. m. fuscus* showed the lowest and highest contribution, respectively, of activity to mean daily MR (40% and 170% increases from resting values, respectively; Table 2). Accounting for diel activity resulted in higher mean daily RWL rates and their relative importance compared with resting values in all species (Table 2). RWL rates of *S. m. fuscus* were the highest among the studied species, although resting values were not different from those of the sympatric *B. judaicus* (Table 1). Nevertheless, the RWL rate of active *S. m. fuscus* was twofold higher than that of *B. judaicus* (Table 2) and translated to respiratory losses of up to 30% of the species' daily EWL at 30°C (Table 2; Fig. 2). Resting RWL proportions for *S. m. fuscus* were not significantly higher than the lowest recorded values for xeric species, as a result of the species' lowest cuticular resistance for water loss among all studied species. In contrast, the unique activity pattern of the species at 30°C contributed to higher rates of gas exchange and thus dramatically increased relative importance of RWL (Table 2). The high activity pattern of hydrated *S. m. fuscus* (Fig. 2) suggests that reduced WLR during prolonged desiccation in this species at 30°C (Gefen and Ar 2004, their fig. 4) may involve behavioral modulation, perhaps coupled with depression of resting gas exchange rates (Gefen 2008). Similarly, the relatively constant WLR for *B. judaicus* during a 2-wk exposure to desiccating conditions (Gefen and Ar 2004) correlates with the species' low levels of activity reported here. Activity bouts lasting even a few minutes result in decreased hemolymph pH in *Pandinus imperator* (Paul et al. 1994). Therefore, different activity patterns such as those exhibited by *S. m. fuscus* and *B. judaicus* at 30°C (Fig. 2) are possibly associated with varying extents of hemolymph acidification or buffering capacities. Tolerance levels of these fluctuations may underlie variation in activity patterns, including the fragmented pattern exhibited by *B. occitanus* (Fig. 3).

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