

Temperature and desiccation effects on the antipredator behavior of *Centruroides vittatus* (Scorpiones: Buthidae)

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Abstract. Temperature can profoundly affect many physiological processes, including muscle performance. Many ectotherms appear sensitive to this relationship, choosing times and locations of activity permitting high body temperatures and, thus, quick escape from predators. High body temperatures, however, can lead to dehydration, which in turn affects muscle performance. Striped bark scorpions *Centruroides vittatus* Say 1821 provide an ideal model for assessing the effects of temperature and water loss on two potentially important antipredator behaviors, sprinting and stinging. Scorpions had significantly higher sprint speeds at warmer temperatures, with males significantly faster than females. Additionally, sting latency was longer and sting rate lower when scorpions were cooler. Intriguingly, females appear capable of stinging at a higher rate than males. Desiccation allowed the scorpions to sprint significantly faster than control (hydrated) scorpions, probably due to weight loss. The influence of temperature on sprinting and stinging might thus explain bark scorpions' preference for maintaining high body temperatures during periods when they are exposed to predation. When inactive, however, scorpions may benefit from maintaining lower body temperatures to decrease resting metabolic rate and desiccation.

Keywords: Defensive behavior, scorpions, thermal ecology, sting speed, sexual dimorphism

Ectotherms generally exhibit preferred body temperatures (T_p) that they maintain through behavioral thermoregulation. Temperature profoundly affects many physiological processes including, but not limited to, oxygen consumption, digestion (Bobka et al. 1981; Zhang & Ji 2004), growth (Angilletta et al. 2004), and locomotor performance (Forsman 1999). The latter process is related to temperature primarily due to well-recognized thermal dependencies of muscular contraction and relaxation (Bennett 1984). The influence of temperature on locomotor performance is ecologically important for many organisms, as it impacts both hunting ability and predator avoidance via such activities as sprinting (Waldschmidt & Tracy 1983; Bauwens et al. 1995), flying (Machin et al. 1962), swimming (Turner et al. 1985), and striking (Greenwald 1974; Rowe & Owings 1990; Webb & Shine 1998). Indeed, endothermic enemies are known to take advantage of ectotherms that find themselves with body temperatures (T_b) cooler than they might prefer (Rowe & Owings 1996; Swaisgood et al. 1999, 2003). Sprint speed, in particular, can be critical for an ectotherm attempting escape from a potential predator (van Berkum et al. 1986; Hertz et al. 1988). For this reason, T_p is often strongly correlated with the optimal temperature (T_o) for sprinting capacity (Miller 1982; Bauwens et al. 1995; Forsman 1999), providing evidence that ectothermic organisms typically select body temperatures that maximize their locomotor capabilities. If a prey organism's ability to survive encounters with and escape from predators is dependent on locomotor performance, then maintaining T_p will favor survival in the face of predation; indeed, this has been demonstrated in wild populations (Christian & Tracy 1981).

The match, however, between T_p and T_o is not always perfect (see reviews in Huey & Slatkin 1976; Huey 1982). Some ectothermic organisms may have a broad range of temperatures over which performance varies little (Schmalhofer &

Casey 1999), negating the advantage of finely tuned behavioral thermoregulation. Other species may face competing physiological demands with different T_o s. Side-blotched lizards (*Uta stansburiana*), for example, select microhabitats that maximize their sprint speeds during the morning and late afternoon, but chose sub-optimal, shaded habitats during midday to avoid desiccation (Waldschmidt & Tracy 1983). Water conservation can itself feed back on locomotor performance. Dehydration has been found to decrease endurance but not burst activity in frogs and lizards (Crowley 1985; Moore & Gatten 1989; Wilson & Havel 1989) and to decrease walking velocity in crayfish (Claussen et al. 2000). Because higher temperatures typically increase the rate of water loss (Slobodchikoff 1983), many ectotherms might face a difficult physiological trade-off: a high T_b may support increased performance through its effect on muscle contraction while simultaneously decreasing performance from desiccation.

Desert scorpions provide an excellent model organism for examining the effects of temperature and dehydration on antipredator motor patterns. They flourish within desert ecosystems (Hadley 1974), forming an ecologically important link as the dominant predators of small herbivorous and detritivorous arthropods (McCormick & Polis 1990) and as the prey of many vertebrates (Polis et al. 1981; Ayal 2007). Indeed, the total biomass of these highly successful arachnids can exceed that of all vertebrates combined in some desert systems (Polis 1990). Predation is the dominant mortality factor (Polis 1990), making scorpions especially valuable for studies of antipredator behavior. They tend to exhibit nocturnal, "time-minimizing" activity patterns (Schoener 1971) in which they are rarely active and foraging, preferring to remain in refugia and thus limiting their risk of falling prey (Polis 1980). Surface activity of many scorpions is highest during the earlier hours of the night and gradually decreases as dawn nears (Hadley & Williams 1968; Polis 1980; Warburg &

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Polis 1990; Carlson et al., unpublished data). This may afford them access to sun-warmed substrates, returning to refugia as the surface substrates cool. Additionally, scorpions appear most active during both warm (Polis 1980) and humid (Skutelsky 1996) weather conditions, decisions that may help them maximize body temperature while minimizing water loss.

Anecdotal reports suggest that temperature may indeed affect locomotor performance in scorpions (Hadley 1974; Warburg & Polis 1990), though there is, as yet, little experimental evidence of this. The water loss rates of scorpions, though low (Hadley 1974), are known to rise with temperature (Hadley 1970; Gefen & Ar 2006), and desiccated scorpions exhibit limited functionality of the limbs (Sensenig & Shultz 2004). This is likely due to the use of hydraulics in some locomotor activities (Sensenig & Shultz 2004) and the decreased effectiveness of hydrostatic systems with fluid loss (Anderson & Prestwich 1975). Additionally, dehydration may reduce the oxygen-transporting abilities of the hemolymph, further inhibiting locomotor performance (Gefen & Ar 2005). All of this serves to highlight the potential importance of thermoregulation and water balance for locomotor-based antipredator behaviors. Indeed, the primary defensive mechanisms of scorpions, sprinting (Shaffer & Formanowicz 1996, 2000) and stinging, fall into this category. The purpose of this research is to determine the effects of temperature and desiccation on these antipredator behaviors in a model scorpion.

Centruroides vittatus Say 1821, the striped bark scorpion, is an excellent species for such research. In addition to being the most common and active scorpion in many lithic deserts of the southwestern United States and northern Mexico (Brown et al. 2002), scorpions of the family Buthidae are noted for their high temperature preferences (Warburg & Ben-Horin 1981), low water loss rates (Gefen & Ar 2004), and well-developed osmoregulatory ability (Gefen & Ar 2005). *C. vittatus* is subjected to a wide range of temperatures, from searing summer heat to subfreezing winter nights (Whitmore et al. 1985). Striped bark scorpions appear sensitive to the influence of temperature on their defensive capabilities, as they are less likely to be active on the surface during cool weather (Brown & O'Connell 2000; Brown et al. 2002; Yamashita 2004). And when they are active, they are less likely to seek refuge in bushes (an antipredator tactic; Brown & O'Connell 2000; McReynolds 2004) when temperatures are warm (McReynolds 2008).

Striped bark scorpions are also appropriate because stinging and sprinting are important components of their antipredator behavior. Although bark scorpions (*Centruroides* spp.) are well known for possessing potent neurotoxins that might deter a vertebrate enemy, grasshopper mice (*Onychomys* spp.) are resistant to the lethal effects of the venom and feed voraciously on *Centruroides* (Rowe & Rowe 2006, 2008); an effectively delivered sting, however, often causes sufficient pain for the mouse to drop the scorpion, providing an opportunity for its escape (Rowe & Rowe 2006). The broad range of environmental temperatures to which striped bark scorpions are exposed, coupled with the importance of stinging and sprinting for evading predators, make *C. vittatus* an ideal model for testing hypotheses about scorpion thermal ecology and physiology in relation to defensive behavior. In another report (Carlson et al., unpublished data), we show that *C. vittatus* from two different populations both select substrates generating high body temperatures (36–38°C) when tested in a thermal gradient.

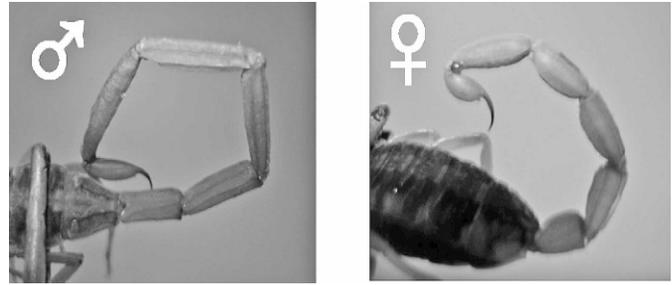


Figure 1.—Sexual dimorphism in the metasomas of male and female *C. vittatus*.

Here, we examine the effects of temperature, and of temperature-induced dehydration, on their defensive ability.

METHODS

Animals.—From a large group (600+) of *Centruroides vittatus* scorpions collected during May 2008 in the Organ Mountains in New Mexico, USA, 180 experimental subjects (60 adult males, 60 adult females, and 60 unsexed juveniles) were selected randomly. All scorpions were kept at room temperature (~25°C) in plastic sweater boxes with gravel substrates, egg crate refugia, and petri dishes for water. The communal nature of *C. vittatus* (McAlister 1966; Polis & Lourenço 1986) allowed us to house 30–60 individuals per box with no signs of aggression. Due to concerns that the added weight and the energetics of digestion may influence thermal ecology, the scorpions were only fed between experiments (i.e., after all trials for a single experiment were completed), and all were fed at the same time. Food items offered included crickets (*Acheta domesticus*), “superworms” (*Zoophobas morio* larvae), and mealworms (*Tenebrio molitor* larvae). To best approximate the light conditions faced by scorpions in the wild (where they are active at night and hiding in crevices or burrows during the day), lights in the room housing the scorpions were kept on 24-h D; a small window nonetheless provided diffuse daylight cueing.

The scorpions were each marked with a unique four-dot pattern of fluorescent paint (Hadley & Williams 1968; Bradley 1988). Individuals were sexed by the length and thickness of the segments of the metasoma (tail). Males have thin and elongate segments whereas females possess shorter and thicker segments (Polis & Sissom 1990; Fig. 1). Pregnancies in females to be tested were noted; because most of the females were gravid (> 90%), this variable could not be avoided while maintaining adequate sample sizes. Individuals were characterized as juveniles based on qualitative attributes, such as a lack of clear sexual dimorphism and smaller total body sizes and masses.

Temperature effects on sprint speed.—All 180 scorpions were used in the sprint speed trials. Because there is significant and heritable variation in sprint speed ability between individuals (Shaffer & Formanowicz 2000), each scorpion was tested at every temperature and compared with its own performance (repeated measures). The scorpions were divided equally into three subgroups (each containing 20 adult males, 20 adult females, and 20 unsexed juveniles) to systematically counter-balance treatment effects (i.e., temperatures) across trials. Trials on the same individual scorpion were separated by a minimum of 48 h.

The sprint speed of each scorpion was assessed at three temperatures; $T_p = 38^\circ\text{C}$ (Carlson et al., unpublished data), 25°C , and 10°C . Test temperatures were chosen to span the range of temperatures experienced by free-ranging striped bark scorpions (Brown et al. 2002; Yamashita 2004; Carlson et al., unpublished data).

Sprint speed trials were performed using the same gradient track unit employed in earlier temperature preference trials (Carlson et al., unpublished data), consisting of a 3.2-mm thick copper base, 1.22 m long by 30.5 cm wide. 10.2-cm-tall aluminum sides enclosed the base and also divided the unit lengthwise into three separate tracks, each approximately 10.2 cm wide by 1.22 m long. The base was covered with approximately 1 cm of fine sand. The experimental temperatures were achieved by placing the track, with its copper bottom, on six hot plates running the length of the unit for the 38°C trials, and on a continuous line of ice packs for the 10°C condition; since the experimental room was kept as close as possible to 25°C , no heating or cooling was needed for this latter treatment. All of the scorpions to be tested at a given temperature were individually contained in small acetate cylinders ($\sim 6\text{ cm} \times 6\text{ cm}$, constructed from overhead transparency sheets) placed in one of the tracks to prevent them from becoming fatigued from excessive movement. They were acclimated to the temperature of the unit for at least 6 min; pilot tests, performed with a Sensortek BAT-12 thermocouple connected to a Harvard Apparatus microprobe inserted into the mesosoma (abdomen), show this is more than sufficient time for a scorpion's T_b to reach the temperature of the substrate upon which it rests. The temperature of the substrate (T_s) inside each scorpion's acetate containment cylinder, and thus the approximate T_b of that scorpion, was taken remotely (preventing disturbance to the scorpion) using an Extech model RH101 infrared thermometer immediately prior to sprint testing.

Sprint speed trials were conducted in the two tracks not used for containment/acclimation. Because of negative photokinetic behaviors in scorpions (Abushama 1964; Warburg & Polis 1990), the end of the track was shaded while the beginning was well-lit to encourage unidirectional movement. Scorpions were placed on the track and, if necessary, startled with a tap on the metasoma to induce running. A stopwatch accurate to 0.01 s was used to record the time elapsed from crossing the starting line to either stopping or reaching a 50 cm "finish line" marked on the track. The distance at the final point was measured for individuals who stopped short. Each individual was induced to sprint three times at each of its test temperatures; within a trial (i.e., test temperature), scorpions were allowed to rest for several minutes between successive sprints. The highest speed achieved by an individual in its three sprints at a given test temperature was used for later analysis. Three individuals (two juveniles and one adult male) that refused to sprint during one or more of its test temperatures were removed from the analysis, reducing the sample size to 177. The sand in the apparatus runway was shifted and smoothed to even out the surface between tests on different individuals.

Temperature effects on sting speed.—A subset of 54 individuals (18 adult females, 18 adult males, and 18 unsexed juveniles) of the original 180 marked scorpions from the sprint

speed trials were selected for sting trials. In the same manner as the sprint speed measurements, these scorpions were split into three equal-sized subgroups that were tested at all three temperatures in counterbalanced order. Once again, successive trials on the same scorpion were separated by a minimum of 48 h. One adult male died before completing all three of his trials and was removed from the analyses.

Trials were conducted using a 9.5-mm thick copper plate, approximately 19 cm \times 16 cm, on top of which was placed a thin layer of fine sand. An acetate cylinder (approximately 7 cm tall, 8 cm long and 2.5 cm wide at the center) similar to those used in the sprint trials was used to contain the scorpion, with the simple modification of partially flattening the cylinder into an ellipse to keep the scorpion oriented perpendicularly to the video camera (see below). Test temperatures were induced by placing the copper plate on ice (10°C), on the lab bench (25°C), or on a hot plate (38°C), using insulation and spacers to fine-tune the temperature. A sting-eliciting probe was constructed from a 15-cm stick, onto which a 2-cm \times 2.5-cm piece of index card was affixed to one end as a target.

Scorpions were placed individually into the acetate ellipse and allowed 6 min to equilibrate to the temperature of the testing apparatus. As with sprint trials, the T_s inside each scorpion's acetate ellipse was taken immediately preceding its sting test. Each test was filmed with a Canon XL2 digital video camera at 30 fps. To elicit a sting, the probe, target end down, was lowered slowly from above and pressed firmly on the 4th or 5th tergite (dorsal cuticular segment) of the scorpion; both the scorpion and the target were oriented perpendicular to the camera. The probe was held in place for at least two seconds after the scorpion stung. Scorpions that did not sting within 10 s were characterized as failing to sting and the trial was terminated.

Video was analyzed frame-by-frame. Elapsed time from first contact of the probe with the scorpion's body to the moment when the scorpion's aculeus (stinger) touched the target was recorded as sting latency. The number of separate contacts between the aculeus and the target (i.e., number of stings) in the following 2 s was used to calculate a sting rate (stings/s). Individuals whose aculeus failed to contact the target were excluded from sting latency analyses. Occasionally, a scorpion's aculeus stuck in the target, or lodged between the target and the scorpion's body; individuals whose aculeus remained stuck for more than 1 s of the 2-s "post-first-sting" filming window were excluded from sting rate analyses.

The speed with which a scorpion can deliver a sting might be influenced not only by temperature, age, or gender, but also by the starting position of its telson (the last tail segment, to which the aculeus is attached) and its metasoma (tail). We therefore used the videotapes to quantify the starting position of each scorpion's telson along its longitudinal axis, employing an ordinal scale from 1–7 (Fig. 2a), generating an estimate of metasomal "curling"; similarly, we used a three-level ordinal scale to quantify the lateral (sagittal) angle of each scorpion's metasoma (Fig. 2b) just prior to being touched with the sting stimulus.

Dehydration effects on sprint speed.—From the marked scorpions that were not employed in the sting experiments, 60 individuals were randomly selected and divided into a control and a treatment group, each with 10 adult males, 10 adult females, and 10 juveniles. All scorpions were measured again

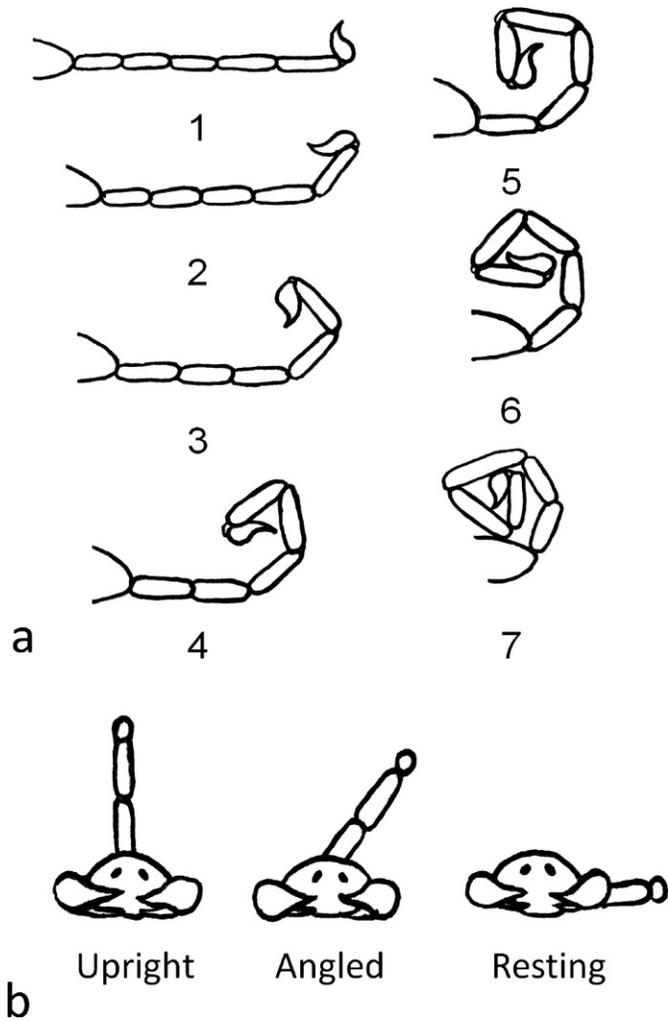


Figure 2.—Ordinal system for quantifying a) degrees of metasomal curling and b) metasomal angle in *C. vittatus* just prior to delivering a sting.

for sprint speed at room temperature (25° C) using the same procedure described earlier. The treatment group was then placed in a glass desiccator with 3.2 cm of Drierite layering the bottom; a porcelain plate covered with a paper towel was used to prevent scorpions from making direct contact with the desiccant. The entire unit, desiccator plus scorpions, was then placed inside a Percival model I36LLC8 environmental chamber for 70 h at 36° C. The control group was placed in a twin desiccator, again with a plate and paper towel barrier, but with petri dishes of water supplied for drinking and no Drierite. The control group was kept in the environmental chamber during the same period as the experimental group, for which mass losses of 10–20% were targeted.

After desiccation, all the scorpions were again tested at 25° C for sprint speed. The change in a scorpion's sprint speed was calculated as a percent of its original speed. The paper towel and porcelain plate barrier was not entirely effective; scorpions that slipped past the barrier and came in contact with either the desiccant or water condensed on the bottom were excluded from subsequent analyses, reducing the control and treatment group sample sizes from 30 each to 19 and 22, respectively.

Statistical analysis.—A mixed-design, repeated measures ANOVA, with one between-group effect (age/sex) and one within-subject effect (temperature), was performed on the sprint speed, sting speed, and sting rate data. The possible influences of sensitization, habituation, or fatigue across trials was assessed by substituting “trial number” for “temperature” in a second set of ANOVAs. Dependent variables (DVs) in each of these six ANOVAs were tested for the standard parametric assumptions of normality, homogeneity of variances, and repeated-measures sphericity (Keppel 1991). Two of the six DVs (sprint speed and sting latency with temperature) violated the sphericity assumption and were thus subjected to the conservative Greenhouse-Geisser correction (Keppel 1991, Field 2005). One DV (sting latency with temperature) violated the normality and homogeneity assumptions and could not be corrected using a data transformation; we therefore applied a conservative level of significance ($P < 0.01$) to this DV to minimize any risk of Type I error (Keppel 1991). Effect sizes (strengths of association) are reported as partial η^2 (partial eta squared). Multiple comparisons for any of the mixed-design ANOVAs with significant main effects were conducted using Bonferroni's adjustments, the preferred post-hoc test for repeated measures (Field 2005).

Two-way independent ANOVAs were used to assess the influences of dehydration and age/sex on two dependent variables, the change in a scorpion's body mass and the change in its sprint speed following ~ 3 days at $T_b = 36^\circ$ C. Both DVs were tested for the standard parametric assumptions of normality and variance homogeneity. Sprint speeds were significantly non-normal and could not be transformed to meet this assumption; we therefore applied a conservative level of significance ($P < 0.01$) to this DV to minimize the risk of Type I error (Keppel 1991). Effect sizes are reported as partial η^2 ; Bonferroni adjustments were again used to assess the significance of multiple comparisons.

Two dichotomous variables were analyzed using the Cochran's Q test for repeated measures (Siegel 1956): whether or not the scorpion sprinted the full 50 cm or stopped short; and whether or not a scorpion's sting “hit” the target. The influence of the starting positions of a scorpion's telson (metasomal curling) and metasoma (metasomal angle) on sting latency were analyzed with a Friedman's non-parametric repeated measures ANOVA, followed by post-hoc tests using Wilcoxon's signed-rank tests (Siegel 1956; Field 2005). The effect of metasomal curling and metasomal angle on sting latency was further explored by conducting, for each test temperature separately, a non-parametric Spearman's rank order correlation (Siegel 1956; Field 2005).

The computer program SPSS (Version 15.0, Chicago, Illinois) was used to perform statistical analyses. Descriptive results are presented in the text as means \pm 1 SE.

RESULTS

Sprint distances.—The experimental protocol was very effective in eliciting “straight-line” sprints from all 177 scorpions tested at each of their three body temperatures. Indeed, 88% of the trials (467/531) resulted in the scorpion sprinting the full 50 cm marked on the track. The average distance of the 64 sprints (12%) that stopped short of the 50-cm mark did not differ considerably across the three test temperatures (30.4 ± 9.14 cm at 10° C, 35.1 ± 5.37 cm at 25°

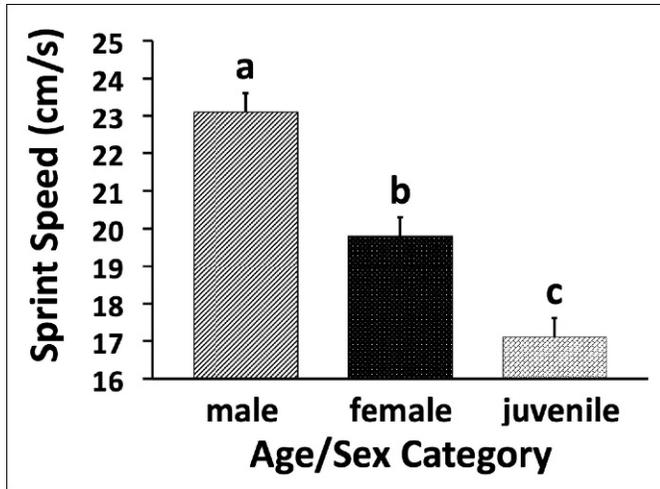


Figure 3.—Mean + SE sprint speeds of *C. vittatus* as a function of age and gender. Different letters signify different mean values at $P < 0.05$.

C, and 35.0 ± 6.20 cm at 38°C , respectively). The proportion of “short sprints” was, however, significantly influenced by a scorpion’s body temperature: only 10/177 tests (5.65%) at 25°C and 5/177 tests (2.82%) at 38°C resulted in the scorpion stopping short, compared to 49/177 (27.68%) truncated runs for scorpions at 10°C ($Q_2 = 64.48$, $P < 0.001$). Moreover, the 10 shortest runs (ranging from 10–23 cm) recorded in all 531 trials were for scorpions tested at their coolest temperature.

Sprint speeds.—There was a highly significant difference in the sprint speeds between each age/sex category ($F = 34.2$; $df = 2$, 174; $P < 0.001$; Fig. 3), with males sprinting fastest (23.1 ± 0.51 cm/s), followed by females (19.8 ± 0.50 cm/s) and then juveniles (17.1 ± 0.51 cm/s); the partial η^2 for this main effect was 0.282. Post-hoc Bonferroni comparisons show that male sprint speeds were significantly faster than either females or juveniles ($P < 0.001$), while females were faster than juveniles ($P = 0.001$). It is worth noting that 57 of the 60 female scorpions involved in these sprint tests were gravid; when we removed the three non-gravid females (one each from the three subgroups of adult females) from the analysis, results were unchanged.

Temperature significantly affected sprint speeds ($F = 1712.42$; $df = 1.45$, 252.67; $P < 0.001$; Fig. 4): at the warm temperature (38°C), scorpions averaged speeds of 32.8 ± 0.65 cm/s; at medium temperatures (25°C), their speed averaged 20.4 ± 0.37 cm/s; at the cooler temperature (10°C), speeds averaged only 6.8 ± 0.15 cm/s. The partial η^2 for this main effect was 0.908. Post-hoc Bonferroni comparisons revealed significant differences between each of the temperature treatments ($P < 0.001$). The positive effects of increasing body temperature on sprint speeds appears more pronounced in males than in females and juveniles, as evidenced by a small (partial $\eta^2 = 0.142$) but nonetheless significant interaction between age/sex and temperature ($F = 14.36$; $df = 2.94$, 252.67; $P < 0.001$). There was no significant effect of trial number on sprint speed ($F = 0.42$; $df = 2$, 348; $P = 0.657$), nor was there a significant interaction between trial number and age/sex ($F = 0.93$; $df = 4$, 348; $P = 0.983$).

Although our test apparatus was unsophisticated (i.e., a copper-bottomed runway placed on ice bags, a counter top, or

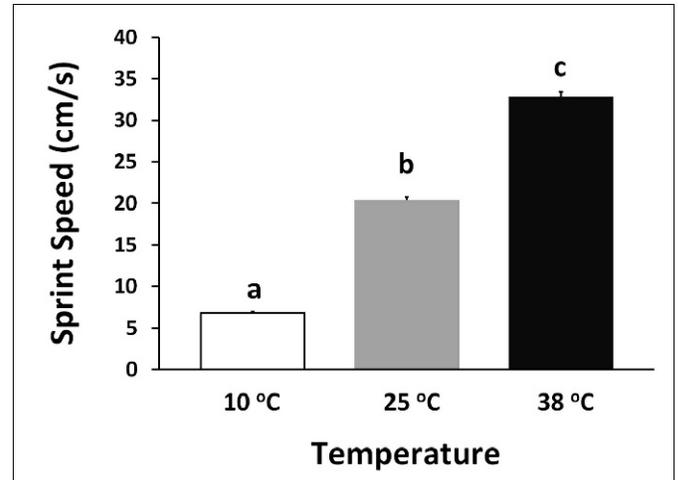


Figure 4.—Mean + SE sprint speeds of *C. vittatus* as a function of temperature. Different letters signify different mean values at $P < 0.05$.

hot plates), the variability in our targeted treatment temperatures (10, 25, and 38°C) was small; the T_s (and, thus, the T_b) for scorpions during their 10°C trial was $10.4 \pm 0.20^\circ\text{C}$; for scorpions during their 25°C trial it was $25.4 \pm 0.05^\circ\text{C}$; and for scorpions in their 38°C trial, it was $40.9 \pm 0.08^\circ\text{C}$. The low variability in substrate temperatures, recorded as they were along the full length of the runway, attests to the effectiveness of the copper plate in diffusing temperatures evenly across the apparatus.

Sting speeds and effectiveness.—Eliciting stings proved more difficult than inducing sprints. Indeed, 24.5% of the 159 sting trials ended with the scorpion either not stinging or attempting to sting but missing the target. Temperature appeared to influence stinging success, as 84.9% and 75.5% of the stings delivered by scorpions when at 25°C and 38°C T_b hit the target, respectively, while only 66.0% of the stings delivered by scorpions at 10°C were so effective ($Q_2 = 6.25$, $P = 0.044$).

For those scorpions who managed to sting the target in each test, temperature had a significant effect on their latency to sting ($F = 13.27$; $df = 1.06$, 23.26; $P = 0.001$; Fig. 5); cooler scorpions (10°C) took significantly longer (Bonferroni adjustment; $P < 0.001$) to deliver a sting (1.67 ± 0.40 s) than either the medium (25°C ; 0.29 ± 0.05 s) or warm (38°C ; 0.32 ± 0.08 s) scorpions, which did not themselves differ. The partial η^2 for this main effect was 0.376. The age and sex of the scorpion had no effect on sting latency ($F = 1.44$; $df = 2$, 22; $P = 0.258$), nor was there a significant interaction between age/sex and temperature ($F = 1.77$; $df = 2.11$, 23.26; $P = 0.191$). Note that 17 of the 18 female scorpions included in this analysis were gravid; when the non-gravid female was removed from the analysis, results were unchanged.

The significant influence of T_b on sting latency is unlikely to be the result of systematic differences in the initial positions of a scorpion’s telson or metasoma. There were no significant differences in metasomal curling ($\chi^2 = 2.14$; $df = 2$; $P = 0.343$) or angle ($\chi^2 = 3.60$; $df = 2$; $P = 0.166$) across the three test temperatures. Moreover, neither metasomal curling ($r_s = 0.218$; $P = 0.208$) nor angle ($r_s = 0.053$; $P = 0.763$) was significantly correlated with sting latency for scorpions during their 10°C test; results at 38°C were similar, with insignificant

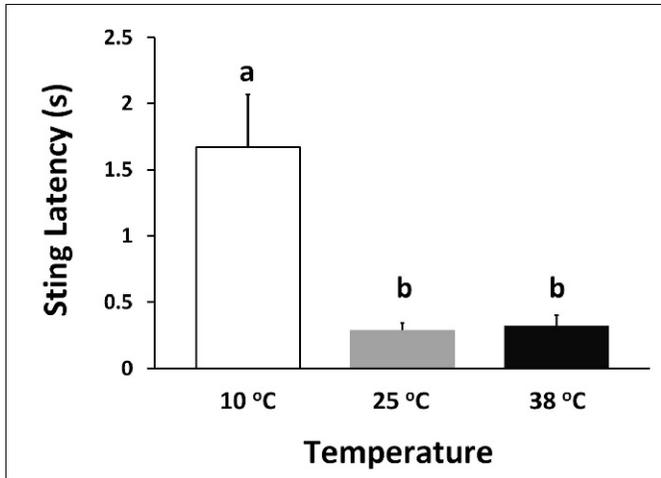


Figure 5.—Mean + SE sting latencies of *C. vittatus* as a function of temperature. Different letters signify different mean values at $P < 0.05$.

correlations of sting latency with metasomal curling ($r_s = 0.049$; $P = 0.762$) and angle ($r_s = 0.077$; $P = 0.637$). Intriguingly, both curling and angle were significantly correlated with sting latency for scorpions at intermediate body temperatures; e.g., at 25° C, scorpions with higher values of metasomal curling (positions 4–6 in Fig. 2a; note that no scorpion had a curling value of 7 at this temperature) delivered slower stings ($r_s = 0.449$; $P = 0.002$) than individuals with lower values (positions 1–3 in Fig. 2a). Similarly, individuals whose metasomas were held at ~45° delivered slower stings than those holding them vertically ($r_s = 0.491$; $P = 0.001$); only one individual at 25° C held its metasoma in a resting position (Fig. 2b), preventing any meaningful comparison for this angle. There was no significant effect of trial number on sting latency ($F = 0.34$; $df = 2, 44$; $P = 0.717$), nor was there a significant interaction between trial number and age/sex ($F = 1.26$; $df = 4, 44$; $P = 0.301$).

A similar pattern was found in the effects of temperature on sting rate ($F = 41.43$; $df = 2, 86$; $P < 0.001$; Fig. 6); cooler scorpions (10° C) delivered significantly fewer (Bonferroni adjustment; $P < 0.001$) stings per second (2.97 ± 0.27) than did scorpions at intermediate (25° C; 6.16 ± 0.39 stings/s) and warm (38° C; 6.33 ± 0.32 stings/s) body temperatures, which themselves did not differ. The partial η^2 for this main effect was 0.491. And while there was no significant interaction between age/sex and temperature on sting rate ($F = 0.32$; $df = 4, 86$; $P = 0.864$), the main effect of age/sex approached significance ($F = 2.81$; $df = 2, 43$; $P = 0.072$). Though caution is merited, it is noteworthy that female bark scorpions appear to deliver rapid, probing stings (5.90 ± 0.39 stings/s) more quickly than either juveniles (4.86 ± 0.38 stings/s) or males (4.71 ± 0.39 stings/s). Removing the sole non-gravid female from sting rate analyses did not influence these results. There was no significant effect of trial number on sting rate ($F = 0.58$; $df = 2, 86$; $P = 0.561$), nor was there a significant interaction between trial number and age/sex ($F = 0.44$; $df = 4, 86$; $P = 0.779$).

Our test apparatus for assessing sting speed and sting rates was, like our apparatus for assessing sprint speeds, rather crude. It was, nonetheless, effective and reliable at generating our targeted test temperatures. The T_s , and thus T_b , for

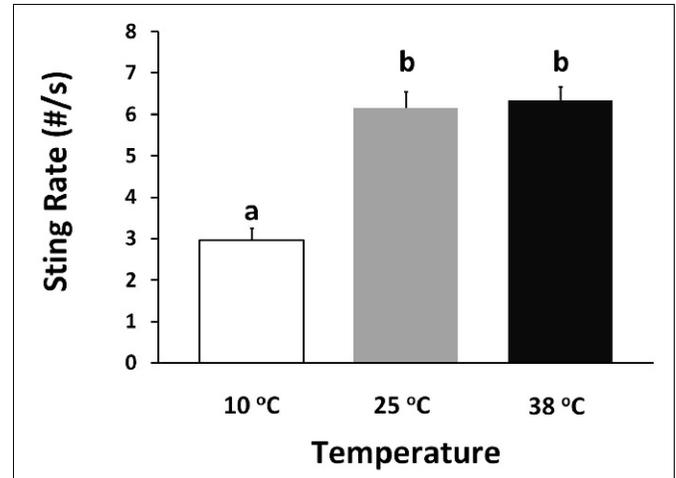


Figure 6.—Mean + SE sting rates of *C. vittatus* as a function of temperature. Different letters signify different mean values at $P < 0.05$.

scorpions tested at their targeted T_b of 10° C was 9.4 ± 0.18 ° C; for scorpions during their 25° C trials, T_s was 25.0 ± 0.05 ° C; and for 38° C trials, T_s was 37.8 ± 0.09 ° C.

Dehydration effects.—The scorpions receiving the desiccation treatment lost a significantly greater percentage of their body mass ($-14.95 \pm 1.3\%$) than did control scorpions ($-0.44 \pm 0.9\%$; $F = 78.32$; $df = 1, 35$; $P < 0.001$; Fig. 7). The partial η^2 for this main effect was 0.691. The effect of age/sex on mass loss was insignificant ($F = 0.97$; $df = 2, 35$; $P = 0.391$), as was the interaction of dehydration/control with age/sex ($F = 0.41$; $df = 2, 35$; $P = 0.670$).

The effect of hydration on sprint speeds was highly significant ($F = 22.84$; $df = 1, 35$; $P < 0.001$; Fig. 8); desiccated scorpions increased their sprint speed by $+7.57 \pm 7.1\%$ between their pre- and post-tests, while control scorpions decreased in speed by $-27.69 \pm 4.8\%$. The partial η^2 for this main effect was 0.395. At first glance, the age and sex of a scorpion also appear to influence how its sprint speed changed ($F = 3.68$; $df = 2, 35$; $P = 0.035$); females suffered the greatest

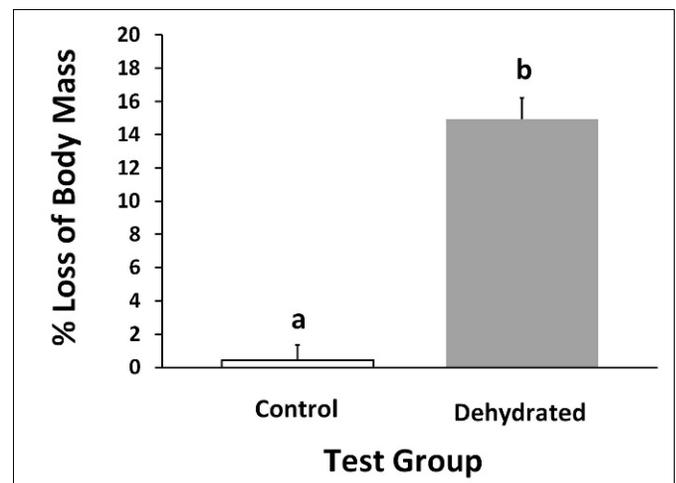


Figure 7.—Mean + SE percent of body mass lost in dehydrated and control *C. vittatus*. Different letters signify different mean values at $P < 0.05$.

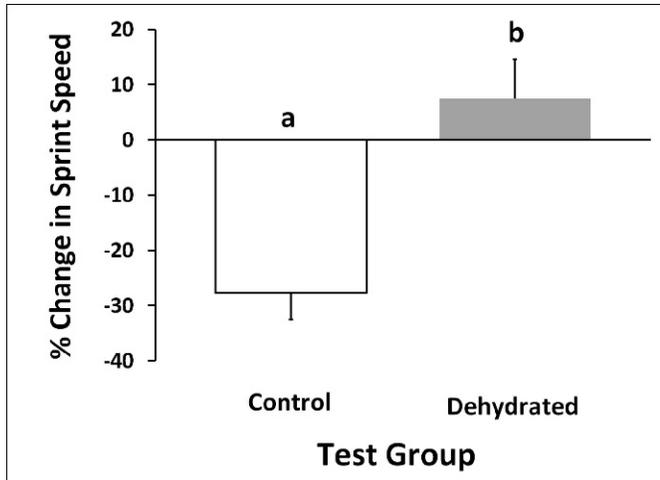


Figure 8.—Mean + SE percent changes between pre- and post-treatment sprint speeds for dehydrated and control *C. vittatus*. Different letters signify different mean values at $P < 0.05$.

reduction in sprint speeds ($-19.52 \pm 6.5\%$) during their time in the environmental chamber, followed by males ($-9.80 \pm 6.8\%$), while juveniles actually ran faster ($+10.17 \pm 8.8\%$) after spending ~ 3 days at 36°C . Note, however, that this DV did not meet the parametric assumption of normality, forcing us to reduce the level of significance (to $P < 0.01$) to minimize Type I error; by this more stringent criterion, age/sex had no significant influence on sprint speeds following desiccation. The highly significant effect of hydration, but not age/sex, on changes in scorpion sprint speeds was confirmed by running a Kruskal-Wallis non-parametric ANOVA (Siegel 1956; Field 2005) on both variables; the former DV remained highly significant ($\chi^2 = 14.37$; $df = 1$; $P < 0.001$), while the latter was not ($\chi^2 = 2.33$; $df = 2$; $P = 0.312$). And finally, the interaction between age/sex and dehydration/control was insignificant ($F = 1.21$; $df = 2, 35$; $P = 0.31$).

DISCUSSION

Carlson et al. (unpublished data) show that striped bark scorpions from two widely separated populations inhabiting ecologically distinct habitats (one a rocky scrub desert in the foothills of the Organ Mountains in southern New Mexico, the other from the piney woods region of southeastern Texas) exhibit activity patterns and microhabitat preferences favoring high T_b 's; moreover, when tested in a thermal gradient in the laboratory, scorpions from both populations had very high T_p 's ($36\text{--}38^\circ\text{C}$). The results presented here may help explain why; i.e., a *C. vittatus* that is warm sprints significantly faster and frequently sprints farther, delivers a quicker and more accurate sting, and delivers more stings per second than when it is cold. The influence of body temperature on this suite of defensive behaviors is the most robust finding from this study, as demonstrated by the uniformly higher effect sizes (partial η^2) for temperature than for age and gender. Temperature appears to have a more profound effect on sprint speed than sting efficacy, as evidenced by 1) the larger effect size (partial $\eta^2 = 0.908$) for maximal sprint velocity than for sting latency (0.376) or sting rate (0.491); and 2) by the significant differences (Bonferroni multiple comparisons) in sprint speeds

across all three body temperatures ($10, 25,$ and 38°C), but only between the coldest (10°C) vs. two warmer (25 and 38°C) temperatures for sting latency and rate. The preference of striped bark scorpions for the hottest of these temperatures may nonetheless make sense; when in the clutches of a grasshopper mouse, even a moderately warm scorpion can deliver a painful sting that will get it dropped, but only the warmest and fastest scorpion might then sprint to safety before the mouse re-attacks (Rowe & Rowe 2006).

Desiccation also had a significant effect on sprint velocity, but not in the manner we originally predicted. Surprisingly, scorpions that had lost nearly 15% of their body mass due to dehydration ran faster than they did prior to desiccation; control scorpions, whose body masses barely changed over the same three-day period while housed at 36°C , had sprint speeds $\sim 1/3^{\text{rd}}$ lower than their initial runs. The lack of any substantive effects of desiccation on sprinting may have several explanations. First, scorpions as a group use hydraulic pressure less in limb extension than most other arachnids (Shultz 1992), suggesting that fluid loss might have little impact on running speed. At high (though unspecified) levels of desiccation, however, scorpions do have difficulty moving (Sensenig & Shultz 2004); it is therefore possible that the amount of water loss in our trials was too low to have produced noticeable locomotor effects. Second, scorpions may, when suffering from dehydration stress, shift to anaerobic metabolism (Gefen 2008), which is less sensitive to the debilitating effects of desiccation than is aerobic metabolism (Weinstein 1998), allowing scorpions to maintain comparable levels of performance across varying levels of hydration. Finally, desiccation appears to affect activity bursts, such as sprinting, much less than it does endurance (Crowley 1985; Wilson & Havel 1989) mediated again through the different sensitivities of anaerobiosis vs. aerobiosis to desiccation. This study was not designed to measure endurance, so conclusions cannot presently be drawn about any possible inhibitory effects of desiccation on scorpion locomotor performance over longer time frames. The small positive effect of dehydration on scorpion sprint speeds ($+7.6\%$ faster following desiccation) is most likely the result of their significant loss of body mass (Crowley 1985).

In contrast, the dramatic reduction in sprint speeds for the control scorpions may reflect the negative physiological effects of supporting a high T_b (36°C) for a moderately long duration (70 h) without feeding. Studies have shown that ectotherms subject to high temperatures, but within the normal range they experience in the field, suffer denaturation of cellular proteins (Hofmann & Somero 1995); replacing these proteins requires energy that must be diverted from other tasks including, perhaps, maintaining the structures required for limb extension and retraction. Moreover scorpions, like many ectotherms, exhibit temperature-sensitive metabolic rates (Lighton et al. 2001); the energetic demands of higher T_b 's would reduce glycogen stores (Sinha & Kanungo 1967), further squeezing the pipeline that fuels locomotion. Whether desiccated scorpions are buffered from protein damage at high T_b 's is unknown. Dehydration, however, might actually protect scorpions from depleting their carbohydrate reserves, as desiccation significantly reduces their metabolic rates (Gefen 2008). Thus, for striped bark scorpions, the cost of maintain-

ing a high T_b is imposed not by desiccation, to which they appear well adapted, but through exhaustion of their energy resources. This cost may help explain the lengthy hiatus that scorpions spend between meals (Bradley 1982; Quinlan et al. 1993) in presumably cool refugia. Although speculative, proximate cues inducing a bark scorpion to leave the safety of its shelter could be a loss of body mass and/or a level of desiccation that maximize its sprint speed.

The influence of age and gender on the defensive behavior of striped bark scorpions also produced both anticipated and novel results. In a simple but elegant study, Shaffer and Formanowicz (1996) demonstrated that non-gravid female *C. vittatus* had significantly faster sprint speeds than gravid females, who themselves were faster than females carrying first-instar larvae on their backs. Moreover, female sprint speed was inversely related to the weight of the clutch they were carrying, either internally or dorsally. Given that all but three of the 60 females used in our sprint speed trials were gravid (and thus heavy, at 0.64 ± 0.016 gm), it is not surprising that their sprint speeds were significantly slower than the much leaner males (0.40 ± 0.12 gm). Juveniles, although light (0.17 ± 0.007 gm), were significantly slower than either males or females, likely resulting from their shorter limbs or incomplete motor development. Our results demonstrating both age and gender effects on sprint speeds thus support and extend the original findings of Shaffer and Formanowicz (1996). Uniquely, however, our results may help explain the dramatic sexual differences in *Centruroides* metasomas (Fig. 1) by pointing, tentatively, to a sexual dimorphism in antipredator behavior. Gestation in *C. vittatus* lasts eight months (Polis & Sissom 1990), a lengthy and risky period for female bark scorpions. Limited by the weight of their larger bodies and developing embryos, and thus incapable of achieving the sprint speeds of males, female *C. vittatus* may have selectively compensated for their increased vulnerability with better stinging ability. The longer, thinner metasomas of males appear to limit their ability to deliver fast, repetitive stings. While possession of a tail morphology capable of probing an enemy's epidermis for a weak spot certainly makes sense for a sluggish female bark scorpion, its absence in males is perplexing. Perhaps the longer and thinner metasoma of males enhances maneuverability, complementing their reliance on quick sprints to safety. Thin tails with an extended reach might also prove useful in courtship, or in male-male combat. We hope to explore these and other functional explanations concerning sexual differences in bark scorpion morphology and defensive behavior in future projects.

Our results documenting the influence of temperature on the defensive behavior of bark scorpions appear relevant to two additional, related aspects of their ecology; namely, their "errancy" and their proclivity for climbing bushes. Bark scorpions (*Centruroides* spp.) have earned the ecomorphological label of "errant" (McCormick & Polis 1990; Polis 1990) because, when hunting, they actively search for prey, quite unlike the ambushing strategy adopted by the majority of scorpion species. A cursorial foraging mode would, we argue, be more likely to attract the attention of visually hunting predators (e.g., grasshopper mice, *Onychomys* spp.; see Rowe & Rowe 2006) than would lying in wait. The foraging behavior of bark scorpions appears sensitive to their greater risk of predation, as evinced by their tendency of climbing into

bushes to evade their enemies (Brown & O'Connell 2000), a behavior that becomes even more pronounced when the moon is bright (McReynolds 2004). Intriguingly, one report suggests that female bark scorpions are more likely than males to use bushes (Yamashita 2004), perhaps reflecting the females' greater vulnerability imposed by their slower sprint speeds. In a recent report, McReynolds (2008) shows that striped bark scorpions shift from foraging in vegetation to foraging on the ground when nighttime air temperatures are extremely warm ($> 30^\circ$ C); the author suggests this shift may be due to increased availability of terrestrial prey during the hottest months of the year. A complementary interpretation is that bark scorpions are more likely to be found foraging on the ground when temperatures are warm enough to permit quick sprints to safety.

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