Hot and not-so-hot females: reproductive state and thermal preferences of female Arizona Bark Scorpions (*Centruroides sculpturatus*)

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Abstract

For ectotherms, environmental temperatures influence numerous life history characteristics, and the body temperatures (T_b) selected by individuals can affect offspring fitness and parental survival. Reproductive trade-offs may therefore ensue for gravid females, because temperatures conducive to embryonic development may compromise females' body condition. We tested whether reproduction influenced thermoregulation in female Arizona Bark Scorpions (*Centruroides sculpturatus*). We predicted that gravid females select higher T_b and thermoregulate more precisely than nonreproductive females. Gravid *C. sculpturatus* gain body mass throughout gestation, which exposes larger portions of their pleural membrane, possibly increasing their rates of transcuticular water loss in arid environments. Accordingly, we tested whether gravid *C. sculpturatus* lose water faster than nonreproductive females. We determined the preferred T_b of female scorpions in a thermal gradient and measured water loss rates using flow-through respirometry. Gravid females preferred significantly higher T_b than nonreproductive females, suggesting that gravid *C. sculpturatus* alter their thermoregulatory behaviour to promote offspring fitness. However, all scorpions thermoregulated with equal precision, perhaps because arid conditions create selective pressure on all females to thermoregulate effectively. Gravid females lost water faster than nonreproductive animals, indicating that greater exposure of the pleural membrane during gestation enhances the desiccation risk of reproductive females. Our findings suggest that gravid *C. sculpturatus* experience a trade-off, whereby selection of higher T_b and increased mass during gestation increase females' susceptibility to water loss, and thus their mortality risk. Elucidating the mechanisms that influence thermal preferences may reveal how reproductive trade-offs shape the life history of ectotherms in arid environments.

Introduction

For terrestrial ectotherms, environmental temperatures impact a variety of biological processes (i.e. growth rate, immune function, locomotor performance; Autumn & de Nardo, 1995; Braña & Ji, 2000; Mondal & Rai, 2001) and thus can have a significant influence on the evolu-

tion of life history strategies in these taxa. The body temperatures (T_b) of ectotherms are largely dependent on ambient temperatures, but individuals can exert control over their T_b through behavioural thermoregulation (Grant & Dunham, 1988; Samietz *et al.*, 2005). Thermoregulatory patterns can be influenced by physiological state and can be observed as a shift in an animal's preferred T_b (Gardner-Santana & Beaupré, 2009) during particular periods, such as the breeding season. Reproduction is an energetically costly activity that has the potential to alter the thermal preference of ectotherms, especially for viviparous species (Graves &

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Duvall, 1993; Le Galliard *et al.*, 2003). For viviparous ectotherms, the internal retention of offspring can buffer embryos from unfavourable environmental temperatures during development (Beuchat, 1988; Shine, 2004; Pincheira-Donoso *et al.*, 2013), thereby increasing offspring survival and fitness (Shine & Harlow, 1993).

The environmental temperatures selected by reproductive females during gestation can have profound effects on offspring survival (Ji *et al.*, 2007). For instance, incubational temperatures experienced by embryos during development can influence gene expression (Arias *et al.*, 2011), organ and tissue differentiation (Berger *et al.*, 2011), developmental rate (Tun-Lin *et al.*, 2000) and the size of offspring at birth (Fischer *et al.*, 2003). Studies addressing these changes have demonstrated that during gestation, gravid females often select higher T_b and exhibit more precise thermoregulation than nonreproductive females (Osgood, 1970; Charland & Gregory, 1990; Gvozdik, 2005). The selection of higher and less variable T_b by reproductive females has been shown to promote proper embryonic development and facilitate the production of larger and more viable offspring (Shine & Harlow, 1993; Lourdais *et al.*, 2004; Telemeco *et al.*, 2010; Wapstra *et al.*, 2010).

Careful thermoregulation by reproductive females may improve the viability of current offspring, but it has the potential to compromise the body condition of breeding females (Huey & Slatkin, 1976; Christian, 1998; Blouin-Demers & Weatherhead, 2001). Thermoregulation consists of movements between suitable microclimates, alterations in body posture in relation to the substrate, and changes in the duration of basking behaviour (Halliday & Adler, 2002). An increase in the frequency with which reproductively active females engage in thermoregulatory behaviours may make these individuals more conspicuous to predators, consequently increasing their mortality risk (Schwarzkopf & Shine, 1992; Brischoux *et al.*, 2011). Further, different physiological processes are not optimized at the same temperature (Blouin-Demers & Nadeau, 2005), and thus, an optimal temperature for one activity (e.g. gestation) may not be conducive to other physiological processes (e.g. body growth and repair, digestion). In these cases, it is possible that the outcome of thermal trade-offs between temperatures favourable to gestation and those beneficial for female health and survival may result in a conflict between a female's physical condition and the viability of her current offspring (Schwarzkopf & Andrews, 2012). Herein, we investigated the influence of reproductive state on the thermoregulatory behaviour of female Arizona Bark Scorpions, *Centruroides sculpturatus*, Ewing 1928 (=*Centruroides exilicauda*, Wood 1863 of some authors; Scorpiones: Buthidae), to gain insight into factors that shape the evolution of life history strategies (Robert *et al.*, 2003; Webb *et al.*, 2006; Li *et al.*, 2009).

Centruroides sculpturatus are nocturnal predators that inhabit the arid desert regions and riparian habitats of south-western North America (Rowe & Rowe, 2008; Webber & Graham, 2013). Female *C. sculpturatus* are viviparous and give birth to offspring ($\bar{X}$ = 20 scorplings, range: 7–42) following a 5.2 ± 2.3 month gestation period (Polis & Sissom, 1990). Unlike other species of desert scorpions, *C. sculpturatus* do not dig burrows and instead escape unfavourable desert temperatures by hiding within vegetation, in rock crevices, or under surface litter (Hadley, 1974; Polis, 1990). Because the selection of higher and less variable T_b by reproductive females can improve offspring fitness, we predicted that gravid *C. sculpturatus* select higher T_b and exhibit more precise thermoregulation, compared to nonreproductive females. Further, reproductive female scorpions move less frequently than nonreproductive females (Shaffer & Formanowicz, 1996). Given that gravid individuals are more sedentary than nonreproductive females, we predicted that there are no significant differences between the preferred diurnal (i.e. inactive) and nocturnal T_b of gravid *C. sculpturatus*. On the contrary, as nonreproductive females exhibit more surface activity than reproductive animals, we predicted that the former exhibit significant shifts in their diurnal and nocturnal T_b.

The morphological and physiological changes that occur in reproductive female *C. sculpturatus* may compromise their survival (Webber & Rodríguez-Robles, 2013), potentially limiting future reproductive opportunities. Throughout gestation, *C. sculpturatus* exhibit significant increases in body mass, and offspring developing within the female's reproductive tract cause considerable distention of the mesosoma (abdomen; M. M. Webber, personal observations). This increase in body mass exposes large portions of the pleural membrane. The pleural membrane consists of the interconnective tissues between the sclerotized plates composing the exoskeleton of scorpions (Hjelle, 1990). Relative to the waxy hardened cuticle, the pleural membrane is significantly more permeable to water (Hadley & Quinlan, 1987). We hypothesized that the greater exposure of the pleural membrane in gravid females heightens their susceptibility to transcuticular water loss, compared to nonreproductive females. Therefore, we also predicted that gravid *C. sculpturatus* exhibit faster rates of water loss than nonreproductive females.

Materials and methods

We collected 111 mature female *C. sculpturatus* from the outskirts of Quartzsite (33°38′9″N, 114°18′15″W), La Paz County, south-western Arizona, USA. We weighed (± 0.01 g) all individuals and housed them in separate plastic containers (15.0 × 9.0 cm) lined with a gravel substrate and maintained at a temperature of 24.0 ± 5.0 °C.

Thermal preferences

To determine the preferred T_b of female *C. sculpturatus*, we constructed a thermal gradient. The gradient consisted of a rectangular glass enclosure [71.0 cm (l) × 15.2 cm (w) × 15.2 cm (h)] lined with a gravel substrate (Webber & Bryson, 2012). We created a linear gradient (23.0–50.0 °C) that increased approximately 3.5 °C every 10.2 cm. The mean humidity of the room containing the gradient was 40%. We initially divided 62 of the females into two classes: nongravid (n = 34) and gravid (n = 28). We determined the body size of each female scorpion by measuring the length of her carapace (± 1 mm) and categorized females as gravid if embryos were visible within the mesosoma.

We fed all scorpions a single prey item (Common House Cricket, *Acheta domesticus*) and allowed them to acclimate for 7 days before placing them in the thermal gradient. Using forceps, we introduced an individual scorpion into the gradient at the mid-point of the enclosure. Scorpions were placed on a 13 h (ambient) light : 11 h dark cycle, which corresponded to natural summer conditions at the collection locality during the time of capture. We allowed the scorpions to acclimate to the gradient enclosure for 12 h prior to data collection. We measured the mesosomal T_b of each female every 2 h over a 24-h period using an infrared thermometer (Model 42505; Extech Instruments, Nashua, NH, USA, precision ± 0.07 °C). We also noted whether females were stationary or actively moving throughout the enclosure at each 2-h period of data collection. We did not record the T_b of females in cases where they were found to be moving within the gradient. We cleaned all enclosures with soap and water and replaced the gravel between all trials. To compare the preferred T_b of nonreproductive and gravid female *C. sculpturatus* during the day (when scorpions exhibit reduced activity), and at night (when scorpions are primarily active on the surface), we divided the 24-h trial period into two components: diurnal (0800 h–1800 h) and nocturnal (2000 h–0600 h). We calculated the mean diurnal and mean nocturnal T_b for females within each reproductive group and compared these values using a profile analysis (a multivariate equivalent to a repeated-measures ANCOVA). This method allowed us to compare the dependent variable of interest (T_b) over time, while also controlling for body size differences among females. We compared the precision of thermoregulation between reproductive groups using Levene's test for the homogeneity of variances.

Water loss

We measured the water loss rates of the remaining 49 female *C. sculpturatus* (nongravid, n = 24; gravid, n = 25) using flow-through respirometry. We followed the same feeding procedure described in the study of thermal preference and allowed individuals to acclimate to laboratory conditions for 7 days prior to the respirometry trials. We placed each scorpion in a 15.0-mL glass cylinder, which was in turn positioned within a temperature-controlled incubator set at 38.0 °C. Silica gel desiccant was used to dry the air, which was then passed through the glass chamber at a flow rate of 50 mL min^{-1}. Excurrent air was passed through a LI-6262 CO_2/H_2O analyzer (Li-Cor, Lincoln, NE, USA), and the voltage output was recorded once every second and analysed using the Datacan V data acquisition and analysis software (Sable Systems International, Las Vegas, NV, USA). We recorded the rate of water loss for each scorpion over a 30-min period. We compared the mean water loss rate of nonreproductive and gravid females using an analysis of covariance (ANCOVA), to control for differences in body size (carapace size) among females.

All statistical tests were performed using SPSS (SPSS 21 Inc., Chicago, IL, USA). Values reported are means ± 1 SD, and all *P*-values are two-tailed. Significance level for all tests was determined at α = 0.05.

Results

Thermal preferences

Nongravid (carapace length, X̄ = 5.70 ± 0.44 mm, range = 4.76–6.85 mm, n = 34) and gravid (X̄ = 5.75 ± 0.29 mm, 5.20–6.40 mm, n = 28) female *C. sculpturatus* had similar body sizes (ANOVA, $F_{1,60}$ = 0.40, P = 0.53). However, gravid females were proportionally heavier than nonreproductive animals (Table 1). After controlling for differences in body size among females, gravid individuals selected significantly higher diurnal and nocturnal T_b, compared to nonreproductive females (Table 1). There was a significant

Table 1 Comparisons of body mass and preferred body temperature (T_b) between nongravid and gravid female *Centruroides sculpturatus*. Carapace length (mm) was used as the covariate for the analysis of covariance (ANCOVA) and the profile analysis.

Reproductive status	Mean (± 1 SD)	Range	n
Body mass (g)			
Nongravid females	0.68 ± 0.17	0.38–1.0	34
Gravid females	0.96 ± 0.19	0.62–1.43	28
ANCOVA; $F_{1,59}$ = 37.8, P < 0.001			
Diurnal T_b (°C) (0800 h–1800 h)			
Nongravid females	40.6 ± 4.34	32.5–48.5	34
Gravid females	42.5 ± 4.75	23.7–48.4	28
Nocturnal T_b (°C) (2000 h–0600 h)			
Nongravid females	37.0 ± 3.25	31.4–42.7	34
Gravid females	39.7 ± 2.90	33.8–44.6	28
Profile analysis; $F_{1,59}$ = 10.2, P = 0.002			

interaction between body size and preferred T_b, as larger gravid *C. sculpturatus* exhibited lower mean T_b than smaller gravid females ($r^2 = 0.20$, $F_{1,27} = 6.6$, $P = 0.02$; Fig. 1). However, body size was not a significant predictor of selected T_b for nongravid animals ($r^2 = 0.06$, $F_{1,33} = 1.9$, $P = 0.18$; Fig. 1). Nonreproductive and gravid females thermoregulated with equal precision during the day (Levene's test; $F_{1,60} = 0.33$, $P = 0.57$) and at night (Levene's test; $F_{1,60} = 0.97$, $P = 0.33$). The preferred average diurnal T_b of gravid females was not statistically different from their mean nocturnal T_b (Tables 1, 2; Fig. 2). Contrary to our prediction, the average diurnal T_b of nongravid females did not differ from their mean nocturnal T_b (Tables 1, 2; Fig. 2). The average number of movements observed within the gradient at each 2-h interval was not statistically different between nongravid ($\bar{X} = 1.44 \pm 1.40$, range = 0–5, $n = 34$) and gravid females ($\bar{X} = 1.07 \pm 1.20$, range = 0–4, $n = 28$; ANOVA, $F_{1,60} = 1.21$, $P = 0.28$).

Water loss

Nonreproductive (carapace length, $\bar{X} = 5.78 \pm 0.63$ mm, range = 4.81–7.02 mm, $n = 24$) and gravid ($\bar{X} = 5.64 \pm 0.42$ mm, range = 4.69–6.66 mm, $n = 25$) females did
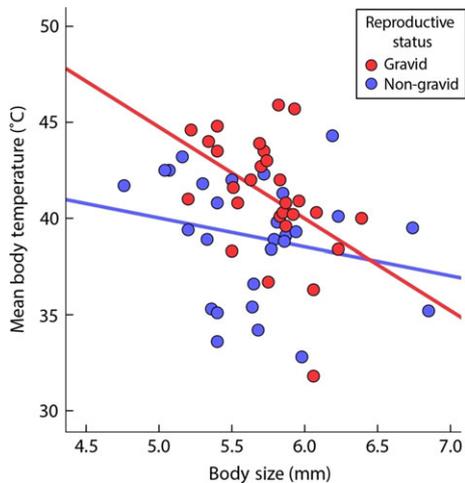

Fig. 1 Mean body temperature (T_b) as a function of body size (carapace length) in nonreproductive and gravid female *Centruroides sculpturatus*.

Table 2 Profile analysis comparing diel shifts in the mean T_b of nonreproductive and gravid female *Centruroides sculpturatus* over a 24-h period.

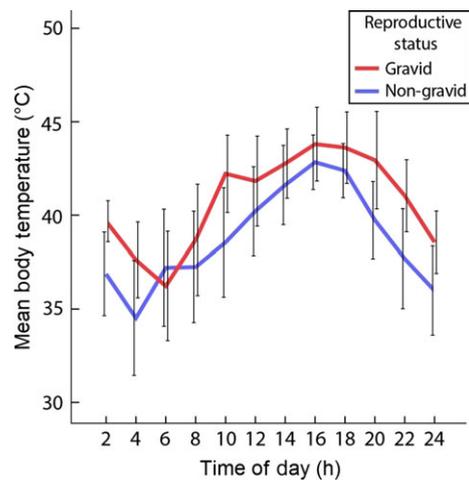| Effect	Wilks' λ	d.f.	F	P
Time	0.985	1	0.92	0.34
Time * Body size (carapace length, mm)	0.994	1	0.36	0.55
Time * Reproductive status	0.994	1	0.37	0.55

Fig. 2 Diel fluctuations in the mean body temperature (T_b) of nonreproductive and gravid female *Centruroides sculpturatus*. Error bars represent 95% CI.

not differ in body size (ANOVA, $F_{1,47} = 0.90$, $P = 0.35$). However, gravid females were proportionally heavier than nonreproductive animals (Table 3). After controlling for differences in body size, gravid females lost water at a faster rate than nongravid individuals (Table 3). Body size was not a significant predictor of water loss rates for either nonreproductive ($r^2 = 0.05$, $F_{1,22} = 1.11$, $P = 0.30$) or gravid ($r^2 = 0.07$, $F_{1,23} = 1.83$, $P = 0.19$) female *C. sculpturatus* (Fig. 3). Similarly, body mass was not a significant predictor of water loss rates for nongravid females ($r^2 = 0.02$, $F_{1,22} = 0.51$, $P = 0.48$; Fig. 4). In contrast, body mass was a significant predictor of water loss rates for gravid females, because heavier individuals lost water at a faster rate than lighter ones ($r^2 = 0.32$, $F_{1,23} = 10.8$, $P = 0.003$; Fig. 4).

Discussion

In viviparous ectotherms, reproductive females often select higher T_b and exhibit increased precision in thermoregulatory patterns during gestation (Osgood, 1970;

Table 3 Comparisons of body mass and rate of water loss between nongravid and gravid female *Centruroides sculpturatus*. Carapace length (mm) was used as the covariate for the analysis of covariance (ANCOVA).

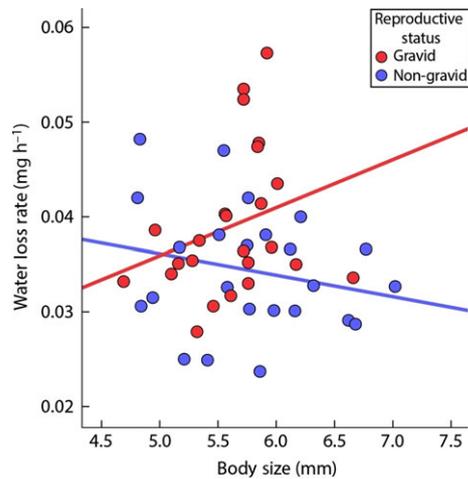| Reproductive status	Mean (± 1 SD)	Range	n
Body mass (g)			
Nongravid females	0.75 ± 0.17	0.42–1.08	24
Gravid females	1.06 ± 0.19	0.76–1.55	25
ANCOVA; $F_{1,46} = 41.3$, $P < 0.001$			
Water Loss Rate (mg h^{-1})			
Nongravid females	0.034 ± 0.007	0.024–0.048	24
Gravid females	0.039 ± 0.007	0.028–0.057	25
ANCOVA; $F_{1,46} = 5.17$, $P = 0.03$			

Fig. 3 Mean water loss rate as a function of body size (carapace length) in nonreproductive and gravid female *Centruroides sculpturatus*.
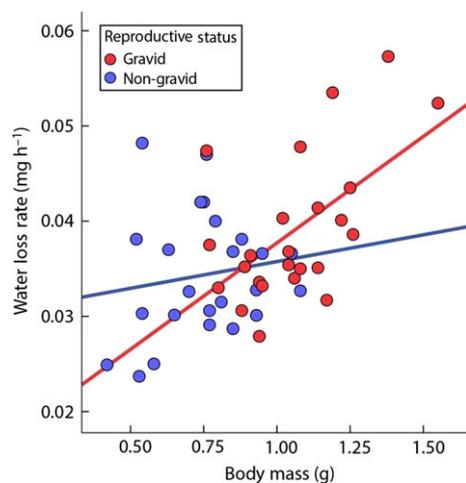

Fig. 4 Mean water loss rate as a function of body mass in nonreproductive and gravid female *Centruroides sculpturatus*.

Charland & Gregory, 1990; Gvozdik, 2005). Although this behaviour may create favourable conditions for offspring development, it may also result in a trade-off for those females, as it negatively affects their body condition, reproductive success and survival, particularly in arid environments. We assessed whether female *C. sculpturatus* altered their preferred T_b during gestation and examined how the morphological and physiological changes that occur in reproductive females affect their ability to conserve water.

Thermal preferences

After controlling for differences in body size, gravid *C. sculpturatus* preferred higher average diurnal and

nocturnal T_b than nongravid females. The selection of higher T_b by gravid *C. sculpturatus* during gestation may promote proper embryonic development, thereby increasing offspring fitness. In addition, active thermoregulation by viviparous ectotherms can shorten the duration of pregnancy (Beuchat, 1988), and thus, the selection of higher T_b by gravid female *C. sculpturatus* may shorten the length of gestation, reducing fitness costs that the females may incur during pregnancy. Further, an elevated T_b can increase the sprint speed and the stinging performance of scorpions (Carlson & Rowe, 2009), which may enable reproductive females to escape predation more effectively. These factors are not mutually exclusive, and all may contribute to the elevated T_b we observed in reproductive female *C. sculpturatus*.

Larger bodied gravid *C. sculpturatus* selected lower mean T_b than smaller gravid females. What physiological factors may account for this result? Larger bodied organisms have a smaller surface-to-volume ratio than smaller individuals, and therefore, the former lose heat at a slower rate than the latter (Blanckenhorn, 2000). For this reason, larger gravid females can select lower environmental temperatures, whereas still maintaining the same preferred T_b as smaller individuals for a given period of time. In contrast, smaller gravid *C. sculpturatus* lose heat faster than larger females and thus may need to select higher environmental temperatures to maintain their preferred T_b during gestation. Alternatively, larger gravid females may select cooler temperatures due to a decrease in the efficiency with which they can thermoregulate at warmer temperatures. At higher temperatures, larger gravid females are unable to lose heat quickly, which may place them at a greater risk of reaching unfavourably higher T_b and suffering heat injury. By selecting cooler T_bs, larger gravid females may decrease their risk of heat-induced mortality.

Contrary to our prediction, gravid females did not exhibit more precise thermoregulation than nonreproductive females during the day, or at night. *Centruroides sculpturatus* inhabit the xeric desert regions of southwestern North America. Arid conditions within these habitats can create substantial selective pressure for water acquisition and conservation, and individuals that do not perform these tasks adequately exhibit high rates of mortality (McKechnie & Wolf, 2010; Moses *et al.*, 2011). Therefore, precise thermoregulation may be necessary for all scorpions (females and males), irrespective of their reproductive status, to reduce rates of water loss when exposed to the higher environmental temperatures in their habitats. At the same time, precise thermoregulation can incur high energetic costs for females. Thermoregulation often consists of frequent movements among thermally preferable microhabitats (Charland, 1995), and this activity may make scorpions more conspicuous to predators. Reducing the frequency of movements would probably decrease predation risk

for female *C. sculpturatus*, but it would also reduce the probability that the scorpions will be able to consistently and reliably select microhabitats in which they can maintain their preferred T_b.

Reproductive *Centruroides vittatus* (Striped Bark Scorpion) females are known to move less frequently than nongravid females (Shaffer & Formanowicz, 1996), and thus, we predicted that gravid *C. sculpturatus* are more sedentary than nonreproductive individuals and do not show daily shifts in their preferred T_b. On the other hand, because nonreproductive females often engage in more surface activity than reproductive animals, we hypothesized that nongravid *C. sculpturatus* exhibit significant differences between their preferred nocturnal (active) and diurnal (inactive) T_b. We did not observe significant differences in the mean number of movements between nongravid and gravid female *C. sculpturatus* within the temperature gradient enclosure, or between the average preferred diurnal and nocturnal T_b of gravid *C. sculpturatus*. Contrary to our prediction, the mean T_b of nongravid females did not change significantly over the 24-h trial period. Collectively, these findings suggest that the time of day does not statistically influence the preferred T_b of female *C. sculpturatus* and that females do not appear to alter their thermoregulatory behaviour in response to ambient light cues. Because environmental temperatures can influence a multitude of behavioural and physiological processes in terrestrial ectotherms (Beuchat, 1988; Hadley, 1994; Telemeco *et al.*, 2010), avoidance of unfavourable temperatures, not responses to the light environment, may be the most prominent factor influencing patterns of surface activity in *C. sculpturatus*.

Water loss

To accommodate developing embryos during gestation, the pleural membrane of the mesosoma of gravid scorpions is stretched, exposing a section of the integument that is significantly more permeable to water than the hardened exoskeleton (Hadley & Quinlan, 1987). Moreover, during gestation developing embryos may place increased oxygen demands on viviparous females (Beuchat & Vleck, 1990; Robert & Thompson, 2000; Weldon *et al.*, 2012). Higher respiration rates may, in turn, increase the rate of water loss in gravid females. The exposure of the permeable pleural membrane and the possible increased respiratory rates of reproductive females were expected to lead to faster rates of water loss for gravid *C. sculpturatus*, compared to nonreproductive females.

Gravid *C. sculpturatus* indeed lost water faster than nonreproductive females, and heavier gravid individuals had higher rates of water loss than lighter reproductive females. These results suggest that water loss rates increase significantly for gravid females as gestation

progresses, probably because growing embryos within the mesosoma cause greater exposure of the pleural membrane. Further, larger gravid scorpions produce larger and more numerous offspring than smaller females (Steffenson & Brown, 2013). Larger offspring or a larger litter may increase the oxygen demands placed on females and induce a greater distention of the mesosoma, resulting in even faster rates of water loss for larger gravid females. In nature, faster dehydration rates may compromise the survival of gravid scorpions through increasing their risk of desiccation in arid environments. Gravid female *C. sculpturatus* may minimize their water loss rates by selecting more humid microhabitats, which may reduce their rates of evaporative water loss.

Evaporative cooling occurs when water evaporates from the body surface of an organism and leads to a reduction in the individual's T_b. Evaporative cooling generally occurs under harsh environmental conditions, such as high temperatures and low humidity (Edney, 1974; Oertli & Oertli, 1990; Hadley, 1994). Although evaporative cooling may enable several species of terrestrial arthropods to survive brief fluctuations in environmental temperatures (Iacarella & Helmuth, 2012; Lahondère & Lazzari, 2012), this benefit may be limited for arid-adapted species, because prolonged periods of water loss in arid environments can deplete an organism's water reserves, increasing its desiccation risk (Toolson, 1987). Moreover, the amount of heat lost through evaporative cooling is often < 10% of the heat generated via metabolic processes (Lighton *et al.*, 2001; M. M. Webber, unpublished). Therefore, evaporative cooling does not appear to be a likely mechanism for reducing T_b in *C. sculpturatus*.

In conclusion, our findings regarding the thermal preferences of breeding *C. sculpturatus* demonstrate the influence of reproductive state on other physiological attributes of these females. Gravid *C. sculpturatus* selected higher T_b, which may positively affect offspring health and survival. However, the preferred higher temperatures and the greater exposure of the pleural membrane in reproductive females increase their water loss rates and consequently the mortality risk of these individuals. Hence, gravid *C. sculpturatus* females may experience an evolutionary trade-off, whereby engaging in current reproduction (i.e. gestation) may limit their survival due to an increase in the risk of mortality through desiccation at higher temperatures. In environments where resources such as thermally preferable habitats or water are limited, as is the case in arid deserts, the outcome of trade-offs experienced by reproductive females may lead to plasticity in the energetic resources invested during reproduction. Elucidating the proximate mechanisms that generate alterations in the daily activities of reproductive females increases our understanding of how ecologically relevant tasks shape the life histories of ectothermic animals.

Acknowledgments

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