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Life history tradeoffs and the costs of reproduction in Arizona Bark Scorpions (Centruroides sculpturatus)

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LIFE HISTORY TRADEOFFS AND THE COSTS OF REPRODUCTION IN

ARIZONA BARK SCORPIONS (*CENTRUROIDES SCULPTURATUS*)

By

Michael Marie Webber

Bachelor of Science

University of Nevada, Las Vegas

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A dissertation submitted in partial fulfillment of

the requirements for the

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Michael Marie Webber

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ABSTRACT

**Life history tradeoffs and the cost of reproduction in Arizona Bark
Scorpions (*Centruroides sculpturatus*)**

by

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Tradeoffs in life history evolution result from conflicts in the time and energy that can be simultaneously invested in activities such as growth, reproduction, and survival. Reproduction is an energetically costly activity for organisms, and is known to elicit alterations in the daily activity patterns of individuals. I investigated reproductive tradeoffs in the Arizona Bark Scorpion, *Centruroides sculpturatus*. To better understand the nature of tradeoffs in this species, I examined the influence of reproductive state on the predatory efficiency and thermal preference of reproductive females. Further, I examined the influence of reproductive activities (i.e. gestation) on the ability of reproductive females to conserve water at high temperatures. Finally, I used morphometric analyses to investigate tradeoffs in weapon and ornament allometry in male and female *C. sculpturatus*. To examine tradeoffs that occurred between reproductive activities and the predatory efficiency of female *C. sculpturatus*, I conducted prey handling trials of non-gravid and gravid females and compared the time it took them to successfully capture and subdue a prey item (Common House Cricket, *Acheta domesticus*). Using Survival Analyses, I determined that pregnancy did not significantly reduce the predatory efficiency of gravid female *C. sculpturatus*, which

suggests that gravid females can maintain their predatory abilities despite significant

increases in body mass and the physiological costs associated with gestation. However,

all female *C. sculpturatus* exhibiting maternal care (i.e. carrying offspring) were unable

to capture prey during the trial period, suggesting that brooding behaviors incur

substantial energetic costs for female *C. sculpturatus*. Thus, female *C. sculpturatus*

experience a tradeoff between caring for current offspring and their ability to acquire

resources during the brooding period. Next, to examine the influence of reproductive

state on the thermal preference of females, I designed and constructed a thermal gradient,

and recorded the body temperatures (T_b) of non-gravid and gravid females over a 24 hour

period. Using Profile Analysis, I documented that gravid females selected significantly

higher diurnal and nocturnal T_b than non-gravid females. The selection of higher T_b by

gravid *C. sculpturatus* may improve offspring fitness by facilitating favorable

temperatures for embryonic development. However, the preferred T_b of gravid females

was close to their critical maximum temperature, which may significantly increase their

risk of heat-induced mortality. The morphological (increased body mass) and

physiological (increased metabolic rate) changes that occur in reproductive females can

increase their susceptibility to water loss, compared to non-reproductive females. To

compare rates of water loss between non-gravid and gravid females, I measured their

water loss rates using flow-through respirometry. Gravid female *C. sculpturatus* lost

water significantly faster than non-gravid females. This is another tradeoff experienced

by reproductive *C. sculpturatus*, because engaging in current reproduction (i.e. gestation)

may increase their risk of mortality through desiccation at higher temperatures. Finally, to

examine possible tradeoffs in weapon and ornament allometry in *C. sculpturatus*, I

measured the length of several distinct morphological characters: carapace, mesosoma, metasomal segments I-V, telson, chela, and walking legs I and IV. Using Principal Component Analysis, Analysis of Covariance, and a correlation analysis, I compared the relative sizes of traits between male and female *C. sculpturatus*. There is sexual dimorphism in the size of the chelae and tail in *C. sculpturatus*, as females had larger chelae than males, and males had significantly longer tails than females. Males exhibited a negative correlation between the relative size of weapons and ornaments (chelae and tail) and total body length (carapace + mesosoma length), because individuals with relatively larger chelae and tails possessed relatively shorter bodies. These data demonstrate the negative influence that weapon development can have on the resources allocated to other body parts. In female *C. sculpturatus*, increases in the relative size of the mesosoma were negatively correlated with the size of the chelae, carapace, and the length of leg IV. Thus, it appears that the allocation of energetic resources to a structure (the mesosoma) that influences reproductive output may reduce the energy available for weapon development and somatic growth in different regions of the female's body. These intersexual differences in the body allometry of male and female *C. sculpturatus* likely reflect the influence that sexual selection can exert on particular traits. Understanding the mechanisms that generate these tradeoffs in life history evolution may help elucidate factors that lead to diversity in the behaviors and reproductive strategies of species in nature.

ACKNOWLEDGMENTS

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CHAPTER 1

LIFE HISTORY TRADEOFFS AND THE COSTS OF REPRODUCTION

Tradeoffs in life history evolution result from temporal and energetic constraints imposed on organisms by resource limitation. When resources are scarce, organisms must divide a finite amount of resources among various life history components (i.e. growth, maintenance and repair, foraging, reproduction). One prominent tradeoff in life history evolution is between the resources invested in current offspring versus the resources invested in parental survival and future reproduction (Williams 1966; Osorno 1999; Hamel et al. 2011; Nicolai 2012; Weatherhead et al. 2012). Reproduction is an energetically costly activity (Beuchat & Vleck 1990; Charland 1995; Schultz et al. 2008), particularly for viviparous (live-bearing) females that continually transfer nutrients to offspring throughout gestation. Despite the considerable cost of viviparity, this reproductive mode is advantageous in unpredictable environments, because it maintains favorable conditions for embryonic development during gestation, and ultimately results in greater offspring fitness (Beuchat 1988; Qualls & Andrews 1999; Shine 2004; Pincheira-Donoso et al. 2013).

Reproductive females often undergo significant physiological and morphological changes during gestation, which have the potential to negatively impact their ability to engage in other ecologically-relevant tasks. Throughout gestation, reproductive females exhibit significant increases in body mass that may lead to decreases in their locomotor performance (Brodie 1989; Shaffer & Formanowicz 1996). Impaired locomotor ability can increase the mortality risk of reproductive females by significantly hindering their

ability to escape predation (Cooper et al. 1990). Furthermore, decreases in the locomotor

efficiency of reproductive females may also decrease their foraging ability (Levri &

Lively 1996), thus limiting their ability to recuperate the energetic resources invested in a

reproductive bout. For species that exhibit maternal care, these reproductive costs may

extend past parturition and continue to negatively influence the survival and reproductive

potential of post-parturient females.

Reproductive state may also elicit behavioral changes in the daily activity patterns

of females. Reproduction can significantly alter the thermoregulatory patterns of

ectothermic females (Graves & Duvall 1993; Le Galliard et al. 2003). Changes in the

thermoregulatory behavior of reproductive females during gestation have been shown to

lead to greater offspring fitness (Shine 1980; Shine & Harlow 1993; Lourdais et al. 2004;

Telemeco 2010; Wapstra et al. 2010). Despite this benefit, changes in the

thermoregulatory patterns may compromise the survival and reproductive potential of

reproductive females (Huey & Slatkin 1976; Christian 1998; Blouin-Demers &

Weatherhead 2001). There may be thermal conflicts in the temperatures at which various

physiological processes are optimized (Blouin-Demers & Nadeau 2005) and optimal

temperatures for reproductive activities may not be conducive to other physiological

processes (i.e. growth and repair, digestion). Hence, reproductive females may

experience a tradeoff between selecting temperatures favorable for offspring

development and those beneficial for female health and survival (Schwarzkopf &

Andrews 2012).

Another important tradeoff in life history evolution is between the energetic

resources allocated to the development of different anatomical structures throughout

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ontogeny. The maximum body size attained by organisms is another life history component that can directly influence an organism's survival and reproductive potential (Buston & Elith 2011; Xu & Wang 2013). For example, reproductive output generally increases with body size, and larger individuals often produce larger or more numerous offspring and experience greater reproductive success than smaller individuals (Magnhagen & Kvarnemo 1989; Wiklund & Kaitala 1995; Steffenson & Brown 2013). However, there are costs associated with a larger body size, because larger organisms may have greater energetic requirements than smaller ones, which may compromise their survival under resource limitation (Wikelski et al. 1997). Individuals typically allocate a greater amount of energetic resources to the growth of defensive and offensive traits (weapons) and traits used to attract mates (ornaments; Emlen et al. 2012). Thus, weapons and ornaments tend to exhibit positive allometry and become larger and more elaborate as individuals increase in body size (MacLaren et al. 2011; Bergmann & Berk 2012; Painting & Holwell 2013). Although larger weapons and ornaments may increase an organism's chances of survival and reproductive success, the growth and maintenance of enlarged body structures may be energetically costly, possibly resulting in reductions in locomotor ability (Madewell & Moczek 2006; Allen & Levinton 2007), decreased immune function (Saino & Møller 1996; Verhulst et al. 1999), and a greater rate of detectability by predators thereby increasing their predation risk (Godin & McDonough 2003). Furthermore, the allocation of resources to weapon and ornament growth may also diminish the size of other anatomical structures (Emlen 2001; Simmons & Emlen 2006), which may have a negative impact on other essential life history components.

I investigated tradeoffs between current reproduction, body growth, and survival in the Arizona Bark Scorpion, *Centruroides sculpturatus*, Ewing 1928 (=*Centruroides exilicauda*, Wood 1863 of some authors). Specifically, I examined whether reproductive status affected the foraging behavior and predatory efficiency of female *C. sculpturatus* (Chapter 2). Additionally, I assessed the potential effect of reproductive state on the thermal preferences of females, and how the physiological and morphological changes experienced by reproductive females influenced their ability to achieve water balance at higher temperatures (Chapter 3). I also explored intersexual differences in the allocation of energetic resources to weapon and ornament development in *C. sculpturatus*, and how investment in those traits may conflict with the development of other anatomical structures (Chapter 4). I summarized the results of my research, and suggested future studies regarding reproductive tradeoffs in male and female *C. sculpturatus* (Chapter 5). My findings contribute to our understanding of how the allocation of resources to current reproduction can influence the survival and future reproductive opportunities of organisms, and how energetic constraints imposed by reproduction shape the evolution of life histories.

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CHAPTER 2

REPRODUCTIVE TRADEOFF LIMITS THE PREDATORY EFFICIENCY OF

FEMALE ARIZONA BARK SCORPIONS (*CENTRUROIDES SCULPTURATUS*)

Abstract

Life history tradeoffs may result from temporal and physiological constraints
intrinsic to an organism. When faced with limited time and energy, compromises occur
and these resources are allocated among essential activities, such as body growth,
maintenance, foraging, mating, and offspring care. I investigated potential tradeoffs that
may occur between reproductive activities and feeding performance in female Arizona
Bark Scorpions (*Centruroides sculpturatus*) by comparing the time taken to capture prey
between non-reproductive and reproductive females (gravid females and females
exhibiting maternal care, i.e. carrying offspring on their backs). Gravid females were as
efficient at catching prey as non-gravid females. To control for variation in the duration
of the maternal care period, I removed all offspring from all post-parturient females after
5 days. Brooding females and females 24 hours following offspring removal (FOR) did
not successfully capture prey within the 900-second trial period. Twenty-eight days FOR,
females caught prey faster than females displaying maternal care and females 24 hours
FOR, but were not as efficient at catching prey as non-gravid and gravid females. When
pursuing prey, *C. sculpturatus* exhibiting maternal care used an active foraging strategy
more frequently than non-gravid, gravid, and females 28 days FOR. In contrast, non-
gravid, gravid, and females 28 days FOR used active and ambush foraging with similar
frequency. My data suggest that reproduction does not significantly reduce the predatory

efficiency of gravid *C. sculpturatus*, and that these females can cope with increasing body mass and the physiological costs of gestation. However, the observation that brooding females and females 24 hours FOR did not catch prey within the trial period indicates that maternal care significantly reduces predatory efficiency in these scorpions. Females 28 days FOR were still not as efficient at catching prey as non-gravid and gravid females, suggesting that reproductive costs extend for at least 4 weeks after the end of the maternal care period. Preferential use of an active foraging strategy by brooding females may increase prey encounter rates, allowing the scorpions to more rapidly replenish energy reserves depleted during reproduction. However, active foraging may be energetically costly and increase predation risk for brooding females. My findings regarding antagonistic interactions between reproduction and feeding in female *C. sculpturatus* demonstrate the pervasive nature of reproductive costs for viviparous females, and may provide insight on factors that influence the diversity of reproductive strategies observed in nature.

Introduction

Life history theory posits that there are high costs associated with reproduction (Formanowicz & Shaffer 1993; Aubret et al. 2002; Hanssen et al. 2005; Fisher & Blomberg 2011), especially for viviparous species (Charland 1995; Shaffer & Formanowicz 1996; Bleu et al. 2013). The internal development of offspring and the allocation of nutrients to offspring during gestation can impose substantial metabolic costs on viviparous females (Beuchat & Vleck 1990; Schultz et al. 2008). To reduce high reproductive costs, physiological and behavioral tradeoffs may occur (Pruitt & Troupe 2010), resulting in alterations in the activity patterns of females during a given

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reproductive bout. Additionally, in species that exhibit maternal care, brooding behaviors by females can be demanding activities (Altman & Samuels 1992; Hunt et al. 2002; Christie et al. 2012) that may extend reproductive costs after parturition, and may potentially conflict with other ecologically relevant tasks essential for survival, such as resource acquisition.

Studies examining reproductive costs for females have shown that decreases in locomotor performance and alterations in defensive strategies may occur as a result of increasing body mass during gestation (Cooper et al. 1990; Formanowicz & Shaffer 1993; Shaffer & Formanowicz 1996). Reproductive costs that result in decreased locomotor ability in gravid females may also hinder movements as they pertain to foraging and prey capture. Numerous reports have investigated the influence of resource availability on the reproductive investments made by females (i.e. reproductive frequency, offspring number, and offspring size; (Reznick & Yang 1993; Festa-Bianchet & Jorgenson 1998; Rindorf et al. 2000; Bonnet et al. 2001), but few studies have addressed the potential antagonistic effects of reproduction (i.e. gestation and maternal care) on the foraging and feeding behaviors of females. Herein I investigated how reproductive status may influence trophic resource acquisition in female Arizona Bark Scorpions (*Centruroides sculpturatus*, Ewing 1928 [=*Centruroides exilicauda*, Wood 1863 of some authors]), a species that inhabits rocky hillsides, outcrops, and riparian habitats in southwestern North America (Polis 1990). *Centruroides sculpturatus* feed on a variety of invertebrates (e.g. spiders, cockroaches, centipedes (McCormick & Polis 1990), and once prey is captured with the chelae (pincers), *C. sculpturatus* envenomate it via the aculeus (stinger) on the end of the metasoma (tail). Occasionally, small or non-

struggling prey items are subdued and consumed without envenomation (Polis 1990).

Female *C. sculpturatus* are viviparous (Polis & Sissom 1990), and following parturition exhibit maternal care by carrying offspring on their backs. Offspring later disperse following their first cycles of ecdysis (molting).

As previously stated, increases in body mass and nutrient allocation to offspring during gestation can result in decreased locomotor performance in reproductive females (Cooper *et al.* 1990; Formanowicz & Shaffer 1993; Shaffer & Formanowicz 1996). This decrease in locomotor ability may also negatively impact a female's ability to capture prey. Accordingly, I predicted that reproductive female *C. sculpturatus* (gravid females and females providing maternal care) exhibit a decrease in predatory efficiency, compared to non-reproductive females, and thus take longer to capture prey than non-reproductive females and females following the maternal care period. In addition, to compensate for decreased locomotor performance, reproductive female *C. sculpturatus* may alter their foraging strategy. *Centruroides sculpturatus* exhibit both active and ambush (sit-and-wait) foraging behaviors (Polis & Sissom 1990). Active foraging involves relatively frequent movements by predators, and often incurs greater locomotor costs, compared to ambush foraging (Bennett & Gorman 1979). The frequent movements made by active foragers can also expose them to a greater predation risk, compared to ambush foragers (Huey & Pianka 1981). Reproductive female *C. sculpturatus* may attempt to reduce the energetic costs of foraging and decrease their predation risk by changing their foraging behavior. Therefore, I also predicted that reproductive female *C. sculpturatus* employ an ambush foraging strategy more frequently than non-reproductive females and post-parturient females.

<center>Materials and methods</center>

I collected 65 mature female *C. sculpturatus* from the outskirts of Quartzsite

(33° 38′ 9″ N, 114° 18′ 15″ W), La Paz County, southwestern Arizona, USA. I weighed

and housed all individuals in separate plastic containers (15 x 9 cm) lined with a gravel

substrate and maintained at $24.0 \pm 5.0°$C. To control for hunger levels, I fed all scorpions

24 hours after capture by placing a prey item (Common House Cricket, *Acheta*

domesticus) within their enclosures, and allowed the arachnids to acclimate for 14 days

prior to the start of the feeding trials. Of the 65 females, 22 were non-gravid and 43 were

gravid. To obtain females exhibiting maternal care, 20 of the gravid females were

maintained separately until parturition. Female scorpions exhibit maternal care for

variable lengths of time (Miranda 2001; M. M. Webber, unpublished data), and to control

for this variation I removed all offspring from all post-parturient females after 5 days.

I began each feeding trial by introducing a Common House Cricket approximately

one-third of the body mass of the scorpion on the opposite end of the container where the

scorpion was housed. Scorpions are nocturnal predators, and therefore I conducted all

feeding trials under low light conditions, and filmed them using a Sony DCR VX2100

Digital Video Camera Recorder. I measured prey capture time from the time of prey

recognition (i.e. alert stance, orientation towards prey, grasp attempt, cheliceral activity;

Bub & Bowerman 1979) until prey ingestion began. To assess potential changes in

predatory efficiency during the later stages of a reproductive bout, I measured anew the

prey capture time of females exhibiting maternal care at 24 hours and 28 days following

offspring removal (FOR). Each trial lasted a maximum of 900 seconds. Logistical reasons

often suggest that a particular trial or study ends at a prespecified time point (cut-off

<center>15</center>

time). The time to the event of interest is known precisely for those subjects that present

the desired event before that time point. For the remaining subjects, the time to the event

of interest is greater than the observation time, or the event never occurs. This is referred

to as administrative censoring, and the incomplete data are called right-censored

(Marubini & Valsecchi 1995). Accordingly, prey capture time for females that failed to

capture prey within the 900-second trial period was right-censored (Tabachnick & Fidell

2007).

I compared the time taken to capture prey among five reproductive classes (non-

gravid, gravid, females exhibiting maternal care, and females 24 hours and 28 days FOR)

using the non-parametric Kaplan-Meier Failure Time Analysis. This method allowed me

to examine the probability of prey capture over time, while accounting for the right-

censored data in the study. To avoid pseudoreplication, I only compared prey-handling

times among independent groups: (i) non-gravid, gravid, and females exhibiting maternal

care; (ii) non-gravid, gravid, and females 24 hours FOR; and (iii) non-gravid, gravid, and

females 28 days FOR. I performed pairwise comparisons of prey capture time among

reproductive groups using the Mantel-Cox Test (Log Rank Test). I used a Cox-

Proportional Hazard Model to examine the potential influence of body size (carapace

length x width, mm^2) and chela size (length x width, mm^2) on prey capture time of

females in each reproductive group. This analysis enabled me to examine the potential

effect of covariates on the hazard rates of prey capture among females. In the context of

this study, hazard rate refers to the rate at which individuals successfully captured prey at

time t (Kalbfleisch & Prentice 2002). Prey capture time was right-censored for females

that failed to capture prey within the 900-second trial period, and thus I excluded these

individuals from the Kaplan-Meier Failure Time Analysis and the Cox-Proportional

Hazards Analysis.

Whenever possible, I recorded the foraging strategy used by each individual, and

scored it as either "active searching" (when females pursued the crickets) or "ambush

predation" (when females remained stationary until prey capture). I compared the

frequency with which females used each foraging behavior using binomial tests (G-tests).

I excluded from this analysis trials in which the foraging strategy used by a female was

unclear, and in which prey behavior circumvented the use of a given foraging behavior

by females (i.e. when the cricket approached the scorpion immediately after being

introduced into the enclosure). All statistical analyses were performed using SPSS (SPSS

20 Inc., Chicago, IL, USA). All values reported are means ± 1 SD, and all P values are

two-tailed.

Results

Non-gravid and gravid females had similar success rates of prey capture (G =

0.001, df = 1, P = 0.97; Table 2.1). Both groups caught prey more frequently than

females exhibiting maternal care (non-gravid females vs. females exhibiting maternal

care, G = 50.1, df = 1, P < 0.001; gravid females vs. females exhibiting maternal care, G

= 51.4, df = 1, P < 0.001), and than females 24 hours FOR (non-gravid females vs.

females 24 hours FOR, G = 45.7, df = 1, P < 0.001; gravid females vs. females 24 hours

FOR, G = 46.8, df = 1, P < 0.001). Non-gravid females were twice as likely to capture

prey as females 28 days FOR (G = 6.1, df = 1, P = 0.014; see APPENDIX A). Similarly,

gravid females were 1.8 times more likely to capture prey than females 28 days FOR (G

= 6.3, df = 1, P = 0.012; see APPENDIX A). Females 28 days FOR caught prey more

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frequently than females exhibiting maternal care (G = 21.0, $df = 1$, $P < 0.001$) and females 24 hours FOR (G = 19.1, $df = 1$, $P < 0.001$).

The Kaplan-Meier Failure Time Analysis revealed that non-gravid and gravid females captured prey with similar speed (Mantel-Cox test, $X^2 = 0.092$, $df = 1$, $P = 0.76$; Table 2.2, Fig. 2.1). In contrast, non-gravid (Mantel-Cox test, $X^2 = 5.97$, $df = 1$, $P = 0.02$) and gravid females (Mantel-Cox test, $X^2 = 5.15$, $df = 1$, $P = 0.023$) caught prey significantly faster than females 28 days FOR. The Cox-Proportional Hazards Model showed that differences in overall body size among non-gravid, gravid, and females 28 days FOR did not significantly affect the prey capture rates of females. However, chela size had a significant effect on prey handling times in the comparison of gravid females and females 28 days FOR (see APPENDIX A). Gravid female *C. sculpturatus* had significantly wider chelae than females 28 days FOR (gravid females: mean ± SD = 1.70 ± 0.14 mm, n = 23; females 28 days FOR: 1.60 ± 0.14 mm, n = 14; ANOVA, F = 4.47, $df = 1$, $P = 0.042$). Nevertheless, after controlling for differences in body size, non-gravid and gravid females caught prey faster than females 28 days FOR, and the hazard ratio of prey capture for non-gravid and gravid females was similar (see APPENDIX A; Fig. 2.2). Because none of the females exhibiting maternal care (n = 20) or females 24 hours FOR (n = 17) successfully captured prey within the 900-second trial period, prey capture time was right-censored for these groups, and these females were excluded from both the Kaplan-Meier Failure Time Analysis and the Cox-Proportional Hazards Analysis.

The foraging strategy used by females differed among reproductive groups (Table 2.3). Non-gravid females used active foraging and ambush predation with similar frequency, compared to gravid (G = 0.051, $df = 1$, $P = 0.82$) and females 28 days FOR

($G = 1.88$, $df = 1$, $P = 0.17$). Gravid females also used active and ambush foraging with similar frequency, compared to females 28 days FOR ($G = 1.26$, $df = 1$, $P = 0.26$). However, females exhibiting maternal care used active foraging more frequently than non-gravid ($G = 11.37$, $df = 1$, $P = 0.001$), gravid ($G = 9.72$, $df = 1$, $P = 0.002$), and females 28 days FOR ($G = 4.39$, $df = 1$, $P = 0.036$). Trials examining the foraging behavior of females 24 hours FOR were excluded from this analysis due to low sample size.

Discussion

For viviparous females, activities associated with reproduction may adversely affect resource acquisition. Increases in body mass due to developing offspring and nutrient allocation to offspring during gestation may hinder locomotion in gravid females (Shaffer & Formanowicz 1996; Cooper et al. 1990). These reproductive costs have the potential to hamper the prey capture abilities of these females (Lourdais et al. 2004). Contrary to my expectations, the predatory efficiency of gravid female *C. sculpturatus* did not decrease as a direct consequence of their reproductive status. This pattern suggests that for gravid Arizona Bark Scorpions, significant increases in body mass do not noticeably inhibit movements as they pertain to pursuing and subduing prey, or significantly deplete the energy necessary for prey capture.

In species that exhibit maternal care, reproductive costs may extend beyond gestation and manifest themselves during and subsequent to the brooding period (Tallamy & Denno 1982; Altman & Samuels 1992). In this study, none of the females exhibiting maternal care or females 24 hours FOR successfully captured prey within the 900-second trial period. The majority of these trials were characterized by failed grasping

attempts, or by the inability of females to maintain a hold of the prey after capturing it

with their chelae. These findings illustrate that reproductive costs in terms of decreased

predatory efficiency are highest for female *C. sculpturatus* after parturition, and that these

females do not immediately recover from the costs associated with giving birth and

providing maternal care. What factors may contribute to the decrease in prey capture

ability in brooding Arizona Bark Scorpions? Following birth, offspring move from inside

the female's abdomen to her back. This redistribution of offspring mass may impede a

brooding female's ability to move efficiently, thus increasing the difficulty of prey

capture. Further, the offspring of scorpions are mobile following birth, and often cling to

the legs, underside, and tails of their mothers (M. M. Webber, personal observations),

which may increase the difficulty in locating or pursuing a prey item, as well as

compromise the stinging mechanics of brooding females, which may increase the time

needed to subdue prey. Although brooding females and females 24 hours FOR clearly

exhibited a decrease in prey capture abilities, female *C. sculpturatus* in the wild may

reduce the negative impacts of maternal care on foraging success by pursuing smaller

prey or different prey types that may be easier to subdue.

The inability of brooding females and females 24 hours FOR to capture prey

suggests that physiological costs associated with maternal care are responsible for the

decrease in the predatory efficiency of these scorpions. Alternatively, the failure of

brooding females and females 24 hours FOR to catch prey could result from a decrease in

the motivation to feed during and subsequent to the brooding period. In 10 separate prey-

handling trials, post-parturient females exhibiting maternal care did not attempt to capture

prey. (As previously stated, these trials were excluded from the statistical analyses of

prey capture frequency and time to prey capture.) Reproductive females may experience seasonal anorexia, a period during which females do not feed, despite the fact that prey is available in their habitats (Brischoux et al. 2011; Webber et al. 2012). Although seasonal anorexia may lead to poor body condition in females subsequent to the reproductive season, this behavior may allow females to compensate for reduced predatory performance by conserving the energy that would be invested in unsuccessful foraging. A reduction in the foraging behavior of female *C. sculpturatus* exhibiting maternal care may also be caused by a behavioral shift in which females refrain from feeding to decrease the chances of offspring injury or mortality resulting from retaliatory behavior of prey. Further, lessened foraging behavior may improve the chances of offspring survival by reducing the probability of filial cannibalism, when females consume their young to replenish energy invested in reproduction (Peterson & Marchetti 1989; Miller & Zink 2012). Nevertheless, an earlier study showed that filial cannibalism by brooding female scorpions is a rare occurrence (Miranda 2001), and indeed I did not observe this behavior in our study. Still, the hypotheses that post-parturient females conserve energetic resources and display behaviors that may decrease the occurrence of filial cannibalism by exhibiting seasonal anorexia are not mutually exclusive, as both outcomes may increase the survival and reproductive fitness of female *C. sculpturatus* in nature.

Females 28 days FOR caught prey with a higher success rate than females displaying maternal care and females 24 hours FOR, but still took significantly longer to capture prey than non-gravid and gravid females. In addition, females 28 days FOR were significantly less likely to capture prey than non-gravid and gravid females. These findings indicate that reproductive costs in *C. sculpturatus* extend at least 4 weeks

beyond the maternal care period. My experimental design required females 28 days FOR to remain in the trials for 21 days longer than non-gravid and gravid females, which may have resulted in stress-induced changes in feeding behavior. Nonetheless, the observation that females 28 days FOR successfully pursued, captured, and ingested prey suggests that the extended time in the experimental trials had a negligible effect on the foraging success of these scorpions. Because the predatory efficiency of female *C. sculpturatus* is compromised during and after the maternal care period, poor feeding performance following parturition may be at least partly responsible for the relatively long recovery time experienced by reproductive females. It is important to point out that to control for differences in the duration of maternal care, I removed all offspring from females after 5 days. Under natural conditions, female scorpions are known to carry offspring for up to 51 days (Polis & Sissom 1990), and hence for female *C. sculpturatus* in nature the negative effects of reproduction on predatory efficiency may be greater and extend for a longer time period than our trials allowed us to observe. The length of recovery time for female *C. sculpturatus* likely has significant fitness consequences, because female Arizona Bark Scorpions that replenish their energetic resources faster may have increased survival rates, as well as a higher likelihood of engaging in additional reproductive bouts.

Differences in overall body size and chela size were not significant predictors of variation in prey-handling time between non-gravid and gravid females, or between non-gravid females and females 28 days FOR. However, chela size significantly affected prey handling time in the comparison between gravid females and females 28 days FOR. The dimensions of scorpion chelae are strongly correlated with maximum pincer force, and individuals with relatively shorter and wider chelae have a greater mechanical advantage

than those with longer, thinner chelae (Van der Meijden et al. 2010). In this study, gravid female *C. sculpturatus* had significantly wider chelae than females 28 days FOR, which may have conferred the former group an advantage when catching and subduing prey by enabling those individuals to maintain a stronger grasp on prey items, thus decreasing their prey-handling time.

I observed differences in the foraging strategies used by females in different reproductive groups. In the 8 prey handling trials in which the foraging strategy used by brooding females could be determined, those scorpions actively pursued prey more frequently than non-gravid, gravid, and females 28 days FOR. Although none of the females providing maternal care successfully captured prey, all individuals included in my analyses attempted to do so, and actively pursued crickets placed in their enclosures. What factors may cause brooding females to prefer active foraging? Post-parturient females often have depleted energy reserves following the birth of offspring (Lambert & Dutil 2000), and females that do not replenish those reserves relatively quickly suffer higher rates of mortality (Koivula et al. 2003). During the maternal care period, females in poor physiological condition may switch from an ambush to an active foraging strategy to increase their frequency of prey encounters. Despite the fact that active foraging may be energetically costly and increase the predation risk for brooding females, the need to quickly replenish energetic resources may offset the potential negative impacts of this foraging strategy. On the other hand, why may non-gravid, gravid, and females 28 days FOR utilize an ambush strategy more frequently than brooding females? Females in those three groups were more successful at catching prey and may be in better physiological condition than brooding females, and thus may rely on their energy

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reserves during periods of low food abundance. Further, for these females the increased energy expenditure and predation risk associated with active searching may outweigh the advantage of increased prey encounter rates associated with wide foraging.

Conclusion

Life history theory suggests that tradeoffs exist in the resources allocated between current and future reproductive episodes, and that the outcome of reproductive investments is dictated by the current physiological state of an organism. I predicted that reproductive costs negatively influence predatory efficiency in both gravid and brooding female *C. sculpturatus*. Contrary to my expectations, gravid females did not exhibit a decrease in their predatory abilities. However, maternal care given to current offspring by female *C. sculpturatus* did lead to a significant reduction in the females' ability to capture prey. Further, even 28 days FOR, females were still not as efficient at capturing prey as non-gravid and gravid females. My results demonstrate that the magnitude of reproductive tradeoffs fluctuates over the course of a reproductive bout, and emphasize the importance of isolating stage-specific costs when investigating reproductive tradeoffs. I also observed changes in the foraging strategy of brooding females, as they used an active foraging strategy more frequently than non-gravid, gravid, and females 28 days FOR. This alteration in foraging behavior may increase the likelihood of encountering prey, but may also negatively impact opportunities for future reproduction by increasing the susceptibility of these females to predation.

My invertebrate model may provide a framework on which to base additional hypotheses regarding physiological, ecological, and evolutionary tradeoffs involving reproduction. For example, females that are in poor body condition may decrease their

current reproductive investment by altering the number or size of offspring produced (King 1993; Guisande et al. 1996), or reduce the duration of maternal care given to offspring (Therrien et al. 2008). Future studies investigating the influence of resource availability and body condition on the reproductive investment (i.e. reproductive frequency, offspring number and size) and survival of female Arizona Bark Scorpions may uncover additional tradeoffs experienced by reproductive females. Finally, my findings regarding antagonistic interactions between feeding and reproduction in female *C. sculpturatus* illustrate the pervasive nature of reproductive costs for viviparous females, and help elucidate how these costs may influence the diversity of reproductive strategies observed in nature.

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Tables

Table 2.1. Frequency of prey capture in female *Centruroides sculpturatus*.

Reproductive status	Success frequency (%)	Failure frequency (%)
Non-gravid females	21 (95.5%)	1 (4.5%)
Gravid females	22 (95.7%)	1 (4.3%)
Females exhibiting maternal care	0 (0%)	20 (100%)
Females 24 hours following offspring removal	0 (0%)	17 (100%)
Females 28 days following offspring removal	9 (64.3%)	5 (35.7%)

Global Likelihood Ratio, G = 97.8, *df* = 4, *P* < 0.001

Table 2.2. Mean prey capture time (seconds) of non-gravid and gravid female *Centruroides sculpturatus,* and of females exhibiting maternal care and females 24 hours and 28 days following offspring removal.

Reproductive status	n	Mean ± SD (seconds)	Range (seconds)
Non-gravid females	22	231.3 ± 191.8	3–>900
Gravid females	23	251.1 ± 195.5	48–588
Females exhibiting maternal care	20	—	—
Females 24 hours following offspring removal	17[a]	—	—
Females 28 days following offspring removal	14[b]	480.8 ± 356.2	21–>900

[a] Three females exhibiting maternal care died less than 24 hours following offspring removal.

[b] Three post-parturient females died less than 28 days following offspring removal.

Table 2.3. Frequency of foraging strategies used by non-gravid and gravid female *Centruroides sculpturatus*, and by females exhibiting maternal care and females 28 days following offspring removal.

Reproductive status	Frequency of foraging strategy	
	Active searching (%)	Ambush predation (%)
Non-gravid females	7 (38.8%)	11 (61.2%)
Gravid females	6 (42.9%)	8 (57.1%)
Females exhibiting maternal care	8 (100%)	0 (0%)
Females 28 days following offspring removal	6 (66.7%)	3 (33.3%)

Global Likelihood Ratio, G = 12.8, df = 3, P = 0.005

Figures

Figure 2.1. Kaplan-Meier Failure Time Analysis. The probability of failure to capture prey over time (trial duration = 900 seconds) among non-gravid, gravid, and female *Centruroides sculpturatus* 28 days following offspring removal (FOR).
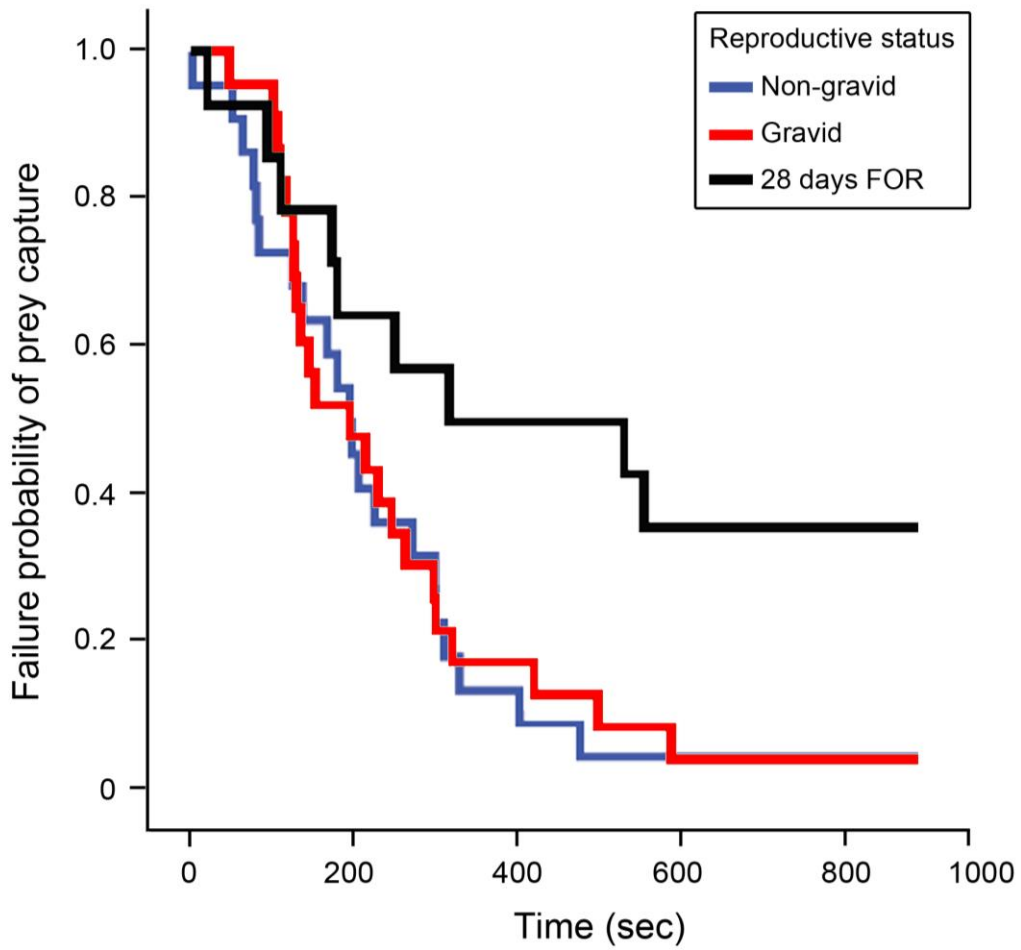
Figure 2.2. Cox Proportional Hazards Model. The cumulative hazard rate of prey capture over time (trial duration = 900 seconds) among non-gravid, gravid, and female *Centruroides sculpturatus* 28 days following offspring removal (FOR).
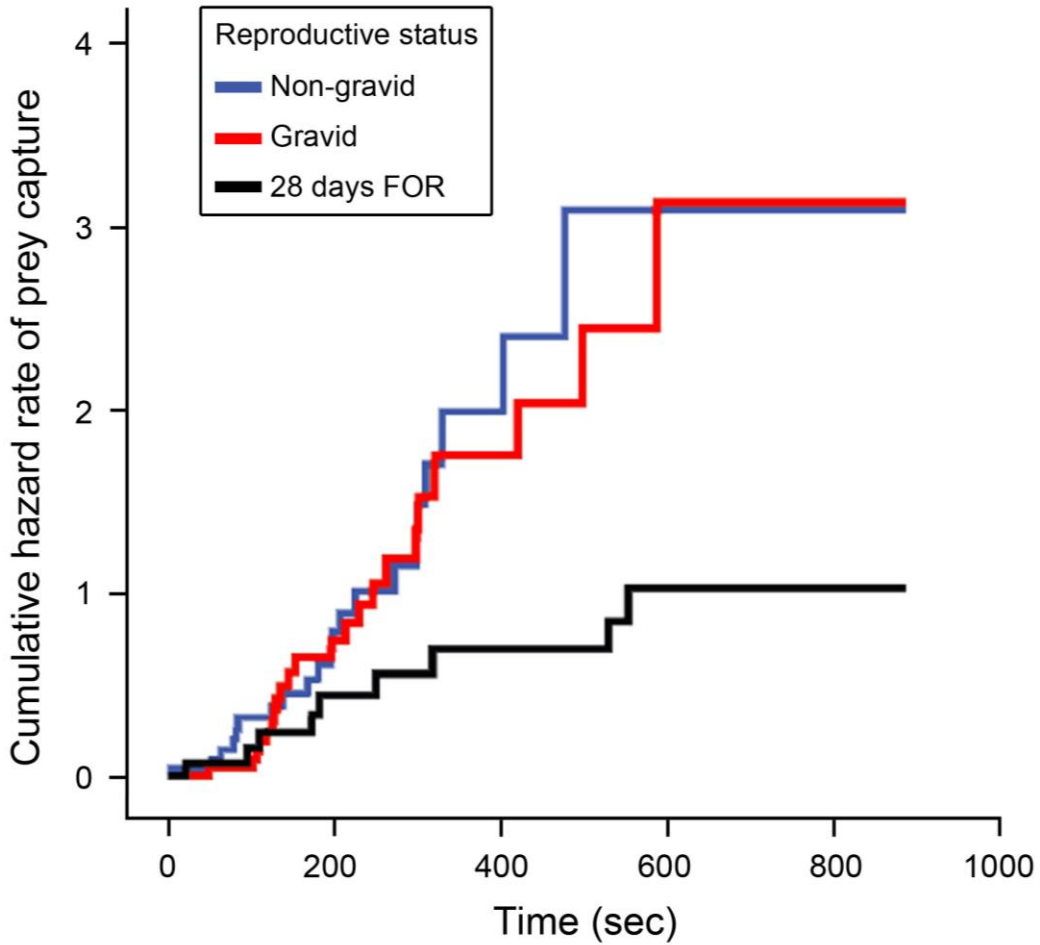
CHAPTER 3

HOT AND NOT-SO HOT FEMALES: REPRODUCTIVE TRADEOFFS

ASSOCIATED WITH THERMOREGULATION IN FEMALE ARIZONA BARK

SCORPIONS (*CENTRUROIDES SCULPTURATUS*)

Abstract

A fundamental tradeoff in life history evolution occurs between resources
invested in reproduction and those allocated to parental survival. For viviparous females,
the transfer of nutrients to offspring throughout gestation incurs high energetic costs.
Still, viviparity provides a mechanism by which females can manipulate the
environmental conditions of offspring during development. In many ectotherms, the
selection of higher and less variable body temperatures (T_b) by viviparous females during
gestation increases offspring viability. These changes in thermoregulatory patterns may
conflict with temperatures favorable for females' health and survival. I tested whether
reproductive status influenced the thermoregulatory patterns of female Arizona Bark
Scorpions (*Centruroides sculpturatus*). I predicted that gravid females select higher T_b
and exhibit more precise thermoregulation than non-reproductive females. As gestation
progresses, reproductive female *C. sculpturatus* exhibit significant increases in body
mass, exposing larger portions of their pleural membranes, which can result in an
increased desiccation risk of the females and compromise their survival. Accordingly, I
also tested whether gravid females lost water faster than non-reproductive individuals. I
determined the preferred T_b of female scorpions in a thermal gradient, and measured their
water loss rates using flow-through respirometry. Gravid females preferred higher T_b than

non-reproductive females, indicating that alterations in thermoregulatory behavior may increase the fitness of their offspring. However, all scorpions thermoregulated with equal precision, suggesting that arid conditions in the wild create selective pressure on females to thermoregulate effectively, irrespective of reproductive status. The mean diurnal T_b (42.5° C) of gravid females was close to their critical thermal maximum of 45º C. Hence, reproductive females may experience a tradeoff, whereby selecting temperatures favorable for offspring development may negatively impact their survival by increasing their risk of mortality through heat stress. Gravid females lost water faster than non-reproductive females, suggesting that greater exposure of the pleural membrane caused by increases in body mass during reproduction enhances the desiccation risk of gravid females, another tradeoff experienced by these individuals. Understanding the mechanisms that result in reproductive tradeoffs may reveal how thermal conflicts shape the life history of ectotherms, particularly in arid environments.

Introduction

A fundamental question in the study of life history evolution is how survival and lifetime reproductive potential are influenced by current reproductive investments. Life history theory predicts that tradeoffs exist between present-day and future reproduction (Williams 1966; Osorno 1999; Nicolai 2012), such that resources invested in current offspring limit the resources available for parental body growth, maintenance, and survival, thereby negatively affecting the probability of future reproduction (Hamel et al. 2011; Weatherhead et al. 2012). These reproductive costs can be especially high for viviparous females (Beuchat & Vleck 1990; Charland 1995; Shaffer & Formanowicz 1996; Schultz et al. 2008; Webber & Rodríguez-Robles 2013), which allocate energetic

resources to offspring throughout gestation in each reproductive bout. Despite its considerable energetic cost, the internal retention of embryos is advantageous in unpredictable environments, because it facilitates favorable conditions for embryos throughout gestation (Qualls & Andrews 1999), thereby increasing offspring survival and fitness (Shine & Harlow 1993).

For ectothermic species, viviparity improves offspring viability by buffering embryos from unfavorable environmental temperatures during development (Beuchat 1988; Shine 2004; Pincheira-Donoso et al. 2013). Consequently, for viviparous ectotherms, 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, Burkot & Kay 2000), and the size of offspring at birth (Fischer et al. 2003). For viviparous females, reproductive state can elicit significant changes in their thermoregulatory patterns (Graves & Duvall 1993; Le Galliard et al. 2003). Studies addressing these changes have demonstrated that gravid females often select higher body temperatures (T_b) and exhibit more precise thermoregulation than non-reproductive females during gestation (Osgood 1970; Charland & Gregory 1990; Gvozdik 2005). The selection of higher and less variable T_b by reproductive females can promote proper embryonic development and facilitate the production of larger and more viable offspring (Shine 1980; Shine & Harlow 1993; Lourdais et al. 2004; Telemeco 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 survival and future reproductive potential of 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 behavior (Halliday & Adler 2002). An increase in the frequency with which reproductively active females engage in thermoregulatory behaviors 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 (i.e. gestation) may not be conducive to other physiological processes (i.e. body growth and repair, digestion). In these cases, it is possible that the outcome of thermal tradeoffs between temperatures favorable to gestation and those beneficial for female health and survival may result in a conflict between female survival and the viability of her current offspring (Schwarzkopf & Andrews 2012). Examination of the influence of environmental temperatures on the behavior, survival, and reproductive success of viviparous ectotherms and their offspring can provide insight on the mechanisms which generate diversity in a species life history (Robert et al. 2003; Webb et al. 2006; Li et al. 2009).

Herein, I investigated the influence of reproductive state on thermoregulatory behavior and possible thermal conflicts between reproduction and survival in female Arizona Bark Scorpions (*Centruroides sculpturatus*, Ewing 1928 (=*Centruroides exilicauda*, Wood 1863 of some authors). *Centruroides sculpturatus* are nocturnal

invertebrates that inhabit the arid desert regions and riparian habitats of southwestern

North America (Polis 1990). Female *C. sculpturatus* are viviparous and give birth to

offspring ($\overline{X}$ = 20 scorplings, range: 7 – 42) following a 5.2 ± 2.3 mo gestation period

(Polis & Sissom 1990). Unlike other species of desert scorpions, *C. sculpturatus* do not

dig burrows, and instead avoid unfavorable 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 has the potential to

improve offspring fitness, I predicted that gravid *C. sculpturatus* select higher T_b and

exhibit more precise thermoregulation, compared to non-reproductive females. Further,

reproductive female scorpions move less frequently than non-reproductive females

(Shaffer & Formanowicz 1996). Given that gravid individuals are more sedentary than

non-reproductive females, I 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, because non-reproductive females exhibit more surface activity than

reproductive animals, I predicted that the former exhibit significant shifts in their diurnal

and nocturnal T_b.

In addition, the morphological and physiological changes that occur in

reproductive female *C. sculpturatus* may compromise their survival, thus limiting future

reproductive opportunities. Throughout gestation, *C. sculpturatus* exhibit significant

increases in body mass, and offspring developing within the reproductive tract of females

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 (Polis 1990). Relative to the waxy hardened cuticle, the plural membrane is significantly more permeable to water (Hadley & Quinlan 1987). I hypothesized that the greater exposure of the pleural membrane in gravid females heightens their susceptibility to transcuticular water loss, compared to non-reproductive females. Besides the increase in their body mass, nutrients transferred to offspring and the enhanced oxygen requirement of developing embryos throughout gestation may also intensify the oxygen demand placed on reproductive females (Beuchat &Vleck 1990; Robert & Thompson 2000; Weldon et al. 2012). Consequently, reproductive females often exhibit higher metabolic rates than non-reproductive females (Birchard et al. 1984; DeMarco 1993; Beaupre & Duvall 1998). An increase in the metabolic rate of reproductive females may also lead to faster rates of water loss via respiration. Therefore, I also predicted that gravid *C. sculpturatus* exhibit faster rates of water loss than non-reproductive females.

Materials and methods

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

Thermal Preference

To determine the preferred T_b of female *C. sculpturatus*, I constructed a thermal gradient. The gradient consisted of a rectangular glass enclosure [71.0 cm (l) x 15.2 cm (w) x 15.2 cm (h)] lined with a gravel substrate (Webber & Bryson 2012). I 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%. I initially divided 62 of the females into two classes: non-gravid (n = 34) and gravid (n = 28). I categorized females as gravid if embryos were visible within the mesosoma.

I fed all scorpions a single prey item (Common House Cricket, *Acheta domesticus*) and allowed them to acclimate for 7 d before placing them in the thermal gradient. Using forceps, I introduced an individual scorpion into the gradient at the midpoint 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. I allowed the scorpions to acclimate to the gradient enclosure for 12 hrs prior to data collection. I measured the mesosomal T_b of each female every 2 hrs over a 24 hr period using an infrared thermometer (Model 42505, Extech Instruments, Nashua, New Hampshire, USA, precision ± 0.07 °C). I also noted whether females were stationary or actively moving throughout the enclosure at each 2 hr period of data collection. I did not record the T_b of females in cases where they were found to be moving within the gradient. I cleaned all enclosures with soap and water and replaced the gravel between all trials. To compare the preferred T_b of non-reproductive and gravid female *C. sculpturatus* during the day (when scorpions exhibit reduced activity), and at night (when scorpions are primarily active on the surface), I divided the 24 hr trial period into two components: diurnal (0800 hrs – 1800 hrs) and nocturnal (2000 hrs – 0600 hrs). I 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 me to compare the dependent variable of interest (T_b) over time, while also controlling for body size differences among

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females. I determined the body size of each female scorpion by measuring the length of her carapace (± 1 mm). I compared the precision of thermoregulation between reproductive groups using Levene's test for the homogeneity of variances.

Water Loss

I measured the water loss rates of the remaining 49 female *C. sculpturatus* (non-gravid, n = 24; gravid, n = 25) using flow-through respirometry. I 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. I put each scorpion in a 15.0 ml glass cylinder, which was placed within a temperature-controlled incubator set at 38.0 ˚C. Silica gel desiccant was used to dry air, which was then passed through the glass chamber at a flow rate of 50 ml/min. Excurrent air was passed through a LI-6262 CO_2/H_2O analyzer (Li-Cor, Lincoln, Nebraska, USA), and the voltage output was recorded once every second and analyzed using Datacan V data acquisition and analysis software (Sable Systems International, Las Vegas, Nevada, USA). I recorded the rate of water loss for each scorpion over a 30 min period. I compared the mean water-loss rate of non-reproductive 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, Illinois, USA). Values reported are means ± 1 SD, and all *P*-values are two-tailed. Significance level for all tests was determined at $\alpha = 0.05$.

<center>Results</center>

Thermal Preference

Non-gravid ($\overline{X}$ = 5.70 ± 0.44 mm, range = 4.76 – 6.85 mm, n = 34) and gravid (

$\overline{X}$ = 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 non-reproductive animals (Table 3.1).

After controlling for differences in body size among females, gravid individuals

selected significantly higher diurnal and nocturnal T_b, compared to non-reproductive

females (Table 3.1). There was a significant 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. 3.1). However, body size was not a significant

predictor of selected T_b for non-gravid females (r^2 = 0.06, $F_{(1,33)}$ = 1.9, P = 0.18; Fig.

3.1). Non-reproductive 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 3.1 & 3.2; Fig. 3.2). Contrary to my

prediction, the mean diurnal T_b of non-gravid females did not differ from their mean

nocturnal T_b (Tables 3.1 & 3.2; Fig. 3.2). The mean number of movements observed

within the gradient at each 2 hour interval was not statistically different between non-

gravid ($\overline{X}$ = 1.44 ± 1.40, range = 0 – 5, n = 34) and gravid females ($\overline{X}$ = 1.07 ± 1.20,

range = 0 – 4, n = 28; ANOVA, $F_{(1,60)}$ = 1.21, P = 0.28).

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Water Loss

Non-reproductive ($\overline{X} = 5.78 \pm 0.63$ mm, range $= 4.81 - 7.02$ mm, n $= 24$) and

gravid ($\overline{X} = 5.64 \pm 0.42$ mm, range $= 4.69 - 6.66$ mm, n $= 25$) females did not differ in

body size (ANOVA, $F_{(1,47)} = 0.90$, $P = 0.35$). However, gravid females were

proportionally heavier than non-reproductive animals (Table 3.3).

After controlling for differences in body size, gravid females lost water at a faster

rate than non-gravid individuals (Table 3.3). Body size was not a significant predictor of

water loss rates for either non-reproductive ($r^2 = 0.05$, $F_{(1,22)} = 1.11$, $P = 0.30$) or gravid

($r^2 = 0.07$, $F_{(1,23)} = 1.83$, $P = 0.19$) female *C. sculpturatus* (Fig. 3.3). Similarly, body mass

was not a significant predictor of water loss rates for non-gravid females ($r^2 = 0.02$,

$F_{(1,22)} = 0.51$, $P = 0.48$; Fig. 3.4). 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 individuals ($r^2 = 0.32$, $F_{(1,23)} = 10.8$, $P = 0.003$; Fig. 3.4).

Discussion

Life history tradeoffs result from conflicts in the amount of time and energy that

can be simultaneously invested in a particular activity at a given time. For viviparous

ectotherms, the selection of higher T_b and increased precision in thermoregulation during

gestation (Osgood 1970; Charland & Gregory 1990; Gvozdik 2005) may create favorable

conditions for offspring development, yet may also incur negative consequences

regarding the body condition, reproductive success, and survival of females. I assessed

whether female *C. sculpturatus* altered their preferred body temperatures during

gestation, and examined how the morphological and physiological changes that occur in

reproductive females may affect their ability to conserve water at higher temperatures.

Thermal Preference

After controlling for differences in body size, gravid *C. sculpturatus* preferred higher mean diurnal and nocturnal T_b than non-gravid females. The selection of higher T_b by gravid *C. sculpturatus* during gestation may promote proper embryonic development, thereby increasing offspring survival. In addition, an elevated T_b can increase the sprint speed and improve the stinging performance of scorpions (Carlson & Rowe 2009), which may enable reproductive females to escape predation more effectively. However, higher temperatures may have negative consequences on the body condition and survival of reproductive females. For example, the preferred diurnal (42.5 °C) and nocturnal T_b (39.7 °C) of gravid females were significantly higher than the preferred diurnal (40.6 °C) and nocturnal T_b (37.0 °C) of non-reproductive individuals, respectively. The critical maximum T_b for *C. sculpturatus* is 45 °C (Hadley & Hill 1969), a temperature at which scorpions show significant signs of heat stress and injury. Gravid female *C. sculpturatus* may thus experience a tradeoff between selecting warmer temperatures conducive to higher offspring fitness, and lower temperatures that reduce their susceptibility to heat-induced mortality. Future studies that monitor the body condition of post-reproductive female *C. sculpturatus* following prolonged exposure to higher temperatures may determine whether the changes we observed in the thermoregulatory behavior of reproductive females have detrimental effects on female body condition.

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). Accordingly, larger gravid females do not lose heat as quickly as smaller ones, and can select lower environmental temperatures while still maintaining the same preferred T_b as smaller individuals for a given period of time. In the same manner, 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 than smaller gravid females due to a decrease in the efficiency in which the former can thermoregulate at warmer temperatures. At high temperatures, larger gravid females are unable to lose heat quickly, which places them at a greater risk of reaching unfavorably high T_b and suffering heat injury. By selecting cooler T_bs, larger gravid females may decrease their risk of heat-induced mortality.

Contrary to my prediction, gravid females did not exhibit more precise thermoregulation than non-reproductive 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 the risk of desiccation when exposed to the high 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 female scorpions are known to move less frequently than non-gravid females (Shaffer & Formanowicz 1996), and thus I predicted that gravid *C. sculpturatus* are more sedentary than non-reproductive individuals and do not show daily shifts in their preferred T_b. On the other hand, because non-reproductive females often engage in more surface activity than reproductive animals, I hypothesized that non-gravid *C. sculpturatus* exhibit significant differences between their preferred nocturnal (active) and diurnal (inactive) T_b. I did not observe a significant difference in the mean number of movements between non-gravid and gravid female *C. sculpturatus* within the gradient enclosure. Also contrary to my prediction, the mean T_b of non-gravid females did not change significantly over the 24 hr trial period. In addition, I did not detect a statistical difference between the average preferred diurnal and nocturnal T_b of gravid *C. sculpturatus*. Collectively, these findings suggest that the time of day does not significantly influence the preferred T_b of female *C. sculpturatus*, and that females do not appear to alter their thermoregulatory behavior in response to ambient light cues. Because environmental temperatures can influence a multitude of behavioral and physiological processes in terrestrial ectotherms (Beuchat 1988; Hadley 1994; Telemeco et al. 2010), avoidance of unfavorable 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, thus 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 place increased oxygen demands on viviparous females, thereby increasing their metabolic rates (Beuchat & Vleck 1990; Robert & Thompson 2000; Weldon et al. 2012). These higher metabolic rates may in turn increase the rate of water loss of gravid females through an increase in their rate of respiration (Birchard et al. 1984; DeMarco 1993; Beaupre & Duvall 1998). The exposure of the permeable pleural membrane and the increased metabolic demands placed on reproductive females were expected to lead to faster rates of water loss for gravid *C. sculpturatus*, compared to non-reproductive females.

Gravid *C. sculpturatus* lost water faster than non-reproductive females. In addition, 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 demand placed on females, and induce a greater distention of the mesosoma, resulting in faster rates of water loss for larger gravid females. In summary, the morphological and physiological changes experienced by gravid *C. sculpturatus* may result in a tradeoff between reproduction and water conservation at higher temperatures. In nature, faster

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rates of water loss have the potential to compromise the survival of gravid *C. sculpturatus* through increasing their risk of desiccation in arid environments. Gravid female *C. sculpturatus* may compensate for increased rates of water loss by selecting more humid microhabitats, which may minimize their rates of evaporative water loss. Moreover, gravid scorpions experience a significant decrease in their locomotor abilities (Shaffer & Formanowicz 1996). Reproductive females may reduce the metabolic costs associated with locomotion by moving less often (Bauwens & Thoen 1981; Shaffer & Formanowicz 1996), which can also reduce the amount of water lost through respiration.

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 and increase its desiccation risk (Toolson, 1987). Further, the amount of heat lost through evaporative cooling is often less than 10% of the heat generated via metabolic processes (Lighton et al. 2001; M. M. Webber, unpublished data). Therefore, evaporative cooling does not appear to be a likely mechanism for reducing T_b in *C. sculpturatus*.

My findings regarding tradeoffs for reproductive *C. sculpturatus* demonstrate the influence of reproductive state on the daily activity patterns of these females. Gravid *C. sculpturatus* selected higher T_b, which may positively affect offspring survival and

fitness. However, the preferred higher temperatures and the greater exposure of the pleural membrane in reproductive females increase the rate of water loss and by extension, the mortality risk of these females. Hence, gravid *C. sculpturatus* females may experience a tradeoff, whereby engaging in current reproduction (i.e. gestation) may limit their survival through an increase in the risk of mortality through desiccation and heat injury at higher temperatures. In environments where resources such as water or thermally preferable habitats are limited, as is the case in arid deserts, the outcome of tradeoffs experienced by reproductive females may lead to plasticity in the energetic resources invested during reproduction. Understanding the proximate mechanisms that generate these reproductive tradeoffs will increase our understanding of how these conflicts shape the life histories of ectothermic animals.

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Tables

Table 3.1. Comparisons of body mass and body temperature (T_b) for the analyses of thermal preferences of non-gravid and gravid female *Centruroides sculpturatus*. Carapace length (mm) was used as the covariate for the Analysis of Covariance and the Profile Analysis.

Reproductive status	Mean (± 1SD)	Range	n
Body mass (g)			
Non-gravid females	0.68 ± 0.17	0.38 – 1.00	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 hrs – 1800 hrs)			
Non-gravid 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 hrs – 0600 hrs)			
Non-gravid females	37.0 ± 3.25	31.4 – 42.7	34
Gravid females	39.7 ± 2.90	33.8 – 44.6	28
Profile Analysis; $F_{(1,59)} = 10.2$, $P = 0.002$			

Table 3.2. Profile Analysis comparing diel shifts in the mean T_b of non-reproductive and gravid female *Centruroides sculpturatus* over a 24 hr period.

Effect	Wilks' λ	*df*	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

Table 3.3. Comparisons of body mass and rate of water loss between non-gravid and gravid female *Centruroides sculpturatus*. Carapace length (mm) was used as the covariate for the Analysis of Covariance.

Reproductive status	Mean (± 1SD)	Range	n
Body mass (g)			
Non-gravid 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)			
Non-gravid females	0.034 ± 0.007	0.024 – 0.048	24
Gravid females	0.039 ± 0.007	0.028 – 0.057	25
ANCOVA; $F_{(1,46)} = 5.17$, $P = 0.03$			

Figure 3.1. Mean body temperature (T_b) as a function of body size (carapace length) in non-reproductive and gravid female *Centruroides sculpturatus*.
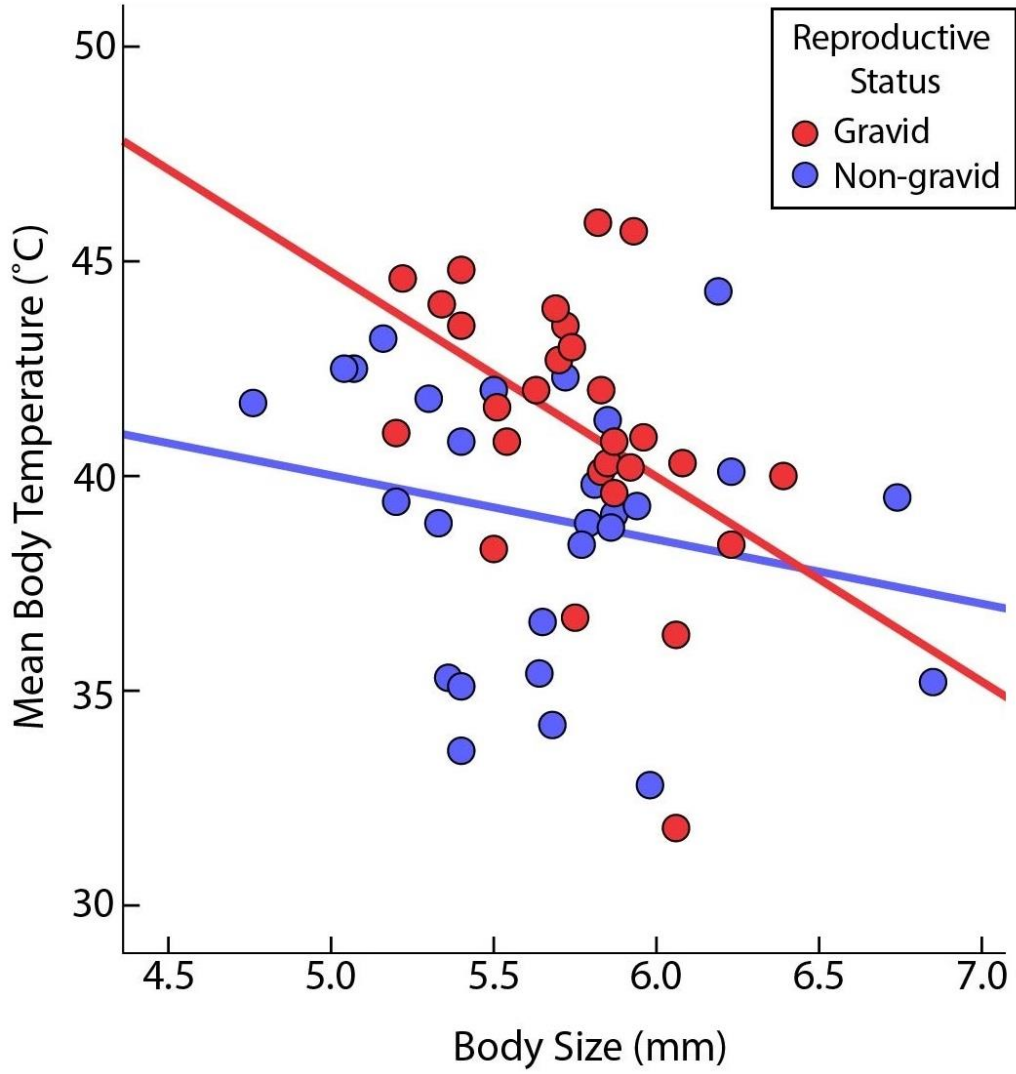
Figure 3.2. Diel fluctuations in the mean body temperature (T_b) of non-reproductive and gravid female *Centruroides sculpturatus*. Error bars represent 95% CI.
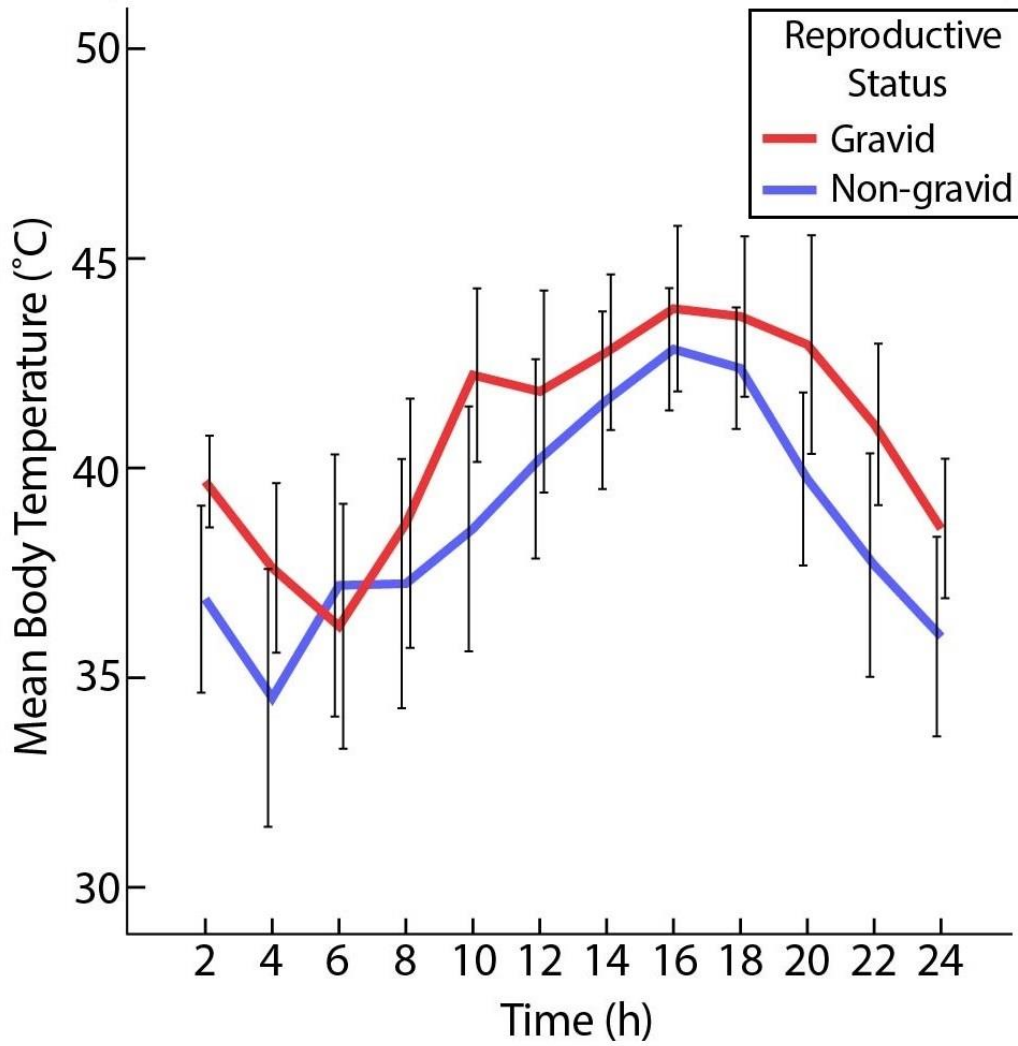
Figure 3.3. Mean water loss rate as a function of body size (carapace length) in non-reproductive and gravid female *Centruroides sculpturatus*.
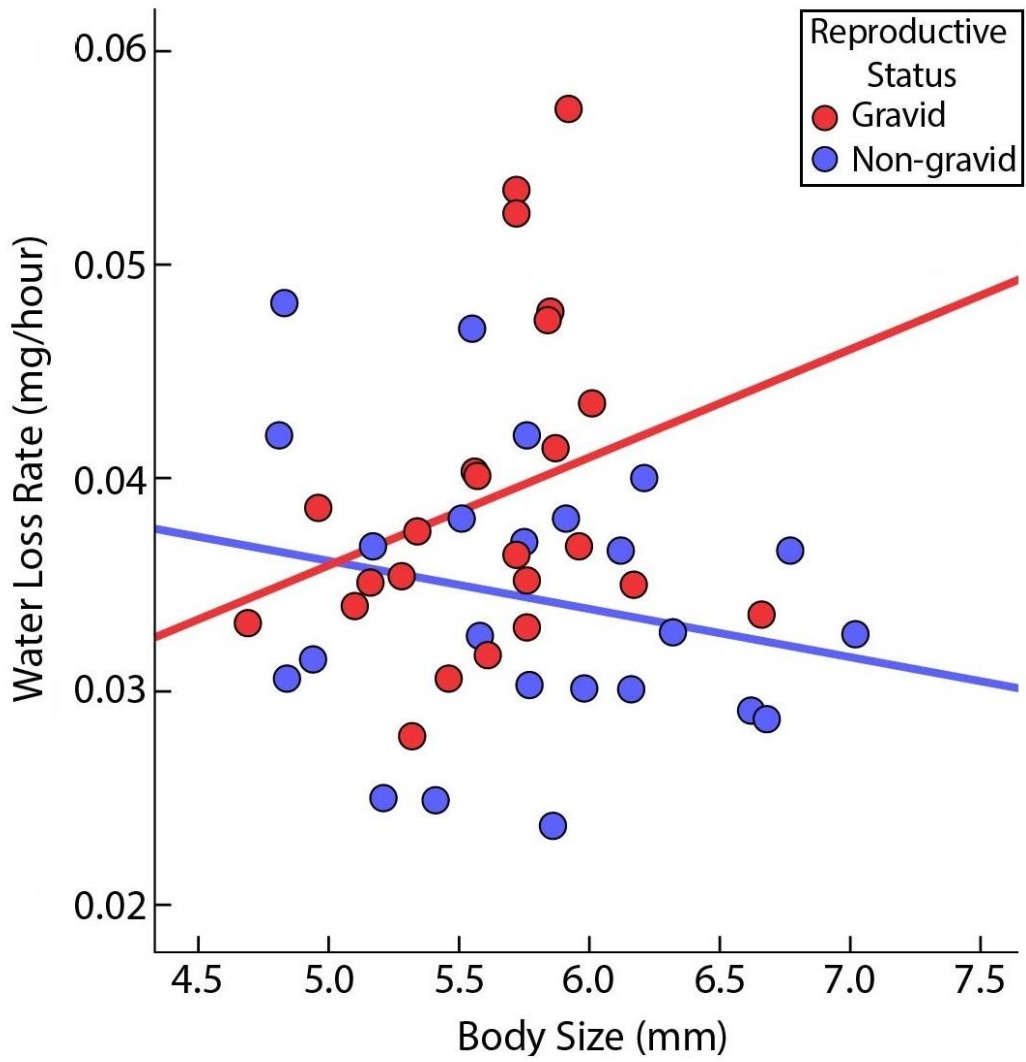
Figure 3.4. Mean water loss rate as a function of body mass in non-reproductive and gravid female *Centruroides sculpturatus*.
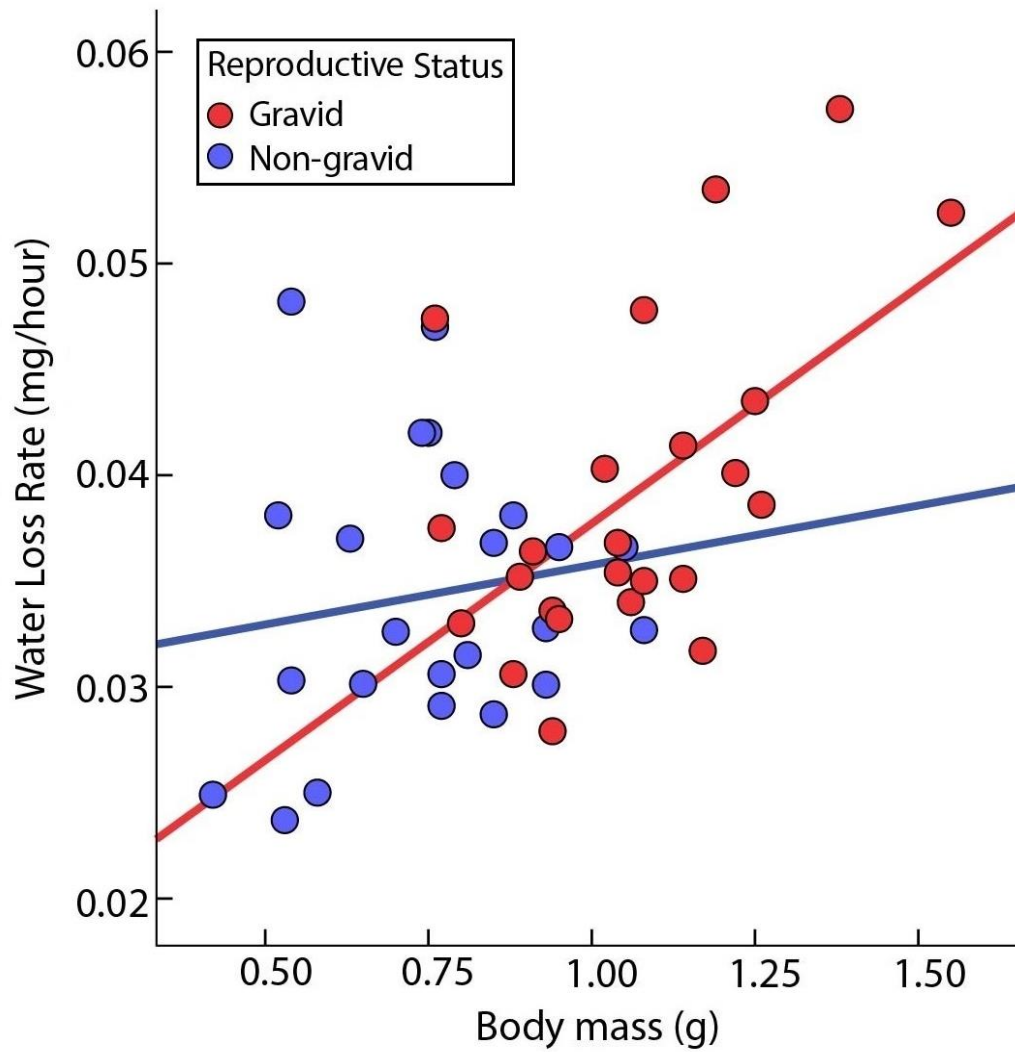
CHAPTER 4

TRADEOFFS IN WEAPON AND ORNAMENT ALLOMETRY IN ARIZONA BARK

SCORPIONS (*CENTRUROIDES SCULPTURATUS*)

Abstract

Life history tradeoffs reflect limitations in the amount of time and energy that

organisms can concurrently allocate to various life history components. One important

tradeoff is the division of energetic resources among different body parts during

ontogeny. Various ecological factors can influence the rates of body growth, and unequal

rates can lead to variation in the body morphology of mature individuals. Organisms

often allocate greater amounts of energetic resources to the development of defensive and

offensive traits (weapons), and to characters used to attract mates (ornaments). Although

weapons and ornaments can increase the survival and reproductive success of individuals,

increased allocation of energy to these features may limit the resources available for the

growth of other somatic structures or reproductive traits. I examined patterns of

allometric growth in male and female Arizona Bark Scorpions, *C. sculpturatus*. For each

scorpion I measured the length of seven distinct morphological traits: carapace,

mesosoma, metasomal segments I-V, telson, chela, leg I, and IV. I assessed how the

growth of weapons (chelae and metasoma) and ornaments (chelae, metasoma and

walking legs in males) influenced patterns of growth in other anatomical structures

(carapace, mesosoma). Although *C. sculpturatus* females are larger than males, males

have significantly longer tails than females. In both sexes, the chelae and metasoma

function as weapons, and enable individuals to defend themselves against predators and to capture prey. In males, the chelae, metasoma, and walking legs also act as ornaments during courtship of females. The relative size of the chelae was negatively correlated with the size of the carapace and mesosoma in females, whereas in males the relative size of the chelae was negatively correlated with total body length. These findings suggest that a greater allocation to weapon growth may limit the growth of other body structures in *C. sculpturatus*. Females exhibited a negative correlation between the relative size of the chelae and the mesosoma, illustrating the negative influence that weapon development can have on characters that affect reproductive investment. The relative size of the tail was negatively correlated with leg IV length in females. These two body parts may grow in a compensatory fashion, as females with relatively longer tails have shorter fourth legs, and females with relatively shorter tails have longer legs IV. These two alternative phenotypes may be functionally equivalent, and enable females to maintain adequate tail function over a relatively wide range of values of tail length. Males did not exhibit a negative correlation between the relative size of the tail and leg IV. The elongated tails of males, perhaps as a result of sexual selection, may allow them to exhibit variation in leg IV length without any negative consequence to their stinging mechanics. In females, allocation of resources to mesosoma growth was negatively correlated with the relative length of the chela, carapace, and leg IV. In males, allocation of resources to chela and tail growth led to relatively shorter bodies. These intersexual differences in the correlation of various traits could have facilitated the origin, and contribute to the maintenance of sexual size dimorphism in *C. sculpturatus*.

Introduction

Tradeoffs in life history evolution result from conflicts between the time and energy that can be simultaneously invested in ecologically relevant tasks. In nature, organisms often must compromise and allocate finite resources among life history components (e.g., body growth, immune function, reproduction). One important tradeoff in life history involves the energetic resources allocated to the development of different body parts throughout ontogeny. Body size is a life history component that can directly influence an organism's survival and reproductive potential (Buston & Elith 2011; Xu & Wang 2013). Reproductive output generally increases with body size, and larger-bodied organisms often produce larger or more numerous offspring, and experience greater reproductive success than smaller individuals (Magnhagen & Kvarnemo 1989; Wiklund & Kaitala 1995; Steffenson & Brown 2013). Furthermore, larger organisms often experience lower predation rates than smaller animals (Werner & Gilliam 1984; Travis et al. 1985). However, there may be negative consequences associated with a larger body size. For example, larger individuals have higher energetic requirements, which may compromise their survival under resource limitation (Wikelski et al. 1997). In addition, larger animals may be less agile, which may decrease their ability to escape predation (Andersson 1994). Larger organisms may require longer to reach reproductive maturity, and thus may experience an increased risk of mortality before reaching reproductive age, compared to smaller and faster-maturing individuals (Blanckenhorn 2000). Understanding the impact of growth rates on life history components may reveal the mechanisms that generate constraints on the maximum body sizes attained by organisms.

Several factors (e.g., temperature, food availability, sexual selection) can generate variation in growth rates during ontogeny (i.e., allometric growth), which ultimately translates into differences in the body proportions of mature individuals (Leigh & Shea 1996; Ohlsson & Smith 2001; Ellis & Bercovitch 2011; Du & Ji 2012). For instance, organisms generally allocate a greater amount of energetic resources to the growth of features used for defense (weapons) and traits used to attract mates (ornaments, Emlen et al. 2012). Weapons and ornaments can increase an organism's fitness by increasing its likelihood of surviving antagonistic encounters and its mating success, respectively. Thus, these traits often exhibit positive allometry, and may become larger and more elaborate as individuals increase in size (MacLaren et al. 2011; Bergmann & Berk 2012; Painting & Holwell 2013). Although larger weapons and ornaments may be advantageous, the growth and maintenance of enlarged body structures is probably energetically costly.

A greater investment in the growth of weapons and ornaments can negatively impact other organismal attributes, and lead, for instance, to significant reductions in locomotor ability (Madewell & Moczek 2006; Allen & Levinton 2007), decreased immune function (Saino & Møller 1996; Verhulst et al. 1999), and to a greater rate of detectability by predators (Godin & McDonough 2003). Furthermore, the production of larger weapons and ornaments is known to result in the reduction of other anatomical structures (Emlen 2001; Simmons & Emlen 2006). Therefore, organisms with relatively larger weapons and ornaments may experience a tradeoff, in which the increased allocation of energetic resources to the growth of these structures has a negative impact

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on other life history components. Examining patterns of allometric growth may therefore shed light on how these energetic constraints shape the evolution of a species life history.

Arizona Bark Scorpions (*Centruroides sculpturatus* Ewing 1928 [=*C. exilicauda* Wood 1863 of some authors]) inhabit the rocky outcrops and riparian habitats within the Sonoran Desert of southwestern North America (Rowe & Rowe 2008; Webber & Graham 2013). *Centruroides sculpturatus* possess dorso-ventrally flattened bodies and have slender and elongated chelae (pincers) and metasoma (tail; Ewing 1928). The chelae and stinger-equipped metasoma of scorpions are primarily used in foraging and prey capture, but also aid in defense against predators (Bub & Bowerman 1979; Shaffer & Formanowicz 1996; Webber & Rodríguez-Robles 2013). The walking legs of scorpions are also instrumental in the acquisition of prey (Bowerman 1975). The first pair of legs is tactile and aids in the manipulation of prey items (Bub & Bowerman 1979), whereas the fourth pair is integral in coordinated locomotion (Bowerman 1975; Herreid & Fourtner 1981), and is also used to lift the posterior end of the body during the stinging and envenomation of prey (M. M. Webber, personal observations). *Centruroides sculpturatus* are sexually dimorphic, as females are generally larger than males (Ewing 1928). Despite being smaller in overall body size, male *Centruroides* spp. possess a longer metasoma than females (Stahnke & Calos 1977), a difference that is most evident in the length of the fifth metasomal segment (Francke & Jones 1982; this study).

Besides their use in foraging and defense, the chelae of male *C. sculpturatus* are used during reproductive activities. During a mating event, male scorpions court females using a series of behaviors referred to as a "*promenade à deux*" (Lourenço 2000). During the promenade, a male scorpion grasps a female by her chelae and engages in a

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procession of movements (juddering, clubbing, sand scraping, pecten movements) to lead

the female to a substrate suitable for spermatophore (the sperm-carrying structure that is

extruded from the male's body; Francke 1979; Lourenço 2000) deposition (Alexander

1959; Polis & Sissom 1990; Tallarovic et al. 2000). If a male experiences female

resistance, he uses his first pair of walking legs to manipulate the pectines (sensory

organs) of the females, or to engage in a drumming display on the substrate (Sánchez-

Quirós et al. 2012). Occasionally during courtship the male uses its metasoma to

administer a "sexual sting" to the pedipalp or cephalothorax of the female, a behavior that

is hypothesized to aid in the pacification of the female, and increase the likelihood that

she engages in the promenade and ultimately accepts the male's spermatophore (Polis &

Sissom 1990).

Fitness-related traits such as weapons and ornaments tend to exhibit positive

allometry and grow proportionally larger as individuals increase in body size (MacLaren

et al. 2011; Bergmann & Berk 2012; Painting & Holwell 2013). The chelae and

metasoma directly influence the survival and reproductive potential of scorpions

(Lourenço 2000; van der Meijden et al. 2012). Hence, the relative size of these traits is

expected to be under selective pressure. Furthermore, ornaments are typically under

directional sexual selection, and larger relative trait size can lead to a higher probability

of reproductive success (Bonduriansky 2007). Accordingly, I predicted that (i) larger

C. sculpturatus have disproportionately larger chelae and longer tails than smaller-bodied

individuals. Because of their role in courtship behavior, larger chelae may allow male

C. sculpturatus to maintain a grip on females during the promenade, thus improving

males' mating success. I therefore hypothesized that (ii) male *C. sculpturatus* have

relatively larger chelae than females. The reproductive success of female scorpions is directly related to their body size, as larger females can produce larger or more numerous offspring than smaller-bodied females (Steffenson & Brown, 2013). Consequently, I predicted that (iii) larger female *C. sculpturatus* have a disproportionately larger mesosoma than smaller-bodied females, and that females possess relatively larger mesosoma than males. Because increased investment in fitness-related traits can limit the growth of other somatic structures, I hypothesized that (iv) male *C. sculpturatus* experience a tradeoff between weapon development and the size of somatic structures, in which individuals that possess larger chelae and tails have relatively smaller (shorter) bodies and shorter walking legs than males with shorter chelae and tails. Finally, I predicted that (v) increased investment in weapon (chelae and tail) size has a negative relationship with the growth of traits which influence reproductive investment (mesosoma) and somatic characters (carapace and walking legs) in female *C. sculpturatus*.

Materials and methods

I collected 195 mature (adult) *C. sculpturatus* (123 females, 72 males) from the outskirts of Quartzsite (33° 38' 9" N, 114° 18' 15" W), La Paz County, southwestern Arizona, USA. I transported all scorpions to the laboratory at the University of Nevada, Las Vegas, where they were euthanized and preserved in 75% ethanol. To compare allometric growth patterns among female and male *C. sculpturatus*, I used a digital caliper (± 0.01 mm; Absolute Digimatic Series 500, Mitutoyo Corporation) to measure the length of several distinct morphological traits: carapace (from the anterior to the posterior margin), mesosoma (from the anterior margin of tergite I to the posterior margin

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of tergite VII), metasoma (from the anterior margin of segment I to the posterior margin of segment V), telson (from the base of the vesicle to the tip of the aculeus), right chela (from the base of the chelal palm to the distal end of the fixed finger), and the length of the first (leg I) and fourth (leg IV) walking legs (from the proximal end of the trochanter to the base of the apotele; Hjelle 1990) on the right side of the body. I also determined total body length (carapace length + mesosoma length) and total tail length (metasoma length + telson length).

All data met the assumptions of normality, and therefore I performed all statistical analyses using non-transformed data. To determine an appropriate index of overall body size and explore patterns of variation among morphological characters, I performed a single principal component analysis (PCA) using data for both female and male *C. sculpturatus*. Next, I compared the relative sizes of morphological characters between female and male scorpions with an analysis of covariance (ANCOVA), using the first principal component (PC1) as the covariate. This method allowed me to compare the relative size of morphological traits between females and males, while controlling for sexual size dimorphism. Finally, I performed a separate correlation analysis for male and female *C. sculpturatus* using the residual values of the seven measured traits (carapace, mesosoma, metasoma, telson, right chela, leg I, leg IV) to investigate positive and negative correlations among characters. All statistical tests were performed using SPSS (SPSS 21 Inc., Chicago, Illinois, USA). Values reported are means ± 1 SD, and all *P*-values are two-tailed. Significance level for all tests was determined at $\alpha = 0.05$.

Results

Principal component analysis

The majority of the variance in overall body size (71.4%) was explained by PC1 (Table 4.1). The carapace, chela, leg I, and leg IV had factor loadings greater than 80%, whereas the factor loadings of the mesosoma (75.4%) and metasoma (37.0%) were lower. (i) *Larger* C. sculpturatus *have disproportionately larger chelae and a longer tail than smaller-bodied individuals.*

Body size (PC1) and the size of the chelae were linearly related in female ($r^2 = 0.87$, $F_{(1,121)} = 788.4$, $P < 0.001$) and male ($r^2 = 0.87$, $F_{(1,70)} = 478.1$, $P < 0.001$) *C. sculpturatus*, as larger individuals had longer chelae than smaller-bodied animals, but the two traits did not differ in proportional scaling (females, slope = $\beta = 0.67$, t = 1.50, *df* = 122, $P = 0.14$; males, $\beta = 0.60$, t = 1.90, *df* = 71, $P = 0.061$; Table 4.2; Fig. 4.1). Body size and total tail length were also linearly related, as larger females ($r^2 = 0.89$, $F_{(1,121)} = 928.9$, $P < 0.001$) and males ($r^2 = 0.83$, $F_{(1,70)} = 334.8$, $P < 0.001$) had longer tails than smaller females and males, respectively (Table 4.3; Fig. 4.2). Tail length exhibited positive allometry in both female ($\beta = 2.45$, t = 3.37, *df* = 122, $P = 0.001$) and male ($\beta = 3.03$, t = 5.48, *df* = 71, $P < 0.001$) *C. sculpturatus*, as the slope of the linear regression of total tail length on PC1 was significantly greater than 1 (Fig. 4.2). However, males exhibited a steeper allometry in comparison to females such that tail length was disproportionately longer in males (Table 4.3; Fig. 4.2).

(ii) *Male* C. sculpturatus *have proportionately larger chelae than females.*

Males ($\overline{X}$ = 9.48 ± 0.64 mm, range = 8.16 – 11.24 mm, n = 72) had

proportionally shorter chelae than females ($\overline{X}$ = 10.53 ± 0.72 mm, range = 8.61 – 12.09

mm, n = 123; ANCOVA, $F_{(1,191)}$ = 9.71, P = 0.002; Table 4.2; Fig. 4.1).

(iii) *Larger female* C. sculpturatus *have a disproportionately larger mesosoma than*

smaller-bodied females, and females possess a relatively larger mesosoma than males.

Body size and mesosoma length were linearly related in female *C. sculpturatus*

(r^2 = 0.34, $F_{(1,121)}$ = 63.0, P <0.001; Table 4.4; Fig. 4.3). Larger females had a

proportionately longer mesosoma than smaller females, as the slope of mesosoma length

in females did not differ significantly from 1 (β = 1.09, t = 0.52, df = 122, P = 0.60; Fig.

4.3). After controlling for overall body size, there was no evidence of sexual dimorphism

in relative mesosoma size in female ($\overline{X}$ = 17.0 ± 1.87 mm, range = 13.11 – 21.45 mm, n

= 123) or male ($\overline{X}$ = 14.7 ± 1.78 mm, range = 11.25 – 19.58 mm, n = 72) scorpions

(ANCOVA, $F_{(1,191)}$ = 3.0, P = 0.09; Table 4.4; Fig. 4.3).

(iv) *Male* C. sculpturatus *that possess relatively larger chelae and a relatively longer tail*

have relatively shorter bodies and walking legs than males with shorter chelae and a

smaller tail.

In males, relative chela size and total body length (carapace + mesosoma length)

were negatively correlated (Fig. 4.4). Relative tail length in males was also negatively

correlated with total body length, whereas the relative size of the mesosoma exhibited a

positive correlation with total tail length (see APPENDIX B).

(v) *Increased investment in weapon (chela and tail) size has a negative relationship with the growth of traits that influence reproductive investment (mesosoma) and with somatic characters (carapace and walking legs) in female* C. sculpturatus.

In females, the relative size of the mesosoma was negatively correlated with the relative size of the chelae, carapace, and the length of leg IV (see APPENDIX C; Fig. 4.5). The relative size of the tail was negatively correlated with the relative size of leg IV. On the contrary, females' mesosomas exhibited a positive correlation with total tail length (see APPENDIX C). The relative size of the chelae of females showed a negative correlation with the relative size of the carapace and with tail length, but had a positive correlation with leg IV length (see APPENDIX C; Fig. 4.5).

Discussion

Life history tradeoffs result from the limited time and energy that organisms can concurrently devote to various activities. Accordingly, increasing the resources invested into one life history component (e.g., foraging, mating, and territorial defense) will likely result in a reduction in the resources that can be invested in others. Although increased allocation to body growth may increase an organism's likelihood of reproductive success (Magnhagen & Kvarnemo 1989; Wiklund & Kaitala 1995; Steffenson & Brown 2013), the costs associated with increased body growth (e.g., decreased agility, immune function, and locomotor efficiency) may place limits on the maximum body sizes reached by organisms (Andersson 1994; Verhulst et al. 1999; Madewell & Moczek 2006). Large amounts of energetic resources are often allocated to the development of weapons and ornaments during ontogeny, increasing the fitness of individuals (Husak et al. 2009). However, finite resources may generate variation in the relative growth rates of

anatomical structures, and may generate plasticity in the morphology of mature individuals (Leigh & Shea 1996; Ohlsson & Smith 2001; Ellis & Bercovitch 2011; Du & Ji 2012). Below I discuss my findings regarding intra- and intersexual patterns of allometric growth in *C. sculpturatus*.

Principal component analysis

The principal component analysis revealed that carapace length was positively correlated with the length of the chela, mesosoma, telson, leg I, and leg IV for female and male *C. sculpturatus*. Therefore, increases in the size of the carapace are associated with a commensurate increase in the size of most anatomical structures measured. Hence, carapace length is a reliable indicator of overall body size in *C. sculpturatus*. However, variation in the length of the metasoma was only minimally accounted for by PC1. This finding suggests that the size of the metasoma varies independently of overall body size. (i) *Larger* C. sculpturatus *have disproportionately larger chelae and a longer tail than smaller-bodied individuals.*

Contrary to my prediction, the size of the chelae in female and male *C. sculpturatus* exhibited a positive linear relationship, with overall body size and chela size scaling isometrically. Larger females possessed longer chelae than smaller females, and larger males had longer chelae than smaller males. Females had proportionately longer chelae than males, indicating that females allocate a greater amount of resources to chela growth, compared to males, and that females maintain this greater allocation to chela growth at larger body sizes. The chelae are multifunctional structures, and are used for prey capture and defense in male and female scorpions (van der Meijden et al. 2010). Thus, there may be functional constraints that maintain the proportional scaling of chela

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size to overall body size in *C. sculpturatus*. For example, it may be necessary for chela size to scale proportionally with body size to maintain adequate mechanical function (i.e., grasping ability, pincer force) at a larger body size.

Larger female and male *C. sculpturatus* had a disproportionately longer tails than smaller females and males, respectively. The tails of scorpions are used during defense and prey capture (van der Meijden et al. 2013), and males also use this structure during the courtship of females. The tail exhibited the greatest sexual dimorphism of all the traits I measured, and male *C. sculpturatus* had disproportionately longer tails at all body sizes and a steeper linear allometry than females. The tails of male *C. sculpturatus* may be under sexual selection, as males with relatively longer tails can increase the range over which they can strike (Fig. 4.6). This ability may be beneficial during the clubbing or stinging of females during a mating event, and may ultimately result in greater reproductive success, compared to males with relatively shorter tails.

(ii) *Male* C. sculpturatus *have proportionately larger chelae than females.*

I predicted that the use of the chelae by males during courtship displays leads to disproportionately larger chelae in male *C. sculpturatus*, compared to females. Contrary to my hypothesis, males had proportionately shorter chelae than females. In species of *Centruroides*, intersexual differences in chela size may become apparent during the developmental stages occurring prior to reaching reproductive maturity (instar IV-V; Francke & Jones 1982). Accordingly, morphological differences in chela size may be under hormonal control, and limitations on the size of chelae in males may result from an overall reduction in the resources allocated to overall body growth throughout ontogeny. The difference in the relative size of the chelae between female and male *C. sculpturatus*

may reinforce sexual dimorphism in this scorpion by limiting the maximum size of prey that males can acquire. In contrast, the smaller chelae of male *C. sculpturatus* may be beneficial during their courtship of females. Scorpions that possess shorter and more robust chelae have a greater mechanical advantage and greater pincer force than scorpions with more elongated chelae (van der Meijden et al. 2010). Shorter chelae may be advantageous to male *C. sculpturatus* by enabling them to maintain a tighter grip on females during courtship, thereby increasing the likelihood that females will remain in close proximity until spermatophore deposition, which may result in increased mating success for males.

(iii) *Larger female* C. sculpturatus *have a disproportionately larger mesosoma than smaller-bodied females, and females possess a relatively larger mesosoma than males.*

Larger females had a proportionately longer mesosoma than smaller females, although there was considerable variation in the size of the females' mesosoma. In female scorpions, fecundity often increases with body size, and larger females can produce larger or more numerous offspring than smaller-bodied individuals (Steffenson & Brown 2013). In female *C. sculpturatus*, increases in body size result in a greater number of offspring, but both large and small-bodied females produce similar-sized offspring (Brown 2004). It thus appears that the reproductive potential of larger female *C. sculpturatus* is enhanced by the allocation of energetic resources to the mesosoma. After controlling for dimorphism in overall body size, I did not detect a statistical difference in the relative size of the mesosoma between female and male *C. sculpturatus*. The mesosoma houses the respiratory, digestive, and circulatory systems of scorpions, and is the primary location for fat storage (Williams 1968; Hjelle 1990). Having a mesosoma proportionate

to their overall body size may allow individuals to maintain the efficiency of their physiological systems. The size of the mesosoma may also influence the reproductive success of male *C. sculpturatus*. The spermatophore develops in the paraxial organ, which is located in the anterior region of the male's body, directly below the carapace, and partially extends into the mesosoma (Francke 1979). If males with a larger mesosoma produce larger spermatophores, those males may experience a reproductive advantage, for an increase in the amount of sperm delivered may increase the probability of successful fertilization of a female's eggs.

(iv) *Male* C. sculpturatus *that possess relatively larger chelae and a relatively longer tail have relatively shorter bodies and walking legs than males with shorter chelae and a smaller tail.*

Increased energetic investment in the production of larger or more elaborate weapons can result in the reduction of resources devoted to the growth of surrounding body structures (Emlen 2001). Therefore, I predicted that male *C. sculpturatus* experience a tradeoff between weapon investment and somatic body growth. Indeed, I documented a negative correlation between the relative size of the chelae and total body length in male *C. sculpturatus*. Contrary to my hypothesis, I did not observe a significant negative correlation between the relative size of weapons (chelae and tail) and the relative size of walking legs I and IV in male *C. sculpturatus*. Smaller body sizes in male *C. sculpturatus* may limit the amount of energetic resources that can be stored in the mesosoma, which may compromise the survival of males under resource limitation. Furthermore, a smaller overall body size in male *C. sculpturatus* may also increase their predation risk by limiting their ability to fend off relatively large-bodied predators.

(v) *Increased investment in weapon (chela and tail) size has a negative relationship with the growth of traits that influence reproductive investment (mesosoma) and with somatic characters (carapace and walking legs) in female* C. sculpturatus.

Relative chela length was negatively correlated with relative carapace and mesosoma length. As with male *C. sculpturatus*, the allocation of energetic resources to chelae may increase the predatory efficiency of females, and enable the latter to better defend themselves against predators. On the contrary, increased resource allocation to chela growth results in females with shorter mesosomas, which may have negative consequences for their reproductive potential. Females with relatively shorter mesosomas may be limited in the maximum number of offspring that they can carry inside their abdomen during gestation. Following the birth of offspring ($\overline{X}$ = 20 scorplings, range: 7 – 42; Polis & Sissom 1990), females exhibit maternal care by carrying offspring on their backs (Lourenço 2000; Webber & Rodríguez-Robles 2013). In females with relatively shorter carapaces and mesosomas, the total surface area that can successfully accommodate offspring during the brooding period is smaller. The relative size of the mesosoma was also negatively correlated with the relative size of the carapace and of leg IV. It thus appears that the allocation of energetic resources to structures that influence reproductive output (mesosoma) in female *C. sculpturatus* reduces the energy available for somatic growth in different regions of the body.

The relative length of the tail exhibited a negative correlation with the relative length of leg IV for female *C. sculpturatus*, as females with longer tails had relatively shorter legs IV. The nature of the interaction between relative tail length and leg IV

length may enable females to maintain adequate tail function during prey capture or defense for a range of values of tail and leg IV lengths. Alternatively, the relative size of the tail and legs IV may be developmentally coupled, so that a relatively longer leg IV and a shorter tail, or a relatively short leg IV and longer tail are two alternative, functionally equivalent phenotypes. In addition, the relative size of females' mesosoma exhibited a positive scaling with total tail length, perhaps because it improves the kinematics of stinging.

Intersexual differences in body allometry

Male *C. sculpturatus* had smaller body sizes than females, yet males possessed disproportionately longer tails. The increased allocation of resources to tail growth may limit the energy available for the growth of other anatomical structures in males, and ultimately result in sexual dimorphism in overall body size, with males being the smaller sex. Other factors may reinforce sexual size dimorphism in *C. sculpturatus*. For instance, body size differences may occur as a result of resource partitioning, such that the morphological differences between the sexes decrease their competition for resources (Temeles et al. 2000). Moreover, the larger sizes of females may result from intersexual differences in the relationship between body size and fecundity, in which a larger body size enhances a female's lifetime reproductive potential by increasing the number or size of offspring produced per reproductive bout (Steffenson & Brown 2013). The larger body sizes of female *C. sculpturatus* may also result from a male preference for larger females, in which the selection of larger females by males increases their reproductive success (Lengagne et al. 2007). Sexual dimorphism in *C. sculpturatus* may also result from sexually antagonistic encounters (Arnqvist & Rowe 2002), in which larger females may

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be more capable of resisting coercion into mating activities by lower quality males. Furthermore, the lifetime reproductive potential of males can be increased by becoming reproductively mature at a relatively early age (Wiklund & Fagerström 1977), as early maturation may allow male *C. sculpturatus* to maximize their total number of mating opportunities (Andersson 1994). All these factors are not mutually exclusive, and they all may influence sexual dimorphism in body size in *C. sculpturatus*.

Conclusion

I predicted that there is a tradeoff between weapon and ornament growth, and the growth of other anatomical structures in Arizona Bark Scorpions, *C. sculpturatus*. Chela length increased proportionally with body size in females and males. Investment in relatively larger chelae led to relatively shorter carapaces and mesosomas in females, and to smaller total body lengths in males. My findings demonstrate that the allocation of resources to weapon development leads to a reduction in the size of other morphological features. Interestingly, female *C. sculpturatus* exhibited a tradeoff between the relative size of the tail and the length of leg IV. This negative correlation suggests that a compensatory association between the two traits is necessary to maintain appropriate stinging performance, and that this interaction is under selection. Furthermore, I observed intersexual differences in the correlation structure of body traits between female and male *C. sculpturatus*. In females, an increase in the relative size of the mesosoma led to a reduction in the size of the chelae, carapace, and legs IV. In males, the relative size of the chelae and the tail were negatively correlated with total body length. These intersexual differences are likely to reflect the influence that sexual selection exerts on particular traits, and the effect of this evolutionary mechanism on the reproductive fitness of males

and females. In summary, the body sizes attained by organisms and the relative scaling of traits to overall body size can have significant functional and ecological implications on the evolution of a species' life history. Understanding the mechanisms that generate phenotypic variation in the allometric growth patterns of individuals may help uncover the natural and sexual selection that molds the body morphology of mature organisms in nature.

<div align="center">Literature cited</div>

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Tables

Table 4.1. Principal component analysis, factor loadings for the first (PC1) and second

(PC2) principal component in female and male *Centruroides sculpturatus*.

Trait	PC1	PC2
Carapace	0.928	−0.167
Metasoma (segments I–V)	0.369	0.918
Chela	0.954	−0.030
Mesosoma	0.754	−0.211
Telson	0.838	0.078
Leg I	0.949	−0.033
Leg IV	0.959	−0.032
Eigenvalue	5.0	0.924
Total Variance (%)	71.43	13.20

Table 4.2. Comparison of chela length (mm) in female and male *Centruroides sculpturatus*. The first principal component (PC1) was used as the covariate for the Analysis of Covariance.

Effect	*df*	MS	F	*P*
Sex	1	0.61	9.7	0.002
PC1	1	69.72	1110.1	<0.001
Sex * PC1	1	0.03	0.5	0.50
Error	191	0.06	—	—

Table 4.3. Comparison of total tail length (metasomal segments I-V + telson length, mm) in female and male *Centruroides sculpturatus*. The first principal component (PC1) was used as the covariate for the Analysis of Covariance.

Effect	*df*	MS	F	*P*
Sex	1	253.5	466.0	<0.001
PC1	1	1349.1	2480.1	<0.001
Sex * PC1	1	14.7	27.1	<0.001
Error	191	0.5	—	—

Table 4.4. Comparison of mesosoma length (mm) in female and male *Centruroides sculpturatus*. The first principal component (PC1) was used as the covariate for the Analysis of Covariance.

Effect	*df*	MS	F	*P*
Sex	1	5.7	3.0	0.086
PC1	1	266.2	137.8	<0.001
Sex * PC1	1	3.1	1.6	0.210
Error	191	1.9	—	—

Figures

Figure 4.1. Chela length (mm) as a function of body size (PC1) in female and male

Centruroides sculpturatus.
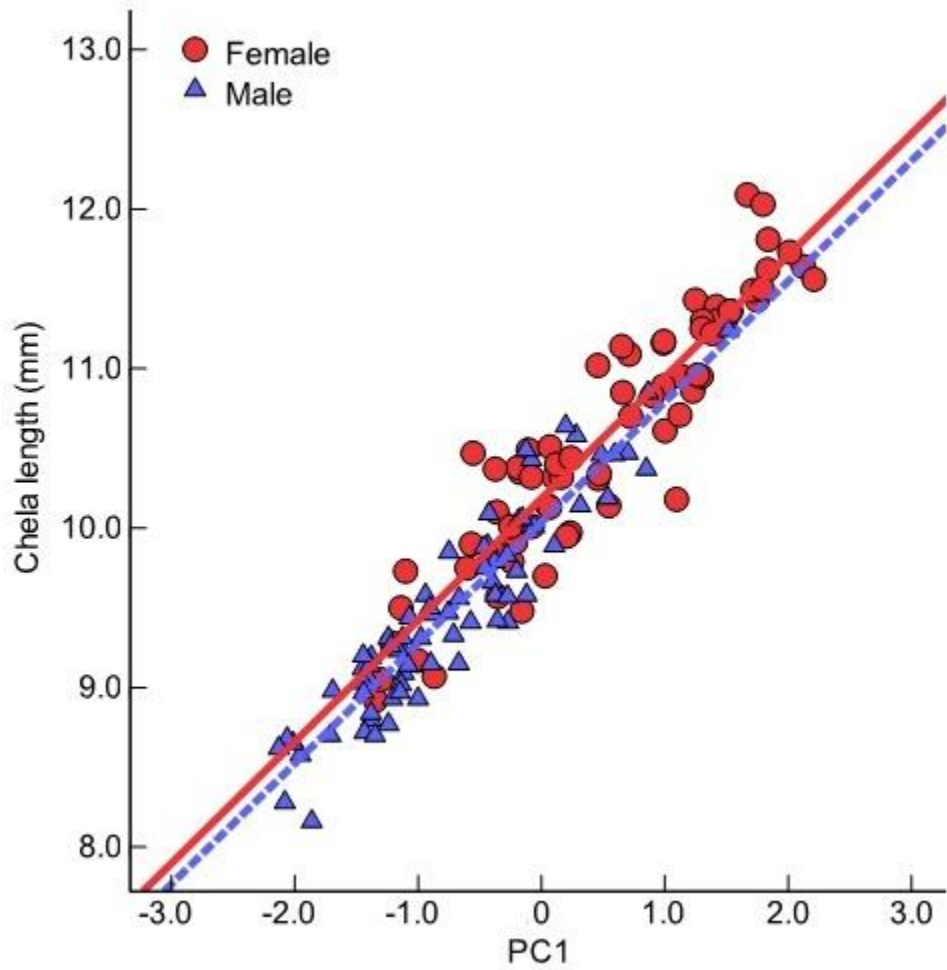
Figure 4.2. Total tail length (mm) as a function of body size (PC1) in female and male

Centruroides sculpturatus.
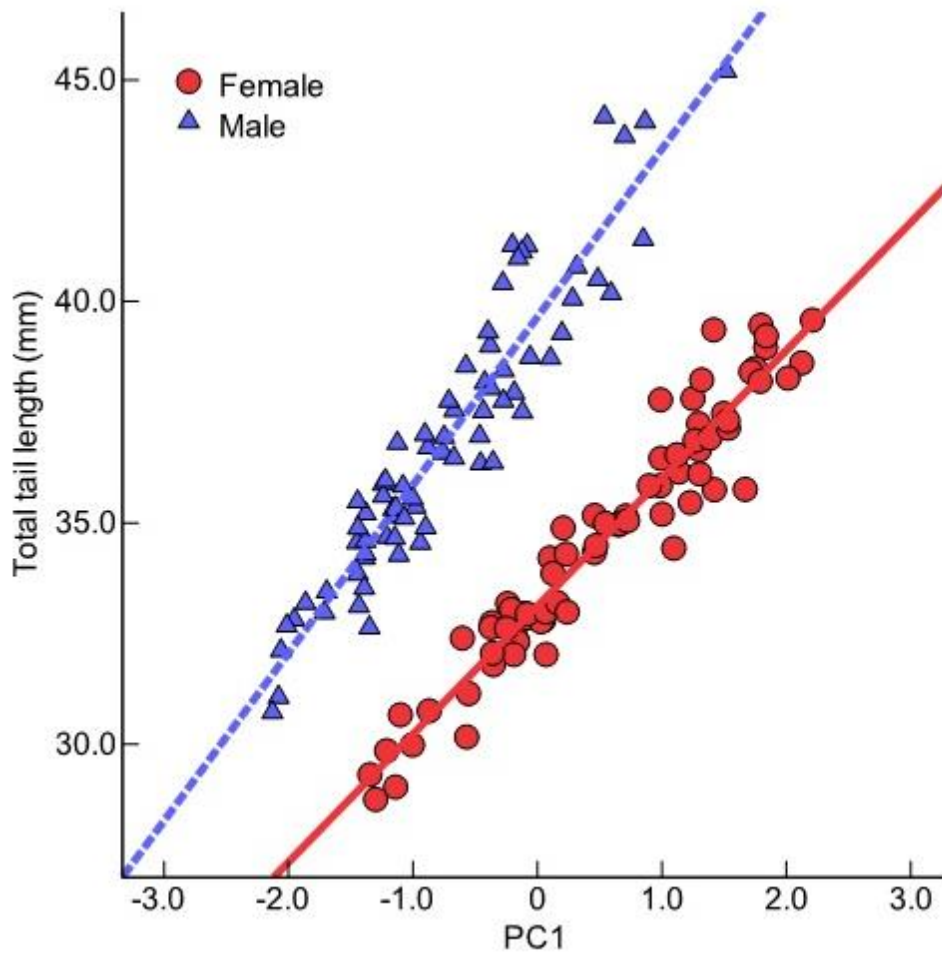
Figure 4.3. Mesosoma length (mm) as a function of body size (PC1) in female and male

Centruroides sculpturatus.

Figure 4.4. Correlation network of the interaction between morphological traits in male

Centruroides sculpturatus.

Figure 4.5. Correlation network of the interaction between morphological traits in female *Centruroides sculpturatus*.

Figure 4.6. The influence of tail length on the strike range of male *Centruroides* *sculpturatus*.

Male 9

Tail length
37.5 mm

Body length   Strike range
20.7 mm   16.8 mm

Male 28

Tail length
41.3 mm

Body length   Strike range
21.0 mm   20.3 mm

CHAPTER 5

LIFE HISTORY TRADEOFFS IN *CENTRUROIDES SCULPTURATUS*

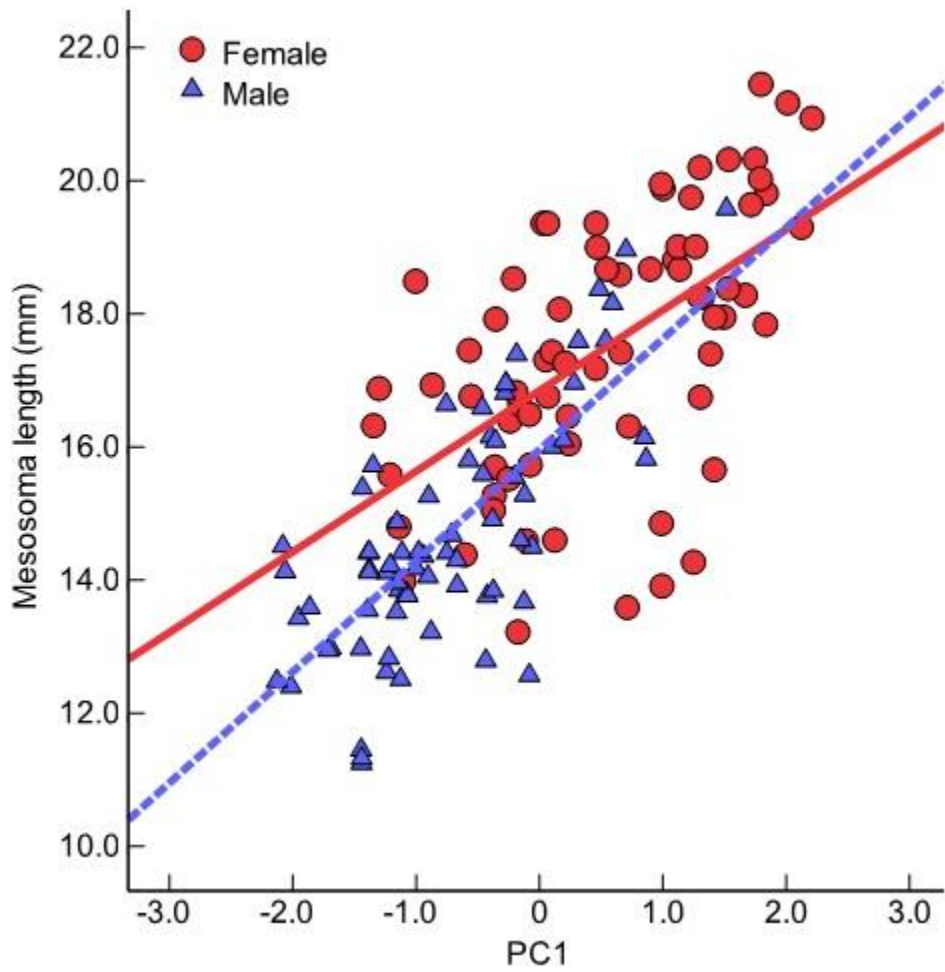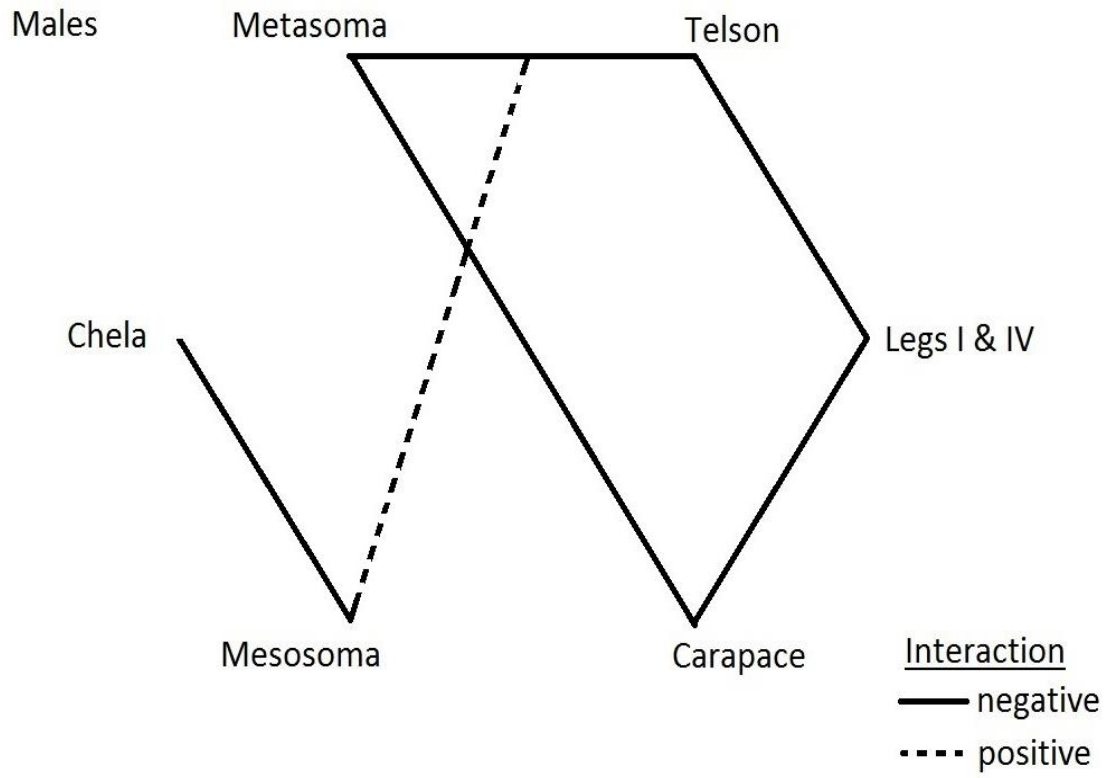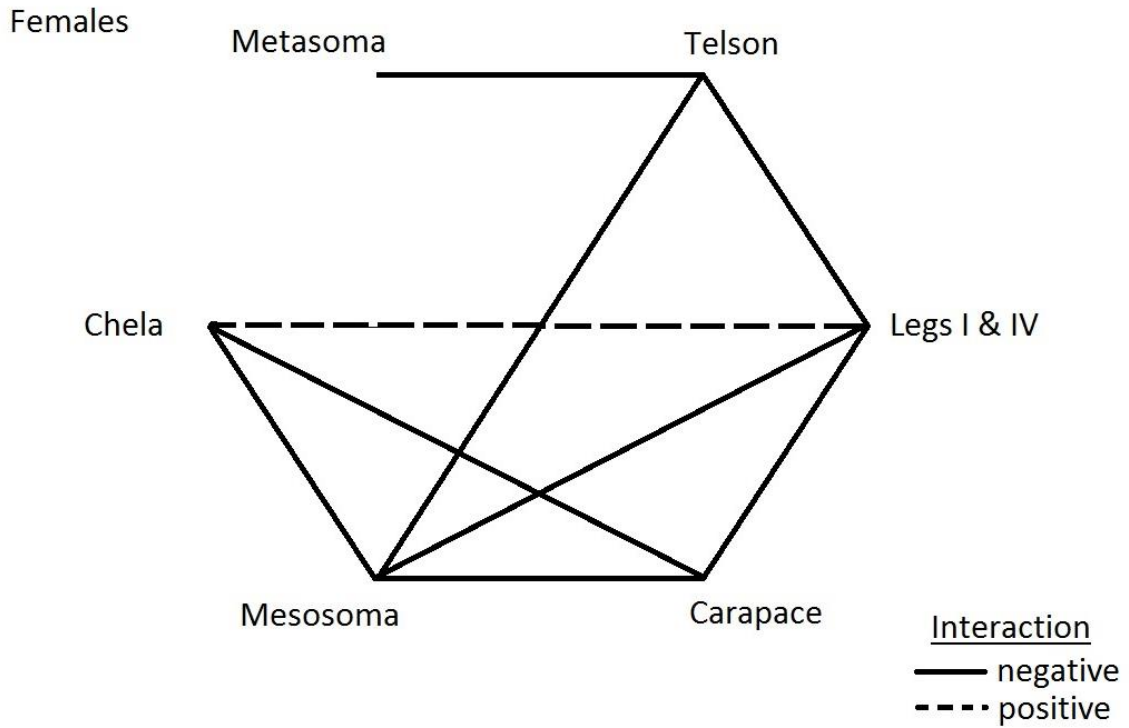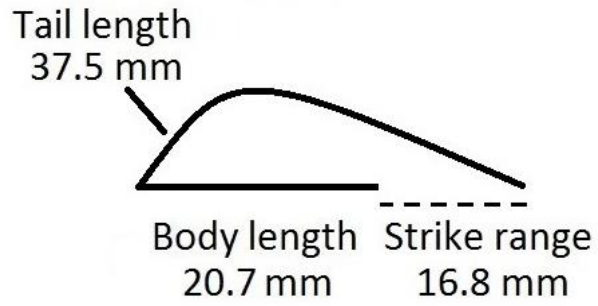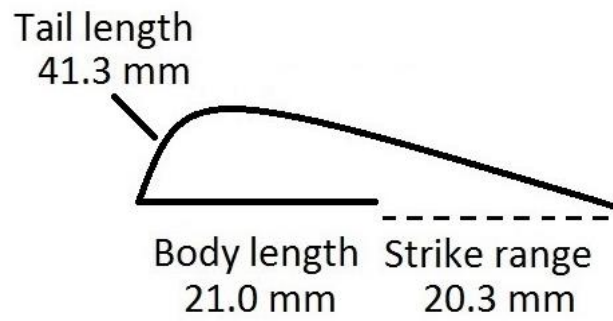Temporal and energetic constraints generate tradeoffs in life history evolution, for organisms must allocate limited resources among various activities. There are high costs associated with reproduction, and these costs are known to have negative consequences on other life history components. I investigated reproductive tradeoffs in female Arizona Bark Scorpions, *Centruroides sculpturatus*. In females, maternal care (i.e. carrying offspring on their backs) significantly reduces predatory efficiency. This tradeoff may compromise the survival of post-parturient females by limiting their ability to recuperate energetic resources invested in reproduction. Thus, post-parturient females may experience significant decreases in body condition following the brooding period, which can compromise their survival, thereby limiting future reproductive opportunities. Additional studies investigating the influence of resource availability and body condition on the reproductive investments made by female *C. sculpturatus* may uncover additional tradeoffs experienced by reproductive females.

I also discovered that reproduction (i.e. gestation) causes alterations in the thermal preferences of female *C. sculpturatus*, because gravid females selected higher body temperatures than non-gravid individuals. This change in the thermoregulatory patterns of reproductive females may increase offspring viability. However, higher body temperatures may make reproductive females more susceptible to heat-induced mortality. Furthermore, the morphological (e.g. increased body mass) and physiological (e.g. higher metabolic rates) changes that occur in reproductive female *C. sculpturatus* caused them

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to lose water at significantly faster rates, compared to non-reproductive females. Therefore, reproductive females experience another tradeoff, as engaging in reproduction increases their rates of water loss and desiccation risk in arid environments. It would be informative to elucidate the precise route of water loss (transcuticular or respiratory) that accounts for the faster rates of water loss observed in reproductive females.

I assessed whether compromises occur in the allocation of resources to the growth of weapons, ornaments and other anatomical structures in male and female *C. sculpturatus*. The chelae of male and female *C. sculpturatus* exhibited isometric growth, suggesting that there may be functional constraints that affect the relative size of the chelae to overall body size in these scorpions. On the contrary, the tails of males and females exhibited positive allometric growth and became disproportionately longer in larger individuals. Moreover, males have significantly longer tails than females. Their longer tails may be the result of sexual selection, if males with relatively longer tails experience greater reproductive success than males with relatively shorter tails. Interestingly, there are also intersexual differences in the correlation of morphological traits in males and females. Increased allocation to chela and tail size reduced total body length in male *C. sculpturatus*. On the other hand, increases in the relative size of the mesosoma led to a reduction in resources allocated to the growth of the carapace, chelae, and leg IV in females. These intersexual differences in the correlation of traits may maintain sexual dimorphism in this species, and may reflect the effect that natural and sexual selection have on the reproductive fitness of male and female *C. sculpturatus*. My dissertation research underscored that examining antagonistic interactions among life

history components can provide valuable insight on how temporal and energetic

constraints shape the evolution of life history strategies observed in nature.

APPENDIX A: COX PROPORTIONAL HAZARD MODEL

The effect of reproductive status and body size on prey capture time among non-gravid and gravid female *Centruroides sculpturatus*, and females 28 days following offspring removal.

Non-gravid females (n = 22) vs. Gravid females (n = 23)				
Covariate	Wald	Exp (β)	*df*	*P*
Reproductive status	0.351	1.20	1	0.554
Body size (carapace length x width, mm^2)	0.493	0.960	1	0.483
Chela size (length x width, mm^2)	2.136	1.168	1	0.144

Non-gravid females (n = 22) vs. Females 28 days following offspring removal (n = 14)				
Covariate	Wald	Exp (β)	*df*	*P*
Reproductive status	6.649	2.951	1	0.010
Body size (carapace length x width, mm^2)	0.023	1.009	1	0.880
Chela size (length x width, mm^2)	0.808	1.111	1	0.369

APPENDIX A Continued.

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Gravid females (n = 23) vs. Females 28 days following offspring removal (n = 14)

Covariate	Wald	Exp (β)	*df*	*P*
Reproductive status	5.834	2.813	1	0.016
Body size (carapace length x width, mm^2)	2.807	0.893	1	0.094
Chela size (length x width, mm^2)	4.460	1.331	1	0.035

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APPENDIX B: CORRELATION MATRIX OF MALE *CENTRUROIDES SCULPTURATUS*

Correlation matrix of the residual size of morphological characters (adjusted for overall size PC1) in male *Centruroides sculpturatus* (n = 72). *P*-values are two-tailed.

	Mesosoma	Chela	Carapace	Leg I	Leg IV	Total tail	Total body
Mesosoma							
r	—	−0.405	−0.186	−0.177	−0.156	0.713	—
P	—	<0.001	0.177	0.137	0.192	<0.001	—
Chela							
r	−0.405	—	−0.058	−0.222	0.021	−0.208	−0.283
P	<0.001	—	0.626	0.060	0.862	0.080	0.016
Carapace							
r	−0.186	−0.058	—	−0.283	−0.370	0.146	—
P	0.117	0.626	—	0.016	0.001	0.222	—

APPENDIX B Continued.

Leg I							
r	−0.177	−0.222	−0.283	—	0.182	−0.030	−0.256
P	0.137	0.060	0.016	—	0.126	0.80	0.030
Leg IV							
r	−0.156	−0.021	−0.370	0.182	—	−0.014	−0.291
P	0.192	0.862	0.001	0.126	—	0.908	0.013
Total tail							
r	0.173	−0.208	0.146	−0.030	−0.014	—	−0.360
P	<0.001	0.080	0.222	0.800	0.908	—	0.002

APPENDIX B Continued.

Total body							
r	—	−0.283	—	0.256	−0.291	−0.360	—
P	—	0.016	—	0.030	0.013	0.002	—

APPENDIX C: CORRELATION MATRIX OF FEMALE *CENTRUROIDES SCULPTURATUS*

Correlation matrix of the residual size of morphological characters (adjusted for overall size PC1) in female *Centruroides sculpturatus* (n = 123). *P*-values are two-tailed.

	Mesosoma	Chela	Carapace	Leg I	Leg IV	Total tail	Total body
Mesosoma							
r	—	−0.347	−0.280	−0.137	−0.317	0.902	—
P	—	<0.001	0.002	0.130	<0.001	<0.001	—
Chela							
r	−0.347	—	−0.184	−0.117	0.194	−0.322	−0.063
P	<0.001	—	0.042	0.199	0.032	<0.001	0.488
Carapace							
r	−0.280	−0.184	—	−0.185	−0.179	−0.111	—
P	0.002	0.042	—	0.040	0.048	0.222	—

APPENDIX C Continued.

Leg I							
r	−0.137	−0.117	−0.185	—	0.023	−0.109	0.029
P	0.130	0.199	0.040	—	0.802	0.230	0.750
Leg IV							
r	−0.317	0.194	−0.179	0.023	—	−0.298	−0.004
P	<0.001	0.032	0.048	0.802	—	0.001	0.963
Total tail							
r	0.902	−0.322	−0.111	−0.109	−0.298	—	−0.028
P	<0.001	<0.001	0.222	0.230	0.001	—	0.761

APPENDIX C Continued.

Total body							
r	—	−0.063	—	0.029	−0.004	−0.028	—
P	—	0.488	—	0.750	0.963	0.761	—

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Publications
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