

Provided for non-commercial research and education use.
Not for reproduction, distribution or commercial use.



This article appeared in a journal published by Elsevier. The attached copy is furnished to the author for internal non-commercial research and education use, including for instruction at the authors institution and sharing with colleagues.

Other uses, including reproduction and distribution, or selling or licensing copies, or posting to personal, institutional or third party websites are prohibited.

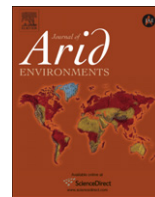
In most cases authors are permitted to post their version of the article (e.g. in Word or Tex form) to their personal website or institutional repository. Authors requiring further information regarding Elsevier's archiving and manuscript policies are encouraged to visit:

<http://www.elsevier.com/copyright>



Contents lists available at ScienceDirect

Journal of Arid Environments

journal homepage: www.elsevier.com/locate/jaridenv

Potential environmental influences on variation in body size and sexual size dimorphism among Arizona populations of the western diamond-backed rattlesnake (*Crotalus atrox*)

Melissa Amarello^{a,*}, Erika M. Nowak^b, Emily N. Taylor^{c,1}, Gordon W. Schuett^d, Roger A. Repp^e, Philip C. Rosen^a, David L. Hardy Sr.^f

^a School of Natural Resources, University of Arizona, Tucson, AZ 85721, USA

^b United States Geological Survey, Southwest Biological Science Center, Colorado Plateau Research Station, Box 5614, Northern Arizona University, Flagstaff, AZ 86011, USA

^c School of Life Sciences, Arizona State University, Tempe, AZ 85287, USA

^d Department of Biology and Center for Behavioral Neuroscience, Georgia State University, 33 Gilmer Street, S.E., Unit 8, Atlanta, GA 30303, USA

^e National Optical Astronomy Observatory, 950 N. Cherry Ave, Tucson, AZ 85719, USA

^f 585 S. Main Ave, Tucson, AZ 85701, USA

ARTICLE INFO

Article history:

Received 16 October 2009

Received in revised form

19 May 2010

Accepted 20 May 2010

Available online 1 July 2010

Keywords:

Ectotherm

Precipitation

Reptile

Resource availability

Seasonality

Temperature

ABSTRACT

Differences in resource availability and quality along environmental gradients are important influences contributing to intraspecific variation in body size, which influences numerous life-history traits. Here, we examined variation in body size and sexual size dimorphism (SSD) in relation to temperature, seasonality, and precipitation among 10 populations located throughout Arizona of the western diamond-backed rattlesnake (*Crotalus atrox*). Specifically, in our analyses we addressed the following questions: (i) Are adult males larger in cooler, wetter areas? (ii) Does female body size respond differently to environmental variation? (iii) Is seasonality a better predictor of body size variation? (iv) Is SSD positively correlated with increased resources? We demonstrate that male and female *C. atrox* are larger in body size in cooler (i.e., lower average annual maximum, minimum, and mean temperature) and wetter areas (i.e., higher average annual precipitation, more variable precipitation, and available surface water). Although SSD in *C. atrox* appeared to be more pronounced in cooler, wetter areas, this relationship did not achieve statistical significance.

© 2010 Elsevier Ltd. All rights reserved.

1. Introduction

Body size affects nearly all aspects of an animal's biology (e.g., growth, reproduction, survival) and differences in resource availability and quality are important influences on intraspecific variation in body size (Bronikowski and Arnold, 1999; Case, 1976; Sears and Angilletta, 2003). Environmental gradients are important determinants of resource variation, and in many species, body size varies along gradients of temperature (Ashton and Feldman, 2003;

James, 1970), primary productivity (Beaupre, 1995a), and/or seasonality (Ashton, 2001; Boyce, 1979). Additionally, body size in males and females may respond differently to environmental gradients and thus result in geographic variation in sexual size dimorphism (SSD; Dobson and Wigginton, 1996; Stillwell et al., 2007).

Temperature is often discussed as the primary driver behind large-scale patterns of body size clines (Stillwell et al., 2007). In general, body sizes of endotherms are negatively (i.e., Bergmann's Rule) and ectotherms positively correlated with temperature (Ashton and Feldman, 2003; James, 1970; but see: Olalla-Tárraga et al., 2006), but there is no general agreement on the proximate determinants responsible for these patterns. In terrestrial ectotherms, for example, regions of warmer climate provide extended periods of activity and potentially more foraging opportunities, which may lead to accelerated growth and, ultimately, larger body size (Blouin-Demers et al., 2002; Bronikowski and Arnold, 1999). Alternatively, high environmental temperatures may limit diurnal

* Corresponding author. Present address: SoLS Graduate Program, PO Box 874601, Arizona State University, Tempe, AZ 85287, USA. Tel.: +1 6024921235; fax: +1 4809650698.

E-mail addresses: melissa.amarello@asu.edu (M. Amarello), erika.nowak@nau.edu (E.M. Nowak), etaylor@calpoly.edu (E.N. Taylor), biogws@langate.gsu.edu (G.W. Schuett), repp@noao.edu (R.A. Repp), pcrosen@email.arizona.edu (P.C. Rosen), dhardysr@theriver.com (D.L. Hardy Sr.).

¹ Present address: Biological Sciences Department, California Polytechnic State University, San Luis Obispo, CA 93407, USA.

activity and cause increases in body temperature, leading to higher maintenance metabolism and a resulting smaller body size (Beaupre, 1995b; Grant and Dunham, 1988).

In arid environments such as deserts, water availability is often severely limited; thus it can be among the most important drivers of primary productivity, which influences the density and availability of prey (Beatley, 1969; Brown and Ernest, 2002; Case, 1976). Precipitation is positively correlated with primary productivity and density of arthropods and small mammals (Beatley, 1969; Brown and Ernest, 2002; Case, 1976). Important to our study, some species of reptiles grow faster and achieve larger adult body sizes in wetter areas (Beaupre, 1995a; Case, 1976).

Several authors have argued that seasonality is a better predictor of body size than other environmental factors (Ashton, 2001; Boyce, 1979). Seasonal environments are characterized by prolonged periods of stressful conditions (e.g., food shortages or drought; Stillwell et al., 2007) and large body size may increase an organism's ability to resist desiccation or starvation (Ashton, 2001; Boyce, 1979; Stillwell et al., 2007). Furthermore, it may be advantageous for long-lived species in an unpredictable climate to invest in growth in order to survive for future reproductive events (Boyce, 1979).

In reptiles and other animals with indeterminate growth, differential allocation strategies between the sexes may provide a proximate explanation for SSD (Beaupre et al., 1998; Taylor and DeNardo, 2008). For example, female pitvipers allocate most of their resources to reproduction once reaching sexual maturity and little to growth, yet males continue to grow (Beaupre, 2002; Beaupre et al., 1998; Taylor and DeNardo, 2008). If the allocation strategy in females is constant, then increased food resources would increase reproductive output, but not increase growth or body size. Thus, in populations with more available resources, SSD is likely to be pronounced (Beaupre, 2002; Winne et al., 2010).

Individual-based models are useful to guide experiments and assess patterns found in nature. Beaupre (2002), for instance, used an individual-based simulation to model time and energy allocation in rattlesnakes. This model predicts several patterns of body size and SSD of populations in varying environments: (i) adult males will be smaller in warmer areas (owing to increased maintenance costs associated with higher body temperatures); (ii) adult males will be larger in areas with more abundant resources; (iii) environmental variation will have little influence on body size of adult females; and (iv) SSD increases curvilinearly with increased resources. An important assumption of this model for predictions (iii) and (iv) is that adult females allocate nearly all (98.5%) available energy (not required for maintenance) to reproduction, while males allocate 100% of their available energy to growth.

Here, we examined variation in body size and SSD among 10 Arizona populations of *Crotalus atrox* (western diamond-backed rattlesnake), a large-bodied ectothermic mesopredator that occupies a variety of habitats throughout the southwestern United States and northern Mexico (Campbell and Lamar, 2004). Across its broad geographic distribution, *C. atrox* shows a wide range of adult body sizes and pronounced male-biased SSD (Campbell and Lamar, 2004; Spencer, 2008). Because of the highly variable physiographic structure of Arizona (Brown, 1994), we sampled a broad range of environmental variation in a relatively small geographic area. Additionally, in *C. atrox* and other squamate reptiles, body size responses to environmental variables are expected to be plastic (Madsen and Shine, 2000; Sears and Angilletta, 2003; Taylor and DeNardo, 2005; Taylor et al., 2005). Accordingly, we predicted that climate influences body size and SSD even at this relatively small geographic scale.

We investigated the influence of temperature, precipitation, surface water, and seasonality on body size of adult *C. atrox* from 10 populations, intensively sampled ($N = 981$) for 2–13 years

(1985–2007) and compared the patterns we found to those predicted by Beaupre's model (2002). Specifically, our analyses were based on the following questions: (i) Are adult males larger in cooler, wetter areas? (ii) Does female body size respond differently to environmental variation? (iii) Is seasonality a better predictor of body size variation? (iv) Is SSD positively correlated with increased resources?

2. Materials and methods

2.1. *C. atrox* natural history

The western diamond-backed rattlesnake (*C. atrox*) is an excellent model to examine geographic variation in body size and SSD in ectothermic vertebrates. Across its broad geographic distribution, body size of adult *C. atrox* increases with latitude (Spencer, 2008), but little variation in body size is explained by latitude alone (linear regression of body size (log snout-vent length (SVL)) against latitude: $r^2 = 0.04$ [adult males] and 0.02 [adult females]; Spencer, 2008). *C. atrox* are sexually dimorphic in size within geographic clades; adult males have 4–13% longer SVL than adult females (Spencer, 2008). Molecular analyses (mtDNA) by Castoe et al. (2007) show gene flow and relatively weak genetic structuring among *C. atrox* populations throughout much of their range in the United States, which suggests that *C. atrox* is best viewed as one species with clinal variation (Spencer, 2008). Therefore, genetic variation is not considered a significant confounding variable in our analyses. Recent laboratory and field studies indicate that growth, reproductive frequency, and SSD are plastic and resource-dependent (e.g., prey) in *C. atrox* (Beaupre et al., 1998; Taylor and DeNardo, 2005, 2008; Taylor et al., 2005).

2.2. Study sites

Located in the arid southwestern United States of America, the State of Arizona provides an exceptional opportunity to examine geographic variation in body size of an ectothermic vertebrate. Within a relatively small area (109–114° W; 31–37° N), elevation varies from 0 to almost 4000 m above sea level, creating a wide variety of vegetation communities from desertscrub to alpine tundra (Brown, 1994). The resulting environmental variation creates a pseudo-natural experimental design by which we investigated populations of *C. atrox*.

We analyzed various aspects of the ecology of *C. atrox* at 10 sites in Arizona (Fig. 1) in vegetation communities ranging from desertscrub to semidesert grassland (described in Brown, 1994; Table 1). Sites 1, 2, 4, and 8 were public areas managed by the National Park Service, dominated by native vegetation, but they contained small areas of human-modified habitats (e.g., housing areas and visitor centers). Site 7 was located near a desert-style golf course and contained a larger percentage of human-modified habitats; site 9 contained a mix of native habitat and private human development (e.g., houses). Site 10 contained a few cattle tanks and sites 3, 5, and 6 were composed primarily of native habitats without human developments other than dirt and asphalt roads.

2.3. Rattlesnake collection and measurement

We captured *C. atrox* by active searches on foot or by vehicle, in funnel traps associated with drift fences, or opportunistically while conducting radio-telemetry. Some combination of these capture methods were used at each study site; thus, it is unlikely that differences in body size were solely due to differences in detection probability associated with different capture methods. We marked individuals with a PIT-tag (passive integrated transponder tag) or

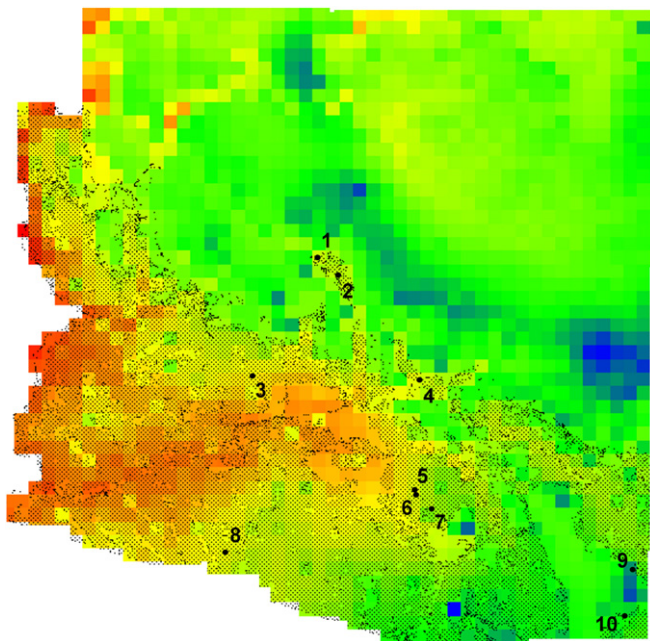


Fig. 1. Map of study sites 1–10 reported herein. The background colors are a graphical representation of PC1: mean-centered, GIS environmental layers (corresponding to each variable in the PCA) were weighted by their PC loadings and summed. Blue denotes coolest and wettest areas, and red denotes warmest and driest areas. The shaded area is the geographical range of *Crotalus atrox* in Arizona (Arizona GAP 1999 coverage H121RS – Western diamondback rattlesnake, USGS Sonoran Desert Research Station, University of Arizona, Tucson, available online: <http://sdrsnet.smr.arizona.edu/>). (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

scale clip, determined sex by probing, measured SVL to the nearest millimeter, and released snakes at their original capture location.

We used SVL from the original capture of each rattlesnake as our measure of individual body size. In an elongate animal such as a snake, length better characterizes body size than mass, mostly because mass often varies seasonally with reproductive status and even daily with feeding (Boback and Guyer, 2003). Furthermore, sexual maturity is best determined by SVL and not age in *C. atrox* (Taylor and DeNardo, 2005). We used published information on minimum size (SVL) at sexual maturity on *C. atrox* populations in Arizona (Goldberg, 2007; Rosen and Goldberg, 2002), verified by observations of reproductive behavior at our study sites, and

Table 1

Crotalus atrox body size varied among study sites by sex. SVL = average snout–vent length in mm ± SEM, N = number of snakes captured; SSD = sexual size dimorphism index ($[(\text{mean adult male SVL})/(\text{mean adult female SVL}) - 1]$); years = range of years at study site; vegetation follows Brown (1994); SG = semidesert grassland; AU = Sonoran desertscrub Arizona upland; LCR = Sonoran desertscrub lower Colorado river; CD = Chihuahuan desertscrub; nps = managed by the National Park Service; u = undeveloped, native vegetation; gc = golf course; eu = exurban development.

Site	Female SVL (N)	Male SVL (N)	SSD	Years	Vegetation
1	836.7 ± 24.3 (26)	940.9 ± 20.3 (45)	0.12	1995–2005	SG (nps)
2	889.4 ± 21.5 (25)	1058.8 ± 30.9 (46)	0.19	1994–2005	AU (nps)
3	749.5 ± 17.2 (26)	844.3 ± 17.3 (53)	0.13	1998–1999	AU (u)
4	812.6 ± 13.3 (26)	868.9 ± 12.1 (50)	0.07	2002–2005	AU (nps)
5	842.0 ± 9.2 (46)	924.5 ± 12.3 (65)	0.10	2001–2007	AU (u)
6	823.8 ± 8.0 (67)	944.7 ± 11.2 (108)	0.15	2000–2004	AU (u)
7	851.2 ± 14.8 (37)	930.3 ± 16.3 (77)	0.09	2002–2006	AU (gc)
8	760.2 ± 9.1 (73)	837.4 ± 11.0 (123)	0.10	1987–2000	LCR (nps)
9	843.6 ± 30.2 (22)	984.4 ± 35.9 (22)	0.17	1998–1999	CD (eu)
10	875.7 ± 46.7 (7)	1029.7 ± 32.7 (37)	0.18	1985–1998	SG (u)

classified snakes 600 mm or longer in SVL as adults. Values reported for SVL are mean ± SEM.

We used the Lovich and Gibbons index (1992) to estimate SSD for each population: $SSD = (\text{mean adult male SVL})/(\text{mean adult female SVL}) - 1$. In this index, if there is no sex difference in mean body sizes, $SSD = 0$; positive index values indicate male-biased dimorphism and negative values indicate female-biased dimorphism. The Lovich and Gibbons index is intuitive and has the most favorable statistical properties of all SSD indices. For example, sex-interactions in ANOVA, or mixed models, are biased by scale effects; thus, an index is the preferred method to investigate variation in SSD among populations (Dobson and Wigginton, 1996; Smith, 1999; Stillwell et al., 2007).

2.4. Environmental data

We obtained environmental data for each study site from Daymet U.S. Data Center (available online: <http://www.daymet.org>). Daymet provides gridded estimates of environmental parameters interpolated from approximately 6000 weather stations (Thornton et al., 1997). We used all available daily surface weather data from 1980 to 2003 to estimate six variables for each study site: T_{max} = average annual maximum temperature; T_{day} = average annual mean temperature; T_{min} = average annual minimum temperature; T_{var} = average within-year variation in temperature; Precip = average annual precipitation; Precip var = average within-year variation in precipitation.

We used Quantum GIS (version 1.0.0 “Kore”; Quantum GIS Development Team, 2009) to characterize surface water availability at each site. Using digital aerial photos, we calculated the total area of natural (riparian areas) and artificial surface water (irrigation ponds and cattle tanks) at each site in hectares (“surface water”).

2.5. Statistical analyses

We used the R statistical package (R Development Core Team, 2008) for all analyses and the R package ggplot2 (Wickham, 2009) for creating graphics. First, we used ANOVA to determine whether there were differences in body sizes among study sites or between the sexes. We used the Lovich and Gibbons index (1992) to analyze SSD instead of including a sex interaction term in this case.

Next, we used principal component analysis (PCA) on the correlation matrix to reduce the number of environmental variables (labdsv package; Roberts, 2010). Most of the environmental variables were highly correlated, and PCA reduces these into fewer non-correlated variables (Everitt, 2005). We used components with eigenvalues greater than 1 to explain variation in SSD and body size (Everitt, 2005). We regressed SSD against principal component scores and used a linear mixed effects model for body size analysis (nlme package; Pinheiro et al., 2008).

Because *C. atrox* shows male-biased SSD, we examined female and male body size in separate linear mixed effects models. We used individual adult SVL for male or female *C. atrox*, principal component scores as fixed variables, and study site as a random variable (to account for potential correlation among individuals within sites and uneven sample sizes among sites; Pinheiro and Bates, 2000) in each mixed model. We examined model residuals for spatial autocorrelation with Moran’s *I* correlograms (Dormann et al., 2007; ncf package; Bjornstad, 2009).

3. Results

We captured and measured 981 adult (355 females:626 males) *C. atrox*, between 1985 and 2007 (Table 1). Body size varied

significantly by sex and study site (ANOVA: $N = 981$, $F_{10,970} = 37.7$, $p < 0.0002$). On average, site 2 had both the largest females (889.4 ± 21.5 mm) and males (1058.8 ± 30.9 mm). We found the largest individual female (1144 mm) at site 9, and the largest individual male (1438 mm) at site 10. The smallest females were from site 3 (749.5 ± 17.2 mm), and the smallest males (837.4 ± 9.1 mm) were from site 8. Overall, males were more variable in size than females: coefficient of variation was 0.12 and 0.16 for females and males, respectively.

Climate and surface water availability varied among study sites. Sites 3 and 8 were the warmest (average annual mean temperature = 24.6°C and 25.4°C , respectively) and sites 9 and 10 were the coolest (average annual mean temperature = 19.3°C and 20.7°C , respectively). Sites 2 and 9 received the most precipitation (average annual precipitation = 41.1 cm and 41.3 cm, respectively) and sites 8 and 10 received the least (average annual precipitation = 25.4 cm and 20.8 cm, respectively). Water was freely available throughout the year at site 7 via irrigation and artificial ponds at the nearby golf course (18.14 ha). Sites 1, 2, 4, and 9 contained native riparian habitats with sections of perennial water flow (3.28–85.79 ha; Sonoran riparian deciduous forest and scrubland; Brown, 1994), and also small areas of irrigation around human developments (not quantified). Site 1 additionally contained a perennial marsh (Sonoran interior marshland; Brown, 1994) and site 10 had several cattle tanks (4.73 ha). Sites 3, 5, 6, and 8 lacked naturally or artificially occurring surface water.

The first two principal components explained 87% of the environmental variation among study sites (Table 2). The first principal component (PC1, 70% variance) had positive loadings for temperature (T_{max} , T_{day} , and T_{min}) and negative loadings for water (precip, precip var, and surface water). The second principal component (PC2, 17% variance) had a high positive loading for seasonality in temperature (T_{var}) and relatively low loadings for all other variables. The remaining principal components had eigenvalues less than 1, thus we did not include them in further analyses (Everitt, 2005).

Sexual dimorphism did not vary significantly with PC1 or PC2 ($r^2 = 0.29$, $F_{2,7} = 2.87$, $p = 0.12$), but there was a strong trend toward a negative correlation between SSD and PC1 ($\beta = -0.01$, $t = -2.17$, $p = 0.07$; Fig. 2).

Body size in *C. atrox* was positively correlated with PC1, but not PC2. Adult females (PC1: $N = 355$, $\beta = -16.5 \pm 3.9$, $t = -4.2$, $df = 7$, $p = 0.004$) and adult males (PC1: $N = 626$, $\beta = -29.3 \pm 6.2$, $t = -4.7$, $df = 7$, $p = 0.002$) were smaller in areas with higher PC1 scores;

Table 2

The first two principal components accounted for 87% of the environmental variation among our study sites: PC1 had positive loadings for temperature and negative loadings for water; PC2 had a large positive loading for seasonality in temperature. Eigenvalues, loadings, and proportion of variance explained for each component are listed below. T_{max} = average annual maximum temperature; T_{day} = average annual mean temperature; T_{min} = average annual minimum temperature; T_{var} = average within-year variation in temperature; Surface water = perennial surface water area; Precip = average annual precipitation; Precip var = average within-year variation in precipitation. All environmental data were obtained from Daymet U.S. Data Center (Thornton et al., 1997): 1980–2003.

Variable	PC1	PC2
Eigenvalue	4.87	1.21
Proportion of total variance	0.70	0.17
T_{max}	0.45	0.09
T_{day}	0.44	0.13
T_{min}	0.41	0.21
T_{var}	0.09	0.86
Surface water	-0.32	0.28
Precip	-0.39	0.31
Precip var	-0.42	0.14

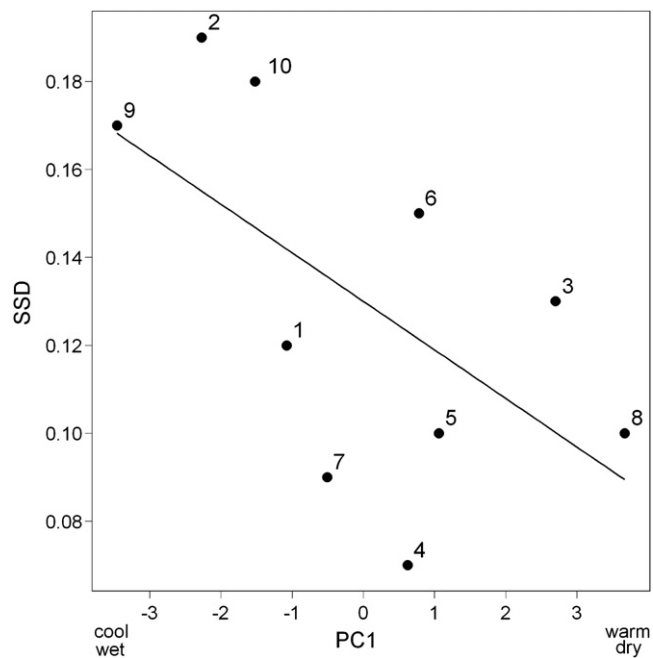


Fig. 2. There was a negative relationship, which approached statistical significance ($\beta = -0.01$, $t = -2.17$, $p = 0.07$), between sexual size dimorphism (SSD) and cooler, wetter areas (PC1) among our populations of Arizona *C. atrox*. Numbers above each point refer to site numbers in Table 1.

thus, body size in *C. atrox* was negatively related to temperature and positively to water (Fig. 3). The effect of PC1 on male body size was greater than on females (effect size = $\beta/\text{standard error}$: -4.73 males; -4.23 females). Seasonality in temperature was not correlated with male (PC2: $N = 626$, $\beta = -6.8 \pm 12.5$, $t = -0.5$, $df = 7$,

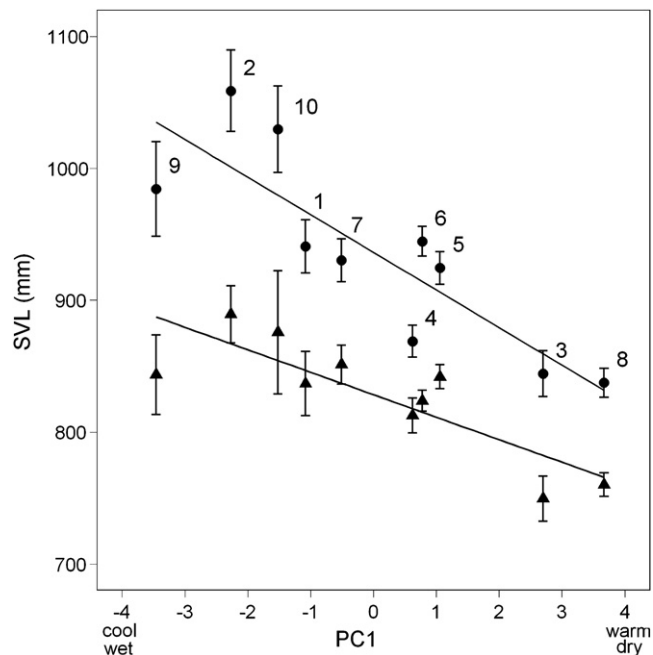


Fig. 3. Adult male and female *Crotalus atrox* are larger in body size (snout–vent length, SVL) in cooler, wetter areas. SVL is negatively correlated with PC1, which is negatively correlated with water and positively correlated with temperature. For each study site, mean male SVL \pm SEM is represented by a circle and mean female SVL \pm SEM is represented by a triangle. Numbers above each circle refer to site numbers in Table 1.

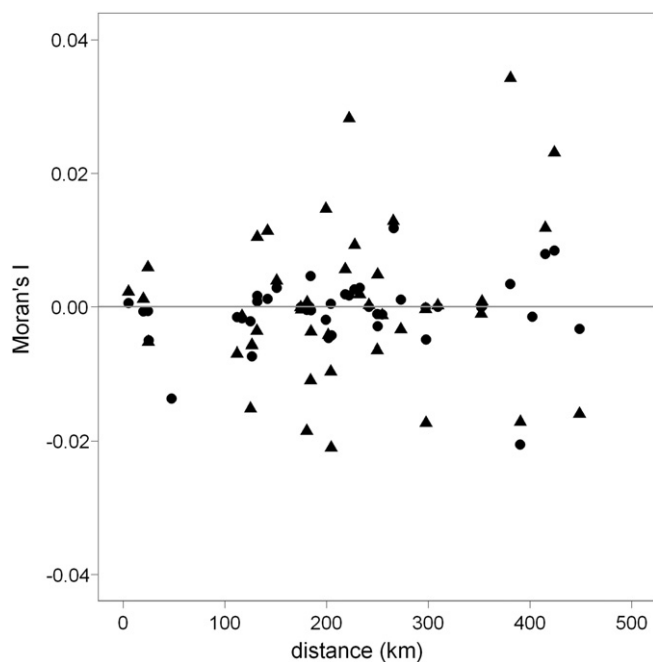


Fig. 4. In the populations of *C. atrox* we investigated, there was no spatial autocorrelation in residuals from male (triangles; Moran's $I = 1.32$, $p = 0.09$) or female (circles; Moran's $I = 1.27$, $p = 0.10$) body size mixed models.

$p = 0.6$) or female body size (PC2: $N = 355$, $\beta = 4.9 \pm 8.5$, $t = -0.6$, $df = 7$, $p = 0.6$).

We found no evidence of spatial autocorrelation for male (Moran's $I = 1.32$, $p = 0.09$) or female (Moran's $I = 1.27$, $p = 0.10$) body size data (Fig. 4).

4. Discussion and conclusions

Here, we demonstrate that *C. atrox* sampled from 10 populations located throughout Arizona are larger in body size (i.e., SVL) in cooler (i.e., lower average annual maximum, minimum, and mean temperature) and wetter areas (i.e., higher average annual precipitation, more variable precipitation, and available surface water). We found SSD to be variable among *C. atrox* populations, but this trend was not significantly correlated with temperature, seasonality, or available water. Arizona has a broad and variable physiographic structure with distinct biomes contained within a narrow latitudinal range, nearly all of which *C. atrox* inhabits. Importantly, our sampling embraced most of this habitat variation, which we assumed also varied in resource availability (e.g., prey, foraging opportunities). Furthermore, owing to the fact that adult SVL in *C. atrox* is variable among the populations we studied, these conditions provided an ideal natural experiment to investigate proximate determinants of geographic variation in body size. Our results (i) support the predictions by *Beaupre's model* (2002) related to SSD and male body size, but not female body size, and (ii) are in general agreement with previous studies of body size variation in ectothermic vertebrates (*Beaupre, 1995a; Bronikowski and Arnold, 1999; Case, 1976*).

Warmer temperatures (along with drier conditions) were associated with smaller, not larger, body sizes in *C. atrox*, in contrast to the general pattern among squamate reptiles (*Ashton and Feldman, 2003*). Likewise, *Beaupre's model* (2002) predicted that adult male rattlesnakes would be smaller in warmer areas. In the relatively warm climate of Arizona, warmer temperatures likely decreased available time to forage and may have increased body temperatures and associated maintenance costs (*Beaupre, 1995b,*

2002). Indeed, at a similarly hot and arid site, small diurnal lizards greatly restricted their activity due to high temperatures (*Grant and Dunham, 1988*). *Crotalus lepidus* (rock rattlesnake) inhabiting a warm, arid site were active less often on the surface, had lower feeding rates, and smaller body sizes than *C. lepidus* inhabiting a nearby cooler, wetter site (*Beaupre, 1995a*). It is thus possible that cooler temperatures provided more opportunities to acquire prey and resulted in increased body size in *C. atrox*, an ectothermic predator with variable growth.

More foraging opportunities do not always promote growth and larger body size in reptiles. *Sears (2005)*, for instance, found that a population of *Sceloporus graciosus* (sagebrush lizards) at low elevation, with more opportunities to forage, grew more slowly than a population at high elevation. In this case, the low elevation population was possibly exposed to greater predation risk and consequently decreased their foraging time to avoid predation (*Sears, 2005*). In contrast, adult rattlesnakes likely do not face the same predation risks as a small lizard such as *S. graciosus*; consequently, such risks may not increase with heightened activity in large-bodied rattlesnakes. In support of this view, mortality rates in some rattlesnake populations are estimated to be as low as 10% for adults (*Crotalus horridus; Brown et al., 2007*). Additionally, *C. atrox* is a cryptic, ambush forager so increased foraging activity may not make *C. atrox* more visible to predators. However, a detailed cost–benefit analysis of increased foraging opportunities in *C. atrox* will be required to test this view.

Precipitation was strongly correlated with body size in male and female *C. atrox*, which suggests that an increase in growth of snakes through bottom-up regulation (i.e., energy from food) may contribute to geographic variation in body size. In deserts, higher primary productivity, and subsequent increases in rodent abundance, results from higher precipitation (*Beatley, 1969; Brown and Ernest, 2002*). This precipitation-driven resource input could influence snake growth and therefore size through a bottom-up pattern of regulation (*Madsen and Shine, 2000; Winne et al., 2010*). *Beaupre's (2002)* model, however, predicted that only male rattlesnakes would increase in body size in resource-rich environments, because adult females allocate nearly all available resources to reproduction, thus additional food had little effect on body size. *Taylor et al. (2005)* experimentally demonstrated that diet supplementation (i.e., rodents) resulted in a significant increase in growth rates of free-living adult female *C. atrox* relative to control subjects (i.e., no supplemented diet). Our results support the findings both of *Beaupre (2002)* and *Taylor et al. (2005)* in that males and females were larger in resource-rich environments, but environmental variation had a larger effect on males than in females.

We found no effect of temperature seasonality on body size in the *C. atrox* populations we studied. Compared to ectotherms with more northern distributions, *C. atrox* experiences relatively short periods of stressful conditions (e.g., food shortages or drought; *Repp and Schuett, 2008; Stillwell et al., 2007*) in Arizona. Thus selection related to seasonality is likely not strong enough to have an effect on body size of *C. atrox* in Arizona.

Though not statistically significant, there was a negative relationship between SSD and PC1 (cooler, wetter areas; Fig. 2) among our populations of Arizona *C. atrox*. In our populations, both adult males and females were larger in resource-rich environments. Although environmental variation had a larger effect on males (-4.73) than females (-4.23), this difference was not great enough to result in a significant relationship between SSD and PC1.

Although the environmental variables we selected were strongly associated with variation in body size in our system, we did not analyze other potentially important factors in this study. Geographic variation in ectotherm body size may also result from

differential mortality (Rosen, 1991; Sears, 2005). Populations of the colubrine snake *Coluber constrictor* (eastern racer) where mortality is largely the result of environmental factors (e.g., overwintering) are larger in body size than those populations where mortality is closely tied to movement activity (e.g., predation; Rosen, 1991). Thus, when mortality is not related to activity, individuals should increase foraging and ultimately attain a larger body size (Rosen, 1991; Sears, 2005).

Differences in body size among populations in this study might be related to differences in age structure or age-related mortality instead of growth and age-specific body size. Without marking, and later recapturing, first-year snakes, it is quite difficult to gauge the exact age of wild snakes with a high level of accuracy (Beaupre, 1995a). However, growth tends to be highly plastic in snakes and influenced by environmental variation (Madsen and Shine, 2000; Taylor et al., 2005), so it is likely that the differences we observed were not related entirely to age.

In gape-limited predators, such as snakes, prey type may be as important as the amount of prey available, and thus prey type could be a potential influence on body size of adults. The diet-alteration hypothesis, for example, predicts that snakes will be larger when larger types of prey, usually mammals or birds, are available, and smaller when only small types of prey (e.g., squamates) are available (Boback, 2003; Forsman, 1991). Furthermore, some snake species appear to reduce (or even eliminate) small prey from their diet as they increase in body size, which is probably due to relative costs associated with pursuit, ingestion, and digestion of one large meal versus many smaller ones (Forsman, 1996; Nowak et al., 2008; Shine et al., 1998; but see Repp and Schuett, 2009). Thus, when only small prey are available, it is less costly to remain relatively small, but when large prey species are available, snakes are predicted to grow sufficiently large to exploit those prey sources. Although we lack information on prey type and abundance for most of our sites, the available data suggest that *C. atrox* may not follow this pattern (Nowak, 2009; Repp and Schuett, 2009; Spencer, 2003). In her examination of 561 museum specimens of *C. atrox* from across their geographic range, Spencer (2003) found no relationship between body size and type of prey (mammal, reptile, bird, or frog) consumed.

In conclusion, we found that adult male and female *C. atrox* were larger in cooler, wetter areas in Arizona. Although not statistically significant, SSD was more pronounced in cooler, wetter areas. Our results are in general agreement with predictions from Beaupre's model (2002); however, we found that female body size was positively correlated with increased resources. Likewise, free-ranging, female rattlesnakes on a supplemented diet increased in growth and reproduced more frequently (Taylor et al., 2005). Our results support the view that females allocate most of their available energy to reproduction, but allocation strategy in female rattlesnakes likely varies among populations with differing prey availability.

Acknowledgements

This research was possible through the cooperation of numerous landowners and managers (National Park Service, Stone Canyon Golf Club, Vistoso Partners, LLC.) and the hard work of many field technicians, collaborators, and volunteers: T. Baker, J. Bortle, J. Capps, C. Cochran, C. Contreras, A. Dee, D. DeNardo, S. Ehret, M. Feldner, L. Gilmore, M. Goode, H. Greene, H.-W. Herrmann, E. Landeen, A. Madara-Yagla, M. Malawy, A.J. Monatesti, E. Oakley, B. Parker, T. Richins, P. Rosenfeld, M. Santana-Bendix, J. Schofer, J. Smith, L. Smith, M. Spille, S. Stumpf, J. Walker, and staff from Montezuma Castle, Tuzigoot, and Tonto National Monuments. We would like to thank the Arizona Game and Fish Heritage Fund, Arizona State University, National Park Service, National Science Foundation

Graduate Research Fellowship (to ENT and MA), the late M. Nowak, US Geological Survey, and the Western National Parks Association for funding aspects of this project. M. Angilletta, C. Montgomery, M. Sears, J. Smith, and members of the K. Lips and M. Sears laboratories improved previous versions of this manuscript. All animal use complies with the current laws of the United States and was approved by Arizona State University, Northern Arizona University, or University of Arizona Institutional Animal Care and Use Committees; snakes were collected under Arizona Game and Fish Commission scientific collection permits issued to each author. The use of trade, firm, or corporation names in this publication is for the convenience of the reader. Such use does not constitute an official endorsement or approval by the U.S. Government of any product or service to the exclusion of others that may be suitable.

References

- Ashton, K.G., 2001. Body size variation among mainland populations of the western rattlesnake (*Crotalus viridis*). *Evolution* 55, 2523–2533.
- Ashton, K.G., Feldman, C.R., 2003. Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution* 57, 1151–1163.
- Beatley, J.C., 1969. Dependence of desert rodents on winter annuals and precipitation. *Ecology* 50, 721–724.
- Beaupre, S.J., 1995a. Comparative ecology of the mottled rock rattlesnake, *Crotalus lepidus*, in Big Bend National Park. *Herpetologica* 51, 45–56.
- Beaupre, S.J., 1995b. Effects of geographically variable thermal environment on bioenergetics of mottled rock rattlesnakes. *Ecology* 76, 1655–1665.
- Beaupre, S.J., 2002. Modeling time–energy allocation in vipers: individual responses to environmental variation and implications for populations. In: Schuett, G.W., Höggren, M., Douglas, M.E., Greene, H.W. (Eds.), *Biology of the Vipers*. Eagle Mountain Publishing, Eagle Mountain, Utah, USA, pp. 463–481.
- Beaupre, S.J., Duvall, D., O'Leile, J., 1998. Ontogenetic variation in growth and sexual size dimorphism in a central Arizona population of the western diamondback rattlesnake (*Crotalus atrox*). *Copeia* 1998, 40–47.
- Bjornstad, O.N., 2009. ncf: Spatial Nonparametric Covariance Functions. <http://CRAN.R-project.org/package=ncf>.
- Blouin-Demers, G., Prior, K.A., Weatherhead, P.J., 2002. Comparative demography of black rat snakes (*Elaphe obsoleta*) in Ontario and Maryland. *Journal of Zoology* 256, 1–10.
- Boback, S.M., 2003. Body size evolution in snakes: evidence from island populations. *Copeia* 2003, 81–94.
- Boback, S.M., Guyer, C., 2003. Empirical evidence for an optimal body size in snakes. *Evolution* 57, 345–351.
- Boyce, M.S., 1979. Seasonality and patterns of natural selection for life histories. *The American Naturalist* 114, 569–583.
- Bronikowski, A.M., Arnold, S.J., 1999. The evolutionary ecology of life history variation in the garter snake *Thamnophis elegans*. *Ecology* 80, 2314–2325.
- Brown, D.E., 1994. Biotic Communities of the Southwestern United States and Northwestern Mexico. University of Utah Press, Salt Lake City, Utah.
- Brown, J.H., Ernest, S.K.M., 2002. Rain and rodents: complex dynamics of desert consumers. *Bioscience* 52, 979–987.
- Brown, W.S., Kery, M., Hines, J.E., 2007. Survival of timber rattlesnakes (*Crotalus horridus*) estimated by capture–recapture models in relation to age, sex, color morph, time, and birthplace. *Copeia* 2007, 656–671.
- Campbell, J.A., Lamar, W.W., 2004. *The Venomous Reptiles of the Western Hemisphere*. Cornell University Press, Ithaca, New York.
- Case, T.J., 1976. Body size differences between populations of the chuckwalla, *Sauromalus obesus*. *Ecology* 57, 313–323.
- Castoe, T.A., Spencer, C.L., Parkinson, C.L., 2007. Phylogeographic structure and historical demography of the western diamondback rattlesnake (*Crotalus atrox*): a perspective on North American desert biogeography. *Molecular Phylogenetics and Evolution* 42, 193–212.
- Dobson, F.S., Wigginton, J.D., 1996. Environmental influences on the sexual dimorphism in body size of western bobcats. *Oecologia* 108, 610–616.
- Dormann, C.F., McPherson, J.M., Araujo, M.B., Bivand, R., Bolliger, J., Carl, G., Davies, R.G., Hirzel, A., Jetz, W., Kissling, W.D., Kuhn, I., Ohlemüller, R., Peres-Neto, P.R., Reineking, B., Schroder, B., Schurr, F.M., Wilson, R., 2007. Methods to account for spatial autocorrelation in the analysis of species distributional data: a review. *Ecography* 30, 609–628.
- Everitt, B.S., 2005. *An R and S-Plus® Companion to Multivariate Analysis*. Springer, London.
- Forsman, A., 1991. Variation in sexual size dimorphism and maximum body size among adder populations: effects of prey size. *The Journal of Animal Ecology* 60, 253–267.
- Forsman, A., 1996. An experimental test for food effects on head size allometry in juvenile snakes. *Evolution* 50, 2536–2542.
- Goldberg, S.R., 2007. Testicular cycle of the western diamond-backed rattlesnake, *Crotalus atrox* (Serpentes: Viperidae), from Arizona. *Bulletin of the Maryland Herpetological Society* 43, 103–107.

- Grant, B.W., Dunham, A.E., 1988. Thermally imposed time constraints on the activity of the desert lizard *Sceloporus merriami*. *Ecology* 69, 167–176.
- James, F.C., 1970. Geographic size variation in birds and its relationship to climate. *Ecology* 51, 365–390.
- Lovich, J.E., Gibbons, J.W., 1992. A review of techniques for quantifying sexual size dimorphism. *Growth Development and Aging* 56, 269–281.
- Madsen, T., Shine, R., 2000. Silver spoons and snake body sizes: prey availability early in life influences long-term growth rate of free-ranging pythons. *Journal of Animal Ecology* 69, 952–958.
- Nowak, E.M., 2009. Ecology and management of venomous reptilian predators. Unpublished Ph.D. Dissertation, Northern Arizona University, Flagstaff.
- Nowak, E.M., Theimer, T.C., Schuett, G.W., 2008. Functional and numerical responses of predators: where do vipers fit in the traditional paradigms? *Biological Reviews* 83, 601–620.
- Olalla-Tárraga, M.Á., Rodríguez, M.Á., Hawkins, B.A., 2006. Broad-scale patterns of body size in squamate reptiles of Europe and North America. *Journal of Biogeography* 33, 781–793.
- Pinheiro, J.C., Bates, D.M., 2000. *Mixed-effects Models in S and S-Plus*. Springer, New York, NY, USA.
- Pinheiro, J., Bates, D., DebRoy, S., Sarkar, D., R Development Core Team, 2008. nlme: Linear and Nonlinear Mixed Effects Models. <http://CRAN.R-project.org/package=nlme>.
- Quantum GIS Development Team, 2009. Quantum GIS Geographic Information System. Open Source Geospatial Foundation Project. <http://qgis.osgeo.org>.
- R Development Core Team, 2008. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.R-project.org>.
- Roberts, D.W., 2010. labdsv: Ordination and Multivariate Analysis for Ecology. <http://CRAN.R-project.org/package=labdsv>.
- Repp, R.A., Schuett, G.W., 2008. Western diamond-backed rattlesnakes, *Crotalus atrox* (Serpentes: Viperidae), gain water by harvesting and drinking rain, sleet, and snow. *The Southwestern Naturalist* 53, 108–114.
- Repp, R.A., Schuett, G.W., 2009. *Crotalus atrox* (western diamond-backed rattlesnake). Adult predation on lizards. *Herpetological Review* 40, 353–354.
- Rosen, P.C., 1991. Comparative ecology and life history of the racer (*Coluber constrictor*) in Michigan. *Copeia* 1991, 897–909.
- Rosen, P.C., Goldberg, S.R., 2002. Female reproduction in the western diamond-backed rattlesnake *Crotalus atrox* (Serpentes: Viperidae), from Arizona. *Texas Journal of Science* 54, 347–356.
- Sears, M.W., 2005. Geographic variation in the life history of the sagebrush lizard: the role of thermal constraints on activity. *Oecologia* 143, 25–36.
- Sears, M.W., Angilletta, M.J., 2003. Life-history variation in the sagebrush lizard: phenotypic plasticity or local adaptation? *Ecology* 84, 1624–1634.
- Shine, R., Harlow, P.S., Keogh, J.S., Boeadi, 1998. The influence of sex and body size on food habits of a giant tropical snake, *Python reticulatus*. *Functional Ecology* 12, 248–258.
- Smith, R.J., 1999. Statistics of sexual size dimorphism. *Journal of Human Evolution* 36, 423–459.
- Spencer, C.L., 2003. Geographic variation in the morphology, diet and reproduction of a widespread pitviper, the western diamondback rattlesnake (*Crotalus atrox*). Unpublished Ph.D. Dissertation, The University of Texas at Arlington.
- Spencer, C.L., 2008. Geographic variation in western diamond-backed rattlesnake (*Crotalus atrox*) morphology. In: Hayes, W.K., Beaman, K.R., Cardwell, M.D., Bush, S.P. (Eds.), *The Biology of the Rattlesnakes*. Loma Linda Press, Loma Linda, California, pp. 55–78.
- Stillwell, R.C., Morse, G.E., Fox, C.W., 2007. Geographic variation in body size and sexual size dimorphism of a seed-feeding beetle. *The American Naturalist* 170, 358–369.
- Taylor, E.N., DeNardo, D.F., 2005. Sexual size dimorphism and growth plasticity in snakes: an experiment on the western diamond-backed rattlesnake (*Crotalus atrox*). *Journal of Experimental Zoology* 303A, 598–607.
- Taylor, E.N., DeNardo, D.F., 2008. Proximate determinants of sexual size dimorphism in the western diamond-backed rattlesnakes (*Crotalus atrox*). In: Hayes, W.K., Beaman, K.R., Cardwell, M.D., Bush, S.P. (Eds.), *The Biology of Rattlesnakes*. Loma Linda Press, Loma Linda, CA, USA, pp. 91–100.
- Taylor, E.N., Malawy, M.A., Browning, D.M., Lemar, S.V., DeNardo, D.F., 2005. Effects of food supplementation on the physiological ecology of female western diamond-backed rattlesnakes (*Crotalus atrox*). *Oecologia* 144, 206–213.
- Thornton, P.E., Running, S.W., White, M.A., 1997. Generating surfaces of daily meteorological variables over large regions of complex terrain. *Journal of Hydrology* 190, 214–251.
- Wickham, H., 2009. ggplot2: An Implementation of the Grammar of Graphics. <http://had.co.nz/ggplot2>.
- Winne, C.T., Willson, J.D., Gibbons, J.W., 2010. Drought survival and reproduction impose contrasting selection pressures on maximum body size and sexual size dimorphism in a snake, *Seminatrix pygaea*. *Oecologia* 162, 913–922.