

# Geographic variation in body size and sexual size dimorphism of North American Ratsnakes (*Pantherophis* spp. s.l.)

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**Abstract:** Because body size affects nearly all facets of an organism's life history, ecologists have long been interested in large-scale patterns of body-size variation, as well as why those large-scale patterns often differ between sexes. We explored body-size variation across the range of the sexually dimorphic Ratsnake complex (species of the genus *Pantherophis* Fitzinger, 1843 s.l.; formerly *Elaphe obsoleta* (Say in James, 1823)) in North America. We specifically explored whether variation in body size followed latitudinal patterns or varied with climatic variables. We found that body size did not conform to a climatic or latitudinal gradient, but instead, some of the populations with the largest snakes occurred near the core of the geographic range and some with the smallest occurred near the northern, western, and southern peripheries of the range. Males averaged 14% larger than females, although the degree of sexual size dimorphism varied between populations (range: 2%–25%). There was a weak trend for male body size to change in relation to temperature, whereas female body size did not. Our results indicate that relationships between climate and an ectotherm's body size are more complicated than linear latitudinal clines and likely differ for males and females.

**Key words:** Bergmann's rule, body size, climatic variability, latitudinal clines, North American Ratsnake, *Pantherophis* spp., sexual dimorphism, temperature.

**Résumé :** Comme la taille du corps a une incidence sur presque toutes les facettes du cycle biologique d'un organisme, les écologistes s'intéressent depuis longtemps aux motifs de variation à grande échelle de la taille du corps, ainsi qu'aux causes des différences entre les sexes de ces motifs. Nous avons examiné les variations de la taille dans un complexe de serpents ratiers caractérisés par un dimorphisme sexuel (les espèces du genre *Pantherophis* Fitzinger, 1843 s.l.; anciennement *Elaphe obsoleta* (Say dans James, 1823)) en Amérique du Nord. Nous avons plus particulièrement examiné si les variations de la taille du corps suivaient des motifs latitudinaux ou variaient en fonction de variables climatiques. Nous avons constaté que la taille du corps ne se conforme pas à un gradient climatique ou latitudinal, mais plutôt que certaines des populations comprenant les plus grands serpents se trouvaient plus près du centre de l'aire de répartition géographique et que certaines des populations comprenant les plus petits individus étaient près des bordures nord, ouest et sud de cette aire. Les mâles sont en moyennes 14 % plus grands que les femelles, bien que le degré de dimorphisme sexuel varie d'une population à l'autre (fourchette : 2 % – 25 %). Il y a une faible tendance de la taille du corps des mâles à varier en fonction de la température, qui n'est pas observée chez les femelles. Nos résultats indiquent que les relations entre le climat et la taille du corps d'un ectotherme sont plus compliquées que de simples clines latitudinaux linéaires et sont probablement différentes pour les mâles et les femelles. [Traduit par la Rédaction]

**Mots-clés :** règle de Bergmann, taille du corps, variabilité climatique, clines latitudinaux, serpent ratier nord-américain, *Pantherophis* spp., dimorphisme sexuel, température.

## Introduction

Understanding patterns of geographical variation in body size among and within species has long been a goal of evolutionary ecology because body size affects nearly all life-history traits of an organism (Brown et al. 2004). Although well-defined patterns have been identified and explanatory hypotheses proposed, it is unclear whether any universal pattern and explanation exists. For example, in many taxa, body size increases with latitude (Bergmann

1847; Ashton 2002; Ashton and Feldman 2003), which Bergmann (1847) proposed was a result of lower surface to volume ratios providing larger individuals an energetic advantage at higher latitudes. Although this ecological “rule” has been remarkably valid for many species and taxa, it is far from uniform (Meiri and Dayan 2003; Olson et al. 2009). Among other species, the opposite pattern has been observed, with body size declining with latitude (Mousseau 1997; Ashton and Feldman 2003; Olalla-Tarraga et al. 2006). Other investigations have found that patterns in body size

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are idiosyncratic and weak (Ashton 2004) or that no geographic trends are discernable (Pincheira-Donoso and Meiri 2013).

Geographic patterns in body size of ectotherms have been particularly challenging to detect and explain. Smaller size at higher latitudes among ectotherms seems likely to be related to shorter growing seasons (Blanckenhorn et al. 2007), although that explanation might be more relevant to species that have a single growing season (e.g., most arthropods) than to those that grow over multiple years (e.g., fishes, amphibians, and reptiles). Often, the body size of ectotherms tends to vary according to particular resources rather than latitude or longitude (Amarello et al. 2010; Pincheira-Donoso and Meiri 2013; Feldman and Meiri 2014). For example, moisture is often a more powerful driver of body-size variation in organisms than latitude or temperature (James 1970; Yom-Tov and Geffen 2006; Stillwell et al. 2007). Dry environments might select for larger individuals that are more resistant to dehydration. Alternatively, body size may be correlated to primary productivity, which might be directly linked to rainfall resulting in larger individuals in wetter areas (Yom-Tov and Geffen 2006). Seasonality is also an important driver of variation in body size (Cushman et al. 1993; Arnett and Gotelli 1999; Schauble 2004; Amarello et al. 2010). Similarly, larger body size might allow individuals to cope better with especially variable climates (Meiri 2008). Particularly, it may be that larger individuals have greater starvation resistance during periods of resource scarcity (Ashton 2001). Further complicating matters is that the body size of individuals within a population may be driven by local factors such as predation or age-specific mortality (Rosen 1991), which can obscure larger geographic patterns of body size. Given the range of patterns of geographic variation in size that have been reported and the various factors that have been proposed to explain those patterns, predicting how body size might vary geographically for a particular ectothermic species is far from straightforward (Pincheira-Donoso and Meiri 2013).

Our first goal was to document body-size variation among populations of Ratsnakes (species of the genus *Pantherophis* Fitzinger, 1843 s.l.; formerly *Elaphe obsoleta* (Say in James, 1823)), one of the largest snakes in North America (maximum body length of 256 cm) that occurs from Ontario, Canada, to southern Florida and central Texas, USA (Ernst and Ernst 2003). Ashton and Feldman (2003) reported that 73% of snakes and lizards follow a reverse Bergmann's cline, with individuals from populations at lower latitudes attaining larger sizes than those at higher latitudes. However, other studies have failed to find a latitudinal trend in the body size of reptiles (Oufiero et al. 2011; Brandt and Navas 2013; Pincheira-Donoso and Meiri 2013). Ratsnakes near the northern extent of their geographic range live longer and grow more slowly than snakes in the central portion of their range (Blouin-Demers et al. 2002), although how that affects body size across the range is currently unknown. Lacking a clear basis on which to hypothesize how size should vary geographically, we explore how size varies with latitude, longitude, elevation, temperature, rainfall, and seasonality.

An additional component of geographic variation in body size involves the extent to which males and females conform to the same pattern. Any geographic change in an environmental factor that affects the body size of one sex more than the other can lead to geographic variation in the magnitude and direction of sexual size dimorphism (Teder and Tammaru 2005; Blanckenhorn et al. 2007; Stillwell et al. 2007; Howes and Loughheed 2007). Thus, our second goal was to document variation in sexual size dimorphism (SSD) across the range of Ratsnakes. SSD is widespread among snakes (Shine 1978). Most often females grow larger than males, although the reverse is true in species in which males engage in combat to attain access to reproductive females (Shine 1994). Male–male combat is well documented in Ratsnakes (Gillingham 1980) and males generally grow larger than females, with larger

males realizing a reproductive advantage (Blouin-Demers et al. 2005).

It seems likely that the extent of SSD in a population should reflect the extent to which males compete for access to reproductive females. Thus, shorter active seasons at higher latitudes might cause females to reproduce less frequently than those at lower latitudes (e.g., every other year rather than every year: Sperry and Weatherhead 2009, 2012). Assuming males are able to breed every year, less frequent reproduction by females would cause the operational sex ratio (Emlen and Oring 1977) to become male biased, thereby increasing competition among males. In this case, we hypothesize that SSD should increase with latitude. Here, we examine whether SSD and body size vary by location and with environmental factors.

## Materials and methods

### Study animals

To explore variation in the body size of Ratsnakes across their geographic range, we compiled body-size measurements from 10 Ratsnake populations, ranging from Texas and Florida in the south, to Kansas (USA) in the west, and Ontario in the north (Fig. 1). All measurements were either collected by the authors or were solicited from other researchers. For all comparisons and analyses of body size, we used snout–vent length (SVL) measured in millimetres. Although all researchers who provided data for this study also provided tail-length and body-mass measurements, we chose to include only SVL because both tail length and body mass can vary widely on account of injury (tail length) and body condition or time since last meal (mass). SVL is a standard measurement and is robust and repeatable (Blouin-Demers 2003). For analyses, we included only data from snakes greater than 800 mm SVL, as this is the smallest reported adult size (Ernst and Ernst 2003). For snakes captured multiple times, we randomly excluded all but one capture to avoid pseudoreplication. For studies that used radiotelemetry, we used the size of the snake before it was implanted with a transmitter because transmitters can affect growth (Weatherhead and Blouin-Demers 2004).

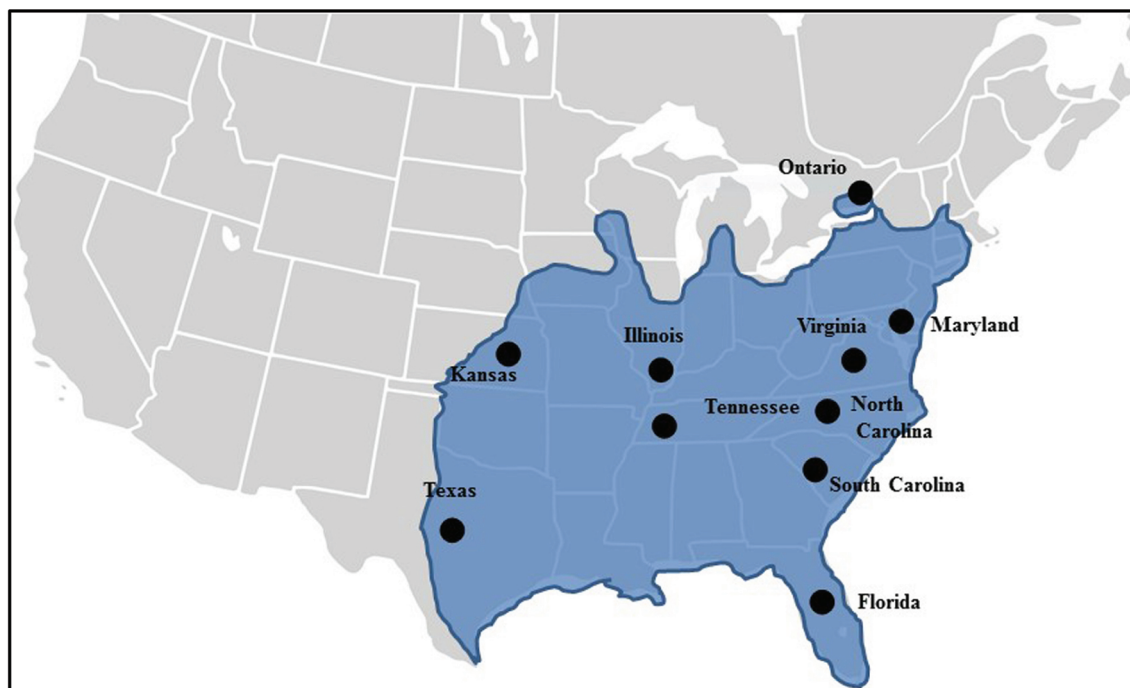
### Geographic variation in body size

To explore sex-specific geographic variation in the body size of Ratsnakes, we first compared the mean SVL of snakes from each of the 10 study populations. We were interested in understanding if the body sizes of adult Ratsnakes vary between populations, as well as within populations (i.e., sexual dimorphism). We used a factorial ANOVA to test for differences in size between males and females and among the 10 study populations, with an interaction term for location and sex. We then used Hochberg post hoc tests to make all pairwise comparisons between sexes and populations. SVL data were tested for normality and homogeneity of variance before analysis and were square root transformed to better meet the ANOVA assumptions, as this data transformation technique best satisfied the assumptions of the test. If we found evidence of geographic variation in body size of Ratsnakes, then we then explored correlations with body size and climatic and location variables.

### Influence of environmental variables on body size

To explore the relationship of population location and climate with snake body size, we used a linear mixed effect model. For each population, we used publicly available National Oceanic and Atmospheric Administration (NOAA) weather stations and Google Earth to calculate growing degree days (GDD), frost-free days (FFD), maximum annual temperature, minimum annual temperature, mean annual rainfall, latitude, longitude, and elevation. GDD represents the amount of thermal energy available in a given day and was calculated as  $[(T_{\max} + T_{\min}) / 2] - T_{\text{base}}$  (Wang 1960). We used 10 °C as  $T_{\text{base}}$  because Ratsnakes are rarely active below this temperature (Weatherhead et al. 2012). FFD provides an index of

**Fig. 1.** Geographic range of Ratsnakes (*Pantherophis* spp. s.l.) within North America (shaded region) and location of sampled populations (black dots). The northernmost location represents a disjunct population found in eastern Ontario, Canada. Ratsnake range data from Ernst and Ernst (2003) are superimposed on the base map from Lokal\_Profil (reproduced under CC BY 2.5). Color version online.



growing season length and was calculated as the number of days between the mean last frost date in the spring and the mean first frost date in the fall. We also calculated two indices of seasonal variability that have been correlated with geographic variation in body sizes of wildlife (Henderson et al. 2003; Verdú et al. 2006): annual temperature range (mean July temperature – mean January temperature) and rainfall variability (mean monthly rainfall in wettest month – mean monthly rainfall in driest month).

To reduce the number of climate variables in subsequent analyses and to avoid using highly correlated variables, we first conducted a principal components analysis (PCA). We used GDD, FFD, maximum annual temperature, minimum annual temperature, mean annual rainfall, annual temperature range, and rainfall variability as factors in the PCA. We also included latitude, longitude, and elevation of each population location in the PCA because these can be highly correlated with climatic variables. The first three principal components explained 95% of the variation in the data and we generated component scores for each component to be used in subsequent analyses (Table 1). Because all of the temperature variables and latitude loaded heavily onto the first component, PC1 can be interpreted as a temperature index, with higher scores corresponding to a warmer climate and lower latitude. PC2 comprised longitude, elevation, and precipitation range and best represents a gradient of sites from west (higher elevation, variable precipitation) to east (lower elevation, rain evenly distributed across the year). Annual temperature range, precipitation range, and elevation loaded heavily onto the third component; thus, PC3 can be interpreted as climate variability, with a higher score indicating higher annual variability in both temperature and rainfall.

We used a linear mixed effect model with Proc Mixed in SAS version 9.4 (SAS Institute Inc., Cary, North Carolina, USA) to explore the relationship between snake SVL and population location and climate data. We used the Kenward–Roger method to best account for uneven sample sizes between the populations (Kenward and Roger 1997). We used snake SVL (square root transformed) as the dependent variable and PC1, PC2, PC3, sex, and

**Table 1.** Three principal components (PC) explained 95% of variation in climate and location between our 10 Ratsnake (*Pantherophis* spp. s.l.) populations.

	PC1	PC2	PC3
Eigenvalue	6.9	1.85	0.79
Proportion of variance explained	0.69	0.19	0.08
Loading			
Latitude	–0.99	0.07	0.07
Longitude	0.71	–0.66	0.01
Elevation	0.26	0.81	–0.41
Frost-free days	0.97	–0.14	–0.08
Growing degree days	0.98	–0.07	–0.11
Temperature range	–0.87	0.44	0.13
Temperature maximum	0.97	0.15	–0.02
Temperature minimum	0.98	–0.15	–0.08
Annual precipitation	0.76	–0.36	0.40
Precipitation range	0.43	0.61	0.64

**Note:** PC1 had substantial loadings of latitude, frost-free days, growing degree days, temperature range, temperature maximum, and temperature minimum. PC2 had large loadings for longitude, elevation, and precipitation range. PC3 was primarily loaded with precipitation range, annual precipitation, and elevation. Table 1 shows the eigenvalues, proportion of variance explained, and loadings for each component.

interaction terms between sex and each of the principal components as fixed factors. We used population location as a random effect to account for autocorrelation of snake body size within each population.

#### Sexual size dimorphism

To explore the magnitude and direction of SSD, we calculated an index of sexual size dimorphism (SSDI) for each population based on the methods described by Lovich and Gibbons (1992). We calculated SSDI as  $(-\text{mean size of males} / \text{mean size of females}) + 1$ . The value is negative if males are larger than females and positive if females are larger than males. To avoid bias associated with variable sample sizes among populations, we included only the

**Table 2.** Sample sizes, sex ratios, mean and maximum snout–vent length (SVL), and sexual size dimorphism index of Ratsnakes (*Pantherophis* spp. s.l.) collected from 10 populations within their geographic range.

	Total no. of captures	No. of adult males	No. of adult females	Male SVL (mm)		Female SVL (mm)		Sexual size dimorphism index: 5%
				Mean	Maximum	Mean	Maximum	
Florida	106	48	23	1128	1545	990	1455	−0.18
Texas	210	59	50	1145	1555	1093	1340	−0.10
South Carolina	388	75	65	1259	1900	1175	2207	−0.02
Tennessee	40	23	13	1208	1485	1175	1380	−0.08
North Carolina	246	73	82	1172	1790	1096	1500	−0.15
Virginia	22	13	7	1338	1590	1145	1345	−0.25
Maryland	208	61	38	1208	1593	1187	1385	−0.15
Kansas	512	149	102	1139	1945	1078	1370	−0.22
Illinois	228	55	47	1238	1706	1143	1504	−0.16
Ontario	4459	748	655	1091	1624	1040	1475	−0.10

**Note:** Total number (no.) of captures include juveniles, recaptures, and snakes that had missing measurement or sex data. The no. of adult males and no. of adult females excludes recaptures, records with missing data, and all snakes below 800 mm SVL (the smallest reported adult size). Populations are listed by latitude from lowest (Florida, USA) to highest (Ontario, Canada).

largest 5% of captured females and the largest 5% of captured males from each population when calculating SSDI. Fitch (1981) demonstrated that for a variety of reptiles using the body sizes of the largest 5 or 10 individuals to calculate SSDI was a reliable approximation of the population mean. An additional benefit of including only the largest snakes encountered at each location is that we excluded data from small adults that are still growing and generated a more accurate indication of how large snakes in each population grow (i.e., maxima). Although we limited our calculation to the 5% of largest snakes captured at each location, the minimum number of snakes that we included for SSDI calculation for each site was five individuals of each sex. To then explore the relationships between location and climate factors with SSDI, we used multiple regression analyses (Proc Reg) regressing SSDI with the factors PC1, PC2, and PC3.

## Results

### Geographic variation in body size

In total, we collected SVL measurements from 6479 individual Ratsnakes from 10 populations across the geographic range of the species. The number of individuals measured from each population ranged from 22 (Virginia) to 4459 (Ontario), with a mean of 219 SVL measurements per population. After excluding recaptures and juvenile snakes, we included SVL measurements from 2386 adult Ratsnakes in subsequent analyses (Table 2).

A factorial ANOVA indicated that SVL (square root transformed) varied among populations ( $F_{[9,20]} = 28.29$ ,  $P < 0.01$ ). Populations with the largest snakes were located near the center of the range of the species (Fig. 2). For instance, snakes in Ontario (northernmost site) were, on average, smaller ( $P < 0.04$ ) than snakes from every population sampled with the exception of Florida, the southernmost site. Snakes from the Florida population were, on average, smaller than snakes from all other populations except Ontario ( $P \geq 0.99$ ), Texas ( $P = 0.98$ ), and Kansas (the westernmost population;  $P > 0.99$ ). Conversely, individuals from populations in the central portion of the species' range including Maryland, Virginia, Illinois, and South Carolina contained the largest individuals that were sampled (Fig. 2).

### Influence of environmental variables on body size

Body size of Ratsnakes was strongly correlated with sex ( $F_{[1,2383]} = 80.34$ ,  $P < 0.001$ ,  $\beta = -0.46$ ), with males being larger than females in all populations. The interaction term between PC1 and sex was also statistically significant ( $F_{[1,2383]} = 4.23$ ,  $P = 0.039$ ,  $\beta = -0.041$ ), indicating that body size of males and females responded to PC1 differently. Male SVL increased at a higher rate with increasing PC1 values than female SVL (Fig. 3), indicating that male SVL increases more markedly with decreasing latitude and in-

creasing temperature than female SVL. We found no relationship between body size and PC1 ( $F_{[1,5,63]} = 0.06$ ,  $P = 0.817$ ,  $\beta = -0.031$ ), PC2 ( $F_{[1,5,7]} = 0.79$ ,  $P = 0.41$ ,  $\beta = -0.013$ ), PC3 ( $F_{[1,5,91]} = 1.15$ ,  $P = 0.032$ ,  $\beta = -0.063$ ), or between the interaction terms sex and PC2 ( $F_{[1,2383]} = 2.0$ ,  $P = 0.158$ ,  $\beta = 0.055$ ), or sex and PC3 ( $F_{[1,2384]} = 1.05$ ,  $P = 0.307$ ,  $\beta = -0.061$ ).

### Sexual size dimorphism

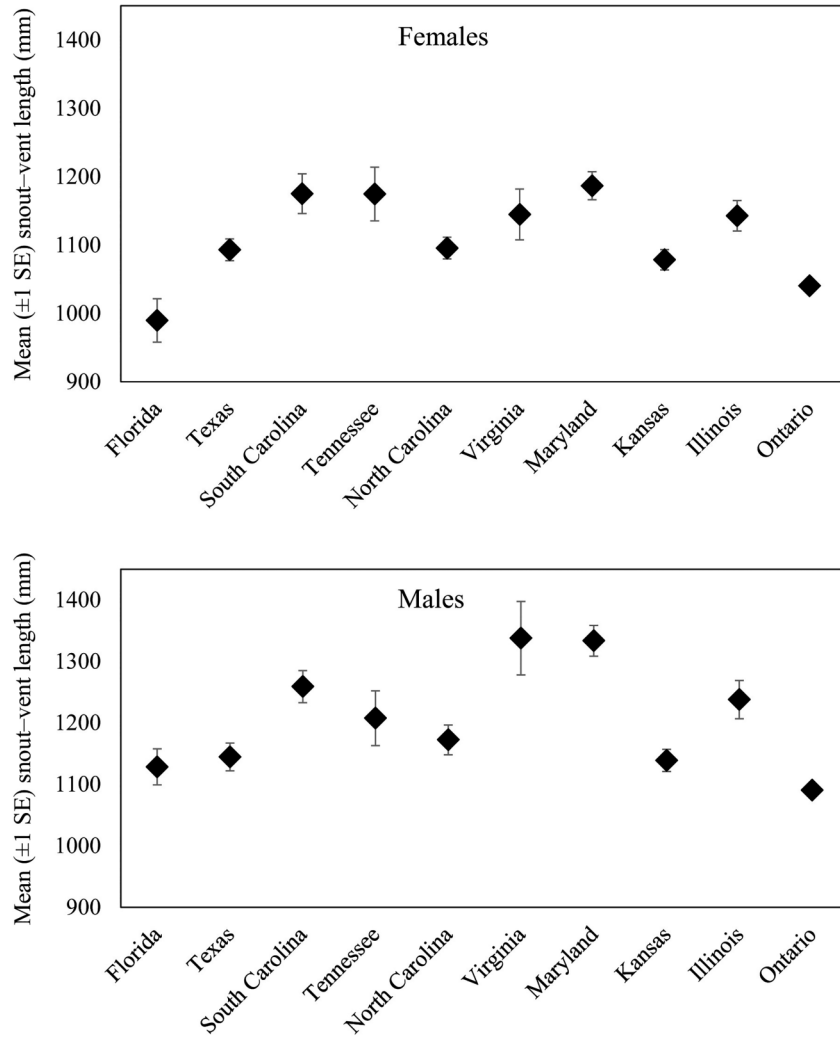
Mean SVL of Ratsnakes varied between the sexes ( $F_{[1,20]} = 27.12$ ,  $P < 0.01$ ). Within populations, males were always longer than females, with males averaging  $1136 \pm 199$  mm (mean  $\pm$  1 SD) and females averaging  $1069 \pm 149$  mm. There was also a significant interaction between sex and population location ( $F_{[9,20]} = 1.86$ ,  $P < 0.04$ ), indicating that degree of sexual dimorphism varied geographically (Table 2). Male Ratsnakes were, on average, 14% larger than females. The SSDI ranged from 22% to 25% in Kansas and Virginia to only 2% in South Carolina (Fig. 4). Virginia might be biased by small sample sizes, but Kansas and South Carolina have large samples (512 and 388 individuals, respectively) collected over many years. We did not detect any relationship between SSDI and any of the principal components representing latitude and temperature, longitude, or seasonality ( $P > 0.25$ ).

## Discussion

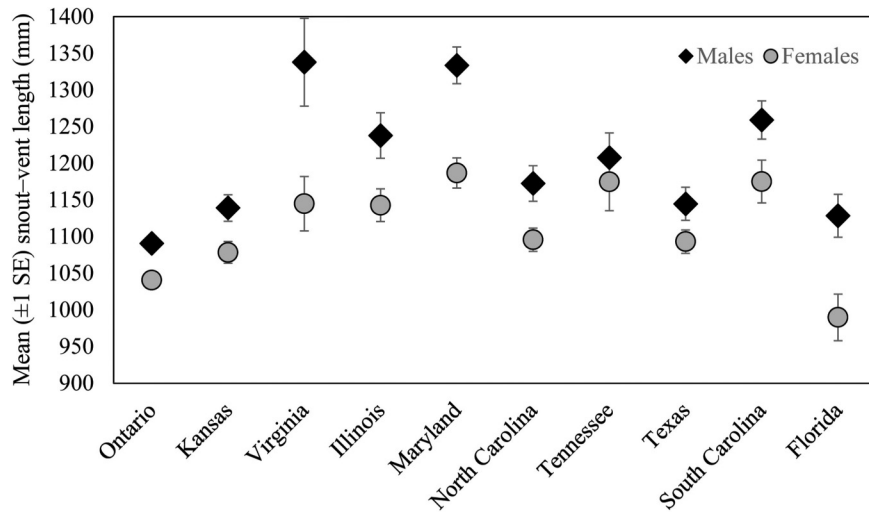
We found that the size of Ratsnakes varied geographically, but we found no evidence of a latitudinal cline in body size for Ratsnakes, unlike what has been reported for many other species of snakes and lizards (Ashton and Feldman 2003). Larger ectotherm body size at lower latitudes is generally attributed to the longer growing seasons that allow animals to grow for longer periods of the year (Blanckenhorn et al. 2007). For Ratsnakes, growing season length is related to growth rates (Blouin-Demers et al. 2002), but not apparently to overall size of individuals within the population, potentially because individuals from populations where growth is slow also live longer (Blouin-Demers et al. 2002). We found no relationship between the body size of Ratsnakes and the principal component that contained GDD and FFD, two indices of growing season length that have previously been correlated to body size of other species (Henderson et al. 2003; Verdú et al. 2006).

Our results indicate that the body size of Ratsnakes is not directly related to broad location (latitude, longitude, or elevation) or climatic (temperature, precipitation, seasonality) factors. In fact, some of the populations with the largest snakes (Maryland, Tennessee, Virginia, South Carolina) occurred near the center of the species' geographic range (Fig. 2), while some with the smallest occurred near the periphery of the geographic range in the north (Ontario), west (Kansas), and south (Florida and Texas). We

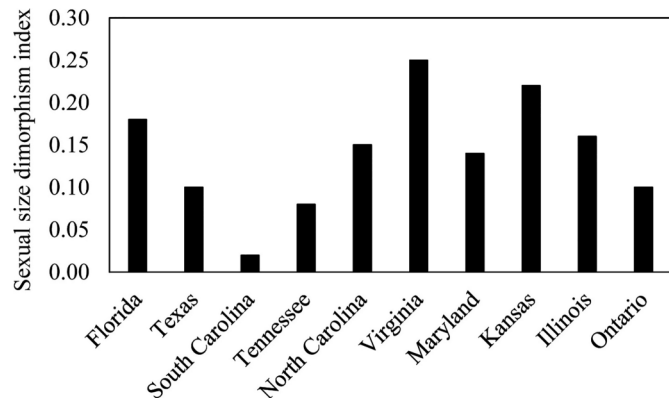
**Fig. 2.** Mean ( $\pm 1$  SE) snout-vent length (mm) of female and male Ratsnakes (*Pantherophis* spp. s.l.) from 10 populations across North America. Populations are arranged by increasing latitude.



**Fig. 3.** Mean ( $\pm 1$  SE) snout-vent length (mm) of female and male Ratsnakes (*Pantherophis* spp. s.l.) from 10 populations across North America arranged in order from coolest to warmest (determined by the first principal component). Analyses indicated that male body size changed more rapidly in response to this variable than female body size.



**Fig. 4.** Sexual size dimorphism index of Ratsnakes (*Pantherophis* spp. s.l.) across 10 populations in North America. Populations are arranged from highest to lowest latitude.



should note, however, that this pattern was not ubiquitous: snakes in North Carolina were relatively small. Whereas researchers have long acknowledged that a species should be most abundant near the geographic center of its distribution (i.e., the abundant center hypothesis; Brown 1984), we are unaware of trends in body size of an organism conforming to a similar pattern. Our results indicate that environmental conditions near the center of a species' range might provide optimal conditions for growth relative to those at the periphery. However, many snakes apparently show larger body size at lower latitudes (Ashton and Feldman 2003), indicating that extended annual growing seasons might offset more rapid growth at range centers.

The direction of SSD reported here (i.e., males being larger than females) corresponds with the prediction that male-male combat drives SSD in snakes. Because Ratsnakes engage in combat (Gillingham 1980) and because larger males are more successful at siring young (Blouin-Demers et al. 2005), we should expect males to attain larger body sizes than females (Shine 1978, 1994). However, we found that the magnitude of SSD varied considerably across populations (males being 2%–25% larger than females). We predicted that SSD would increase with latitude because Ratsnakes at northern locations may only reproduce every 2–3 years (Weatherhead et al. 2012), whereas those in southern locations may breed annually (B.A. DeGregorio, personal observation). If females at northern locales only reproduce every 2–3 years, then the operational sex ratio would be male biased, thereby increasing competition among males for access to females, which would favor larger males. However, we found no evidence supporting this trend nor did we find support for SSD varying with temperature or precipitation. Similar to patterns in overall ectotherm body size, the factors responsible for the observed geographic variation are likely operating on finer spatial scales related to particular resources or resource allocation differences between the sexes and cannot be detected in coarse investigations using broad climatic variables (Amarello et al. 2010; Pincheira-Donoso and Meiri 2013; Feldman and Meiri 2014).

Although we uncovered a pattern of geographic body-size variation in Ratsnakes, this pattern does not conform to previous hypotheses proposed to explain the latitudinal variation in reptile body size (e.g., Ashton 2002). Instead, the pattern conforms to recent studies that suggest that variation in body size is driven by local resources that are difficult to quantify (Amarello et al. 2010; Pincheira-Donoso and Meiri 2013; Feldman and Meiri 2014). It is likely that local effects such as differences in age-specific mortality between populations or differences in prey availability might account for much of the variation in body size between populations (Rosen 1991). For Ratsnakes, some of the largest mean body sizes occurred in populations near the center of the species' geo-

graphic range and some of the smallest occurred near the periphery of the geographic range. A logical extension of our study would be to measure resource availability (i.e., prey availability) for each of the studied populations to potentially better explain the observed pattern of body-size variation, although it is unclear whether snakes exhibit strong density dependence (Halliday and Blouin-Demers 2016). Similarly, better documenting the reproductive cycles of females in each population, the density of snakes of each population, and the influence of resource availability on reproduction would allow us to gain a better understanding of what mechanisms cause the trends in SSD that we observed.

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