

# Climate shapes patterns of sexual size and shape dimorphism across the native range of the green anole lizard, *Anolis carolinensis* (Squamata: Dactyloidae)

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Geographical variation in sexual size dimorphism (SSD) can result from the combined effects of environmental and sexual selection. To understand the determinants of SSD across geographical landscapes, we tested for relationships between SSD and climatic variables in the widespread lizard *Anolis carolinensis*. To distinguish alternative hypotheses for observed patterns of variation in SSD, we also examined sex-specific patterns of body size evolution and asked whether SSD was associated with certain patterns of sexual shape dimorphism. We found strong evidence for Rensch's rule (an increase in male-biased SSD with average body size) in *A. carolinensis* and evidence for the reversed version of Bergmann's rule (an increase in body size towards warmer environments) in males. Across populations, SSD was positively related to temperature; however, female body size was not related to any climatic variable, suggesting that the latitudinal gradient of SSD might be driven by a gradient in the intensity of sexual selection acting on males. Sexual size dimorphism was positively correlated with sexual dimorphism in head shape and negatively correlated with limb length dimorphism, suggesting that sexual selection in males might drive the evolution of SSD and that differences in size and limb shape between sexes might represent alternative strategies to avoid competition for the same resources.

**ADDITIONAL KEYWORDS:** Bergmann's rule – body size – climatic gradient – dimorphism – Rensch's rule – shape.

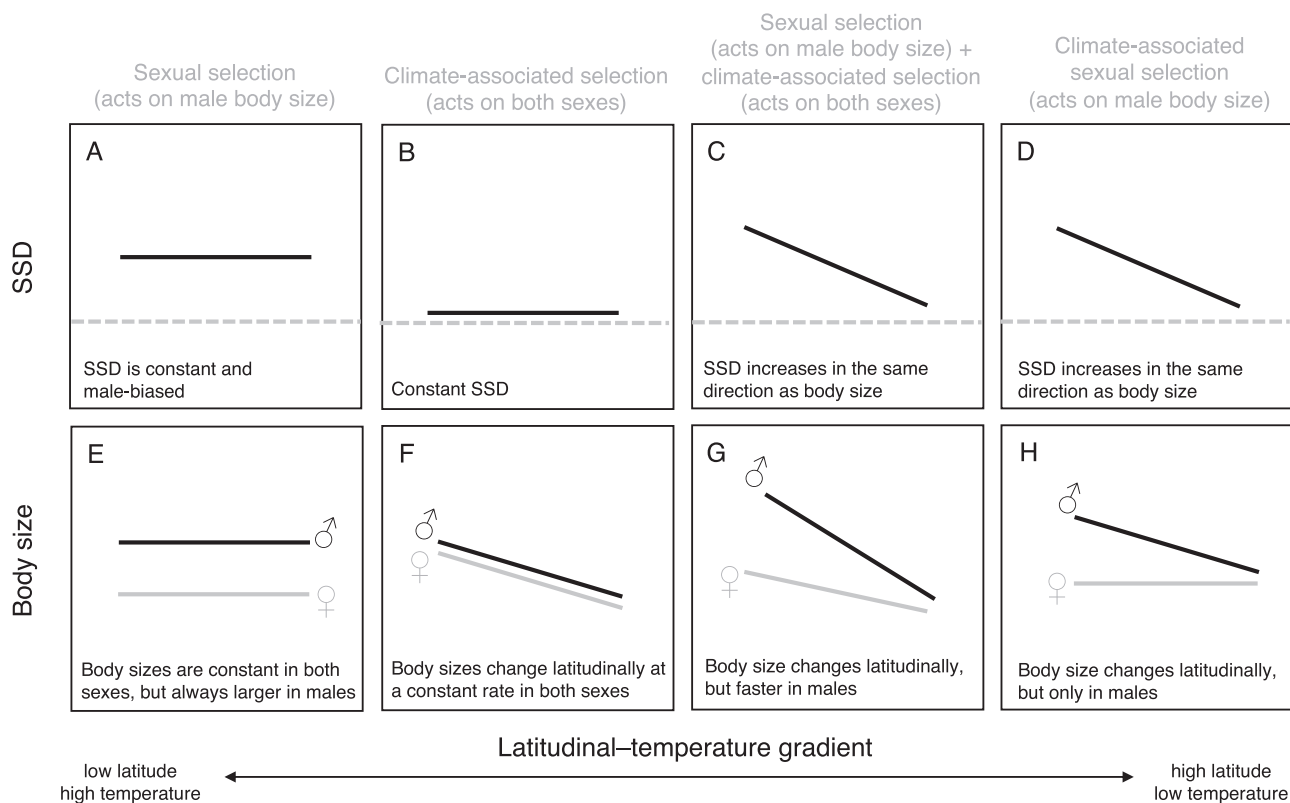
## INTRODUCTION

Sexual dimorphism occurs when males and females of a species differ in body size [i.e. sexual size dimorphism (SSD); Fig. 1A, E] or other aspects of the phenotype. Darwin first related the prevalence of male-biased SSD to sexual selection (Darwin, 1874), because large sizes seemed to confer reproductive benefits to males by enhancing performance in intrasexual competition, a mechanism that has since been confirmed in many systems (Fairbairn *et al.*, 2007). A common trend in sexual dimorphism is Rensch's rule, which describes a pattern wherein the ratio of male size to female size increases with the body size of the species (Rensch, 1950, 1959; Meiri & Liang, 2021). Rensch's rule patterns could emerge if males experience strong sexual selection for increased combat performance,

simultaneously driving the evolution of both large male size (assuming size and performance are positively correlated) and increased SSD (assuming females do not experience similar selection) (Zeng, 1988; Fairbairn, 1997; De Lisle & Rowe, 2013). Ultimately, the evolution of male and female size underlies SSD and Rensch's rule patterns, so any factors directing or constraining the evolution of body size might, in turn, influence the evolution of these patterns.

Given its central importance to ecology and physiology (Calder, 1984), body size is expected to be under strong environmental selection. Such selection, which need not align with sexual selection, has been suggested to drive large-scale ecological and evolutionary patterns. One such pattern, Bergmann's rule, describes a geographical gradient in body size in which, within a group of related species or populations, those with larger sizes are found in colder climates (e.g. at higher latitudes or elevations; Bergmann, 1847; Meiri, 2011). The proposed selective

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**Figure 1.** Four scenarios for the evolution of sexual size dimorphism (SSD; top row) and body size (bottom row) under sexual and/or climatic selection. In the top row, dashed grey lines represent size monomorphism (i.e.  $SSD = 0$ ), and continuous black lines represent predicted trends in SSD (y-axis) across a latitude or temperature gradient (x-axis). In the bottom row, continuous grey and black lines represent corresponding body size values for females and males, respectively, across the same gradient. A, E, under sexual selection alone, SSD should be constant and male-biased across latitudes (A), because the relative ratio of male-to-female body size is also expected to be constant (E). B, alternatively, if sexual selection is absent, but the environment imposes selection on body size across a climatic gradient, SSD is not expected to evolve across the climate gradient, because the latter does not impose sex-specific selection pressures. F, however, body size in both sexes should evolve in a similar manner across the gradient, depicted here following the reversed Bergmann's rule. C, if sexual selection for large males and climatic selection for small size in cool climates (i.e. reversed Bergmann's rule) occur simultaneously, SSD should decrease at cooler latitudes, resulting in a latitudinal version of Rensch's rule. G, this is because while both male and female body size evolve in the same direction owing to climatic selection, and sexual selection favours large males everywhere, the effects of sexual selection on males are increasingly balanced by climatic selection for smaller males at cooler latitudes. D, H, if the only selection pressure affecting body size is latitudinally varying sexual selection (e.g. selection for larger males at lower latitudes), SSD should increase in the direction of body size increase, again resulting in a latitudinal version of Rensch's rule (D); in this case, however, as long as the sexes can respond independently to selection, only male body size should vary across the climatic gradient (H).

mechanism driving this pattern, which was originally described in endotherms, stems from the heat-conservation hypothesis, which states that better heat conservation is achieved at larger sizes because of an allometric decrease in the surface area-to-volume ratio. Since its postulation, Bergmann's rule has been confirmed for many groups of endotherms (e.g. Ashton *et al.*, 2000; Ashton, 2002; Meiri & Dayan, 2003; Blackburn & Hawkins, 2004). However, given the same heat-conservation principle, ectotherms are expected to follow a reversed version of Bergmann's

rule (henceforth, 'reversed Bergmann's rule'; Fig. 1B, F) because the need to gain heat from external sources must be balanced against any benefits of volume-associated heat conservation, and consequently, the surface area-to-volume ratio should be increased at higher latitudes and in colder climates (Stevenson, 1985). In support of this hypothesis, several studies have identified the reversed Bergmann's rule in ectotherms, such as salamanders (Olalla-Tárraga & Rodríguez, 2007) and squamates (Ashton & Feldman, 2003).

If a species simultaneously experiences natural selection on body size following Bergmann's rule or its opposite and sexual selection consistent with Rensch's rule (i.e. selection for larger male size), an interesting possibility emerges: if SSD is driven by size-associated sexual selection, as expected based on the mechanisms proposed for Rensch's rule, we would expect the magnitude of SSD to decrease geographically in the same direction as an environmentally driven decrease in size (e.g. towards cooler regions in taxa that follow the reversed pattern of Bergmann's rule; Fig. 1C, G; Blanckenhorn *et al.*, 2006). Furthermore, if SSD is driven by sexual selection on males, any such environmentally mediated change in SSD should be primarily attributable to the evolution of the male phenotype rather than the female one (assuming the sexes respond independently to selection), but body size in both sexes would be expected to exhibit a relationship with climate (Fig. 1G).

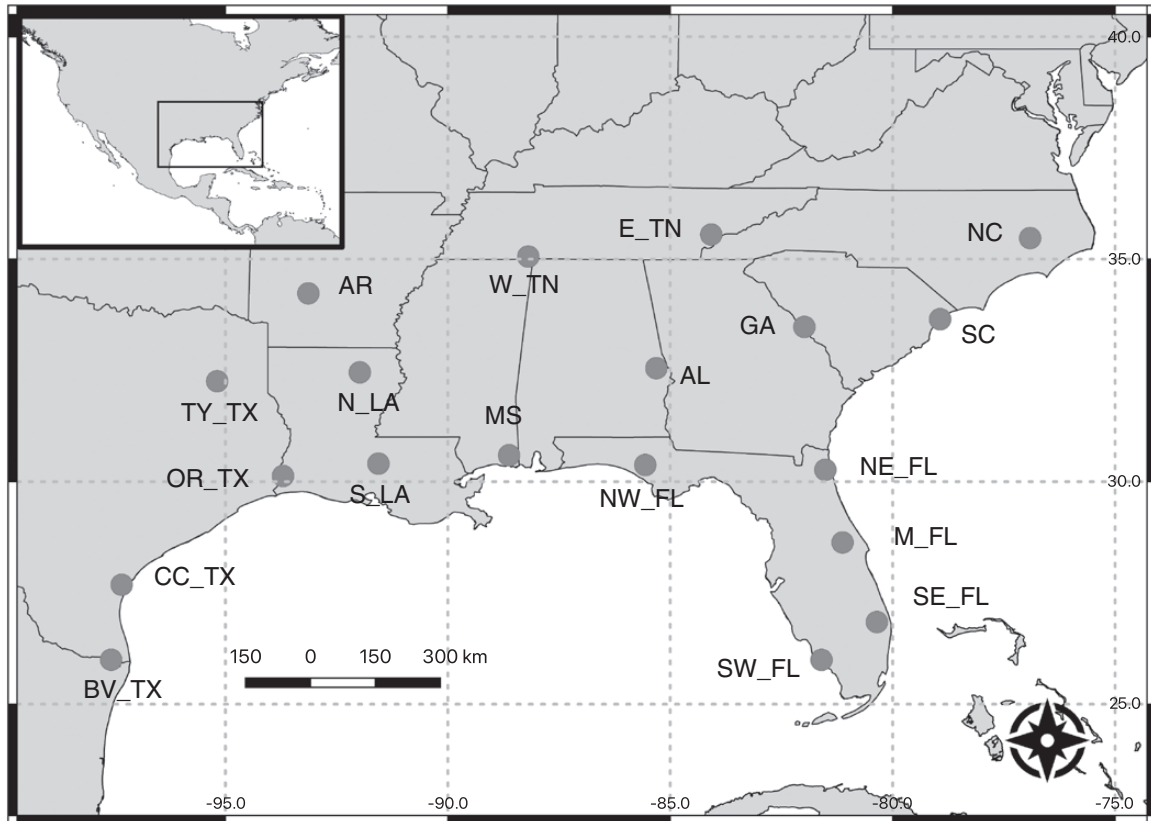
Alternatively, sexual selection itself might be variable across latitudes, resulting in latitudinal patterns of SSD, without any role of ecological selection on body size (Fig. 1D, H). This might occur if, for example, factors influencing competition for mates, such as abundance or territoriality, exhibit latitudinal trends, as has been proposed for many groups (Schemske *et al.*, 2009; Machado *et al.*, 2016). In this case, SSD would, of course, be related to climate (Fig. 1D), but this relationship would be expected to arise from climate-associated effects of selection for increased male (but not female) body size (Fig. 1H). Indeed, Tarr *et al.* (2019) found a latitudinal gradient of SSD in Central and North American lizards, in which species with higher levels of SSD were found at lower latitudes and in warmer environments. This pattern was driven by latitudinal variation in male body size, as expected if sexual selection for large body size in males is stronger in aseasonal environments owing to the long-term benefits of defending territories or mates from rivals when reproduction occurs continuously throughout the year (Machado *et al.*, 2016).

Despite the potential for both climatic selection and sexual selection to influence the evolution of SSD patterns across geographical gradients, these factors are seldom considered together in comparative studies (but for a pioneering example, see Blanckenhorn *et al.*, 2006). Here, we study the green anole (*Anolis carolinensis*), a widespread lizard species, to investigate whether Rensch's rule and the reversed Bergmann's rule combine to shape intraspecific patterns of sexual dimorphism. Green anoles occur across 11 states in the south-eastern USA (Fig. 2), spanning ~22° longitude and 10° latitude (Minesky, 1999) and occurring in climatically varied environments (Campbell-Staton *et al.*, 2016). They exhibit male-biased SSD, and males compete for territories that overlap those of females,

thereby securing opportunities to mate (Jenssen *et al.*, 1995, 2000; Jenssen & Nunez, 1998). In *A. carolinensis*, body size has been shown to vary across latitudes (Goodman *et al.*, 2013) and to be positively correlated with attributes favoured by sexual selection, such as bite strength, locomotor performance, dominance and territory size (reviewed by Lailvaux *et al.*, 2004). In this context, the widespread geographical distribution of *A. carolinensis* and its reported variability in body sizes across populations present an exceptional opportunity to test how environmental gradients might affect sexual dimorphism at the intraspecific level.

In this study, we investigate whether intraspecific patterns of SSD are consistent with conflicting pressures of sexual and ecological selection on body size (Fig. 1C, G) or with an environmental gradient of sexual selection (Fig. 1D, H). We first test for Rensch's rule among populations of *A. carolinensis*. Second, we investigate whether SSD is related to climate and whether this hypothetical relationship can be explained by sex differences in the relationship between climate and body size. We expect populations of *A. carolinensis* to follow Rensch's rule, indicating an effect of sexual selection on male body size, and we also expect SSD to increase towards warmer, low-latitude regions, as predicted under both a reversed Bergmann's rule and a scenario in which sexual selection is more intense in warmer climates. If there is a latitudinal conflict between ecological and sexual selection on male body size, we expect male and female body size to be positively related to temperature (following the reversed Bergmann's rule, as expected in squamates), with male body sizes being more variable because of sexual selection (Fig. 1G). However, if only male body size is related to temperature, this would suggest that the relationship between SSD and climate is attributable primarily to sexual selection on male body size (Fig. 1H).

It can be challenging to disentangle the effects of alternative evolutionary mechanisms solely by studying evolutionary patterns, even when such mechanisms make distinctive predictions (e.g. Fig. 1). Such efforts will be more powerful if it is possible to test for signatures of mechanisms of interest in more than one type of data. Thus, to complement our analyses of body size dimorphism, we also quantified sexual dimorphism in several dimensions of morphological shape that are predicted to covary with size in distinctive ways if subjected to environmental or sexual selection gradients. Specifically, we use a recently developed analytical technique (Adams *et al.*, 2020) to quantify shape dimorphism in traits for which dimorphism is thought predominantly (although not exclusively) to reflect sexual selection (head shape; Olsson *et al.*, 2002; Lappin *et al.*, 2006),



**Figure 2.** Geographical locations of sampled populations of *Anolis carolinensis*. For details about particular localities, see Goodman *et al.* (2013: supplemental materials).

fecundity selection (pelvis and body shape; Olsson *et al.*, 2002; Kratochvíl *et al.*, 2003) and ecological selection (hindlimbs; Butler *et al.*, 2007), then asked whether patterns of size and shape dimorphism were concordant or discordant. We expected SSD and head shape dimorphism to increase together along a climatic gradient of sexual selection, assuming that sexual selection simultaneously selects for larger body size and relatively larger head size in males and that evolution is not constrained for either trait (e.g. Fig. 1D, H; Vitt & Cooper, 1985). Alternatively, if the evolution of large size is environmentally constrained (e.g. Fig. 1C, G), head shape dimorphism and SSD could exhibit a negative relationship, because head dimorphism might represent an alternative way to increase reproductive success for size-limited males. Given that *A. carolinensis* exhibits male-biased (and not female-biased) SSD and that its sexual dimorphism is thus unlikely to derive from fecundity selection (Cox *et al.*, 2007), we expected no relationship between SSD and dimorphism in traits related to fecundity. Finally, sexual differences in relative limb dimensions might facilitate resource partitioning in much the same way that SSD might, because sexes with different sizes and/or relative limb lengths

should be able to use different microhabitats or other scarce resources (Schoener, 1967; Butler, 2007; Butler *et al.*, 2007). If these two measures of dimorphism represent alternative strategies to decrease ecological intraspecific competition, we would expect them to be related negatively.

## MATERIAL AND METHODS

### MORPHOLOGICAL DATA

We collected 29–42 adult lizards from each of 19 populations of *A. carolinensis* throughout the southeastern USA in May–June of 2006 and 2007 (Fig. 2; Supporting Information, Table S1; see Goodman *et al.*, 2013). Collection sites included natural and human-modified habitats. Sites were limited to areas in which there were no major artificial water sources, because moisture levels during incubation can affect hatching size and subsequent growth rates (Du & Shine, 2008; Robbins & Warner, 2010). Lizards were measured for snout–vent length (SVL, to 0.5 cm) within 48 h of collection. Afterwards, they were euthanized via inhalation of isoflurane and preserved in 10% formalin. Only individuals > 80% of the maximum

individual SVL found within each population and sex group were considered in the present study (in a preliminary examination, we determined that this threshold confidently excludes subadult specimens; data not shown).

In the laboratory, preserved lizards were taped to a flat piece of plastic to standardize body position and X-rayed dorsally in a HP Faxitron 43805N machine with a metal standard in each exposure. The X-rays were scanned and converted to digital images. From these images, the following measurements were taken by K.S.T. using IMAGEJ software: head length; head width; pelvis width; humerus, radius, femur and tibia length; and inter-limb distance. Additionally, the following measurements were taken from the specimens by R.M.G. using digital callipers: head height; pelvis height; and pectoral height. The values for all morphological traits were ln-transformed, and averages for each trait were calculated for males and females for each population. An index of SSD was also calculated for each population as ln(average male SVL/average female SVL).

To define morphological shape, we assumed strict geometrical definitions of size and shape such that two populations show the same average morphological shape if their individuals show, on average, the same proportions (Mosimann, 1970; Klingenberg, 2016). To this end, we first defined size as the geometric mean of all traits except SVL (i.e. the mean of ln-transformed trait values; Mosimann, 1970). Then, we subtracted this new size variable from each ln-transformed trait, which resulted in a vector of shape variables (note that the resulting shape variable might contain negative values). We repeated this process to obtain shape variables for each sex within each population.

We removed two populations (SW\_FL and BV\_TX in the paper by Goodman *et al.*, 2013) from all analyses because data for only one or two females were available for them. Also, for our main analyses, we removed two additional Florida populations (SE\_FL and M\_FL; henceforth, ‘Florida populations’) because individuals from these populations had particularly small body sizes and because these populations were the only two that did not (or in the case of M\_FL, potentially did not; see Tollis *et al.*, 2012) fall within the widespread clade of *Anolis* that is distributed from the Gulf Coast to North Carolina (Campbell-Staton *et al.*, 2012; Tollis *et al.*, 2012). We show results from our analyses including those two populations in the Supporting Information.

#### INDICES OF SEXUAL SHAPE DIMORPHISM

We estimated indices of sexual shape dimorphism (SSHD) for several suites of traits for each population, following the methodology described by Adams *et*

*al.* (2020). This technique involves the calculation of a distance-based index of multivariate shape dimorphism that can include several morphological traits. This index was calculated using the following expression:

$$\text{SSHD} = \sqrt{\sum_{i=1}^p \{[\ln(Y_{i,M}) - \text{size}_M] - [\ln(Y_{i,F}) - \text{size}_F]\}^2}$$

Here, SSHD is a measure of multivariate morphological distance between sexes,  $p$  is the number of traits,  $Y_i$  is the value of the  $i$ th morphological trait,  $\text{size}_M$  and  $\text{size}_F$  are the new size variables described in the previous section for males and females within each population, and  $[\ln(Y_{i,M}) - \text{size}_M]$  and  $[\ln(Y_{i,F}) - \text{size}_F]$  represent the size-corrected shape variables of males and females for a given trait, also as described in the previous section (for details, see Adams *et al.*, 2020).

Traits fulfilling different functions can show distinct patterns of sexual dimorphism (Braña, 1996; Olsson *et al.*, 2002; Schwarzkopf, 2005). For that reason, we grouped the shape variables into three categories and calculated SSHD indices for each separately. The first group included the three head traits: head length, head width and head height. We grouped these traits because the head is the main weapon that male lizards use in intrasexual combat, and its dimensions are thus expected to show sexual dimorphism (Vitt & Cooper, 1985; Lailvaux *et al.*, 2004). We termed the obtained SSHD index  $\text{SSHD}_{\text{head}}$ . The second group included pelvis width, pelvis height and the distance between fore- and hindlimbs. These traits are known to be proportionally larger in females as a consequence of fecundity selection (Olsson *et al.*, 2002; Frydlová *et al.*, 2011; Pincheira-Donoso & Hunt, 2017); therefore, we expected dimorphism in these traits to evolve in similar directions. In this case, the resulting SSHD index was termed  $\text{SSHD}_{\text{pelvis}}$ . Finally, the third group included femur and tibia lengths. We calculated a SSHD index based on these traits ( $\text{SSHD}_{\text{h-limbs}}$ ) because hindlimbs are known to have implications for locomotion and habitat use in anoles that have been shown to be divergent between sexes (e.g. Schoener, 1967; Butler & Losos, 2002).

Given that the SSHD indices return only positive values, such that male- and female-biased dimorphism is indistinguishable, we assigned positive signs to the SSHD indices when the sum of the size-corrected trait values of males was larger than that of females and negative signs when the opposite was true (e.g. Adams *et al.*, 2020).

#### CLIMATIC DATA

Climatic data were downloaded from the National Oceanic and Atmospheric Administration’s Global

Surface Summary of Day database (<http://www.ncdc.noaa.gov>; National Climatic Data Center, Asheville, NC, USA) for a 20-year period (1986–2006 and 1987–2007 for populations collected in 2006 and 2007, respectively). Weather data were taken from weather stations closest to a collection site. GPS locations for weather stations are reported by [Goodman \*et al.\* \(2013\)](#). For each month within a year, the lowest recorded temperature, total precipitation, and monthly averages of daily mean, maximum, minimum and dewpoint temperatures were calculated. These variables were then used to calculate the following historical estimates: average of lowest recorded temperature and total precipitation in each year (averaged among years); average of mean, maximum, minimum and dewpoint temperatures (calculated first among months within years, then among years); average of within-year variance of maximum, minimum and dewpoint temperatures (calculated first among months within years, then among years); and average of within-year variance in total precipitation (from averaging total precipitation among years).

Climatic data were summarized by conducting a principal components analysis (PCA) on the correlation matrix of the 11 climatic variables. The first two principal components (PCs) explained 95% of the variability in the data. Principal component 1 represented a ‘temperature’ axis (henceforth,  $PC1_{\text{climate}}$ ), where positive values were related to higher temperatures and lower temperature variability ([Table 1](#)). Principal component 2 (henceforth,  $PC2_{\text{climate}}$ ) was related strongly and positively to total precipitation and within-year variance in precipitation ([Table 1](#)). The value of  $PC1_{\text{climate}}$  was strongly and negatively correlated with latitude ( $r = -0.96$ ). We retained the scores of each population along these two PC axes for further analyses.

**Table 1.** Loadings for the two first principal components ( $PC1_{\text{climate}}$  and  $PC2_{\text{climate}}$ ) from a principal components analysis performed on climatic variables

Variable	PC1	PC2
Average of temperature	0.33	-0.12
Average of dewpoint temperature	0.33	0.01
Average of maximum temperature	0.33	-0.06
Average of minimum temperature	0.32	-0.16
Average of total precipitation	0.04	0.75
Average of lowest recorded temperature	0.33	-0.11
Average of within-year variance in temperature	-0.33	-0.01
Average of within-year variance in dewpoint temperature	-0.33	-0.03
Average of within-year variance in maximum temperature	-0.32	0.07
Average of within-year variance in minimum temperature	-0.33	-0.03
Average of within-year variance in total precipitation	0.18	0.61

## RENSCH’S RULE

We tested for Rensch’s rule, which states that SSD increases with body size when males are the larger sex but decreases with body size when the opposite is true ([Rensch, 1950](#); [Meiri & Liang, 2021](#)), by evaluating patterns of SSD allometry among populations of *A. carolinensis*. The rule was originally proposed for interspecific comparisons, given the presence of the pattern among higher taxonomic levels ([Fairbairn, 1997](#)), but has also been tested intraspecifically ([Fairbairn & Preziosi, 1994](#); [Blanckenhorn \*et al.\*, 2006](#); [Liao \*et al.\*, 2015](#)).

We calculated the slope of an ordinary least squares (OLS) regression of  $\ln(\text{average female SVL})$  on  $\ln(\text{average male SVL})$  for all populations, where the null hypothesis states that the slope is isometric ( $b = 1$ ; i.e. as female size increases, there is a proportional increase in male size). In this case, a slope lower than one (male size increases allometrically relative to female size) would support the presence of Rensch’s rule, indicating that greater evolutionary change in male body size, as expected under sexual selection, could be driving SSD patterns. We chose to use an OLS regression rather than a reduced major axis regression, as is common in studies of allometry ([Fairbairn, 1997](#)), because OLS slopes should provide more reliable estimations of scaling relationships between traits and better describe the variation of a trait relative to size ([Kilmer & Rodríguez, 2017](#); see also discussion by [Liang \*et al.\*, 2022](#)). We used the R package *lmodel2* ([Legendre & Oksanen, 2018](#)) to conduct OLS regressions and obtain 95% confidence intervals for the slopes.

## SEXUAL DIMORPHISM, SIZE AND CLIMATE

To test whether SSD varied as a function of climate, we regressed SSD on each of the first two climate

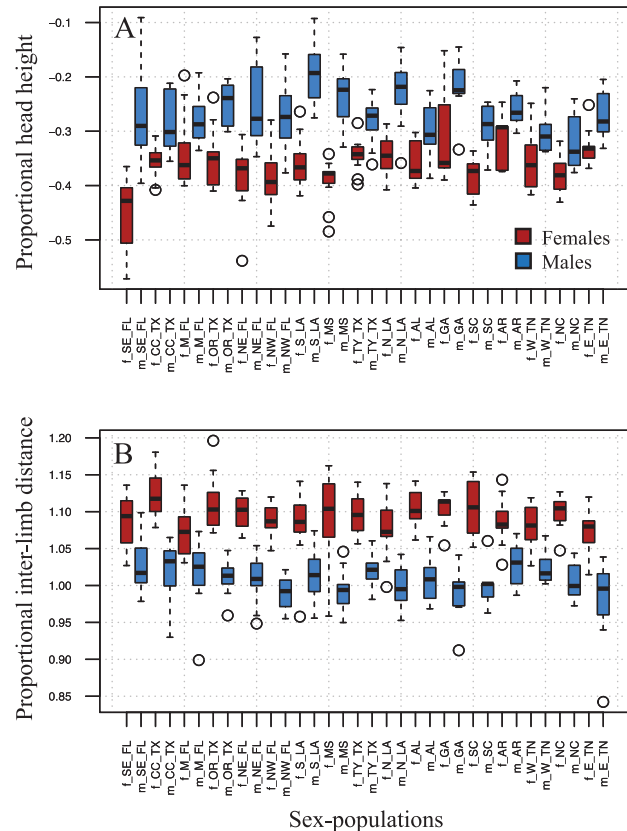
PCs ( $PC1_{\text{climate}}$  and  $PC2_{\text{climate}}$ ). Then, to examine whether the observed patterns in SSD resulted from changes primarily in males or in females, we regressed body size on each of the climate PCs for each sex independently. Additionally, we performed analyses of covariance (ANCOVA) of size on each climatic variable, with sex as a covariate (e.g.  $\text{size} \sim PC1_{\text{climate}} \times \text{sex}$ ), to test for differences in slope between sexes in the size–climate relationship within a single model. A positive relationship between SSD and  $PC1_{\text{climate}}$ , with males showing a steeper positive relationship between size and  $PC1_{\text{climate}}$  compared with females, would suggest that climatic gradients of SSD are driven by conflict between sexual and ecological selection at latitudes where smaller body sizes are selected ecologically. Alternatively, the lack of a relationship between  $PC1_{\text{climate}}$  and female body size would suggest that climatic patterns of SSD variation are driven by latitudinal changes in the intensity of sexual selection. We also performed a linear regression between population-level average body size (mean of male and female sizes) and  $PC1_{\text{climate}}$  to test for a reversed Bergmann's rule. Finally, we performed pairwise regressions between each of the SSHD indices and SSD to test whether each of these measures of shape dimorphism is related to size dimorphism.

## RESULTS

The average SVL for *A. carolinensis* in this study was 60.94 mm for males and 52.97 mm for females. Males and females from south-eastern Florida (SE\_FL) showed, on average, the smallest sizes for each sex among populations (51.88 and 44.50 mm, respectively), whereas males and females from south-eastern Texas (OR\_TX) showed the largest average sizes for each sex (70.53 and 58.00 mm, respectively) (Supporting Information, Table S1). Males were always larger than females within individual populations when considering both SVL and geometric size as measures of overall size (Supporting Information, Fig. S1). For body proportions, males showed proportionally larger heads than females (Fig. 3A), whereas females showed proportionally larger pelvic dimensions and proportionally longer inter-limb distances (Fig. 3B). The sexes did not differ consistently in other traits (Supporting Information, Fig. S1).

### RENSCH'S RULE

The linear relationship between female and male size among populations revealed a strong pattern of male-divergent allometry that was significantly different

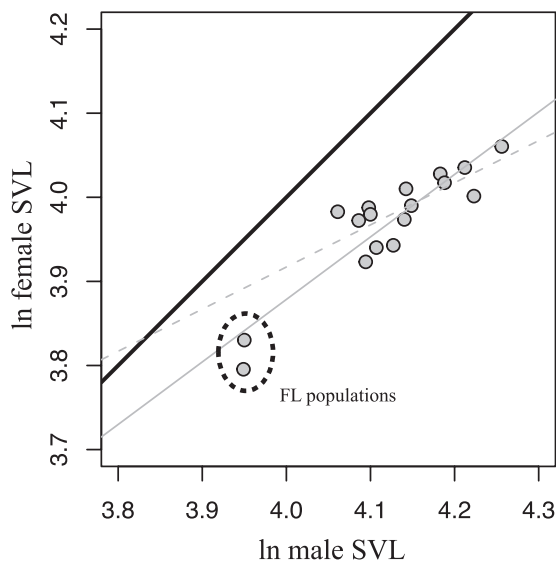


**Figure 3.** Sexual shape dimorphism in *Anolis carolinensis*. The boxplots show values of relative head height (A) and relative inter-limb distance (B) for each sex within each population. Males show proportionally higher heads but shorter inter-limb distances when compared with females, as expected under sexual and fecundity selection. Populations are shown in increasing latitudinal order (higher latitudes to the right), preceded by 'f' for females and 'm' for males. Boxplots are shown in red for females and in blue for males.

from isometry ( $b = 0.50$ , 95% confidence interval = 0.25–0.76; Fig. 4). When including the Florida populations, the linear relationship still showed a significant pattern of male-divergent allometry ( $b = 0.74$ , 95% confidence interval = 0.55–0.93; Fig. 4).

### SEXUAL DIMORPHISM, SIZE AND CLIMATE

We found a significant positive relationship between SSD and  $PC1_{\text{climate}}$  (Fig. 5A), but no relationship between SSD and  $PC2_{\text{climate}}$  (Fig. 5B). The individual regressions showed that male size was significantly and positively related to  $PC1_{\text{climate}}$  (Fig. 5C), but no relationship was found for female size (Fig. 5C). No relationships between size and PC2 were detected for either of the sexes (Fig. 5D). The results of the ANCOVA indicated that males had larger sizes



**Figure 4.** The allometry of sexual size dimorphism (SSD) in populations of *Anolis carolinensis*. Each point represents a population. The continuous black line represents a 1:1 relationship ( $b = 1$ ), the grey continuous line represents the slope of an ordinary least squares regression that considers all populations, and the dashed grey line represents the slope of an ordinary least squares regression that does not consider Florida populations (encircled in the figure).

than females for a given value of  $PC1_{\text{climate}}$  ( $t = 9.68$ ,  $P < 0.001$ ). However, they also indicated that size was not significantly related to  $PC1_{\text{climate}}$  ( $t = 1.03$ ,  $P = 0.312$ ) and that the slope of this relationship was not different between sexes ( $t = 1.22$ ,  $P = 0.233$ ). The results of analyses including all populations can be found in the [Supporting Information \(Fig. S2\)](#). We found a positive but non-significant increase in average body size with temperature ( $R^2 = 0.25$ ,  $t = 2.09$ ,  $P = 0.057$ ), providing weak support for the reversed Bergmann's rule in *A. carolinensis*.

For the indices of SSHD, we found a positive and significant relationship between  $SSHD_{\text{head}}$  and SSD ( $t = 2.27$ ,  $P = 0.041$ ; [Fig. 6A](#)), no discernible relationship between  $SSHD_{\text{pelvis}}$  and SSD ([Fig. 6B](#)), and a negative and significant relationship between  $SSHD_{\text{h-limbs}}$  and SSD ( $t = -2.45$ ,  $P = 0.029$ ; [Fig. 6C](#)). The results of analyses including all populations can be found in the [Supporting Information \(Fig. S3\)](#).

## DISCUSSION

### *ANOLIS CAROLINENSIS* FOLLOWS RENSCH'S RULE AND (WEAKLY) REVERSES BERGMANN'S RULE

Like most anoles ([Fitch & Hillis, 1984](#); [Stamps \*et al.\*, 1997](#)), *A. carolinensis* showed male-biased SSD in all

populations, with SSD ratios (male size/female size) ranging from 1.08 to 1.25. These values fall close to the average SSD ratios found among Greater Antilles anoles and are higher than for most anole species found in mainland habitats, but lower than for most anole species found on small islands (median SSD for Greater Antilles anoles = 1.16; mainland anoles = 1.03; small island anoles = 1.32; [Siliceo-Cantero \*et al.\*, 2016](#)). Our results indicated a trend of male-divergent allometry (i.e. a slope less than one, reflecting greater phenotypic variation in males) in *A. carolinensis*, which is concordant with Rensch's rule ([Fig. 4](#)). A pattern of male-divergent allometry has been suggested to arise as a consequence of stronger selection on male body sizes, which is predicted under a model of sexual selection (e.g. [Székely \*et al.\*, 2004](#); [Dale \*et al.\*, 2007](#)).

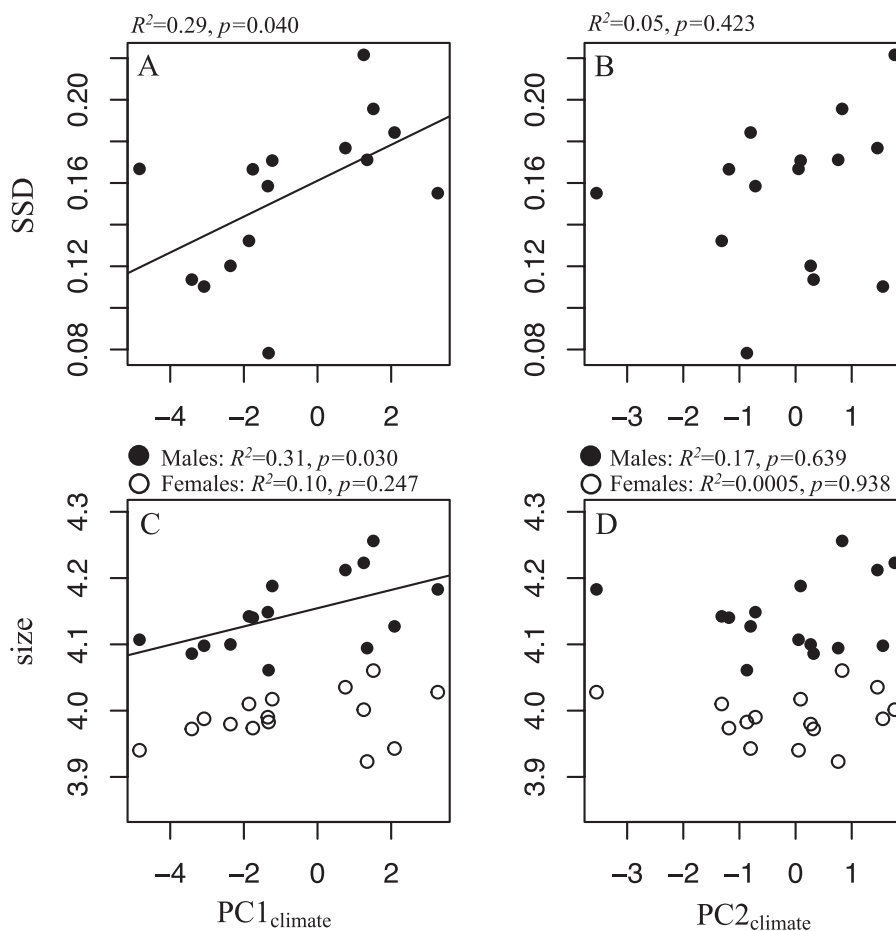
Our results show that populations of *A. carolinensis* exhibit a weak (i.e. non-significant) trend consistent with the reversed Bergmann's rule. Bergmann's rule states that vertebrates from cool climates tend to be larger than close relatives from warmer ones ([Bergmann, 1847](#)). However, it has been shown that squamates usually invert this rule, probably because of the lower thermoregulatory efficiency of large body sizes in ectotherms ([Ashton & Feldman, 2003](#)). Although we show such a reversed pattern of Bergmann's rule among populations of *A. carolinensis* (albeit non-significantly;  $P = 0.057$ ), this pattern seems to be driven only by the association between male body size and temperature, because female body size is not related to climate. This suggests that the reversed Bergmann's rule might not, in this case, be attributable to a direct effect of climate on body size.

### THE EFFECT OF CLIMATE ON SEXUAL SIZE DIMORPHISM

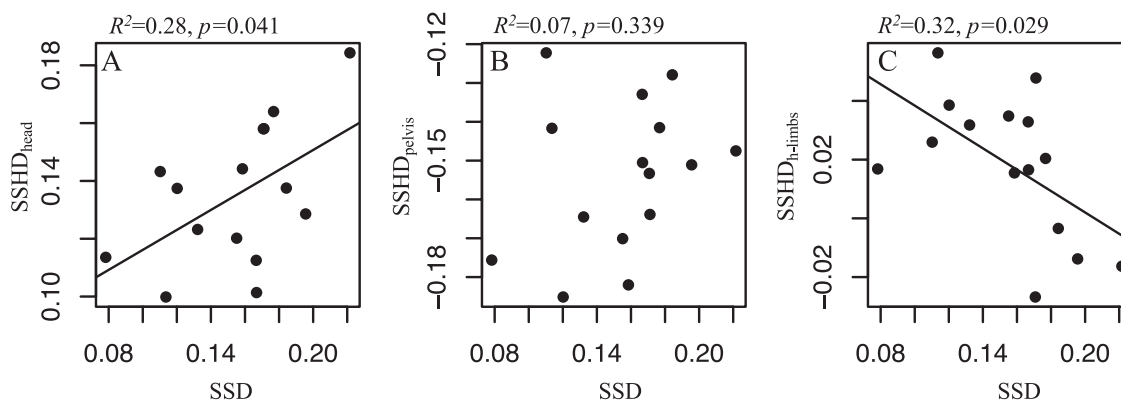
Our results showed that SSD was positively related to temperature ([Fig. 5A](#)) and again suggest that this relationship is driven by variation in male sizes, which were larger in populations that experience higher temperatures and which were more variable than female sizes across the observed temperature gradient ([Fig. 5C](#)). We found no relationship between female body size and temperature ([Fig. 5C](#)), which suggests that the positive relationship between SSD and temperature, in addition to the reversed Bergmann's rule pattern described in the previous section, are likely to be driven primarily by sexual selection acting on male body size.

These results are consistent with the findings of previous studies. For example, [Blanckenhorn \*et al.\* \(2006\)](#) showed that, across a variety of taxonomic groups, many species exhibited latitudinal versions of Rensch's rule as a result of males and females





**Figure 5.** Relationships between: (A) sexual size dimorphism (SSD) and principal component 1 (PC1<sub>climate</sub>; temperature); (B) SSD and PC2<sub>climate</sub> (precipitation); (C) size and PC1<sub>climate</sub>; and (D) size and PC2<sub>climate</sub>. Each data point represents a population. In C and D, filled and open circles represent males and females, respectively. Results from linear regressions between each pair of variables (and for each sex in C and D) are shown at the top of each panel. SSD =  $\ln(\text{average male snout-vent length}/\text{average female snout-vent length})$ . Continuous lines represent significant fitted models.



**Figure 6.** Relationships between each of the sexual shape dimorphism (SSHD) indices and sexual size dimorphism (SSD). Results from linear regressions between each pair are shown at the top of each panel. SSD =  $\ln(\text{average male snout-vent length}/\text{average female snout-vent length})$ . Continuous lines represent significant fitted models.

showing different latitudinal gradients of body size. However, they did not differentiate between a scenario in which males and females respond in different ways to environmental factors and one in which only one sex responds to a gradient of selection (e.g. sexual selection). Populations of *A. carolinensis* appear to illustrate the second scenario. This pattern is also consistent with results of the study by Tarr *et al.* (2019), who found a latitudinal gradient of SSD in Central and North American lizard species driven by a higher variability in male body sizes, but found no relationship between female body size and temperature, suggesting that the former pattern is mainly attributable to a gradient of sexual selection on male body size. Tarr *et al.* (2019) had originally hypothesized that a latitudinal gradient of SSD could arise as a result of latitudinal changes in the relative intensity of sexual and fecundity selection, as proposed by the ‘reproductive selection hypothesis’. This hypothesis predicts that the limited breeding periods found in seasonal environments should result in females producing larger clutches and/or hatchlings, such that reproductive output is maximized during the short breeding season (Shine, 1988; Olsson *et al.*, 2002; Pincheira-Donoso & Tregenza, 2011). In this context, female-biased SSD is expected to evolve at higher latitudes. Conversely, as reproduction becomes more frequent throughout the year in aseasonal environments (Meiri *et al.*, 2012), males are expected to evolve large body sizes, given the greater benefits of the long-term control of mates, potentially resulting in male-biased SSD at lower latitudes (Machado *et al.*, 2016). Examining body size, Tarr *et al.* (2019) found evidence consistent with sexual selection, but not fecundity or ecological selection, causing latitudinal gradients of SSD. Our results are broadly concordant with those of Tarr *et al.* (2019), suggesting that patterns of SSD in *A. carolinensis* could be arising as a consequence of climate-associated sexual selection on male body size.

#### PATTERNS OF SEXUAL SHAPE DIMORPHISM

Morphological shape data can be a rich source of information about organismal function (Wainwright & Reilly, 1994); as such, they have the potential to shed additional light onto the causes of SSD patterns (Adams *et al.*, 2020). Shape has been a surprisingly little-studied aspect of sexual dimorphism in anoles, although it is often acknowledged that males and females occupy partly non-overlapping regions of morphological space (Butler & Losos, 2002; Butler *et al.*, 2007; Stuart *et al.*, 2021). In populations of *A. carolinensis*, SSD is correlated with sexual dimorphism in certain shape variables, and these relationships shed light on the likely mechanisms underlying observed patterns of SSD.

Head shape dimorphism (SSHD<sub>head</sub>) was positively related to SSD. This result supports a scenario in which, in the absence of climatic constraints on size (Fig. 1D, H), SSD and head dimorphism evolve in the same direction under the effect of a climatic gradient of sexual selection. This results in the most size-dimorphic populations also showing the most proportionally dimorphic heads. Several previous studies have demonstrated that dimorphism in intrasexually selected weapons (e.g. head size in lizards) can evolve in parallel to SSD (e.g. through positive allometry in males; Vitt & Cooper, 1985; Kodric-Brown *et al.*, 2006; Bonduriansky, 2007). In contrast, other studies have shown how shape dimorphism in sexually selected characters can also evolve in the absence of SSD (e.g. Schwarzkopf, 2005; Gienger & Beck, 2007), potentially representing an alternative strategy to increase reproductive output when the evolution of size is constrained. In *A. carolinensis*, populations with low SSD also have low levels of SSHD<sub>head</sub>, suggesting that both dimorphic patterns are likely to be attributable to those populations experiencing low degrees of sexual selection.

As we had expected for a species with male-biased SSD, pelvic shape dimorphism (SSHD<sub>pelvis</sub>) was not related to SSD. Our results showed no evidence for any pattern of climate-dependent fecundity selection on female body size (e.g. as predicted if female-biased SSD evolves at latitudes where reproduction is time limited; Shine, 1988; Olsson *et al.*, 2002; Pincheira-Donoso & Tregenza, 2011). In contrast, our data support the idea that SSD in *A. carolinensis* is a consequence mainly of sexual selection on male body size. Nonetheless, fecundity-related morphology might be constrained regardless of the effect of fecundity selection on size. For example, Michaud & Echternacht (1995) studied several populations of *A. carolinensis*, describing how egg size and pelvic width increased with female mass. They noted how egg size seemed to be constrained in some populations relative to pelvic width, in accordance with a ‘pelvic constraint model’, in which optimal egg size might not be obtainable in some populations owing to a constraint imposed by the pelvic girdle aperture (Congdon & Gibbons, 1987). In addition to this apparent anatomical constraint, the morphologies of fecundity-related traits, including the pelvic girdle and inter-limb length, are also important for many aspects of locomotion and habitat use in *Anolis* and other lizard groups (e.g. Melville & Swain, 2000; Tinius *et al.*, 2018), and those activities might also constrain their evolution. Based on our results and those of previous studies, it might be that the evolution of fecundity-related traits is highly constrained. If true, the proportional dimensions in these traits in females relative to males would not exceed certain limits, regardless of the variation in

fecundity selection across latitudes (e.g. Congdon & Gibbons, 1987).

Dimorphism in hindlimb length ( $SSH_{h-limbs}$ ) was negatively related to SSD. Males showed proportionally longer hindlimbs than females in populations with low levels of size dimorphism, but only small differences between sexes were observed in populations with higher SSD. The *Anolis* radiation is particularly well known for the tight links between limb morphology and microhabitat use that have evolved independently across several of its lineages (Losos, 2009). Famously, the evolution of different limb morphologies as a consequence of the use of different microhabitats is not restricted to the species level in *Anolis*, but has also been observed at the intraspecific level, and even between sexes in several species, including *A. carolinensis* (e.g. Jenssen & Nunez, 1998; Irschick *et al.*, 2005). In this context, the negative relationship between  $SSH_{h-limbs}$  and SSD, ranging from low SSD and high male-biased limb length dimorphism to high SSD and modest female-biased limb length dimorphism, could, in theory, be driven by a decreasing level of resource overlap between sexes as differences in size increase (Schoener, 1967). In other words, differences in relative limb dimensions and differences in size could reflect alternative ecomorphological strategies for habitat partitioning between sexes (although this would not explain why limb dimorphism becomes slightly female biased, as opposed to simply monomorphic, with high SSD). Although longer limbs can be sexually selected in males, because they could increase the ability of males to guard territories, fight or display (Husak *et al.*, 2006; Losos, 2009), the negative relationship between  $SSH_{h-limbs}$  and SSD suggests that sexual selection is not a significant factor behind the evolution of limb dimorphism in *A. carolinensis*. Future studies that include quantification of habitat use and performance tests for males and females will be needed across populations to test directly how  $SSH_{h-limbs}$  relates to such functions.

In the present study, we have shown how sexual size dimorphism is associated with climate and several measures of shape dimorphism in populations of *A. carolinensis*. We have shown how populations of this species follow Rensch's rule and, at least on the surface, seem to reverse Bergmann's rule. We have also shown how patterns of SSD arise as a consequence of males and females showing different latitudinal gradients of body size. However, our results suggest that the latitudinal patterns of SSD and reversed Bergmann's rule observed across populations might be explained entirely by a latitudinal gradient of sexual selection acting on males (e.g. owing to increased competition for mates in warmer habitats), because female body size did not show any relationship with climatic variables. Head shape dimorphism was positively related to SSD,

supporting the role of a sexual selection gradient in driving the observed pattern of SSD, whereas relative limb length dimorphism was negatively related to SSD, suggesting that size and limb dimorphism could represent alternative strategies for resource partitioning between the sexes.

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## DATA AVAILABILITY

The data underlying this article will be shared on reasonable request to the corresponding author.

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## SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Figure S1.** Sexual shape dimorphism in *Anolis carolinensis*. A–D, the boxplots show the values of relative head length (A), head width (B), head height (C) and humerus length (D). E–L, values of relative femur length (E), relative tibia length (F), relative pelvis width (G), relative pelvis height (H), relative distance between fore- and hindlimbs (I), relative pectoral height (J), geometric size (K) and  $\ln(\text{snout-vent length})$  (L). Populations are shown in increasing latitudinal order (higher latitudes to the right) preceded by 'f' for females and 'm' for males. Boxplots are shown in red for females and in blue for males.

**Figure S2.** Relationships between sexual dimorphism and climate, and between size and climate, including data from Florida populations: (A) SSD and  $\text{PC1}_{\text{climate}}$  (temperature); (B) SSD and  $\text{PC2}_{\text{climate}}$  (precipitation); (C) size and  $\text{PC1}_{\text{climate}}$ ; and (D) size and  $\text{PC2}_{\text{climate}}$ . Each data point represents a population. In C and D, black and white points represent males and females, respectively. Results from linear regressions between each pair of variables (and for each sex in C and D) are shown at the top of each panel. SSD =  $\ln(\text{average male SVL}/\text{average female SVL})$ . Abbreviations: PC, principal component; SSD, sexual size dimorphism; SVL, snout–vent length.

**Figure S3.** Relationships between each of the sexual shape dimorphism (SSHD) indices and sexual size dimorphism (SSD), including data from Florida populations. Results from linear regressions between each pair are shown on top of each panel. SSD =  $\ln(\text{average male snout-vent length}/\text{average female snout-vent length})$ . A continuous line represents a significant fitted model.

**Table S1.** Coordinates, sample sizes ( $N$ ) and average trait measurements (in millimetres) for each of the populations of *Anolis carolinensis* considered in the study. Data are shown for females and males separately. Data ranges are shown in parentheses. Abbreviation: SVL, snout–vent length. Data are only from individuals > 80% of the size of the largest individual from their population–sex group.