Biological Journal of the Linnean Society, 2026, **147(1)**, blaf141
https://doi.org/10.1093/biolinnean/blaf141

Original Article

Sexually selected traits vary over a latitudinal gradient in green anole lizards (*Anolis carolinensis*)

Simon P. Lailvaux[1,*], Mahaut Sorlin[1], Jamie Marks[2], Margaret A. Duerwachter[3], Jerry F. Husak[3]

[1]Department of Biological Sciences, The University of New Orleans, New Orleans, LA 70148, United States
[2]Department of Integrative Biology, Kellogg Biological Station, Michigan State University, Hickory Corners, MI 49060, United States
[3]Department of Biology, University of St Thomas, St Paul, MN 55105, United States

[*]Corresponding author. Department of Biological Sciences, University of New Orleans, 2000 Lakeshore Drive, New Orleans, LA 70148, United States.
E-mail: slailvaux@gmail.com.

ABSTRACT

Species frequently exhibit ecogeographical trends such that phenotypes in different populations vary according to local conditions along a geographical cline or gradient. Latitudinal gradients for traits such as body size and shape are thought to be driven by variation in environmental temperature, but we currently lack an understanding of how such variation affects both sexual size dimorphism and the expression of secondary sexual traits. We measured sexual size dimorphism and the relative size of dewlap area, bite force, and head morphology in four populations of green anole (*Anolis carolinensis*) lizards spanning a latitudinal gradient in the eastern United States. We found that while populations at lower latitudes exhibit greater sexual size dimorphism than those further from the equator, the relative expression of secondary sexual traits did not consistently follow this pattern, with bite force and dewlap area exhibiting negative and positive relationships with latitude, respectively. We also found that bite force and head shape are decoupled in male green anoles at both the highest and lowest latitudes, suggesting that other selective forces are acting on head morphology in these populations as well.

Keywords: sexual selection; *Anolis*; latitude; performance; dewlap; bite force

INTRODUCTION

Species in nature can exhibit considerable intraspecific variation across their geographical range (Mayr 1942). Most notably, organisms may show systematic changes in size, shape, or coloration at higher latitudes as compared to conspecific populations closer to the equator (Ashton and Feldman 2003, Meiri and Dayan 2003, Nudds and Oswald 2007, Galván *et al.* 2018). Proximate explanations for these ecogeographical trends commonly interpret latitude as a proxy for the thermal environment. For example, local thermal conditions are thought to explain observed latitudinal variation in both size (Bergmann's rule; Bergmann 1847) and shape (Allen's rule; Allen 1877), such that organisms in cooler environments at higher latitude are both larger and exhibit proportionately shorter appendages than those in more tropical environments as adaptations to limit heat exchange (Partridge and Coyne 1997, McQueen *et al.* 2022), although other potential drivers include prey size (McKnab 1971) and fasting endurance (Millar and Hickling 1990), amongst others. Rensch's rule states that sexual size dimorphism (SSD) increases with body size in those taxa where males are the larger sex (Rensch 1950, Abouheif and Fairbairn 1997), and several studies have linked this allometry of SSD to both sexual selection (Szekely *et al.* 2004, Dale *et al.* 2007) and latitude (Blanckenhorn *et al.* 2006). Although these results suggest that the strength of sexual selection should vary over latitudinal gradients, studies testing for intraspecific effects of latitude on the expression of both secondary sexual traits and SSD are uncommon.

Sexual selection drives the evolution of exaggerated secondary sexual traits (Andersson 1994), the relative expression of which is often considered a surrogate for the strength of sexual selection (Gontard-Daneck and Møller 1999). SSD, by contrast, has been shown to be inconsistently related to the strength of pre-copulatory sexual selection across animal taxa (Soulsbury *et al.* 2014, Janicke and Fromonteil 2021). Although one could predict that higher latitude populations might experience higher levels of male–male competition due to the truncated breeding seasons associated with the relatively shorter warmer periods in these regions (Hau 2001, Moore *et al.* 2019), several previous studies have instead

---

Received 8 September 2025; revised 5 November 2025; accepted 7 November 2025

suggested that sexual selection is experienced most intensely by organisms at lower latitudes. For example, Fujimoto *et al.* (2015) observed male competition, male courtship, and female choice in *Oryzias latipes* medaka fish across a latitudinal gradient and found that all three sexual selection pressures were strongest in the lower latitude population. Matsumara *et al.* (2023) reported a similar result in *Tribolium castaneum* beetles, but only for males, while Sumarto *et al.* (2020) showed that latitude influenced sexual dimorphism in southeast Asian Adrianichthyidae fish. Although several factors beyond temperature might contribute to latitudinal variation in sexual selection pressures, ectothermic organisms might be expected to be particularly sensitive to variation in the thermal environment. Indeed, ectotherms such as reptiles and amphibians are of interest in this context because they tend to subvert the ecogeographical trends exhibited by many endothermic taxa (Adams and Church 2008, Muñoz *et al.* 2014). Nonetheless, the evaluation of ecogeographical trends in sexual selection across populations that vary in thermal characteristics has been generally neglected in evolutionary ecology (García-Roa *et al.* 2020, Leith *et al.* 2022).

Green anole lizards (*Anolis carolinensis*) exhibit a broad latitudinal distribution across the eastern United States, extending from southern Florida to as far north as North Carolina and Tennessee. Genetic studies show that the northward expansion of this ancestrally tropical species into more temperate regions of the United States over the past 100000 years is associated with positive selection on genes involved in cold tolerance and behaviour (Bourgeois and Boissinot 2019), and indeed anoles from Tennessee are more cold tolerant than those from lower latitude populations (Wilson and Echternacht 1987). Previous studies have also shown that green anole populations at higher latitudes exhibit relatively wider and deeper heads than those from warmer and less seasonal populations at lower latitudes (Jaffe *et al.* 2016) and are also reported to be larger in body size due to both larger egg size and higher growth rates as compared to lower latitude animals (Goodman 2010). Collectively, these findings demonstrate that green anoles in the United States vary in characters at least partially in response to thermal conditions across their latitudinal gradient in general accordance with both Bergmann's and Allen's rules (Jaffe *et al.* 2016). However, despite the large literature on green anoles and their status as a model system for reproductive biology and ecology and evolution (Lovern *et al.* 2004), no studies to date have tested whether sexual selection or related phenotypes follow a latitudinal gradient in this species.

We measured sexual size dimorphism, bite force, head shape, and dewlap size in four populations of green anoles spanning their latitudinal distribution in the eastern United States. *Anolis* species vary in sexual dimorphism, with the extent of that dimorphism being positively linked to sexual selection across 97 species of anoles (Toyama *et al.* 2025). As in most lizard species, *Anolis* mating systems are dominated by male combat, and bite force has been shown to be a key determinant of male combat outcomes, and thus subject to sexual selection (Husak *et al.* 2009, Husak 2016) in many lizard taxa (Huyghe *et al.* 2005, Husak *et al.* 2006), including several species of *Anolis* lizards (Lailvaux and Irschick 2007) and green anoles specifically (Lailvaux *et al.* 2004), whereas head shape is an important morphological predictor of bite force (Herrel and O'Reilly 2006, Huyghe *et al.* 2009, Wittorski *et al.* 2016). Dewlaps are used in a variety of social contexts in *Anolis*, including male–male interactions, and relative bite force has been positively linked to relative dewlap size in the males of territorial anole species (Vanhooydonck *et al.* 2005b, Lailvaux and Irschick 2007), green anoles among them (Vanhooydonck *et al.* 2005a, Lailvaux *et al.* 2012), suggesting that rivals may glean information on a given male's bite force from the size of its extended dewlap (Vanhooydonck *et al.* 2005b, Lailvaux *et al.* 2012). Individual male green anole dewlaps also change size seasonally, with dewlap area becoming larger over the course of the breeding season and smaller during the non-breeding season (Irschick *et al.* 2006) due to stretching and shrinking of the dewlap skin associated with increased dewlap signalling, and thus dewlap extension, and decreased dewlap signalling and extension, respectively (Lailvaux *et al.* 2015). Dewlaps are thus an important component of anole mating systems, and dewlap design might therefore be expected to reflect variation in sexual selection pressures as well (but see Henningsen and Irschick 2012, Summers and Ord 2022).

We tested the hypothesis that sexual selection is affected by latitude in green anoles, as reflected in the measured phenotypic traits across the four measured populations. Specifically, we predicted that green anole populations at lower latitudes will be more sexually dimorphic, and exhibit relatively larger dewlaps, bite forces, and head sizes compared to populations at higher latitudes. Given the noted variation in head shape across green anole populations, we also tested the related hypothesis that the relationship between male bite force and overall head shape will vary across the measured latitudinal range.

METHODS

We sampled four green anole populations comprising 218 animals in June and July 2022: Monroe County, Tennessee (TN; 26 males and 22 females); Charleston, South Carolina (SC; 29 males and 25 females); New Orleans, Louisiana (NOLA; 26 males and 26 females); and Punta Gorda, Florida (PG; 30 males and 25 females). Four populations has been considered sufficient for capturing existing latitudinal gradients both in previous meta-analyses (e.g. Eo *et al.* 2008) and in empirical studies (Geißel *et al.* 2025), and the four chosen populations also span the entire continental distribution of green anoles across the eastern United States. Following capture, we measured morphology, bite force, and dewlap size in all animals following standard methods. We measured snout–vent length (SVL) and head dimensions to the nearest 0.01 mm using Mitutoyo calipers. Dewlap area was measured by extending the dewlap using forceps and photographing it against a known scale using a Sony RX10 digital camera. We then digitized each image using tpsDig 2.3.2 to estimate the total area of extended dewlap (as in Vanhooydonck *et al.* 2005a, Irschick *et al.* 2006, Lailvaux *et al.* 2012, 2015). It is important to note here that despite the demonstrated elasticity of the green anole dewlap, changes in dewlap size associated with stretching manifest only over long periods of time, and previous studies have found measurements of dewlap area made using the described method to be repeatable in the short term (Vanhooydonck *et al.* 2005b). We measured bite force using an isometric type 9023 Kistler (Winterthur, Switzerland) piezoelectric force transducer connected to a type 5058a Kistler charge amplifier and attached to custom-made bite plates in such a way that biting down on the plates stretched the transducer, allowing us to measure the maximum force (newtons) exerted (see Herrel *et al.* 1999 for a detailed description; Anderson *et al.* 2008, Lappin and Jones 2014). Bite plates had a thin layer of padding to prevent tooth breakage during trials. We measured bite force five times per individual, and retained the highest measured value as our estimate of maximum bite force (Lailvaux *et al.* 2004, 2019, Husak *et al.* 2021). The thickness of the bite plates prevented us from measuring the bite force of adult females from the PG population, as these animals were often as small as or smaller than subadults from other green anole populations.

Statistical analysis

We used R 4.4.2 for all analyses (R Core Team 2024). We used Box–Cox transformations to transform as required to meet assumptions of normality. To test for an effect of population on sexual size dimorphism, we fit an ANOVA with SVL as a dependent variable and population, sex, and the interaction between population and sex as factors. To test for an effect of population on the relative magnitude of dewlap area, head shape, and bite force, we fit a MANCOVA to these variables with sex, population, and the interaction between sex and population as factors. Note that due to the missing bite forces for female green anoles from the PG population (see above), the test for the multivariate interaction between sex and population here is conservative. We used the R package *emmeans* (Lenth 2019) to calculate Tukey-protected post-hoc contrasts among factor levels as required. To test for variation in the relationships between overall male head size and bite force across the four populations, we calculated the geometric mean of head length, head width, and head height (Lappin and Jones 2014) and fit a linear model with transformed bite force as a dependent variable, and SVL, population size, head size, and the interaction between population and head size as predictor variables. We used the *emtrends* command in *emmeans* to calculate the slopes of the relationship between head size and bite force in each of the four populations, and the *emmip* command to calculate contrasts. In all cases, units of contrasts correspond to transformed units of measurement.

RESULTS

The ANOVA for SVL yielded a significant interaction between sex and population size ($F_{3,201} = 16.677$, $P < .001$). While males were always significantly larger than females regardless of source population, the largest size dimorphisms were observed in the lowest latitude populations, where the female–male contrasts for PG and NOLA were −0.0853 (±0.007 SE; $t_{201} = -12.95$, $P < .001$) and −0.1096 (±0.007 SE; $t_{201} = -16.25$, $P < .001$) respectively, as compared to −0.048 (±0.007 SE; $t_{201} = -7.242$, $P < .001$) for SC and −0.06 (±0.007 SE; $t_{201} = -8.451$, $P < .001$) for TN. The PG anoles are the smallest lizards overall, with the average PG males being as large as the average NOLA female (Fig. 1). However, NOLA harboured the largest males overall, with NOLA males being larger than males in PG (contrast PG–NOLA = −0.011 ± 0.007 SE, $t_{201} = -16.652$, $P < .001$), SC (NOLA–SC contrast = 0.03 ± 0.007 SE, $t_{201} = 3.972$, $P < .001$), and TN (NOLA–TN contrast = 0.034 ± 0.0074 SE, $t_{201} = 5.035$, $P < .001$). By contrast, while there was no difference in SVL between the SC and TN males (SC–TN contrast = 0.008 ± 0.007 SE, $t_{201} = 1.198$, $P = .629$), SC females were significantly larger than those from the TN population (SC–TN contrast = 0.019 ± 0.007 SE, $t_{201} = 2.72$, $P < .036$). NOLA females were significantly smaller than those from SC (NOLA–SC contrast = -0.035 ± 0.007 SE, $\mathrm{t}_{201} = -5.21$ $P < .001$), but were not significantly different in SVL from TN females (NOLA–TN contrast = −0.016 ± 0.007 SE, $t_{201} = -2.291$, $P = .1$). The MANCOVA on the combined effects of sex and population on head morphology, dewlap area, and bite force with SVL as a covariate yielded significant effects of sex (Pillai's trace = 0.8756, $F_{5,151} = 212$, $P < .001$) and population (Pillai's trace = 0.518, $F_{15,459} = 6$, $P < .001$) on the measured traits, but no significant interaction between sex and population (Pillai's trace = 0.028, $F_{10,304} = 0$, $P = .934$). Males exhibited larger size-corrected dewlaps than females in all four populations ($F_{1,155} = 180.53$, $P < .001$), but while the smallest relative dewlap areas were seen in PG lizards for both sexes, the relative dewlap areas across the LA, SC, and TN lizards were similar to each other for both males and females (Fig. 2A). By contrast, the highest bite forces relative to body size were seen in the lower latitude populations, with PG males biting the hardest of all the four populations following correction for body size (Fig. 2B). Although bite forces could not be recorded for PG females

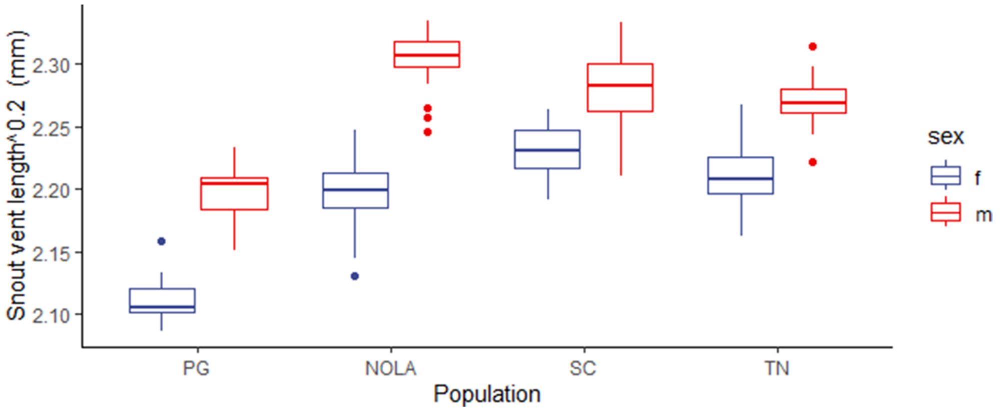

Figure 1. Transformed snout–vent length (SVL) for males and females from each of the four sampled populations. Populations are arranged along the *x*-axis in order of increasing latitude.

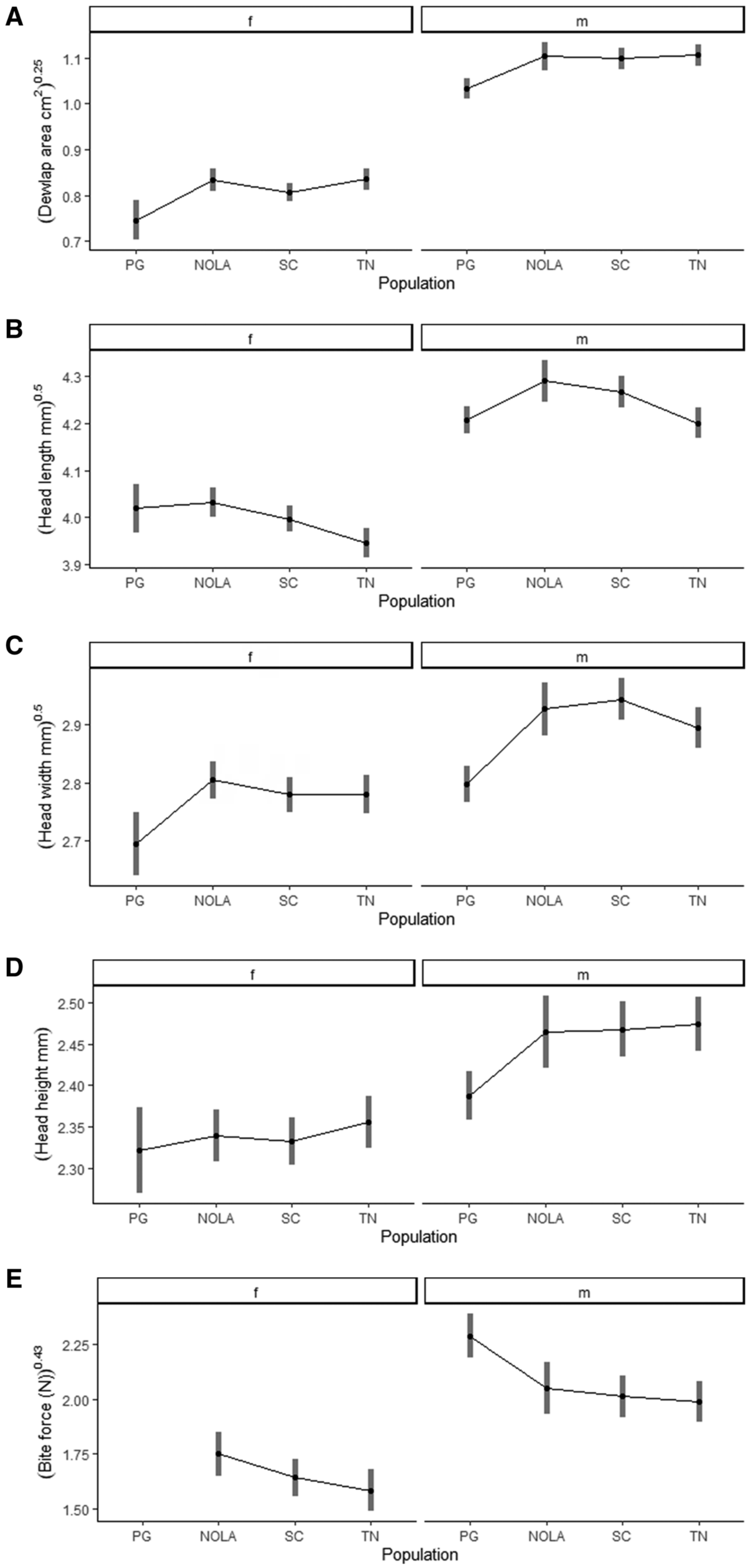

Figure 2. Predicted marginal means ± 95% confidence intervals representing: A, dewlap area$^{0.25}$; B, head length$^{0.5}$; C, head width$^{0.5}$; D, head height; and E, bite force$^{0.43}$, for males and females from each of the four sampled populations. Populations are arranged along the *x*-axis in order of increasing latitude.

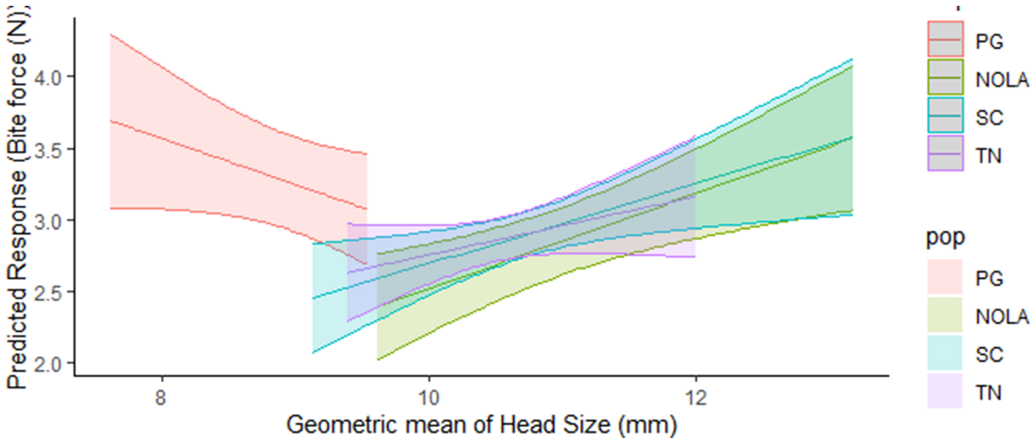

Figure 3. Marginal trends ± 95% confidence intervals for male bite force$^{0.6}$ and the geometric mean for male head shape after accounting for SVL within each of the four green anole populations. The 95% confidence intervals for both the PG and Tennessee males marginally include 0.

(see above), the linear model for male bite force as a function of composite head size (as captured by the geometric mean of head length, head width, and head height) and population with SVL as a covariate yielded a significant interaction between population and head size, indicating that the slopes of the size-free head size/bite force relationships differ among populations. Specifically, the slopes of this relationship in the NOLA and SC lizards are positive, whereas the PG and TN populations exhibited negative slopes over the measured head size range (Fig. 3), the 95% confidence intervals of which marginally crossed 0 in both cases (Table 1).

Table 1. Slopes of the size-free relationship between the geometric mean of male head length, head width, and head height and bite force$^{0.6}$ in each of the four sampled green anole populations, as well as the respective standard errors (SE) and upper and lower 95% confidence intervals.

Population	**Slope**	**SE**	**d.f.**	**Lower CI**	**Upper CI**
Punta Gorda	−0.322	0.187	90	−0.6933	0.0498
New Orleans	0.33	0.103	90	0.1251	0.5353
South Carolina	0.278	0.108	90	0.0629	0.4929
Tennessee	0.202	0.135	90	−0.0654	0.4687

DISCUSSION

Populations of green anoles are known to vary across latitudinal gradients, with populations at high latitudes in particular showing both genomic and phenotypic evidence of increased cold tolerance relative to other populations. We tested the hypothesis that the expression of sexually selected traits would exhibit a similar ecogeographical gradient and predicted that lower latitude populations should experience increased sexual selection, as evidenced by greater sexual dimorphism, and larger heads, dewlaps, and bite forces.

Our prediction was partially supported. There was a general trend of greater sexual size dimorphism at lower latitudes, such that the PG and NOLA populations exhibited the greatest difference in body size between males and females compared to the SC and TN populations. However, the greatest such dimorphism was observed in the NOLA population, rather than in the PG animals at the lowest latitude (Fig. 1). Mayr (1942) emphasized that ecogeographical trends are probably influenced by multiple factors as opposed to single conditions such as temperature, and further that exceptions to a general population trend are probably due to conflict between those selective factors (Mayr 1956). With regard to SSD specifically, Toyama *et al.* (2025) showed that patterns of SSD in *Anolis* lizards are generally as expected if such dimorphism evolved under the auspices of sexual selection, but also found that sexual selection was likely to be much stronger on island species compared to mainland anoles. *Anolis carolinensis* has been present on the US mainland for 4–6 Myr, and thus can hardly be considered an island species. Nonetheless, green anoles have historically not been subject to the community dynamics experienced by mainland anoles in Central and South American communities, typically facing little competition or interspecific interactions until the introduction of Caribbean congeners over the last several decades. Furthermore, previous authors have suggested that urban populations of green anoles in particular might experience heightened sexual selection compared to green anoles in rural or less disturbed habitats because the artificial and discontinuous nature of urban green anole habitat forces males into close proximity with each other (Bloch and Irschick 2006, McMillan and Irschick 2010, Lailvaux 2020), in much the same way that insular lizard species tend to be subject to stronger sexual selection and resource competition (Novosolov *et al.* 2013). The extreme dimorphism exhibited by the urban green anoles in New Orleans might therefore be explained by the intense sexual competition experienced by males in this population. On the other hand, the green anoles from South Carolina also derive from primarily urban habitats, yet are not particularly sexually dimorphic. It may be that the sexual selection and latitudinal effects may mask or cancel each other out in urban populations at higher latitudes, although we cannot conclude this with confidence from our current dataset. However, it is also important to note here that the NOLA and PG populations harbour the largest and smallest lizards respectively in terms of total body size, and yet both of these populations are also more dimorphic than the two high-latitude populations. The general trend of higher dimorphism closer to the equator therefore does hold within our sample, variation in dimorphism among those low-latitude populations notwithstanding, suggesting that these populations both probably experience more intense sexual selection than those further from the equator.

Dewlap area and bite force showed opposite latitudinal trends to each other after accounting for body size, with higher latitude lizards exhibiting the largest relative dewlap sizes (Fig. 2A), while the highest bite forces were observed in green anole populations closer to the equator (Fig. 2B). Consequently, while our results for bite force mirror our SSD data in support of our prediction of stronger sexual selection at lower latitudes, the dewlap size data do not. An important caveat to our results for dewlap size is the known plasticity in dewlap size in green anoles. Lailvaux *et al.* (2015) showed that the dewlap skin in male green anoles shows a significantly lower elastic modulus—i.e. is significantly less resistant to stretching—compared to belly skin during the breeding season, resulting in dewlaps stretching over the course of that season when males are allowed to extend their dewlaps as part of their displays, and shrinking when they are prevented from doing so. Given this dewlap elasticity, any trend towards greater dewlap size at low latitudes could be masked if males at higher latitudes display at relative greater rates. Although we would not expect this to be the case based on sexual selection alone, anoles are also known to display their dewlaps in other selective contexts, including during interactions with predators (Leal 1999), during interspecific interactions (Losos 1985, Tokarz and Beck 1987, Leal *et al.* 1998), and in non-directed territorial displays (Greenberg and Noble 1944, Jenssen *et al.* 1995). Few data are available on intraspecific variation in dewlap display frequencies within green anoles. Bloch and Irschick (2006) showed that green anole males in an urban population in New Orleans displayed roughly twice as much as males from a nearby rural population, whereas Lovern *et al.* (1999) compared male displays among populations from Georgia, Florida, and Hawai'i, and found few differences among populations in display duration, although display frequency was not measured. Lailvaux *et al.* (2012) further showed that dewlap area is insensitive to resource availability in juvenile anoles, suggesting that dewlap display frequency is the major known source of dewlap plasticity. In the absence of a similar latitudinal gradient in dewlap display frequency, the pattern for dewlap area therefore opposes that for bite force and SSD. Summers and Ord (2022) argue that dewlap size is primarily a function of signal detectability, which could be relevant here; the PG population is unique among other green anole populations in its lack of red coloration, instead being a greyish colour (Macedonia *et al.* 2003). However, Macedonia *et al.* (2003) did not find that the grey coloration made the dewlap more visible in the light environment compared to red-dewlapped males in their respective populations. Furthermore, an analysis of headbob displays place PG males within the range of variation of headbob displays of red-dewlapped anoles (Macedonia *et al.* 2015). It is unclear why the PG anoles have grey dewlaps unlike other green anole populations, or what that means for dewlap size in particular or sexual signalling in general, but the unique dewlap may simply be due to a bottleneck during Pleistocene sea-level changes (Tollis and Boissinot 2014, Macedonia *et al.* 2015).

Our second hypothesis, that the relationship between head size and bite force would vary across the latitudinal range, was supported. Head morphology is a primary determinant of bite force in lizards (Herrel *et al.* 2001, 2007, Verwaijen *et al.* 2002), and we therefore expected that variation in relative head dimensions would track variation in relative bite force across the measured populations. Our results show that PG males exhibit both the widest and flattest heads relative to body size of the four populations we examined. However, despite these lizards exhibiting the largest bite forces relative to their body size, the relationship between overall head size and bite force showed a marginally non-significant negative slope once the effects of body size are accounted for (Table 1). The 95% confidence intervals of the positive slope between head size and bite force similarly included zero in the Tennessee green anole males (Table 1). Bite force in anoles is generally a function of head width and head height, with lizards with taller and wider heads yielding higher bite forces (Wittorski *et al.* 2016, De Meyer *et al.* 2019). Our data show that male PG lizards have the shallowest and narrowest heads relative to body size, yet the highest bite forces. The reasons for this decoupling between head size and bite force are not apparent from our dataset, but could be related to dietary or habitat differences in the PG population (Bonneaud *et al.* 2016). Indeed, lizards in the TN population are unique in our sample since they make frequent use of rocky outcrops in their local habitat, particularly during the winter when crevices act as a thermal refuge (Bishop and Echternacht 2004). Saxicolous lifestyles are associated with reduced bite forces in cordylid lizards that exhibit dorsoventrally flattened body plans for making use of crevices, including shallow heads and necessarily short jaw adductor muscles (Broeckhoven and Mouton 2014). Despite the known effects of sexual selection on both bite force and head size in green anoles (Lailvaux *et al.* 2004), other selective pressures probably affect head shape as well.

Although latitudinal trends were evident in dewlap size, bite force, and head dimensions after accounting for effects of body size, these trends typically mirrored each other in males and females, as evidenced by the lack of a significant interaction between sex and population in any of the measured traits. The green anole mating system is based on female defence polygyny (Nunez *et al.* 1997, Jenssen and Nunez 1998), and as such the expression of sexually selected traits is shaped primarily by male combat in these animals. The similar expression of dewlap size, bite force, and head dimensions in both sexes across the measured populations therefore represents either common selection pressures on each beyond sexual selection or, more likely, a lack of sex limitation in the relative expression of these sexually selected male traits. Lailvaux *et al.* (2019) found evidence for unresolved intralocus sexual conflict involving head shape and bite force in a New Orleans population of green anoles, such that the mechanical burden of larger than optimal heads in females—probably caused by sexual selection for large heads in males (Lailvaux *et al.* 2004)—compromises female sprint speed. The parallel latitudinal trends of these traits in males and females therefore suggests that similar conflict may exist across the measured population, and that females probably suffer costs of sexual selection for traits related to male competition that are not compensated for (for a review see Husak and Swallow 2011) in each.

Our data collected across four populations of green anoles show evidence for a latitudinal gradient in the strength of sexual selection in these lizards; after accounting for body size, lizards at lower latitudes are on average more dimorphic, with wider heads and higher bite forces compared to those at higher latitudes, but with smaller dewlap areas. Rensch's rule says that SSD tends to scale positively with allometry in species where males are the larger sex (Fairbairn 1997). However, our data show that the green anole populations exhibiting the largest SSD were those harbouring lizards with both the largest and the smallest average body sizes among the four populations studied. One possibility is that the lack of thermal selection for larger body size in southern populations compared to SC and TN populations, combined with higher sexual selection at low latitudes, has resulted in the patterns of dimorphism we found. These data, in conjunction with the finding that lower latitude green anoles also exhibit higher relative bite forces, therefore support the interpretation of SSD expression as a function of the strength of sexual selection in these animals (Szekely *et al.* 2004), and further show that sexual selection is likely to be stronger at lower latitudes in green anoles, as it seems to be in several other organisms (Blanckenhorn *et al.* 2006). Empirical studies that directly measure the strength of natural and sexual selection across this gradient would be useful for confirming or rejecting this notion.

ACKNOWLEDGEMENTS

We thank J. Macedonia, S. Echternacht, and J. Bush for advice on anole sampling locations; E. McElroy for collecting SC lizards; and M. Chopra, M. Melchior, and R. Yusuf for help with laboratory data collection. The manuscript was improved by comments from Santiago Claramunt and from the Lailvaux Integrative Ecology and Evolution lab.

SUPPLEMENTARY DATA

Supplementary data are available at *Biological Journal of the Linnean Society* online.

CONFLICT OF INTEREST

None declared.

FUNDING

This study was partially funded by a UST Young Scholars Grant to M.A.D.

DATA AVAILABILITY STATEMENT

Data will be deposited in permanent online data repository upon acceptance. Data and code are deposited at Figshare and can be accessed via 10.6084/m9.figshare.30689591.

REFERENCES

Abouheif E, Fairbairn DJ. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. *The American Naturalist* 1997;**149**:540–62.

Adams DC, Church JO. Amphibians do not follow Bergmann's rule. *Evolution; International Journal of Organic Evolution* 2008;**62**:413–20.

Allen JA. The influence of physical conditions in the genesis of species. *Radical Review* 1877;**1**:108–40.

Anderson RA, McBrayer LD, Herrel A. Bite force in vertebrates: opportunities and caveats for use of a nonpareil whole-animal performance measure. *Biological Journal of the Linnean Society* 2008;**93**:709–20.

Andersson M. *Sexual Selection*. Princeton, NJ: Princeton University Press, 1994.

Ashton KG, Feldman CR. Bergmann's rule in nonavian reptiles: turtles follow it, lizards and snakes reverse it. *Evolution; International Journal of Organic Evolution* 2003;**57**:1151–63.

Bergmann C. *Über die Verhältnisse der Wärmeökonomie der Thiere zu ihrer Grösse*. Göttingen: Vandenhoeck und Ruprecht, 1847.

Bishop DC, Echternacht AC. Emergence behavior and movements of winter-aggregated green anoles (*Anolis carolinensis*) and the thermal characteristics of their crevices in Tennessee. *Herpetologica* 2004;**60**:168–77.

Blanckenhorn WU, Stillwell RC, Young KA *et al.* When Rensch meets Bergmann: does sexual size dimorphism change systematically with latitude? *Evolution; International Journal of Organic Evolution* 2006;**60**:2004–11.

Bloch N, Irschick DJ. An analysis of inter-population divergence in visual display behavior of the green anole lizard (*Anolis carolinensis*). *Ethology* 2006;**112**:370–8.

Bonneaud C, Marnocha E, Herrel A *et al.* Developmental plasticity affects sexual size dimorphism in an anole lizard. *Functional Ecology* 2016;**30**:235–43.

Bourgeois Y, Boissinot S. Selection at behavioural, developmental and metabolic genes is associated with the northward expansion of a successful tropical colonizer. *Molecular Ecology* 2019;**28**:3523–43.

Broeckhoven C, Mouton PL. Under pressure: morphological and ecological correlates of bite force in the rock-dwelling lizards *Ouroborus cataphractus* and *Karusasaurus polyzonus*. *Biological Journal of the Linnean Society* 2014;**111**:823–33.

Dale J, Dunn PO, Figuerola J *et al.* Sexual selection explains Rensch's rule of allometry for sexual size dimorphism. *Proceedings of the Royal Society B: Biological Sciences* 2007;**274**:2971–9.

De Meyer D, Irschick DJ, Vanhooydonck B *et al.* The role of bite force in the evolution of head shape and head shape dimorphism in *Anolis* lizards. *Functional Ecology* 2019;**33**:2191–202.

Eo SH, Wares JP, Carroll JP. Population divergence in plant species reflects latitudinal biodiversity gradients. *Biology Letters* 2008;**4**:382–4.

Fairbairn DJ. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics* 1997;**28**:659–87.

Fujimoto S, Miyake T, Yamahira K. Latitudinal variation in male competitiveness and female choosiness in a fish: are sexual selection pressures stronger at lower latitudes? *Evolutionary Biology* 2015;**42**:75–87.

Galván I, Rodríguez-Martínez S, Carrascal LM. Dark pigmentation limits thermal niche position in birds. *Functional Ecology* 2018;**32**:1531–40.

García-Roa R, Garcia-Gonzalez F, Noble DWA *et al.* Temperature as a modulator of sexual selection. *Biological Reviews of the Cambridge Philosophical Society* 2020;**95**:1607–29.

Geiβel JP, Espinosa-Novo N, Giménez L *et al.* Trends in early larval traits of a global invader at home across a latitudinal gradient: the European shore crab, *Carcinus maenas*. *Journal of Biogeography* 2025;**52**:e15143.

Gontard-Daneck MC, Møller AP. The strength of sexual selection: a meta-analysis of bird studies. *Behavioral Ecology* 1999;**10**:476–86.

Goodman RM. Evidence of divergent growth rates among populations of the lizard *Anolis carolinensis* based on experimental manipulations of egg size. *Population Ecology* 2010;**52**:113–22.

Greenberg B, Noble GK. Social behavior of the American chameleon (*Anolis carolinensis* Voigt). *Physiological Zoology* 1944;**17**:392–439.

Hau M. Timing of breeding in variable environments: tropical birds as model systems. *Hormones and Behavior* 2001;**40**:281–90.

Henningsen JP, Irschick DJ. An experimental test of the effect of signal size and performance capacity on dominance in the green anole lizard. *Functional Ecology* 2012;**26**:3–10.

Herrel A, McBrayer LD, Larson PM. Functional basis for sexual differences in bite force in the lizard *Anolis carolinensis*. *Biological Journal of the Linnean Society* 2007;**91**:111–9.

Herrel A, O'Reilly JC. Ontogenetic scaling of bite force in lizards and turtles. *Physiological and Biochemical Zoology: PBZ* 2006;**79**:31–42.

Herrel A, Spithoven L, van Damme R *et al.* Sexual dimorphism of head size in *Gallotia galloti*: testing the niche divergence hypothesis by functional analyses. *Functional Ecology* 1999;**13**:289–97.

Herrel A, Van Damme R, Vanhooydonck B *et al.* The implications of bite performance for diet in two species of lacertid lizards. *Canadian Journal of Zoology* 2001;**79**:662–70.

Husak JF. Measuring selection on physiology in the wild and manipulating phenotypes (in terrestrial nonhuman vertebrates). *Comprehensive Physiology* 2016;**6**:63–85.

Husak JF, Lappin AK, Fox SF *et al.* Bite-performance predicts male dominance in male venerable collared lizards (*Crotaphytus antiquus*). *Copeia* 2006;**2006**:301–6.

Husak JF, Lappin AK, Van Den Bussche RA. The fitness advantage of a high-performance weapon. *Biological Journal of the Linnean Society* 2009;**96**:840–5.

Husak JF, Rohlf CM, Lailvaux SP. Immune activation affects whole-organism performance in male but not female green anole lizards (*Anolis carolinensis*). *Journal of Comparative Physiology. B, Biochemical, Systemic, and Environmental Physiology* 2021;**191**:895–905.

Husak JF, Swallow JG. Compensatory traits and the evolution of male ornaments. *Behaviour* 2011;**148**:1–29.

Huyghe K, Herrel A, Adriaens D *et al.* It is all in the head: morphological basis for differences in bite force among colour morphs of the Dalmatian wall lizard. *Biological Journal of the Linnean Society* 2009;**96**:13–22.

Huyghe K, Vanhooydonck B, Scheers H *et al.* Morphology, performance and fighting capacity in male lizards, Gallotia galloti. *Functional Ecology* 2005;**19**:800–7.

Irschick DJ, Ramos M, Buckley C *et al.* Are morphology-performance relationships invariant across different seasons? A test with the green anole lizard (*Anolis carolinensis*). *Oikos* 2006;**114**:49–59.

Jaffe AL, Campbell-Staton SC, Losos JB. Geographical variation in morphology and its environmental correlates in a widespread North American lizard, *Anolis carolinensis* (Squamata: Dactyloidae). *Biological Journal of the Linnean Society* 2016;**117**:760–74.

Janicke T, Fromonteil S. Sexual selection and sexual size dimorphism in animals. *Biology Letters* 2021;**17**:20210251.

Jenssen TA, Greenberg N, Hovde KA. Behavioral profile of free-ranging male lizards, *Anolis carolinensis*, across breeding and post-breeding seasons. *Herpetological Monographs*, 1995;**9**:41–62.

Jenssen TA, Nunez SC. Spatial and breeding relationships of the lizard, *Anolis carolinensis*: evidence of intrasexual selection. *Behaviour* 1998;**135**:981–1003.

Lailvaux SP. It's not easy being green: behavior, morphology, and population structure in urban and natural populations of green anole (*Anolis carolinensis*) lizards. *Frontiers in Ecology and Evolution* 2020;**8**:570610.

Lailvaux SP, Cespedes AM, Houslay TM. Conflict, compensation, and plasticity: sex-specific, individual-level trade-offs in green anole (*Anolis carolinensis*) performance. *Journal of Experimental Zoology A* 2019;**331**:280–9.

Lailvaux SP, Gilbert RL, Edwards JR. A performance-based cost to honest signalling in male green anole lizards (*Anolis carolinensis*). *Proceedings of the Royal Society B: Biological Sciences* 2012;**279**:2841–8.

Lailvaux SP, Herrel A, Vanhooydonck B *et al.* Performance capacity, fighting tactics and the evolution of life-stage male morphs in the green anole lizard (*Anolis carolinensis*). *Proceedings of the Royal Society of London. Series B: Biological Sciences* 2004;**271**:2501–8.

Lailvaux SP, Irschick DJ. The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. *The American Naturalist* 2007;**170**:573–86.

Lailvaux SP, Leifer J, Kircher BK *et al.* The incredible shrinking dewlap: signal size, skin elasticity, and mechanical design in the green anole lizard (*Anolis carolinensis*). *Ecology and Evolution*, 2015;**5**:4400–9.

Lappin AK, Jones MEH. Reliable quantification of bite-force performance requires use of appropriate biting substrate and standardization of bite out-lever. *The Journal of Experimental Biology* 2014;**217**:4303–12.

Leal M. Honest signalling during predator-prey interactions in the lizard *Anolis cristatellus*. *Animal Behaviour* 1999;**58**:521–6.

Leal M, Rodriguez-Robles JA, Losos JB. An experimental study of interspecific interactions between two Puerto Rican *Anolis* lizards. *Oecologia* 1998;**117**:273–8.

Leith NT, Fowler-Finn KD, Moore MP. Evolutionary interactions between thermal ecology and sexual selection. *Ecology Letters* 2022;**25**:1919–36.

Lenth RV. emmeans: Estimated marginal means, aka Least-Squares Means. *R package version 1.3.5.1*, https://CRAN.R-project.org/package=emmeans, 2019.

Losos JB. An experimental demonstration of the species-recognition role of *Anolis* dewlap color. *Copeia* 1985;**1985**:905–10.

Lovern MB, Holmes MM, Wade J. The green anole (*Anolis carolinensis*): a reptilian model for laboratory studies of reproductive morphology and behavior. *ILAR Journal* 2004;**45**:54–64.

Lovern MB, Jenssen TA, Orrell KS *et al.* Comparisons of temporal display structure across contexts and populations in male *Anolis carolinensis:* signal stability or lability? *Herpetologica* 1999;**55**:222–34.

Macedonia JM, Clark DL, Cherry LE *et al.* Comparison of headbob displays in gray-dewlapped and red-dewlapped populations of green anoles (*Anolis carolinensis*). *Herpetologica* 2015;**71**:117–24.

Macedonia JM, Echternacht AC, Walg JW. Color variation, habitat light, and background contrast in *Anolis carolinensis* along a geographical transect in Florida. *Journal of Herpetology* 2003;**37**:467–78.

Matsumara K, Wakabayashi K, Kawakami R *et al.* Latitudinal cline in reproductive traits in the red flour beetles *Tribolium castameum*. *Behavioral Ecology and Sociobiology* 2023;**77**:85.

Mayr E. *Systematics and the Origin of Species*. New York: Columbia University Press, 1942.

Mayr E. Geographical character gradients and climatic adaptation. *Evolution* 1956;**10**:105–8.

McKnab BK. On the ecological significance of Bergmann's rule. *Ecology* 1971;**52**:845–54.

McMillan DM, Irschick DJ. Experimental test of predation and competition pressures on the green anole (*Anolis carolinensis*) in varying structural habitats. *Journal of Herpetology* 2010;**44**:272–8.

McQueen A, Klaassen M, Tattersall GJ; Australasian Wader Studies Group *et al.* Thermal adaptation best explains Bergmann's and Allen's rules across ecologically diverse shorebirds. *Nature Communications* 2022;**13**:4727.

Meiri S, Dayan T. On the validity of Bergmann's rule. *Journal of Biogeography* 2003;**30**:331–51.

Millar JS, Hickling GJ. Fasting endurance and the evolution of mammalian body size. *Functional Ecology* 1990;**4**:5–12.

Moore IT, Vernasco BJ, Escallon C *et al.* Tales of testosterone: advancing our understanding of environmental endocrinology through studies of neotropical birds. *General and Comparative Endocrinology* 2019;**273**:184–91.

Muñoz MM, Wegener JE, Algar AC. Untangling intra- and interspecific effects on body size clines reveals divergent processes structuring convergent patterns in *Anolis* lizards. *The American Naturalist* 2014;**184**:636–46.

Novosolov M, Raia P, Meiri S. The island syndrome in lizards. *Global Ecology and Biogeography* 2013;**22**:184–91.

Nudds RL, Oswald SA. An interspecific test of Allen's rule: evolutionary implications for endothermic species. *Evolution; International Journal of Organic Evolution* 2007;**61**:2839–48.

Nunez SC, Jensse TA, Ersland K. Female activity profile of a polygynous lizard (*Anolis carolinensis*): evidence of intersexual asymmetry. *Behaviour* 1997;**134**:205–23.

Partridge L, Coyne JA. Bergmann's rule in ectotherms: is it adaptive? *Evolution* 1997;**51**:632–5.

R Core Team. *R: A Language and Environment for Statistical Computing*. Vienna, Austria: R Foundation for Statistical Computing, 2024. https://www.R-project.org/.

Rensch B. Die Abhängigkeit der relativen Sexualdifferenz von der Körpergrösse. *Bonner Zoologische Beiträge* 1950;**1**:58–69.

Soulsbury CD, Kervinen M, Lebigre C. Sexual size dimorphism and the strength of sexual selection in mammals and birds. *Evolutionary Ecology Research* 2014;**14**:63–76.

Sumarto BKA, Kobayashi H, Kakioka R *et al.* Latitudinal variation in sexual dimorphism in a freshwater fish group. *Biological Journal of the Linnean Society* 2020;**131**:898–908.

Summers TC, Ord TJ. Signal detection shapes ornament allometry in functionally convergent Caribbean *Anolis* and southeast Asian Dracos. *Journal of Evolutionary Biology* 2022;**35**:1508–23.

Szekely T, Freckleton RP, Reynolds JD. Sexual selection explains Rensch's rule of size dimorphism in shorebirds. *Proceedings of the National Academy of Sciences* 2004;**101**:12224–7.

Tokarz RR, Beck JW. Behavior of the suspected lizard competitors *Anolis sagrei* and *Anolis carolinensis*—an experimental test for behavioral interference. *Animal Behaviour* 1987;**35**:722–34.

Tollis M, Boissinot S. Genetic variation in the green anole lizard (*Anolis carolinensis*) reveals island refugia and a fragmented Florida during the Quaternary. *Genetica* 2014;**142**:59–72.

Toyama KS, Losos JB, Herrel A *et al.* Sexual size dimorphism as a deteminant of biting performance dimorphism in *Anolis* lizards. *Journal of Evolutionary Biology* 2025;**38**:251–60.

Vanhooydonck B, Herrel A, Van Damme R *et al.* The relationship between dewlap size and performance changes with age and sex in a green anole (*Anolis carolinensis*) lizard population. *Behavioral Ecology and Sociobiology* 2005a;**59**:157–65.

Vanhooydonck B, Herrel AY, Van Damme R *et al.* Does dewlap size predict male bite performance in Jamaican *Anolis* lizards? *Functional Ecology* 2005b;**19**:38–42.

Verwaijen D, Van Damme R, Herrel A. Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Functional Ecology* 2002;**16**:842–50.

Wilson MA, Echternacht AC. Geographic variation in the critical thermal minimum of the green anole, *Anolis carolinensis* (Sauria: Iguanidae) along a latitudinal gradient. *Comparative Biochemistry and Physiology A*, 1987;**87**:757–60.

Wittorski A, Losos JB, Herrel A. Proximate determinants of bite force in *Anolis* lizards. *Journal of Anatomy* 2016;**228**:85–95.