JOURNAL OF
Evolutionary Biology

.·**eseb**
European Society for Evolutionary Biology

Sexual size dimorphism as a determinant of biting performance dimorphism in *Anolis* lizards

Ken S. Toyama[1], **Jonathan B. Losos**[2], **Anthony Herrel**[3,4,5,6], **D. Luke Mahler**[1]

[1]Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, Canada
[2]Washington University, CB 1137, One Brookings Drive, St. Louis, MO 63130, USA
[3]Mécanismes Adaptatifs et Evolution, UMR 7179, Département Adaptation du Vivant, Muséum national d'Histoire naturelle CNRS, Paris, France
[4]Department of Biology, Evolutionary Morphology of Vertebrates, Ghent University, Ghent, Belgium
[5]Department of Biology, University of Antwerp, Wilrijk, Belgium
[6]Naturhistorisches Museum Bern, Bern, Switzerland

Handling editor: Rebekah Rogers, Associate editor: Nicola Nadeau

Corresponding author: Ken S. Toyama, Department of Ecology and Evolutionary Biology, University of Toronto, Toronto, M5S 3B2 ON, Canada.
Email: ken.toyama@mail.utoronto.ca

Abstract

Rensch's rule describes a pattern of interspecific allometry in which sexual size dimorphism (SSD) increases with size among closely related species (i.e., among a group of related species, the largest ones tend to show more male-biased SSD). Sexual selection is often invoked to explain Rensch's rule, as larger male body size is assumed to be favoured by sexual selection for increased fighting performance in contests for mating opportunities. Often, however, the correlation between size and performance is not well described. We studied a sexually selected performance trait, bite force in *Anolis* lizards, to determine whether patterns of SSD are linked to size-associated patterns of performance dimorphism at the macroevolutionary level, as expected under the sexual selection hypothesis for Rensch's rule. Additionally, we tested whether allometric patterns of performance dimorphism differ between mainland and island species, as the latter have likely evolved under a stronger sexual selection regime. We found that SSD overwhelmingly explains the relationship between performance dimorphism and size in anoles, as expected under a sexual selection model for Rensch's rule. However, residual performance dimorphism was higher in island than in mainland species, suggesting that these groups differ in performance dimorphism for reasons unrelated to size. Head size dimorphism was associated with residual performance dimorphism, but did not fully explain the difference in performance dimorphism between island and mainland species. Together, these findings highlight the need to interpret Rensch's rule patterns of body size evolution cautiously, as allometric patterns of performance dimorphism and size dimorphism might not be equivalent.

Keywords: bite force, head shape, insularity, performance, Rensch's rule, sexual dimorphism

Introduction

A common pattern in sexually reproducing species is that sexual dimorphism in body size becomes increasingly male-biased in larger species within a particular evolutionary group (Andersson, 1994; Fairbairn, 1997; Rensch, 1950). This pattern of body size evolution, which is a special case of Rensch's rule (Adams et al., 2020; Toyama, 2024), is frequently thought to arise from sexual selection for large male sizes in species that exhibit male–male competition for mating opportunities (e.g., Dale et al., 2007; Liang et al., 2022; Plard et al., 2011; Székely et al., 2004; Webster, 1992). As such, this hypothesis assumes a positive association between fighting performance and body size (Clutton-Brock, 1985; Fairbairn, 1997; Fairbairn et al., 2007; Lailvaux et al., 2004; Lindenfors et al., 2002; Shine, 1978). Indeed, in many species, size is a strong predictor of mating contests between males. For example, in polygynous animals, larger males typically win fights against smaller males, excluding them from access to females and increasing their own fitness (e.g., Clutton-Brock et al., 1977; Haley et al., 1994; Olsson, 1992; Plavcan, 2001).

Surprisingly, although male body size commonly correlates with competitive ability, the role of male competitive performance in driving Rensch's rule patterns of body size evolution is seldom explicitly tested. Instead, this size-based performance mechanism is often taken for granted in comparative tests of Rensch's rule (Abouheif and Fairbairn, 1997; Dale et al., 2007; Fairbairn, 1997; Liang et al., 2022; Székely et al., 2004; Webster, 1992), probably because of the difficulty of measuring performance at comparative scales (i.e., in phylogenetic-scale studies, which typically include dozens of species). In this study, we ask whether a key measure of fighting performance follows the predictions of Rensch's rule in a group of lizards exhibiting a Rensch's rule pattern of body size evolution. We note that although Rensch's rule is most commonly associated with the study of the allometry of SSD (Abouheif & Fairbairn, 1997; Meiri & Liang, 2021), Rensch's original observations were related not only to sexual differences in body size but to any relative difference between sexes, including differences in the relative sizes of particular anatomical structures (i.e., allometric "shape" differences) (Rensch, 1950, 1959; Toyama, 2024). Only recently, however, has the study of Rensch's rule begun to incorporate traits other than size (e.g., Adams et al., 2020; Machado et al., 2021; Santos & Machado, 2016),

in line with Rensch's original ideas. To date, however, tests of Rensch's rule have not investigated the evolution of fighting performance itself, which should be the direct target of sexual selection in such systems. As we show below, a direct investigation of the evolution of performance can shed new light on the dynamics of size and shape evolution in organisms that follow Rensch's rule.

Given a group of taxa that follows Rensch's rule in body size, shows male-biased SSD, and in which performance is sexually selected in males, three types of results can be obtained when testing for Rensch's rule in performance. First, if a universal evolutionary association between performance and size is followed by males and females (i.e., performance in males and females follows the same allometric trajectory; Figure 1A), performance differences between sexes should directly reflect the observed size differences between sexes. This simple mapping of performance to size is implicitly assumed in comparative studies of body size evolution that explain Rensch's rule patterns as the result of sexual selection on size-associated performance. If true, geometrically removing the size component from our measure of performance should eliminate the association between performance dimorphism and size in a group of species following this model (Figure 1D). This is what we expect if sexual selection on performance is the primary determinant of SSD evolution and if size is the overwhelming determinant of performance (i.e., if performance-based selection on size is sufficient to explain a Rensch's rule pattern of body size evolution).

However, Rensch's rule-like patterns of body size evolution may also be compatible with more complex underlying mechanisms of performance evolution, and the direct study of performance dimorphism evolution has the potential to identify such scenarios. The next two potential outcomes consider the possibility that the positive relationship between performance and body size could differ between males and females (i.e., sexes could differ in some aspect of the allometry of performance). For example, if males have greater values of a performance-linked trait after controlling for size (e.g., a male-biased shape dimorphism in some morphological or physiological trait that is linked to fighting ability), performance may always be relatively higher in males than in females, even if performance scales with size according to the same allometric exponent for both sexes (i.e., same slope but different allometric intercept for performance in males and females, Figure 1B). Another option is that males could gain additional performance benefits at larger sizes when compared to females (i.e., the allometric slope of performance in males is steeper than in females, Figure 1C). This might occur
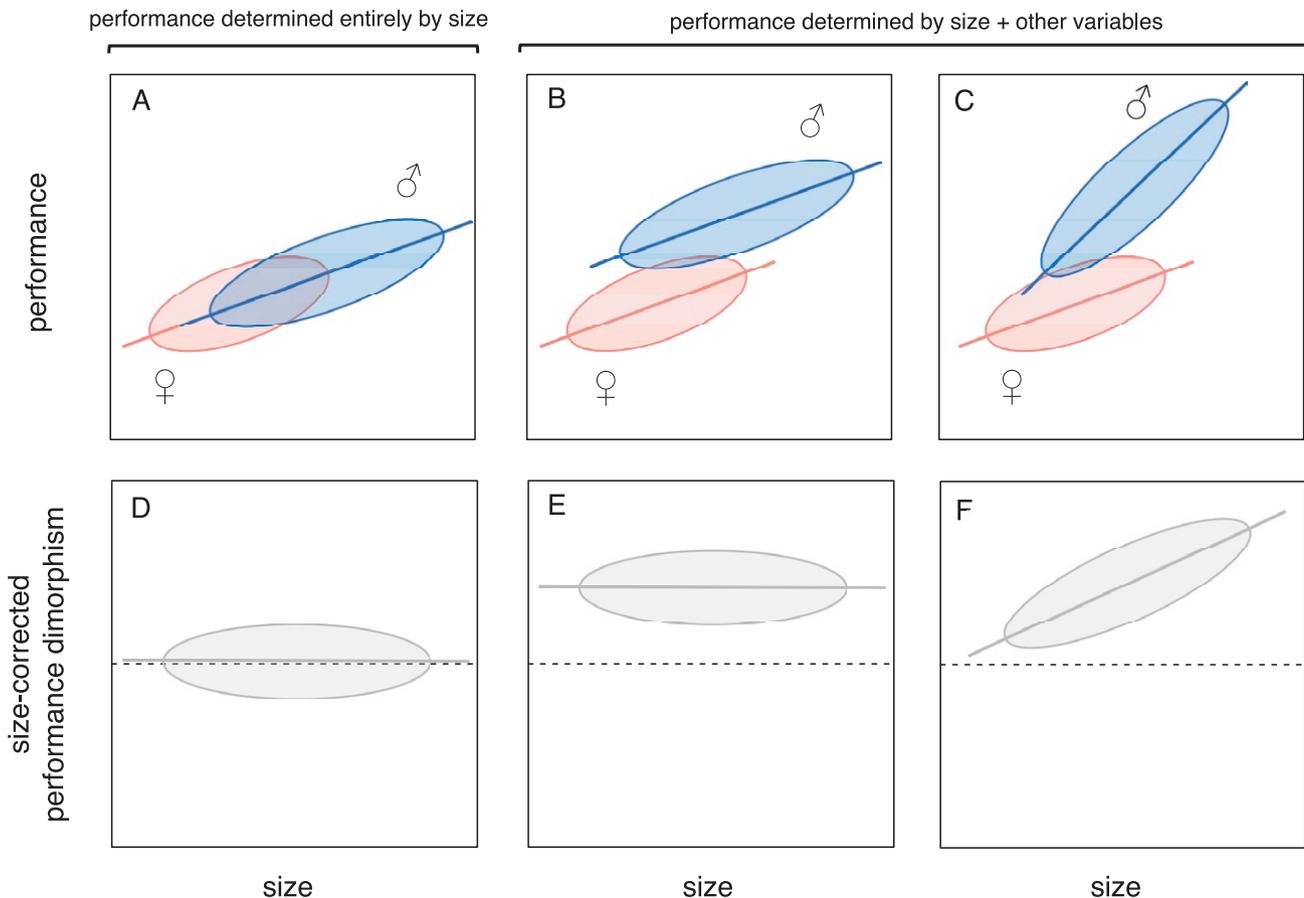

Figure 1. Different scenarios for the evolution of performance dimorphism in a group of species for which body size follows Rensch's rule. (A) If performance shows the same allometric trajectories in males and females (i.e., same intercept and slope) in a group of species that follows Rensch's rule in body size, then (D) dimorphism in size-corrected performance should be ~0 across the size distribution. Alternatively, (B) performance in males and females can have different allometric intercepts while sharing a similar slope (here males have higher intercepts). In this case, (E) size-corrected performance dimorphism will be constant but positive, with the intercept reflecting a global sex-specific performance advantage. (C) Finally, if allometric slopes differ between sexes (here the male slope is steeper), (F) size-corrected performance dimorphism will also be positively associated with size because performance scales with positive allometry in males.

if selection for male fighting performance simultaneously drives the evolution of SSD (by selecting for larger males) and sexual shape dimorphism (by selecting for shape traits that enhance fighting ability). In both such alternative cases, an observed Rensch's rule pattern of body size evolution would underestimate the real performance differences between sexes—by a constant in the first case, and disproportionately in larger species in the second case.

One potential way to distinguish these alternative mechanisms is to examine the allometry of size-corrected performance dimorphism.[1] In the first of these alternative cases, there should be no association between size-corrected performance dimorphism and body size (slope = 0), but size-corrected performance dimorphism should be higher than zero, representing a uniform performance difference between sexes across the size distribution (Figure 1E). In the second case, removing the size component from performance would not eliminate an association between performance dimorphism and size (slope > 0), because performance scales with size more steeply in males than in females (Figure 1F).

In this study, we test the correspondence between macroevolutionary patterns of SSD and sexual dimorphism in bite force, a sexually selected performance trait, in *Anolis* lizards. Anole species have diversified in a wide variety of ecological settings, resulting in the evolution of high levels of ecological and morphological diversity (Losos, 2009). Anoles are known to follow Rensch's rule in body size (Boyko, 2017) and most species show male-biased SSD, although the genus exhibits considerable diversity in SSD, with both positive (male-biased) and negative (female-biased) SSD values represented (Butler et al., 2000; Siliceo-Cantero et al., 2016; Supplementary Figure S1). In most anole species for which mating behaviour has been studied, males engage in combat with other male conspecifics for access to mating opportunities, using their jaws to bite each other (Johnson et al. 2010; Losos, 2009). Moreover, in individual contests between males, bite force has been shown to predict fighting success in anoles (De Meyer et al., 2019; Lailvaux and Irschick, 2007; Lailvaux et al., 2004).

Although male–male interactions seem to have been an important factor shaping the evolution of anoles, and some degree of competition among males for mates is typically expected, anole species can vary considerably in the strength of sexual selection they experience. For example, consistent with predictions of life history theory (Pianka 1970; Stearns 1989; Palkovacs 2003; Knell 2009; Schwarz & Meiri 2017; Montiglio et al. 2018; Terborgh 2023), many insular anole species exhibit slower growth rates, greater ages of sexual maturity, longer lifespans, higher population densities, more intense male-male competition, and higher levels of SSD than their mainland counterparts (Andrews, 1976, 1979). These differences support the idea that island anole species are selected for long-term competition and are under a stronger

influence of sexual selection compared to mainland species (Andrews, 1979).

Thus, we also ask whether ecological context (i.e., island vs. mainland) affects the evolutionary relationship between performance dimorphism and SSD in anoles. One option is that all anoles (including both males and females) follow a universal performance-size relationship (e.g., Figure 1A and D). We expect this if size is the sole driver of performance differences between sexes. Alternatively, there may be other determinants of performance dimorphism, and these may differ between regions as a function of differences in the intensity of sexual selection. For example, if insularity is associated with stronger sexual selection, island and mainland species could differ in their performance dimorphism patterns due to the evolution of additional (i.e., non-size) traits that enhance insular male performance, like secondary sexual traits or behaviour (e.g., Figure 1B, C, E, and F). Indeed, it is known that sexual selection can drive the evolution of larger heads in some lizards to increase biting performance (Lailvaux et al., 2004; Scharf & Meiri, 2013; Vitt & Cooper, 1985), and a similar pattern could be observed in insular anoles. This is not unlikely, as it is known that island and mainland anole species can diverge in aspects of their phenotype that are related to performance (Toyama et al., 2024). In this scenario, a Rensch's rule pattern in body size would underestimate the actual patterns of performance dimorphism in insular species.

Using data on both biting performance and body size for a large sample of insular and mainland anoles we test (a) whether dimorphism in bite force, a measure of intrasexual fighting performance in anoles, is overwhelmingly defined by body size differences; and (b) whether different sexual selection regimes, represented by insular and mainland environments, have resulted in the evolution of different performance–size relationships in anoles, consequently resulting in a discordance between SSD and performance dimorphism in those species under a stronger sexual selection regime (i.e., insular species). We also test whether such a mismatch could be explained by the evolution of exaggerated secondary sexual traits (i.e., large head sizes) in males under stronger sexual selection (i.e., males of insular species).

Materials and methods

Data

Bite force measurements were taken from 4,279 individual lizards representing males and females of 97 *Anolis* species. All measurements were taken *in vivo* by the same observer (AH) using an isometric Kistler force transducer (type 9203, Kistler Inc.) and the custom-fabricated bite plates and measurement protocol described in Herrel et al. (1999). The highest bite force recorded for each individual out of five trials was considered for further analysis. For each lizard in the performance data set, the same individual also measured body size (as snout-vent length, or SVL), head width, head height, and the jaw closing in-lever (measured as the distance between the quadrate and the coronoid process of the mandible, with the position of the latter approximated by the posteroventral corner of the jugal; Verwaijen et al., 2002) using a Mitutoyo digital calliper (± 0.01 mm) (Supplementary Figure S2). All measurements were natural log-transformed prior to analysis. Preliminary investigation revealed that the largest species in our dataset did not exhibit the patterns followed by most anoles (see Supplementary Materials), so

---

[1] In this paper, we adopt Klingenberg's "Gould-Mosimann" definitions of size and shape (Klingenberg 2016). We thus regard size as the scale of an object, and we regard shape as the proportional geometry of an object. The shape component of a particular measurement can be obtained by standardizing that measurement by its size (i.e., via size correction). According to the Gould-Mosimann School of allometry, a shape component obtained this way may contain variation that correlates with size (even though it has been size-corrected), and this variation represents the shape's allometry. Here we treat performance as a shape variable, and we study the allometry of performance dimorphism by examining the relationship between size-corrected performance dimorphism and body size.

we decided to exclude species of exceptional size from the dataset prior to analysis. We defined such species as those falling outside the interval defined by ±2 standard deviation from the mean of species body size (the sex-specific average of body size for each species). This resulted in the exclusion of five large species (*Anolis barahonae*, *A. chamaeleonides*, *A. cuvieri*, *A. equestris*, and *A. princeps*; Supplementary Figure S3), but no small species. These especially large anoles, which evolved in three different clades, all have relatively low levels of SSD, which we speculate could be a consequence of selective pressures specific to the evolution of extremely large body sizes in arboreal anoles.

For all analyses, we only included individuals that reached at least 75% of the maximum size reported for their species and sex. We calculated mean values of bite force, SVL, and head measurements for each sex of each species. For subsequent phylogenetic comparative analyses, we used the time-calibrated phylogeny of *Anolis* of Poe et al. (2017), with branches pruned to match our data set and with phylogenetically-compatible substitutions made to include species that were present in our data, but not in the phylogeny. Our final data set included data for males and females of 73 species of *Anolis* (males: mean number of individuals per species = 20.44; range of individuals per species = 1–161; females: mean number of individuals per species = 16.41; range of individuals per species = 1–78), which we categorized as "island" or "mainland" species, based on their region of origin.

Measures of sexual dimorphism

Sexual dimorphism in performance

For each species, we calculated sexual dimorphism in raw performance as ln(male bite force) – ln(female bite force). We calculated dimorphism in size-corrected performance as described below.

Accounting for the role of size in shape dimorphism is straightforward when size and shape have the same dimensionality (i.e., when the expected allometric slope between them is 1; Adams et al., 2020). However, for performance relationships, it is common for measures of size and performance to have different dimensions (Schmidt-Nielsen, 1984; note that performance-linked morphologies, such as muscle cross-sectional area, and direct performance measurements, such as bite force, can both be considered geometric "shape" if scale is removed). Indeed, in many cases, performance may scale with body size according to system-specific power relationships that must be estimated empirically (Herrel & O'Reilly, 2006; Schmidt-Nielsen, 1984), and it is necessary to account for the difference in dimensionality between size and shape when correcting for size to study sexual dimorphism in performance. Thus, to study performance dimorphism in anoles, we first determined the power at which bite force (measured in N) scales with body size (SVL, measured in mm).

To do this, we first averaged the male and female values of SVL and bite force respectively for each species to obtain single values of these variables per species. We then performed a phylogenetic generalized least squares (PGLS) regression of ln(average species bite force) on ln(average species SVL) using the package nlme (Pinheiro et al., 2023). In this and the rest of the phylogenetic linear models tested in this work, we assumed that residuals were distributed following Pagel's lambda model of evolution. We then used the slope of this regression (2.84 [± 0.19 SE]) to calculate size-corrected bite force as a geometric shape variable in which the effect of scale has been removed in a manner that accounts for the difference in dimensionality between our measures of performance and size (size-corrected bite force = ln(bite force) – 2.84 * ln(SVL)). Finally, we calculated size-corrected bite force dimorphism as size-corrected male bite force – size-corrected female bite force. Note that all subsequent statements about allometry will describe deviations from the above system-specific empirical scaling relationship between performance and size (i.e., in what follows, we will assume this relationship to reflect the isometric effect of scale on biting performance).

Sexual dimorphism in relative head size

To calculate sexual dimorphism in relative head size (a shape variable), we first calculated the average absolute head size for all individuals of each sex of each species, which we computed as the geometric mean of the natural log-transformed measurements of head width, head height, and the jaw closing in-lever (Mosimann, 1970). Note that we measured head size using these variables because they are strongly predicted to influence lizard bite force (De Meyer et al., 2019). Next, we calculated relative (i.e., size-corrected) head size as the log ratio of absolute head size to average body size for the same individuals (relative head size = geometric head size – ln(SVL); *note that all variables in this equation are unidimensional*). Finally, we calculated sexual dimorphism in relative head size for each species as the relative head size of males – the relative head size of females.

Analyses

First, to examine whether anoles follow Rensch's rule for body size, we performed a PGLS regression to test for a relationship between SSD [calculated as ln(male body size) – ln(female body size)] and average species size (Adams et al., 2020). Since insular species are known to show relatively higher levels of male-biased SSD than mainland species (Andrews, 1976, 1979; Siliceo-Cantero et al., 2016) we added a "region" term in our model, which indicates whether a species occurs on an island or the mainland. We began by testing a full model, including an interaction between average species size and region, and performed backward model selection until our model contained only significant terms.

We then performed a PGLS regression to test for a relationship between dimorphism in absolute (i.e., not size-corrected) bite force and average species size. We again added "region" (island vs. mainland) as a term in this model (i.e., absolute bite force dimorphism ~ species size * region) and used backward model selection to remove non-significant effects. If sexual differences in bite force are chiefly defined by sexual differences in size, we expected the effect of species size to be positive and significant in this model.

Next, if the evolution of SSD is sufficient to explain bite force dimorphism, removing the effect of size from bite force should result in bite force dimorphism being non-allometric and having an average value of zero. In other words, the Rensch's rule pattern observed for both body size and absolute bite force should not be observed for size-corrected bite force (Figure 1A and D). We tested this by performing a PGLS regression of size-corrected bite force dimorphism on average species size. If SSD fully explains the allometry of bite force dimorphism, we expect the slope of this relationship to be zero (Figure 1D). To test whether average size-corrected bite force dimorphism (i.e., the intercept) differs from zero,
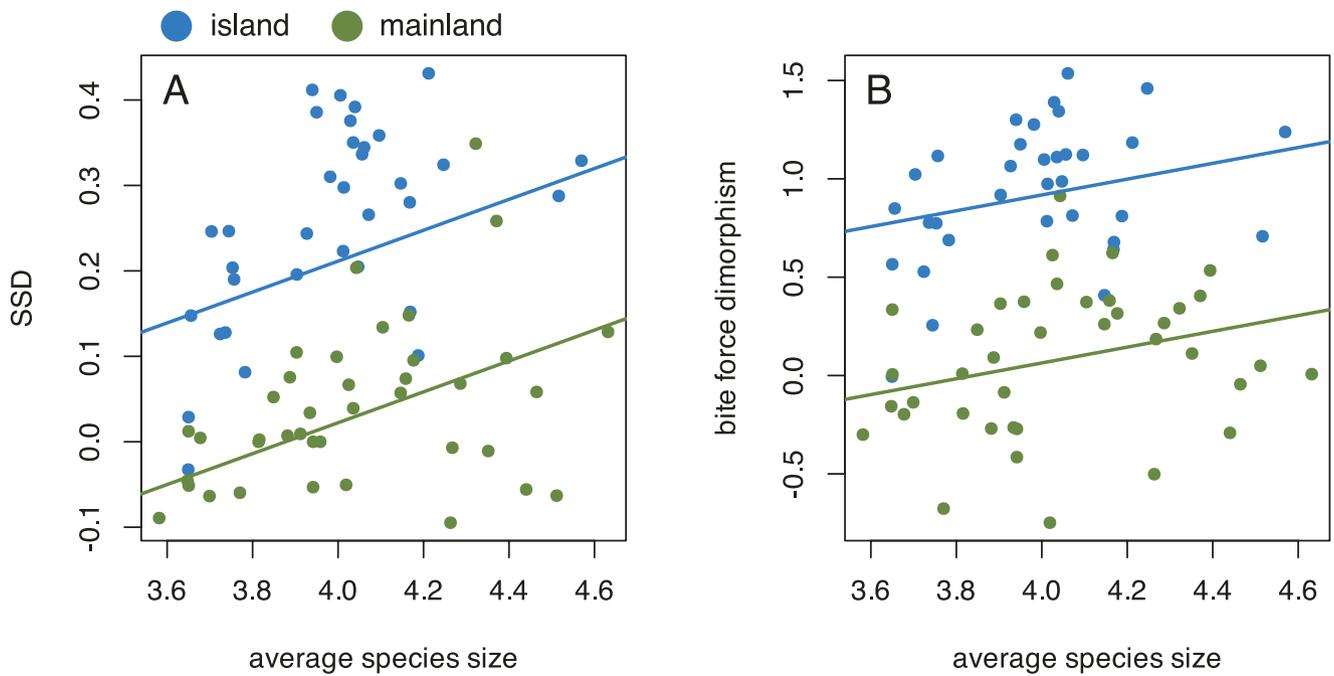
Figure 2. (A) Relationship between sexual size dimorphism (SSD) and average species size (SVL). The relationship is significant (i.e., *Anolis* body size follows Rensch's rule) but island and mainland species show significantly different intercepts. (B) Relationship between absolute bite force dimorphism and average species body size. The relationship is significant but island and mainland species show different intercepts. Solid lines represent PGLS regressions fitted for island and mainland species, separately.

we calculated 95% confidence intervals (CIs) around the mean value of island and mainland species and evaluated whether the intervals overlapped zero. The average value of size-corrected performance dimorphism should be no different from zero under this model (Figure 1D). However, if the evolution of other traits not represented by SSD (e.g., relative head size) also influences bite force dimorphism, these terms may differ from zero. Specifically, if sexes differ nonallometrically in a trait that affects bite performance (e.g., an among-sex difference in shape that does not vary with size, Figure 1B), only the intercept should differ from zero (Figure 1E), and if they differ allometrically in such a trait (Figure 1C), the slope should differ from zero (Figure 1F). As in the above analyses, we included "region" as a term in our PGLS model to test whether island and mainland anoles, which differ in the expected strength of sexual selection on males (Andrews 1976, 1979), differ in the allometry of relative bite force and/or its average value.

Finally, because we observed among-region differences in the allometry of size-corrected bite force dimorphism, we asked whether these differences could be explained by region-specific trends in the evolution of relative head size, a morphological shape trait that is commonly sexually dimorphic in lizards (e.g., Scharf & Meiri, 2013; Vitt & Cooper, 1985) and is strongly linked to bite performance in anoles (Herrel et al., 2007; Wittorski et al., 2016). To test whether relative head size dimorphism influences bite force dimorphism independently of SSD, we performed a PGLS regression of size-corrected bite force dimorphism on relative head size dimorphism, with region as an additional variable (size-corrected bite force dimorphism ~ relative head size dimorphism * region). If head size influences bite force independently of size, we expect this relationship to be positive. Additionally, if differences in relative head size dimorphism entirely explain observed differences in size-corrected

performance dimorphism between regions, the effects of "region" should be non-significant in this model.

Results

A PGLS regression of SSD on average species size was significant, confirming that body size in anoles follows a Rensch's rule pattern ($t = 4.13$, $p < .001$; Figure 2A). The "region" intercept term in this model was also significant, indicating that although island and mainland anoles follow Rensch's rule, island species show higher levels of male-biased SSD than mainland species for a given average species size ($t = -4.17$, $p < .001$; Figure 2A). Island and mainland slopes did not differ, however.

A PGLS regression of absolute bite force dimorphism on average species size was also significant ($t = 2.40$, $p = .019$; Figure 2B), illustrating the dependence of sexual differences in performance on size. For a given species size, bite force dimorphism was larger in island than in mainland species ($t = -8.44$, $p < .001$; Figure 2B), but island and mainland anoles did not have different slopes.

A PGLS regression of size-corrected bite force dimorphism on average species size was not significant ($t = -0.94$, $p = .348$; Figure 3A) providing no support for Rensch's rule in size-standardized biting performance. However, our model included a significant intercept effect of region ($t = -6.20$, $p < .001$), indicating that, for a given size, size-corrected bite force dimorphism is higher in island species (Figure 3A). There was no evidence for an interaction between region and size in this model. Average size-corrected performance dimorphism was no different from zero in mainland species (mean = −0.022, 95% CI = −0.082 to 0.038, Figure 3A), suggesting that SSD is sufficient to account for observed performance dimorphism on the mainland (compare Figures 1D and 3A). However, island species showed significant residual
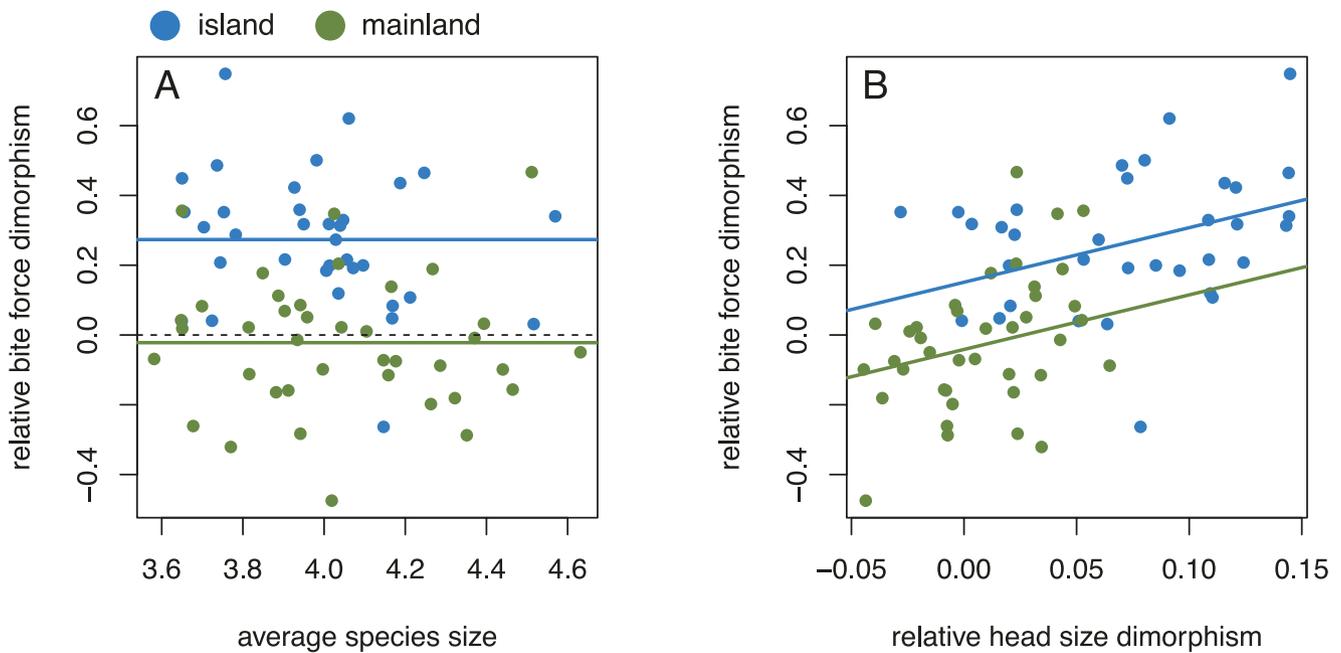
Figure 3. (A) Relationship between size-corrected bite force dimorphism and average species body size (SVL). Solid lines represent the mainland and island fits for the PGLS relationship between these variables. The horizontal dashed line indicates a dimorphism value of zero. None of the relationships shown are significant (solid lines have a slope of 0 and an intercept equal to the mean size-corrected bite force dimorphism of each group), but island species show, on average, significantly higher values of size-corrected bite force dimorphism than mainland species. (B) Relationship between size-corrected bite force dimorphism and relative head size dimorphism. Solid lines represent the mainland and island fits for the PGLS relationships between these variables. The relationship between these variables is significant, as is the difference in size-corrected bite force dimorphism between island and mainland species.

performance dimorphism after size correction (mean = 0.273, 95% CI = 0.209–0.338; compare Figures 1E and 3A).

A PGLS regression showed that size-corrected bite force dimorphism is positively dependent on size-corrected head size dimorphism ($t = 2.93$, $p = .005$; Figure 3B). However, island species still showed higher size-corrected bite force dimorphism than mainland species ($t = -3.75$, $p < .001$; Figure 3B). There was no evidence for an interaction between region and relative head size in this model.

Discussion

Rensch's rule patterns of body size evolution are most commonly explained via a sexual selection hypothesis, which assumes that the evolution of large male size results from selection for increased intrasexual fighting performance (Dale et al., 2007; Serrano-Meneses et al., 2008; Webster, 1992). However, the link between Rensch's rule and performance is seldom directly tested. Here we present evidence that a critical fighting performance metric evolves in accordance with the predictions of a simple size-based sexual selection model in *Anolis* lizards, indicating that body size is the overwhelming determinant of performance dimorphism in this system. While anoles follow Rensch's rule in body size, we found no evidence for additional performance advantages in males of larger species, other than those provided by size, rejecting the possibility that large size confers hyper-allometric performance advantages in anoles (this is true even considering giant species; see Supplementary Figure S4). Interestingly, however, anoles from regions that differ in the inferred intensity of sexual selection also differ in the magnitude of sexual dimorphism in size-corrected performance. Specifically, our results suggest that island species are subject to additional

contributors to performance dimorphism, including increased male-biased dimorphism in relative head size, but that these are observed across the entire size distribution (i.e., they are unrelated to size, or non-allometric). Through the study of biting performance, a locus of sexual selection, our approach sheds light on the mechanisms underlying the evolution of sexual dimorphism.

According to the ecomorphological paradigm, performance is the direct target of selection (Arnold, 1983; Emerson & Arnold, 1989; Irschick et al., 2008; Kingsolver & Huey, 2003; Wainwright & Reilly, 1994). Thus, studies that include direct measures of performance should increase our understanding of macroevolutionary patterns observed in related aspects of the phenotype. Numerous previous studies of Rensch's rule in body size have attributed the appearance of this pattern to sexual selection, as larger size is typically thought to result in superior performance in competing for mates. However, performance itself is not typically measured in these studies. Rather, associations between SSD and an indirect proxy of the intensity of male-male competition are tested instead (e.g., Cox et al., 2003; Dale et al., 2007; Fairbairn & Preziosi, 1994; Serrano-Meneses et al., 2008; Székely et al., 2004). Our study breaks new ground by directly measuring dimorphism in a performance metric related to fighting ability, and then testing for its association with SSD at the macroevolutionary level.

A positive relationship between size-corrected bite force dimorphism and size would indicate that sexual differences in bite force become proportionally larger in larger species. We did not find such a relationship in anoles. This suggests that, within each region, performance scales with a common allometric exponent in both males and females such that once the isometric effect of scale is removed, performance

dimorphism is size-independent. The majority of Rensch's rule studies assume that the allometry of SSD mirrors the allometry of performance dimorphism but do not actually test this, meaning that mismatches between sexual differences in size and performance can go unnoticed. In fact, it has been previously shown that this assumption is sometimes not met. For example, performance-associated secondary sexual traits like weapons or coloration have been found to follow Rensch's rule despite there being no such Rensch's rule pattern in body size in some groups (e.g., Machado et al., 2021; Santos & Machado, 2016). More recently, Juarez & Adams (2022) reported patterns of evolutionary allometry in locomotor performance dimorphism in anurans, despite SSD being isometric. Our work adds to these recent advances in the study of sexual dimorphism by testing Rensch's rule in a performance attribute thought to be a direct target of sexual selection. In our case, body size evolution indeed appears to explain the observed pattern of biting performance dimorphism evolution.

Even if sexual dimorphism in bite force is proportional to SSD, as suggested by our test of Rensch's rule, bite force differences between sexes can still be influenced by more than just size. In anoles, we found this to be true in island taxa, which typically occur at higher densities than mainland taxa (Andrews, 1976, 1979), and which previous studies suggest are subjected to stronger sexual selection in the form of male-male competition for access to mates or territories (Novosolov et al., 2013). We found that island species have a significant amount of residual performance dimorphism even after removing the influence of size (note how island species in Figure 3A follow the pattern illustrated in Figure 1E), indicating that there is an additional contributor to performance dimorphism across the entire size distribution of species in this group. In contrast, size seems to be the only substantial driver of performance dimorphism in mainland species (mainland species in Figure 3A follow the pattern illustrated in Figure 1D).

The evolution of secondary sexual traits used as weapons is one mechanism by which organisms can enhance fighting performance without necessarily increasing body size (Graham et al., 2022; Machado et al., 2021). Given that relative head size is known to affect bite force positively and to show relative male-biased dimorphism in anoles and other lizards (e.g., De Meyer et al., 2019; Lappin et al., 2006; Sagonas et al., 2014; Verwaijen et al., 2002), we expected head size dimorphism to explain the residual performance dimorphism we observed. We indeed found that size-corrected head size dimorphism was strongly associated with residual performance dimorphism across all anole species, supporting its role as a secondary sexual trait. This suggests that, as observed for relative bite force, the average level of dimorphism in relative head size is independent of size. This is consistent with findings by others that sexually selected traits do not always show positive evolutionary allometry (e.g., Painting et al., 2024; Tidière et al. 2017). The reasons for such patterns in some traits remain unclear, but one possibility is that the evolution of increasingly exaggerated structures at larger sizes is limited by natural selection due to physical constraints (Painting et al., 2024; Tidière et al. 2017).

However, relative head size dimorphism could not entirely explain island-mainland differences in size-corrected performance dimorphism, indicating that additional variables not considered in this study likely influence biting performance,

especially in males from island species. Previous studies have identified the *adductor externus* and the *pseudotemporalis* muscle groups in the heads of *Anolis* individuals as important determinants of bite force (Herrel et al., 2007; Wittorski et al., 2016). Although our linear measurement of relative head size should broadly correlate with the size of such muscles, part of the residual variation in performance could potentially be explained by a more detailed morphological and anatomical characterization of the *Anolis* head. Behavioral differences between species might also play a role in determining performance dimorphism, as it is known for lizards that more aggressive individuals tend to have stronger bites (Donihue et al., 2016; Herrel et al., 2009).

We found a constant degree of size-corrected performance dimorphism across body sizes in insular species, meaning that males from small species bite relatively harder than females in the same way males from large species do (this remains true even considering giant species, see Supplementary Figure S4). If size-corrected performance dimorphism can be understood as a proxy for sexual selection, and if sexual selection has been hypothesized to drive the evolution of large size, why are small species on average just as sexually dimorphic as large ones in terms of size-corrected performance? Several alternatives will need to be explored in future studies. For example, the evolution of body size dimorphism via sexual selection might have been limited in some species because of climatic, ecological, and physiological constraints (e.g., niche partitioning, or energetic constraints; Webster, 1992), but this might not have halted the evolution of dimorphism in secondary sexual traits (i.e., head size) and performance (i.e., bite force) in such species. Alternatively, if sexual selection is indeed stronger in larger species, the evolution of exaggerated head sizes in males of large species might have been limited by natural selection, such that survival costs associated with a bulky head do not outweigh the associated reproductive benefits (Tidière et al., 2017). For example, the evolution of disproportionately large heads through sexual selection could be constrained by habitat use (e.g., Kaliontzopoulou et al., 2015; Vanhooydonck & Van Damme, 1999). Relative biting performance dimorphism might also result from selection for niche partitioning between sexes. Previous research on anole lizards suggests that sexual dimorphism in morphological features is associated with sexual differences in ecology such as habitat use, home range, and diet (Schoener, 1967, 1968; Schoener & Schoener, 1982). In particular, sexual differences in head morphology and bite force performance in anoles have been associated with sexual differences in trophic niche (Herrel et al., 2006). Thus, dimorphism in relative bite force might have evolved independently of size in insular species to favour trophic niche partitioning as a response to the intense intraspecific competition found on islands due to high population densities (Andrews, 1979).

The consistent presence of relative performance differences across body sizes (e.g., via secondary sexual traits) is not incompatible with Rensch's rule in body size but rather should be viewed as one of several plausible scenarios consistent with Rensch's rule (e.g., Figure 1). As shown by insular anoles, size differences can be complemented by the occurrence of secondary sexual traits (and possibly other types of traits) in one of the sexes to maximize performance, even though these differences scale isometrically. Nonetheless, this demonstrates the need to interpret Rensch's rule-like patterns of body size evolution cautiously and to consider that patterns

of size dimorphism and performance dimorphism need not be aligned, especially when intrasexual competition and secondary sexual traits are known to occur in a particular group.

Supplementary material

Supplementary material is available at *Journal of Evolutionary Biology* online.

Data availability

The data underlying this article are available in the Dryad Digital Repository at https://doi.org/10.5061/dryad.bcc2 fqzpc.

Author contributions

Ken Toyama (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Investigation [equal], Writing - original draft [equal], Writing - review & editing [equal]), Jonathan Losos (Conceptualization [equal], Investigation [equal], Funding acquisition [equal]), Anthony Herrel (Data curation [equal], Resources [equal], Writing - review & editing [equal]), and Luke Mahler (Conceptualization [equal], Data curation [equal], Formal analysis [equal], Investigation [equal], Writing - original draft [equal], Writing - review & editing [equal], Funding acquisition [equal]).

Conflicts of interest

We have no conflict of interest to declare.

References

Abouheif, E. & Fairbairn, D. J. (1997). A comparative analysis of allometry for sexual size dimorphism: Assessing Rensch's rule. *The American Naturalist*, *149*(3), 540–562. https://doi.org/10.1086/286004

Adams, D. C., Glynne, E., & Kaliontzopoulou, A. (2020). Interspecific allometry for sexual shape dimorphism: Macroevolution of multivariate sexual phenotypes with application to Rensch's rule. *Evolution*, *74*(9), 1908–1922. https://doi.org/10.1111/evo.14049

Andersson, M. (1994). *Sexual selection*. Princeton University Press.

Andrews, R.M. (1976). Growth rate in island and mainland anoline lizards. *Copeia*, 1976, 477–482.

Andrews, R. M. (1979). Evolution of life histories: a comparison of Anolis lizards from matched island and mainland habitats. *Breviora*, *454*, 1–51.

Arnold, S. J. (1983). Morphology, performance and fitness. *American Zoologist*, *23*(2), 347–361. https://doi.org/10.1093/icb/23.2.347

Boyko, J. D. (2017). *The effect of congeners on trait evolution and sexual dimorphism in Lesser Antillean* Anolis *lizards*. University of Toronto.

Butler, M. A., Schoener, T. W., & Losos, J. B. (2000). The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution*, *54*(1), 259–272.

Clutton-Brock, T. H. (1985). Size, sexual dimorphism, and polygyny in primates. In W.L. Jungers (Ed.), *Size and scaling in primate biology* (pp. 51–60). Springer.

Clutton-Brock, T. H., Harvey, P. H., & Rudder, B. (1977). Sexual dimorphism, socionomic sex ratio and body weight in primates. *Nature*, *269*(5631), 797–800. https://doi.org/10.1038/269797a0

Cox, R. M., Skelly, S. L., & John-Alder, H. B. (2003). A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. *Evolution*, *57*(7), 1653–1669.

Dale, J., Dunn, P. O., Figuerola, J., … Whittingham, L. A. (2007). Sexual selection explains Rensch's rule of allometry for sexual size dimorphism. *Proceedings of the Royal Society B: Biological Sciences*, *274*(1628), 2971–2979. https://doi.org/10.1098/rspb.2007.1043

De Meyer, J., Irschick, D. J., Vanhooydonck, B., … Herrel, A. (2019). The role of bite force in the evolution of head shape and head shape dimorphism in *Anolis* lizards. *Functional Ecology*, *33*(11), 2191–2202. https://doi.org/10.1111/1365-2435.13438

Donihue, C. M., Brock, K. M., Foufopoulos, J., & Herrel, A. (2016). Feed or fight: Testing the impact of food availability and intraspecific aggression on the functional ecology of an island lizard. *Functional Ecology*, *30*(4), 566–575. https://doi.org/10.1111/1365-2435.12550

Emerson, S. B. & Arnold, S. J. (1989). Intra-and interspecific relationships between morphology, performance, and fitness. In D.B. Wake, G. Roth (Eds), *Complex organismal functions: Integration and evolution in vertebrates* (pp. 295–314).

Fairbairn, D. J. (1997). Allometry for sexual size dimorphism: Pattern and process in the coevolution of body size in males and females. *Annual Review of Ecology and Systematics*, *28*(1), 659–687. https://doi.org/10.1146/annurev.ecolsys.28.1.659

Fairbairn, D. J., Blankenhorn, W. U., & Székely, T. (Eds.). (2007). *Sex, size and gender roles: Evolutionary studies of sexual size dimorphism*. Oxford University Press.

Fairbairn, D. J. & Preziosi, R. F. (1994). Sexual selection and the evolution of allometry for sexual size dimorphism in the water strider, *Aquarius remigis*. *The American Naturalist*, *144*(1), 101–118. https://doi.org/10.1086/285663

Graham, Z. A., Kaiser, N., & Palaoro, A. V. (2022). Biomechanics influence sexual dimorphism in the giant mesquite bug, *Thasus neocalifornicus*. *Zoology*, *150*, 125988. https://doi.org/10.1016/j.zool.2021.125988

Haley, M. P., Deutsch, C. J., & Le Boeuf, B. J. (1994). Size, dominance and copulatory success in male northern elephant seals, *Mirounga angustirostris*. *Animal Behaviour*, *48*(6), 1249–1260. https://doi.org/10.1006/anbe.1994.1361

Herrel, A., Andrade, D. V., De Carvalho, J. E., … Navas, C. (2009). Aggressive behavior and performance in the tegu lizard *Tupinambis merianae*. *Physiological and Biochemical Zoology*, *82*(6), 680–685. https://doi.org/10.1086/605935

Herrel, A., Joachim, R., Vanhooydonck, B., & Irschick, D. J. (2006). Ecological consequences of ontogenetic changes in head shape and bite performance in the Jamaican lizard *Anolis lineatopus*. *Biological Journal of the Linnean Society*, *89*(3), 443–454. https://doi.org/10.1111/j.1095-8312.2006.00685.x

Herrel, A., McBrayer, L. D., & Larson, P. M. (2007). Functional basis for sexual differences in bite force in the lizard *Anolis carolinensis*. *Biological Journal of the Linnean Society*, *91*(1), 111–119. https://doi.org/10.1111/j.1095-8312.2007.00772.x

Herrel, A. & O'Reilly, J. C. (2006). Ontogenetic scaling of bite force in lizards and turtles. *Physiological and Biochemical Zoology*, *79*(1), 31–42. https://doi.org/10.1086/498193

Herrel, A., Spithoven, L., Van Damme, R., & De Vree, F. (1999). Sexual dimorphism of head size in *Gallotia galloti*: Testing the niche divergence hypothesis by functional analyses. *Functional Ecology*, *13*(3), 289–297. https://doi.org/10.1046/j.1365-2435.1999.00305.x

Irschick, D. J., Meyers, J. J., Husak, J. F., & Le Galliard, J. F. (2008). How does selection operate on whole-organism functional performance capacities? A review and synthesis. *Evolutionary Ecology Research*, *10*(2), 177–196.

Johnson, M. A., Revell, L. J., & Losos, J. B. (2010). Behavioral convergence and adaptive radiation: Effects of habitat use on territorial behavior in *Anolis* lizards. *Evolution*, *64*(4), 1151–1159. https://doi.org/10.1111/j.1558-5646.2009.00881.x

Juarez, B. H. & Adams, D. C. (2022). Evolutionary allometry of sexual dimorphism of jumping performance in anurans. *Evolutionary Ecology*, *36*(4), 717–733.

Kaliontzopoulou, A., Carretero, M. A., & Adams, D. C. (2015). Eco-morphological variation in male and female wall lizards and the macroevolution of sexual dimorphism in relation to habitat use. *Journal of Evolutionary Biology*, *28*(1), 80–94. https://doi.org/10.1111/jeb.12540

Kingsolver, J. G. & Huey, R. B. (2003). Introduction: The evolution of morphology, performance, and fitness. *Integrative and Comparative Biology*, *43*(3), 361–366. https://doi.org/10.1093/icb/43.3.361

Klingenberg, C. P. (2016). Size, shape, and form: Concepts of allometry in geometric morphometrics. *Development Genes and Evolution*, *226*(3), 113–137. https://doi.org/10.1007/s00427-016-0539-2

Knell, R. J. (2009). Population density and the evolution of male aggression. *Journal of Zoology*, *278*(2), 83–90. https://doi.org/10.1111/j.1469-7998.2009.00566.x

Lailvaux, S. P., Herrel, A., VanHooydonck, B., … Irschick, D. J. (2004). 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*, *271*(1556), 2501–2508. https://doi.org/10.1098/rspb.2004.2891

Lailvaux, S. P. & Irschick, D. J. (2007). The evolution of performance-based male fighting ability in Caribbean *Anolis* lizards. *The American Naturalist*, *170*(4), 573–586. https://doi.org/10.1086/521234

Lappin, A. K., Hamilton, P. S., & Sullivan, B. K. (2006). Bite-force performance and head shape in a sexually dimorphic crevice-dwelling lizard, the common chuckwalla [*Sauromalus ater* (= *obesus*)]. *Biological Journal of the Linnean Society*, *88*(2), 215–222. https://doi.org/10.1111/j.1095-8312.2006.00615.x

Liang, T., Meiri, S., & Shi, L. (2022). Sexual size dimorphism in lizards: Rensch's rule, reproductive mode, clutch size, and line fitting method effects. *Integrative Zoology*, *17*(5), 787–803. https://doi.org/10.1111/1749-4877.12569

Lindenfors, P., Tullberg, B. S., & Biuw, M. (2002). Phylogenetic analyses of sexual selection and sexual size dimorphism in pinnipeds. *Behavioral Ecology and Sociobiology*, *52*(3), 188–193.

Losos, J. (2009). *Lizards in an evolutionary tree*. University of California Press.

Machado, G., Buzatto, B. A., & Samia, D. S. (2021). It is not always about body size: Evidence of Rensch's rule in a male weapon. *Biology Letters*, *17*(6), 20210234.

Meiri, S. & Liang, T. (2021). Rensch's rule—Definitions and statistics. *Global Ecology and Biogeography*, *30*(3), 573–577. https://doi.org/10.1111/geb.13255

Montiglio, P. O., Dammhahn, M., Dubuc Messier, G., & Réale, D. (2018). The pace-of-life syndrome revisited: The role of ecological conditions and natural history on the slow-fast continuum. *Behavioral Ecology and Sociobiology*, *72*(7), 1–9.

Mosimann, J. E. (1970). Size allometry: Size and shape variables with characterizations of the lognormal and generalized gamma distributions. *Journal of the American Statistical Association*, *65*(330), 930–945. https://doi.org/10.2307/2284599

Novosolov, M., Raia, P., & Meiri, S. (2013). The island syndrome in lizards. *Global Ecology and Biogeography*, *22*(2), 184–191. https://doi.org/10.1111/j.1466-8238.2012.00791.x

Olsson, M. (1992). Contest success in relation to size and residency in male sand lizards, *Lacerta agilis*. *Animal Behaviour*, *44*, 386–388. https://doi.org/10.1016/0003-3472(92)90046-c

Painting, C. J., Symonds, M. R., & Holwell, G. I. (2024). The evolution of positive allometry and exaggerated traits in a diverse beetle clade. *Functional Ecology*, *38*, 1265.

Palkovacs, E. P. (2003). Explaining adaptive shifts in body size on islands: A life history approach. *Oikos*, *103*(1), 37–44. https://doi.org/10.1034/j.1600-0706.2003.12502.x

Pianka, E. R. (1970). On r-and K-selection. *The American Naturalist*, *104*(940), 592–597.

Pinheiro J, Bates D, R Core Team (2023). *nlme: Linear and Nonlinear Mixed Effects Models. R package version 3.1-164*.

Plard, F., Bonenfant, C., & Gaillard, J. M. (2011). Revisiting the allometry of antlers among deer species: Male–male sexual competition as a driver. *Oikos*, *120*(4), 601–606.

Plavcan, J. M. (2001). Sexual dimorphism in primate evolution. *American Journal of Physical Anthropology*, *116*(S33), 25–53. https://doi.org/10.1002/ajpa.10011.abs

Poe, S., Nieto-Montes de Oca, A., Torres-Carvajal, O., … Latella, I. (2017). A phylogenetic, biogeographic, and taxonomic study of all extant species of *Anolis* (Squamata; Iguanidae). *Systematic Biology*, *66*(5), 663–697.

Rensch, B. (1950). Die Abhängigkeit der relativen Sexualdifferenz von der Körpergrösse. *Bonner Zoologische Beiträge*, *1*, 5869.

Rensch, B. (1959). *Evolution above the species level*. Columbia University Press.

Sagonas, K., Pafilis, P., Lymberakis, P., … Valakos, E. D. (2014). Insularity affects head morphology, bite force and diet in a Mediterranean lizard. *Biological Journal of the Linnean Society*, *112*(3), 469–484. https://doi.org/10.1111/bij.12290

Santos, E. S. A. & Machado, G. (2016). Sexual dichromatism in wing pigmentation of New World dragonflies follows Rensch's rule. *Journal of Evolutionary Biology*, *29*(7), 1447–1454. https://doi.org/10.1111/jeb.12885

Scharf, I. & Meiri, S. (2013). Sexual dimorphism of heads and abdomens: Different approaches to "being large" in female and male lizards. *Biological Journal of the Linnean Society*, *110*(3), 665–673. https://doi.org/10.1111/bij.12147

Schmidt-Nielsen, K. (1984). *Scaling: why is animal size so important?* Cambridge University Press.

Schoener, T. W. (1967). The ecological significance of sexual dimorphism in size in the lizard *Anolis conspersus*. *Science*, *155*(3761), 474–477. https://doi.org/10.1126/science.155.3761.474

Schoener, T. W. (1968). The *Anolis* lizards of Bimini: Resource partitioning in a complex fauna. *Ecology*, *49*(4), 704–726. https://doi.org/10.2307/1935534

Schoener, T. W. & Schoener, A. (1982). Intraspecific variation in home-range size in some *Anolis* lizards. *Ecology*, *63*(3), 809–823. https://doi.org/10.2307/1936801

Schwarz, R. & Meiri, S. (2017). The fast-slow life-history continuum in insular lizards: A comparison between species with invariant and variable clutch sizes. *Journal of Biogeography*, *44*(12), 2808–2815. https://doi.org/10.1111/jbi.13067

Serrano-Meneses, M. A., Cordoba-Aguilar, A., Azpilicueta-Amorín, M., … Szekely, T. (2008). Sexual selection, sexual size dimorphism and Rensch's rule in Odonata. *Journal of Evolutionary Biology*, *21*(5), 1259–1273.

Shine, R. (1978). Sexual size dimorphism and male combat in snakes. *Oecologia*, *33*(3), 269–277. https://doi.org/10.1007/BF00348113

Siliceo-Cantero, H. H., García, A., Reynolds, R. G., … Lister, B. C. (2016). Dimorphism and divergence in island and mainland anoles. *Biological Journal of the Linnean Society*, *118*(4), 852–872.

Stearns, S. C. (1989). Trade-offs in life-history evolution. *Functional Ecology*, *3*(3), 259–268. https://doi.org/10.2307/2389364

Székely, T., Freckleton, R. P., & Reynolds, J. D. (2004). Sexual selection explains Rensch's rule of size dimorphism in shorebirds. *Proceedings of the National Academy of Sciences of the United States of America*, *101*(33), 12224–12227. https://doi.org/10.1073/pnas.0404503101

Terborgh, J. (2023). The "island syndrome" is an alternative state. *Journal of Biogeography*, *50*(3), 467–475. https://doi.org/10.1111/jbi.14530

Tidière, M., Lemaître, J. F., Pélabon, C., Gimenez, O., & Gaillard, J. M. (2017). Evolutionary allometry reveals a shift in selection pressure on male horn size. *Journal of Evolutionary Biology*, *30*(10), 1826–1835.

Toyama, K. S. (2024). *Beyond size dimorphism: The past, present, and future of Rensch's rule*. bioRxiv, https://doi.org/10.1101/2024.10.30.621038, preprint: not peer reviewed.

Toyama, K. S., Tinius, A., & Mahler, D. L. (2024). Evidence supporting an evolutionary trade-off between material properties and architectural design in *Anolis* lizard long bones. *Evolution*, *78*(2), 315–328. https://doi.org/10.1093/evolut/qpad208

Vanhooydonck, B. & Van Damme, R. (1999). Evolutionary relationships between body shape and habitat use in lacertid lizards. *Evolutionary Ecology Research*, *1*(7), 785–805.

Verwaijen, D., Van Damme, R., & Herrel, A. (2002). Relationships between head size, bite force, prey handling efficiency and diet in two sympatric lacertid lizards. *Functional Ecology*, *16*(6), 842–850. https://doi.org/10.1046/j.1365-2435.2002.00696.x

Vitt, L. J. & Cooper Jr, W. E. (1985). The evolution of sexual dimorphism in the skink *Eumeces laticeps*: An example of sexual selection. *Canadian Journal of Zoology*, *63*(5), 995–1002. https://doi.org/10.1139/z85-148

Wainwright, P. C. & Reilly, S. M. (Eds.). (1994). *Ecological morphology: Integrative organismal biology*. University of Chicago Press.

Webster, M. S. (1992). Sexual dimorphism, mating system and body size in New World blackbirds (Icterinae). *Evolution*, *46*(6), 1621–1641. https://doi.org/10.1111/j.1558-5646.1992.tb01158.x

Wittorski, A., Losos, J. B., & Herrel, A. (2016). Proximate determinants of bite force in *Anolis* lizards. *Journal of Anatomy*, *228*(1), 85–95. https://doi.org/10.1111/joa.12394