Evolution, 2026, **80**(**3**), 570–583
https://doi.org/10.1093/evolut/qpaf243
Advance access publication 3 December 2025
Original Article

Interspecific allometry of sexual shape dimorphism in small-bodied and large-bodied geckos

Elizabeth Glynne and Dean C. Adams

Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, Iowa, United States

Corresponding author: Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, Iowa, 50010, United States. Email: glynne.elizabeth@gmail.com

Abstract

At macroevolutionary scales across species, sexual dimorphism often covaries with body size, generating allometric trends. Such patterns are most evident for body size dimorphism, while trends in sexual shape dimorphism remain underexamined. Additionally, how small body sizes (miniaturization) affects such patterns is largely unknown. We evaluated allometry in sexual shape dimorphism in two families of geckos to determine whether changes in body size associate with changes in shape dimorphism. Using surface scans of head shape from nearly 600 individuals across 99 species, we found considerable variation in levels of sexual shape dimorphism across taxa, with some species displaying little dimorphism and others exhibiting large sexual differentiation. Interspecific trends differed between the two families, with strong negative allometry in Sphaeorodactylidae (a family with many small-bodied species), while Phyllodactylidae (a family containing few small-bodied species) displayed isometry and no discernible trend. Notably, greater sexual shape dimorphism was displayed in small-bodied sphaerodactylid species, and corresponded with females exhibiting more robust heads; consistent with sex-specific foraging strategies and dietary differences observed in this group. Our study reveals that interspecific allometry in traits other than body size can have a pervasive influence on patterns of phenotypic diversity across the tree of life.

Keywords: sexual dimorphism, morphometrics, miniaturization, allometry

Introduction

A near-ubiquitous pattern displayed by animals is that of sexual dimorphism, the systematic differences between males and females of the same species (Andersson, 1994; Darwin, 1871; Fairbairn, 2013). Males and females frequently differ in one or more phenotypic characteristics, including morphological attributes such as size, shape, or coloration, as well as exhibiting behavioral and physiological differences (Cox et al., 2003; Fairbairn, 1997). Sex-specific differences in body size, or sexual size dimorphism (SSD), is one of the most conspicuous patterns of sexual dimorphism, and is found in a wide variety of taxa (Fairbairn, 2013; Piross et al., 2019; Rensch, 1950; Reyes-Puig et al., 2023; Székely et al., 2004; among others). Yet increasingly, it is becoming apparent that organisms also display strong patterns of sexual shape dimorphism (SShD), both in overall body shape, as well as in the shapes of particular anatomical traits (e.g., Adams et al., 2020; Berns & Adams, 2013; Cruz-Elizalde et al., 2020; Dursun et al., 2022; Gidaszewski et al., 2009; Kelly et al., 2013; Kaliontzopoulou et al., 2015; Toyama et al., 2023). Deciphering how and why such patterns of sexual dimorphism emerge is the subject of considerable scrutiny. From an evolutionary perspective, sexual differences are likely to evolve whenever natural or sexual selection is sex-specific (McGlothlin et al., 2019). For example, sex-specific habitat use (Butler et al., 2000; Kaliontzopoulou et al., 2015) or the partitioning of trophic resources (Li & Kokko, 2021; Schoener, 1967) can result in enhanced patterns of sexual dimorphism. Likewise, fecundity selection on female body size, or sexual selection for increased male body size, are both expected to lead to increased levels of SSD (Fairbairn et al., 2007; Horne et al., 2020; Janicke & Fromonteil, 2021; Székely et al., 2000; Winkler et al., 2024).

Across taxa, the degree of sexual dimorphism is rarely uniform. Rather, the extent of sexual dimorphism often differs between species, with some species exhibiting little sexual dimorphism while others display considerable differences between the sexes. When viewed comparatively, differences in the degree of sexual dimorphism are often found to vary systematically with species' body sizes, resulting in allometric trends of sexual dimorphism at macroevolutionary scales (Abouheif & Fairbairn, 1997; Fairbairn, 1997; Rensch, 1950, 1960). The past several decades have seen considerable interest in deciphering interspecific allometry patterns of sexual size dimorphism in particular, as biologists seek to understand the evolution of sexual dimorphism and its underlying causes (e.g., Abouheif & Fairbairn, 1997; Blanckenhorn et al., 2006; Ceballos et al., 2013; Dale et al., 2007; Johnson et al., 2017; Liao et al., 2013; Regis & Meik, 2017). However, while sexual differences in overall body size, or the sizes of particular anatomical traits (Machado et al., 2021), are most commonly interrogated, interspecific allometry of sexual dimorphism is not restricted to this aspect of the organismal phenotype. In fact, Rensch's (1950, 1960) original work describing interspecific trends of sexual dimorphism was based on observations of sex-specific differences in body size, as well as differences in numerous other anatomical traits (see Adams et al., 2020; Toyama, 2025).

Received August 7, 2025; revisions received October 21, 2025; accepted November 7, 2025
Associate Editor: Emma Sherratt; Handling Editor: Hélène Morlon
© The Author(s) 2025. Published by Oxford University Press on behalf of The Society for the Study of Evolution (SSE). This is an Open Access article distributed under the terms of the Creative Commons Attribution License (https://creativecommons.org/licenses/by/4.0/), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.

Downloaded from https://academic.oup.com/evolut/article/80/3/570/8363668 by Iowa State University Library user on 06 March 2026

Correspondingly, researchers have recently begun investigating macroevolutionary trends in sexual dimorphism in other phenotypic attributes, revealing allometric patterns in behavioral and performance traits (Juarez and Adams, 2022; Toyama et al., 2025), as well as aspects of organismal shape (Adams et al., 2020).

One factor that likely influences patterns of SShD is miniaturization, the extreme reduction of adult body size, often identified in comparison to ancestral taxa (Carvalho de Oliveira et al., 2021; Hanken & Wake, 1993). Miniaturization has evolved independently many times across the vertebrate tree of life, and is associated with a wide range of structural modifications. These include numerous skeletal alterations, such as increased neurocranial expansion, the fusion of bones, reduced ossification, and other skeletal simplifications (Hanken & Wake, 1993; Meiri et al., 2015; Rieppel 1984b; Rieppel, 1996; Vallejo-Pareja, 2018; Yeh, 2002). Other structural changes commonly associated with miniaturization include organ reduction, tissue loss, and enhanced sensory organ size relative to body size, among others (Daza et al., 2008; Ocampo et al., 2018; Perez-Martinez & Leal, 2021). Additionally, changes in body size influence the evolutionary trajectories of morphological traits, resulting in different relative sizes and proportions of body parts (e.g., Itgen et al., 2022; Linke et al., 1986). Such anatomical changes are necessary to maintain organismal functionality at smaller body sizes, yet an inevitable consequence of these shifts is that the relative sizes of different body parts are necessarily altered. Thus, it follows that both body proportions, and the shape of anatomical parts, will likely incur changes as organisms evolve to become smaller (Lobón-Rovira et al., 2024). Furthermore, if selection operates differentially on males and females during the process of miniaturization, one may hypothesize that patterns of sexual shape dimorphism may similarly be altered (Scharf & Meiri, 2013).

Geckos (Gekkota) provide an ideal study system for evaluating patterns of sexual dimorphism relative to the reduction of body size and miniaturization. With over 2,400 species, geckos exhibit extensive variation in both body size and skull morphology, and within the clade there have been multiple independent instances of body size reduction (Glynne & Adams, 2024; Meiri, 2018). Further, prior studies indicate that levels of SSD vary among gecko species, with female-biased SSD frequently observed in smaller-bodied species and male-biased SSD more common in larger-bodied species (Glynne & Adams, 2024; Perez-Martinez & Leal, 2021). In Sphaerodactylidae for instance, many species are small-bodied, and most exhibit female-biased SSD (Cox & Kahrl, 2014; Fitch, 1981), while the larger species in the group display male-biased SSD (Griffing et al., 2018). Additionally, in Sphaerodactylidae, there is significant evolutionary allometry of SSD across taxa (Glynne & Adams, 2024), with increasing size dimorphism in smaller bodied species, which are more female biased. By contrast, the family Phyllodactylidae, which contains few small-bodied species, exhibits no systematic trend in SSD with body size, and instead the pattern is more isometric. Differences in the patterns of evolutionary allometry between the two clades were hypothesized to be associated with reproduction, as miniaturized sphaerodactylid species–whose smaller species tend to be more female-biased–also produce proportionally larger (longer) eggs (Glynne & Adams, 2024) and are only able to produce one egg per clutch (Bustard, 1968). However, whether body size differences among taxa concomitantly influence allometric patterns in other traits such as SShD remains under-examined. Given that the process of miniaturization and size reduction influences skull morphology (neurocranial expansion, bone fusion, proportionally larger eyes: Daza et al., 2008; Rieppel, 1996), one might hypothesize that sex-specific head shape differences may be influenced by the functional trade-offs associated with feeding and performance as species become smaller. Across lizards, fecundity selection results in females with relatively larger abdomens, while sexual selection results in males with relatively larger heads (Scharf & Meiri, 2013). These contrasting selective pressures generate differing patterns of sexual dimorphism in overall body size and body proportions across taxa. In an analogous manner, if selection on cranial elements operates differentially on males and females, such differences may drive the evolution of SShD in head shape as well. The fact that geckos exhibit extensive cranial variation and have witnessed multiple instances of body size change (largely reduction) makes them an ideal system for evaluating the prediction of changes in body size across the phylogeny are associated with changes in patterns of sexual shape dimorphism.

In this study, we quantified variation in sexual shape dimorphism in cranial morphology across a phylogenetically diverse sample of geckos. The goal of our study was to evaluate macroevolutionary patterns of sexual shape dimorphism (SShD) in head shape across the phylogeny of new world geckos, and to discern whether allometric patterns of SShD differed between two families (Sphaerodactylidae and Phyllodactylidae) that also differ in the number of small-bodied species they contain. To accomplish this we leveraged geometric morphometric approaches to characterize cranial morphology from high-resolution surface scans of males and females from 99 species. We then used a series of multivariate and phylogenetic comparative analyses to evaluate evolutionary trends in the SShD, and to test the hypothesis that shifts in body size across the phylogeny were associated with increased levels of SShD in this group.

Materials and methods

Photogrammetry and model processing

Initial high-resolution 3D images of head shape were obtained for 619 adult specimens from 106 species from two families, Sphaerodactylidae and Phyllodactylidae (hereafter referred to as sphaerodactylids and phyllodactylids). The specimens used in this study were from those available in 13 Natural History collections, were formalin-fixed and stored in ethanol, and represented species present on a recent molecular phylogeny for the group (Tonini et al., 2016). When possible, three males and three females were successfully imaged from each species. Specimens observed to exhibit significant shape distortions from desiccation or other preservation effects were removed from the sample. This resulted in a final dataset containing 589 adult individuals from 99 species representing 43 phyllodactylid species and 56 sphaerodactylid species. This sampling comprised approximately 25 percent of the taxonomic diversity of each group. Importantly however, the species selected varied widely in body sizes, and represented nearly the entire extent of body size variation exhibited in each family. Thus,

Downloaded from https://academic.oup.com/evolut/article/80/3/570/8363668 by Iowa State University Library user on 06 March 2026

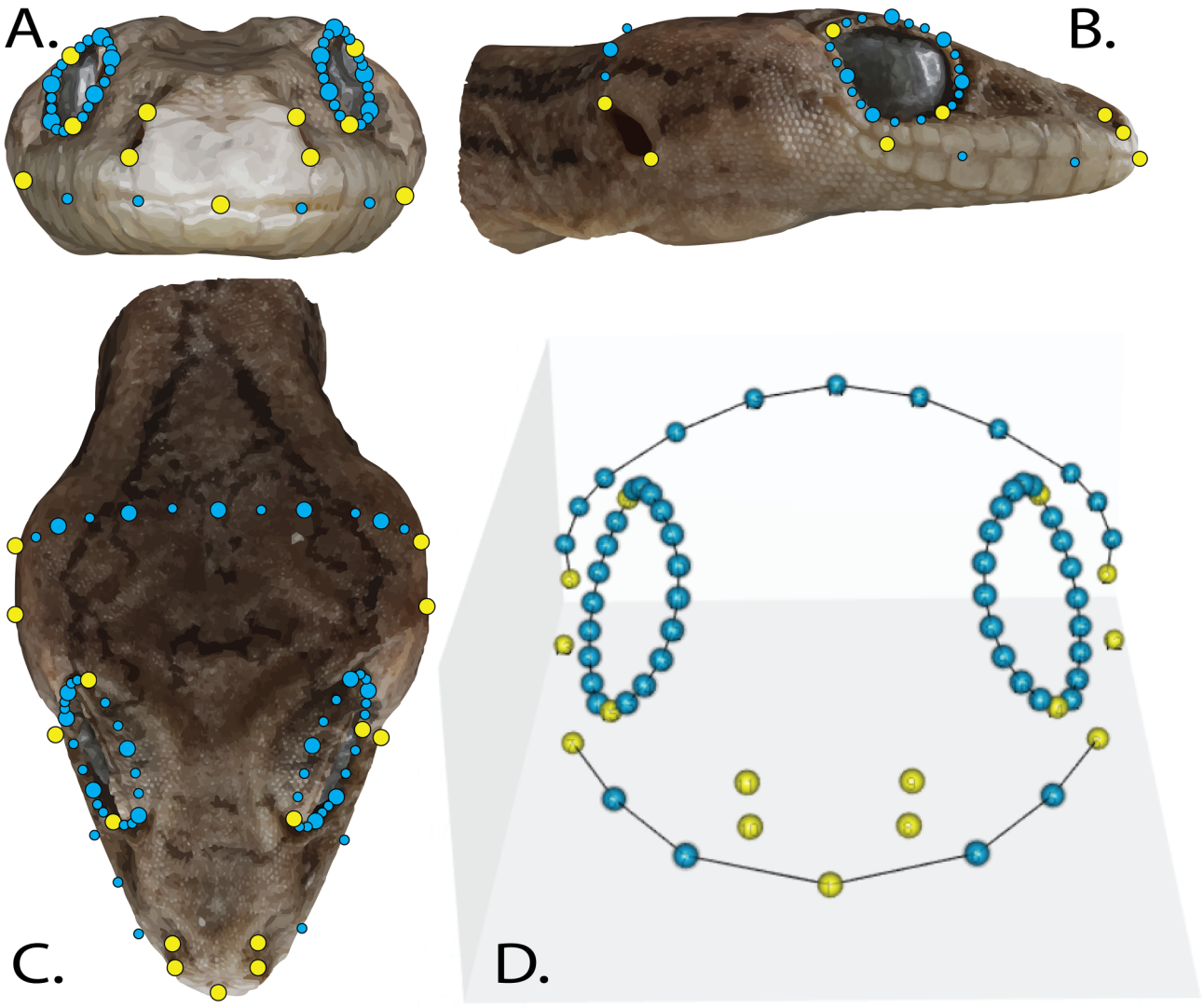


Figure 1. Locations of three-dimensional landmarks and semilandmarks used in this study. Landmarks were placed on specimens in anterior (A), lateral (B), and dorsal (C) views for a resulting configuration of landmarks as seen in the last anterior view (D). Yellow dots represent fixed anatomical landmarks, while blue dots represent sliding semilandmarks placed along curved structures to capture shape variation. Alt text: "Diagram showing the placement of fixed cranial landmarks and sliding semilandmarks on gecko skulls in anterior, lateral, and dorsal views."

allometric trajectories of sexual shape dimorphism estimated below characterized the full range of body sizes known for each family, and are likely accurate representations of these evolutionary trends.

For all observations, specimens were photographed using a Canon Rebel EOS T6 camera equipped with an EFS 18-55mm macro lens (0.25m/0.8ft). A Velcon Videomate IC PH-368 tripod stabilized the camera, allowing precise angle adjustments. To ensure consistent lighting and to minimize shadows, specimens were placed in a light-controlled imaging setup with a motorized turntable and diffuse LED lighting. Images were captured at 30-degree intervals across a full 360-degree rotation, with additional images taken at three tripod angles (0, 15, and 30 degrees) to ensure comprehensive shape capture. For smaller specimens, additional images were taken at finer intervals of 5–15 degrees to improve reconstruction accuracy. The external morphology of each specimen was captured using 25–100 high-resolution images, which were manually inspected to remove blurry images. Next, images were processed using the open-source package AliceVision Meshroom (Griwodz et al., 2021) to generate 3D models (.ply format). Models were then imported into MeshLab, where they were cleaned, scaled, and exported as.obj files for landmarking and subsequent morphological quantification (Callieri et al., 2012).

Landmarking & shape quantification

To quantify head shape, processed 3D models (.obj format) were imported into Stratovan Checkpoint, where a template mesh was used to apply 68 three-dimensional landmarks to each specimen (Figure 1). These landmarks comprised 24 fixed landmarks at anatomically homologous points—such as the premaxilla center, eye corners, nostrils, and jaw margins—while the 44 sliding semilandmarks were placed along curved regions to capture orbital contours, posterior head shape, and mouth morphology. To remove non-shape variation due to differences in position, orientation,

Downloaded from https://academic.oup.com/evolut/article/80/3/570/8363668 by Iowa State University Library user on 06 March 2026

and size, a Generalized Procrustes Analysis (GPA) was performed using the `gpagen` function in `geomorph` 4.0.10 (Adams et al., 2025; Baken et al., 2021). During this procedure, sliding landmarks were iteratively adjusted to minimize bending energy, ensuring an optimal alignment of specimens (Bookstein, 1997; Gunz et al., 2005). Shape variation due to bilateral asymmetry was considered by quantifying shape differences between paired landmarks across the midline, allowing the separation of the symmetric and asymmetric components of shape variation (Klingenberg et al., 2002). The symmetric shape component was then extracted for each individual by mirroring and averaging their landmark configurations to retain only biologically meaningful variation, which was used in all subsequent analyses (Sanger et al., 2013).

Body size and sexual size dimorphism

As an estimate of body size, snout-vent length (SVL) was measured for each individual using digital calipers. Then, to characterize the macroevolutionary dynamics of body size evolution we utilized maximum likelihood (ML) methods (Schluter et al., 1997) to estimate ancestral states, and mapped these onto the phylogeny to visualize evolutionary changes in body size. This facilitated interpretation of shifts to extremely small body sizes (i.e., miniaturization) in the group. Additionally, we obtained estimates of sexual size dimorphism for the taxa used in this study, to evaluate the association between sexual size and sexual shape dimorphism. Here, sexual size dimorphism (SSD) was represented as the distance between logged male and female mean body sizes, which is mathematically equivalent to the absolute value of the logged difference. This SSD measure places sexual dimorphism on a scale from no dimorphism (zero) to increasing dimorphism (positive values), and makes it comparable to the shape dimorphism measure (SShD) used here (see below).

Statistical and analytical procedures

A combination of multivariate statistical and phylogenetic comparative methods were used to quantify the magnitude and evolutionary trajectory of sexual shape dimorphism across species and to evaluate whether miniaturization influenced these patterns. First, to determine whether patterns of sexual shape dimorphism were concordant across species, we performed an extended phylogenetic generalized least squares analysis (E-PGLS: Adams & Collyer, 2024). E-PGLS is a hierarchical linear model in which species effects are accounted for while evaluating other factors of interest. Unlike standard phylogenetic least squares models which use species means as data, E-PGLS can accommodate multiple individuals per species, as well as multiple sub-categories within species (in this case, males and females), while simultaneously conditioning those trends on species-level phylogenetic relationships (Adams & Collyer, 2024). Our E-PGLS model included `species`, `sex`, and the `species × sex` interaction as model effects, with head shape representing the response variables. For the latter, a principal components analysis was first performed to remove redundant dimensions due to superimposition. From this the first 25 PCs, which described 98.4% of the total shape variation in the dataset, were retained and used in the E-PGLS. Phylogenetic non-independence was incorporated using a Brownian motion model of evolution, based on a time-calibrated molecular phylogeny for squamates (Tonini et al., 2016), pruned to our 99 species. Multivariate summary statistics for each model term were then statistically evaluated using residual randomization permutation procedures, which were restricted within-species (see Adams & Collyer, 2024).

A significant `species × sex` interaction from the E-PGLS model would imply that patterns of sexual shape dimorphism were not concordant across species. To evaluate such effects, several subsequent analyses were conducted. First, to visualize species-specific patterns of sexual shape dimorphism, a phylomorphospace was constructed using a principal components analysis (PCA) on species means, with the phylogeny for the group (Tonini et al., 2016) projected into the space. Next, the mean shapes for males and females of each species were projected into the phylomorphospace, to determine whether males or females occupied distinct regions. Additionally, vectors connecting `species × sex` means for each species were overlaid to provide a depiction of the shape changes associated with SShD, producing a visual illustration of the magnitude of SShD exhibited by each species in morphospace, as well as the direction in which sexual dimorphism occurred. Thin-plate spline deformation grids (sensu Bookstein, 1991) were used to illustrate shape changes along the major axes of variation of phylomorphospace. Differences in head shape between families was also evaluated using analysis of variance (ANOVA) and phylogenetic analysis of variance (phylogenetic ANOVA) based on species means.

Second, to evaluate the extent to which patterns of sexual shape dimorphism (SShD) across species varied allometrically as a function of body size, we conducted a phylogenetic regression. For this we first quantified the magnitude of SShD in each species using the sexual shape dimorphism index (SShDi) of Adams et al., (2020). This index measures the Euclidean distance between male and female mean shapes in morphospace, with larger values indicating a greater degree of SShD. Then a phylogenetic regression (Adams, 2014) was used to evaluate whether changes in SShD were associated with changes in species' body sizes across taxa. Phylogenetic regression was performed on each family separately, and regression coefficients were then evaluated against the hypothesis of no allometry using the permutation procedure described in Tejero-Cicuéndez et al., (2023). This approach was used rather than including `family` as a term in a phylogenetic anaylsis of covariance (phylogenetic ANCOVA), because phylogenetic linear models containing discrete factors can display low power when groups are phylogenetically clumped, resulting in a lack of ability to distinguish group-specific effects (Adams & Collyer, 2018). For our data, the two groups (sphaerodactylids and phyllodactylids) were reciprocally monophyletic, leading to complete clumping on the phylogeny, resulting in low statistical power.

Additionally, we used phylogenetic regression to determine whether levels of sexual size dimorphism were associated with levels of sexual shape dimorphism. All phylogenetic comparative analyses evaluating trends in head shape and head shape dimorphism were performed under a Brownian motion model of evolution. Finally, thin-plate spline deformation grids and estimated 3D images were constructed for the average male and female of both the largest and smallest species to facilitate biological interpretation of any sex-specific shape differences found between miniaturized and non-miniaturized species.

Downloaded from https://academic.oup.com/evolut/article/80/3/570/8363668 by Iowa State University Library user on 06 March 2026

Table 1. Multivariate analysis of variance (MANOVA) table of variance components of E-PGLS examining variation in gecko head shape as a function of Species, Sex, and their interaction.

	df	Wilks	Z	P
Species	98	0.863	−30.718	1.000
Sex	1	0.883	2.683	0.009
Species X sex	98	0.002	1.906	0.023

All statistical analyses were conducted in `R` v4.1.1, with morphometric and phylogenetic comparative analyses performed using the `geomorph` v4.1.3 (Adams et al., 2025; Baken et al., 2021) and `RRPP` v1.4.3 packages (Collyer & Adams, 2018). Ancestral state estimation was conducted in `phytools` v2.3.0 (Revell, 2012), and phylogenetic data manipulation and visualization was performed using the `ape` v5.8 (Paradis & Schliep, 2019) and `phytools` (Revell, 2012) libraries.

Results

Extended phylogenetic generalized least squares (E-PGLS) analysis revealed significant differences between males and females, indicating that overall, sexual shape dimorphism was prevalent (Table 1), even when the phylogenetic relationships among species were considered. Additionally, the interaction between `Species` and `Sex` was highly significant (Table 1), revealing that SShD was not uniform across species, and that species exhibited varying degrees of shape differentiation between the sexes. A phylomorphospace obtained from principal components analysis (PCA) confirmed these patterns visually (Figure 2). Here, it was observed that the male and female mean shapes for some species were quite similar to one another (indicating little SShD), while in other species the sexes were considerably more distinct in head shape. Further, males and females across species did not occupy distinct regions of phylomorphospace but overlapped widely across the clade (Figure 2). Thus, while levels of SShD differed across species, there was little evidence of a distinct "male morph" and "female morph" within this group.

Examining the phylomorphospace, we observed that PC1 explained 33.5% of the head shape variation among species. Here, PC1 described differences in skull robustness versus skull elongation (Figure 2), where species toward the negative end of PC1 were proportionately more robust in cranial morphology, while those at the positive end were more elongate. In contrast, PC2 explained 23.8% of the variation. Shape changes aligning with PC2 described differences in the relative sizes of various cranial components, including the post-orbital skull size, orbit size, and snout morphology. Towards the positive extreme of PC2, species displayed relatively longer and wider snouts, with larger orbits and a flatter head. On the other hand, towards the negative extreme of PC2, species showed relatively shorter snouts with smaller, more recessed orbits, and a deeper head (Figure 2).

When the phylomorphospace was scrutinized with respect to family, we found that sphaerodactylids and phyllodactylids were largely distinct, and segregated along PC2 (Figure 3). Most phyllodactylids displayed positive scores along PC2, whereas most sphaerodactylids exhibited negative scores along PC2. Correspondingly, ANOVA revealed that there were significant differences in head shape between the two families ($F = 14.1$, $Z = 4.73$, $P = 0.001$), though this pattern was not significant when phylogeny was considered, as the two families were reciprocally monophyletic (Figure 4) and diverged at the base of the phylogeny (for a discussion of this statistical phenomenon see Adams & Collyer, 2018). In terms of head shape, differences between the families largely reflected patterns described for shape differences along PC2. Specifically, phyllodactylids generally displayed relatively larger orbits and longer, wider snouts, while sphaerodactylids exhibited relatively smaller orbits and shorter snouts.

Examining patterns of sexual dimorphism across the phylogeny, it was revealed that both high levels and low levels of SShD were interspersed widely, with no discernible phylogenetic trend (Figure 4). Likewise, body size variation was also distributed across the phylogeny, though not surprisingly the highest proportion of small-bodied and miniaturized species were sphaerodactylids (Figure 4). Mapping body size on the phylogeny, we noted that small species evolved repeatedly across the phylogeny, but were concentrated within sphaerodactylids. This was not surprising, as many miniaturized species are found in Sphaerodactylidae. Also, consistent with prior work (Glynne & Adams, 2024; Perez-Martinez & Leal, 2021) we found that the ancestral state at the root of sphaerodactylids was small-bodied.

When allometric trends were examined within each family separately, it was revealed that sphaerodactylids displayed strong and significant negative allometry in SShD (Table 2; Figure 5), where smaller species displayed greater sexual shape dimorphism. Permutation tests revealed that the slope of this relationship was significantly different from isometry ($d = 0.020$, $Z = 1.93$, $P = 0.025$). By contrast, macroevolutionary trends in phyllodactylids were found to be isometric, with no significant relationship between SShD and body size (Table 3; Figure 5) and a slope that did not differ from zero ($d = 0.010$, $Z = -0.41$, $P = 0.666$). Thus, allometric changes in SShD were observed in sphaerodactylids but not in phyllodactylids. Additionally, phylogenetic regression found a positive association between SSD and SShD across taxa ($F = 11.172$, $Z = 2.611$, $P = 0.002$), where species exhibiting larger sexual size dimorphism tended to display greater sexual shape dimorphism as well.

Finally, to visually assess the differences in sexual shape dimorphism across body sizes in sphaerodactylids, thin-plate spline deformation grids were generated showing the mean shape differences between sexes for both the smallest and largest species (Figure 6). Within sphaerodactylids, larger species tended to display heads with relatively longer snouts and flatter heads, while smaller species had relatively shorter snouts and relatively deeper and wider heads. With respect to sexual dimorphism, it was observed that males of small species displayed proportionally elongated snouts and dorsoventrally compressed crania, whereas females of small species exhibited more robust, triangular heads with an expanded posterior cranium. In contrast, larger species displayed males with broader, more robust skulls, while females displayed dorsoventrally compressed cranial structures. Thus, sexual shape dimorphism in small-bodied species was best described as a contrast between more robust females and more elongated males, while in larger species the pattern of sexual shape dimorphism was the converse.

Downloaded from https://academic.oup.com/evolut/article/80/3/570/8363668 by Iowa State University Library user on 06 March 2026

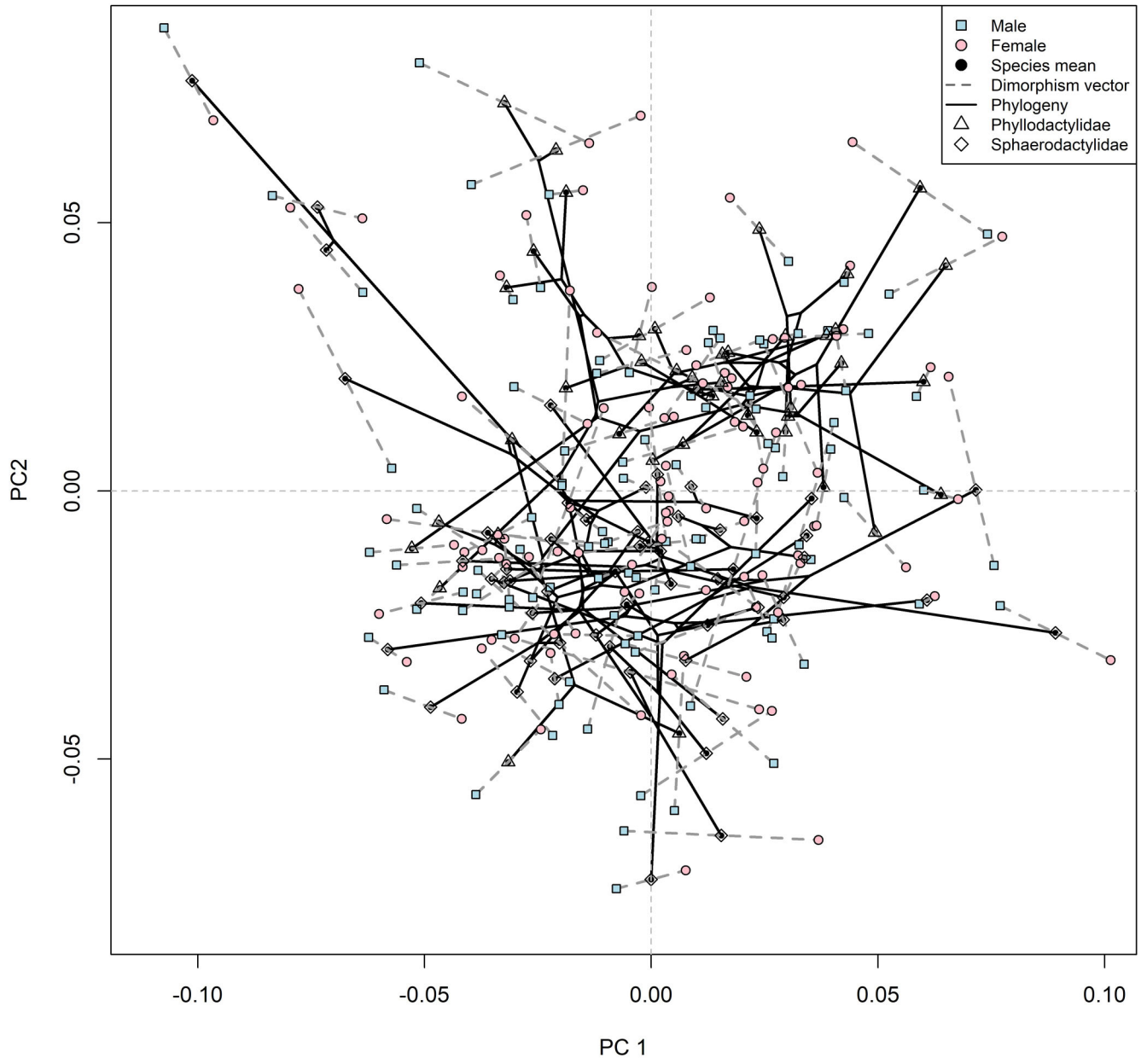


Figure 2. Phylomorphospace obtained from a principal components analysis (PCA) of head shape based on species means. Male and female means of each species have been projected into the morphospace, and the phylogenetic relationships are shown. PC1 and PC2 explain 33.5% and 23.8% of the total shape variation among species means, respectively. Points represent males (light blue squares), females (pink circles), and overall species means (open black symbol) designating Phyllodactylidae (open triangles) and Sphaerodactylidae (open diamonds). Black lines indicate phylogenetic relationships, and dotted grey lines connect male and female means within species, illustrating the magnitude and direction of sexual shape dimorphism (SShD). Thin-plate spline deformations depict morphological variation along PC axes. Alt text: "Plot of gecko species positions in morphospace including males and females, with connecting lines indicating the magnitude and direction of sexual shape dimorphism."

Discussion

How organisms evolve extremely small body size (i.e., miniaturization) and retain biological function is a long-standing evolutionary enigma (Carvalho de Oliveira et al., 2021; Hanken & Wake, 1993; Rieppel, 1996). In vertebrates, miniaturization has evolved independently many times across the tree of life, yet how such trends associate with other phenotypic patterns, such as those related to sexual dimorphism, is less well examined. In this study, we evaluated whether evolutionary changes in body size influenced patterns of sexual shape dimorphism in gecko cranial morphology. We generated a large phenotypic dataset using a combination of high-dimensional 3D surface scans and geometric morphometric methods to characterize patterns of head shape in species from two families of geckos (Sphaerodactylidae and Phyllodactylidae), and interrogated macroevolutionary patterns of SShD using a battery of multivariate and phylogenetic comparative methods. Our results revealed significant variation in SShD across species, with species exhibiting differing magnitudes of shape divergence between the sexes. Additionally, head shape variation was considerable, and differed between the two families.

Downloaded from https://academic.oup.com/evolut/article/80/3/570/8363668 by Iowa State University Library user on 06 March 2026

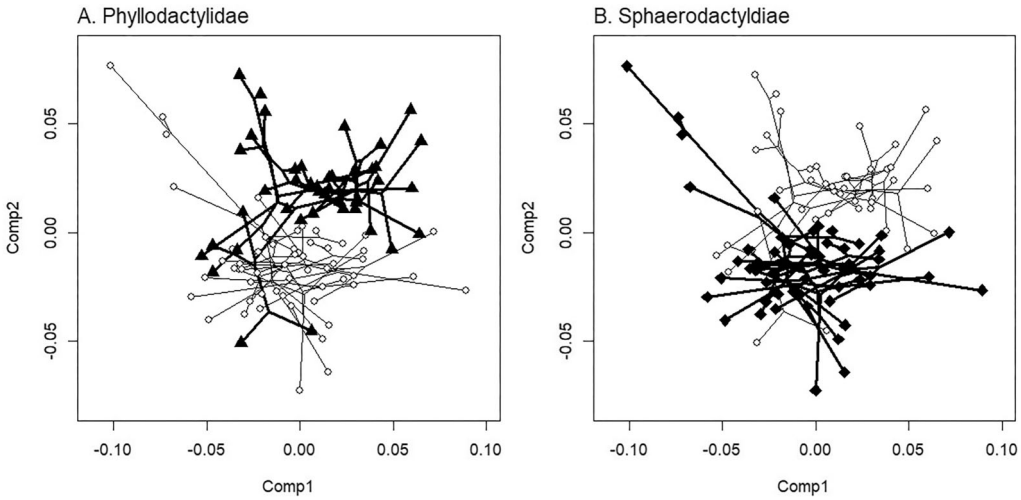


Figure 3. Phylomorphospace obtained from a principal components analysis (PCA) of head shape based on species means, emphasizing family level patterns. The morphospace is the same as in Figure 1. Panel (A) emphasizes species of Phyllodactylidae (black triangles), while the panel (B) emphasizes species of Sphaerodactylidae (black diamonds). The phylogenetic relationships among species are shown. Alt text: "Morphospace plot highlighting clustering patterns by family, showing separation between Phyllodactylidae and Sphaerodactylidae."

When interspecific allometry of sexual shape dimorphism with body size was examined, we found contrasting patterns between the two families. In sphaerodactylids, a group containing many small-bodied and miniaturized species, there was strong negative allometry of SShD with body size, where smaller species exhibited greater SShD. By contrast, phyllodactylids did not show systematic differences in SShD as a function of body size. Overall our work contributes to a growing body of literature documenting patterns of sexual shape dimorphism in vertebrates (e.g., Adams et al., 2020; Berns & Adams, 2013; Cruz-Elizalde et al., 2020; Dursun et al., 2022; Kaliontzopoulou et al., 2015; Kelly et al., 2013; Sanger et al., 2013), and provides several novel insights into how and why such patterns may vary with body size across species.

One result revealed by our analyses was a large difference in head shape between small-bodied and larger-boded sphaerodactylid taxa. Within sphaerodactylids, larger species tended to display heads with relatively longer snouts, relatively flatter heads, and relatively smaller orbits, while smaller species had relatively shorter snouts, relatively wider and deeper heads, and relatively larger orbits (Figure 6). This pattern was similar to that found in studies of other Gekkotan taxa (Lobón-Rovira et al., 2024), where larger species displayed relatively longer snouts with a flatter head in the dorsoventral direction, and smaller species displayed the converse. Anatomically, the differences observed in our study likely correspond with changes in the underlying skeletal elements. Osteological studies in Sphaerodactylid geckos (Daza et al., 2008) have revealed substantial shifts in the relative sizes and positions of the bones in the anterior portion of the skull (the "palatomaxillary unit," sensu Herrel et al., 1999) in miniaturized species (Daza et al., 2008; Rieppel 1984a; Vallejo-Pareja, 2018). Further, it has been suggested that these osteological changes reflect modifications to maintain sensory capabilities, which would be under selective pressure to maintain functionality as species evolve to be smaller (Daza et al., 2008). Specifically, in miniaturized geckos, enlarged orbits and anteriorly shifted cranial elements may allow for enhanced visual input and olfactory sensitivity, preserving the sensory efficacy despite the reduction in skull (Daza et al., 2008). Our findings are in accord with this hypothesis, as the differences in head shape we observed in miniaturized geckos mirror those found in osteological studies.

Another major result of our study was the observation that as sphaerodactylid gecko species become smaller, the degree of sexual dimorphism in head shape increased (Figure 5). Here we found a strong trend of evolutionary allometry in SShD as a function of body size across species. This observation adds to a growing body of macroevolutionary literature suggesting that patterns of sexual dimorphism are not constant across taxa, but can vary systematically with body size. In fact, since the late 20^{th} century there has been renewed interest in the interspecific allometry of sexually dimorphic traits, as researchers have documented such patterns to understand how and why males and females differ within and among species (Adams et al., 2020; Ceballos et al., 2013; Dale et al., 2007; Fairbairn, 1997; Glynne & Adams, 2024; Liang et al., 2022; Peñalver-Alcázar et al., 2019; Reyes-Puig et al., 2023; Székely et al., 2004; Sanger et al., 2013; and many others). This body of work has lead to major insights regarding the evolution of sexual differences, and the mechanistic processes that generate them (Andersson, 1994; Bonduriansky, 2007; Cox et al., 2003; De Lisle & Rowe, 2013, 2017; Fairbairn, 2013). Yet most studies have focused on documenting and explaining patterns of sexual size dimorphism across taxa. Within species, other phenotypic attributes can differ widely between the sexes, including overall body shape and the shape of particular traits (e.g., Adams et al., 2020; Berns & Adams, 2013; Cruz-Elizalde et al., 2020; Dursun et al., 2022; Gidaszewski et al., 2009; Kelly et al., 2013; Kaliontzopoulou et al., 2015; Toyama et al., 2023). Our study provides a link between the two patterns, demonstrating that sexual shape dimorphism can also vary systematically across species with differing body sizes. Indeed, ours is one of several recent studies demonstrating evolutionary allometry of sexual dimorphism in complex multivariate phenotypes (Adams et al., 2020; Rodríguez-Rodríguez & Calderón-Espinosa, 2024; Sanger

Downloaded from https://academic.oup.com/evolut/article/80/3/570/8363668 by Iowa State University Library user on 06 March 2026

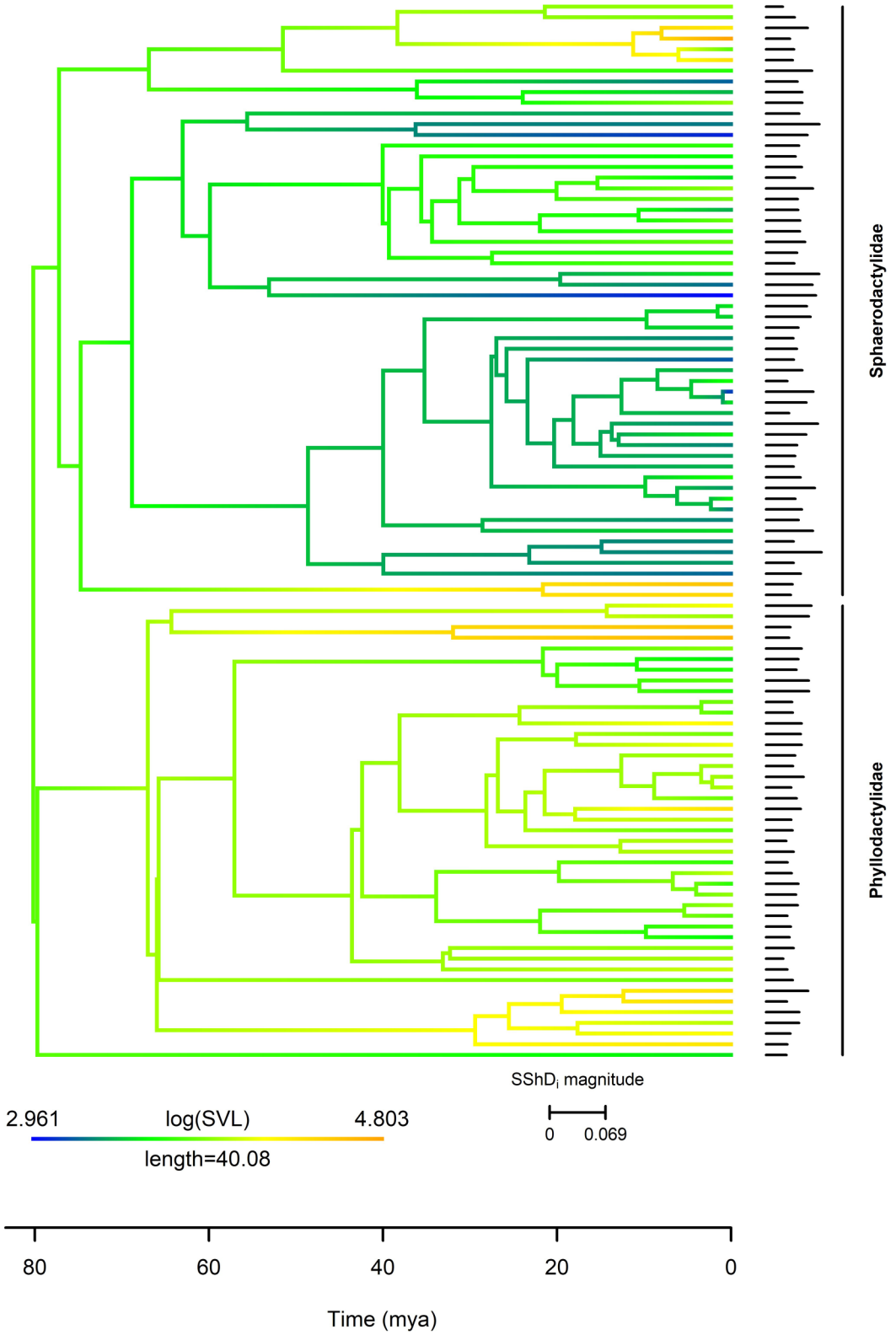


Figure 4. Time-dated phylogeny for reptiles from Tonini et al., (2016) pruned to the 99 species available in this study. Branches display ancestral estimates for body size based on maximum likelihood estimation. Bars at the tips represent the magnitude of sexual shape dimorphism index (SShDi) in each species, scaled by size. Alt text: "Time-calibrated phylogeny with estimated ancestral body sizes and bar plots at the tips showing the magnitude of sexual shape dimorphism."

et al., 2013; Toyama et al., 2023), though there remains a paucity of attention to this area. Our findings suggest the possibility that such patterns may be more widespread, and we therefore recommend that future work on evolutionary patterns of sexual dimorphism concentrate on trends in complex phenotypes like shape.

Downloaded from https://academic.oup.com/evolut/article/80/3/570/8363668 by Iowa State University Library user on 06 March 2026

Table 2. Results of a phylogenetic regression evaluating the degree of sexual shape dimorphism relative to overall body size across 56 Sphaerodactylidae species.

	df	SS	MS	Rsq	F	Z	P
log(SVL)	1	6.69e-05	6.69e-05	0.169	10.955	2.477	0.005
Residuals	54	3.30e-04	6.11e-06	0.831			
Total	55	3.97e-04					

Phylogenetic nonindependence was incorporated using a Brownian motion model of evolution.

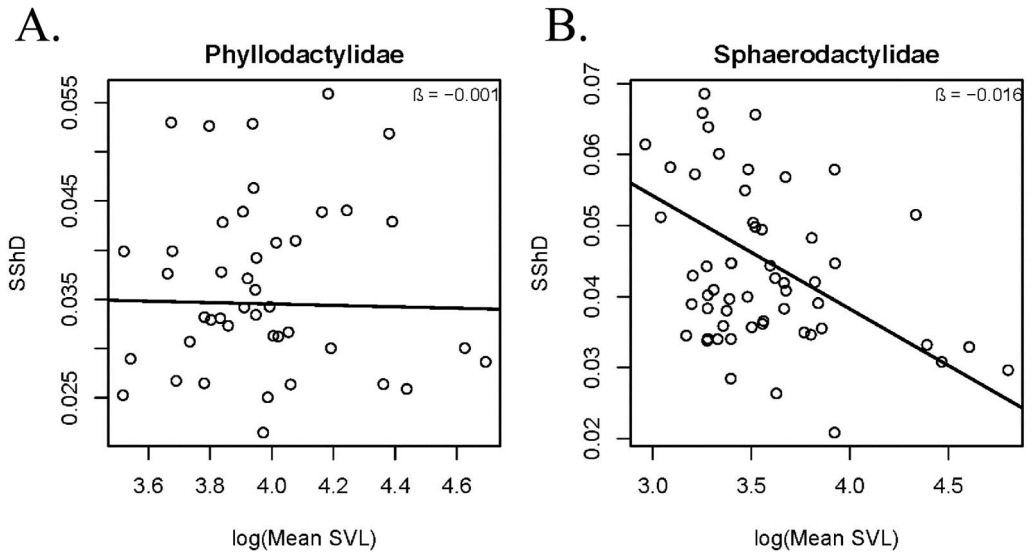


Figure 5. Relationship between sexual shape dimorphism (SShD) and body size for Phyllodactylidae (A) and Sphaerodactylidae (B). The phylogenetic regression line is shown in each figure (black line) with the slope coefficient noted in the top-right corner of each panel. Alt text: "Scatterplots showing the relationship between sexual shape dimorphism and body size for two gecko families, with regression lines indicating negative allometry in Sphaerodactylidae and no trend in Phyllodactylidae."

Table 3. Results of a phylogenetic regression evaluating the degree of sexual shape dimorphism relative to overall body size across 43 Phyllodactylidae species.

	df	SS	MS	Rsq	F	Z	P
log(SVL)	1	3.44e-08	3.44e-08	0.000224	0.009	−1.453	0.922
Residuals	41	1.53e-04	3.74e-06	0.999776			
Total	42	1.53e-04					

Phylogenetic nonindependence was incorporated using a Brownian motion model of evolution.

Examining evolutionary patterns by family, we discovered that interspecific trends of SShD as a function of body size were decidedly allometric in sphaerodactylids, but isometric in phyllodactylids. Specifically, we found a strong and negative relationship between the degree of SShD and body size across species in sphaerodactylids (Figure 5), implying that smaller species exhibited greater levels of dimorphism in head shape. Interestingly, this result mirrored patterns observed in sexual size dimorphism in the same family (Glynne and Adams, 2024), where miniaturized sphaerodactylids were more female biased, and displayed greater levels of size dimorphism than did larger species in the clade. For the latter pattern, it was suggested that in small species, sex-specific selection on females for increased reproductive success resulted in female-biased patterns of size dimorphism. This hypothesis was supported by the fact that smaller species in the family produced relatively larger (longer) eggs (Glynne & Adams, 2024), and thus having larger females would be necessary to accommodate the proportionally greater volume of egg mass. These results were consistent with the prediction that reproductive pressures constrain the lower limit of body size reduction in miniaturized geckos, leading to female biased size dimorphism (see Glynne & Adams, 2024). However, whether similar mechanisms drive the patterns of sexual shape dimorphism observed in this study are less clear.

So why might geckos exhibit sexual shape dimorphism? Male-biased cranial sexual dimorphism in larger sphaerodactylid species has been hypothesized to have evolved in response to intrasexual competition (Griffing et al., 2018). In our study however, we observed the greatest sexual shape dimorphism in small species. Scrutinizing the patterns of head shape dimorphism in more detail it was found that females of miniaturized species displayed heads that were more robust and triangular, with an expanded posterior region relative to their male counterparts (Figure 6). Because our data characterized the external anatomy of the organism, this in-

Downloaded from https://academic.oup.com/evolut/article/80/3/570/8363668 by Iowa State University Library user on 06 March 2026

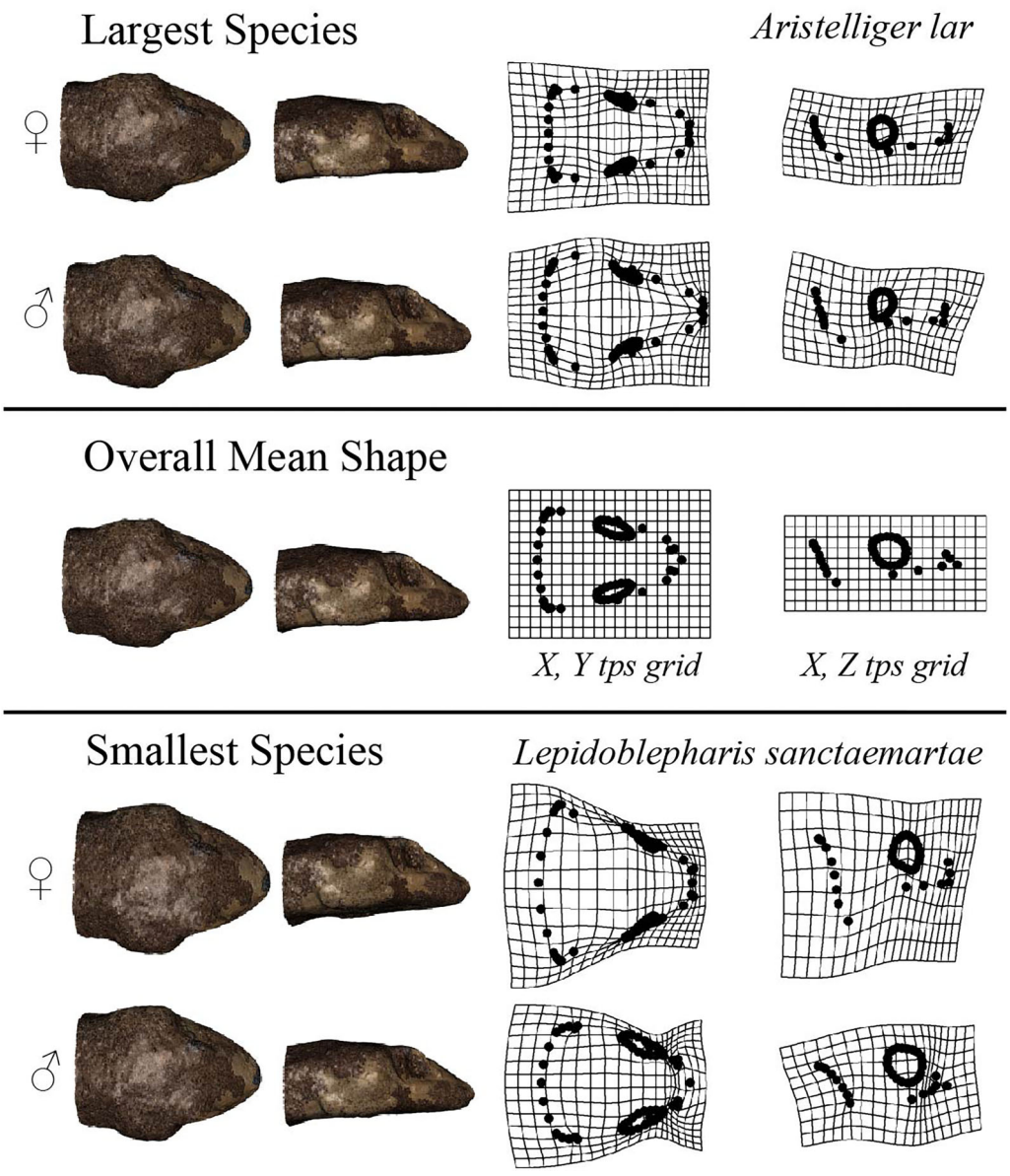


Figure 6. Thin-plate spline deformation grids and 3D shape visualizations of males and females across body size categories in Sphaerodactylidae, illustrating patterns of sexual shape dimorphism in head shape in the group. Male (bottom) and female (top) head shapes are displayed for the largest species (*Aristelliger lar*, top) and the smallest species (*Lepidoblepharis sanctaemartae*, bottom) represented in the dataset. 3D images represent unwarped images to group means from the specimen nearest to the overall mean. Alt text: "Shape comparison showing male and female skull morphology in the smallest and largest species of Sphaerodactylidae, illustrating differences in head shape between sexes and across body size".

crease in the posterior region of the head in females corresponded with greater jaw adductor musculature (Daza et al., 2011; Rieppel 1984b), which may be associated with foraging difference between males and females. There is evidence of sex-specific foraging in lizards (Andrews & Asato, 1977; Parmelee & Guyer, 1995; Perry, 1996), where females exhibit more active foraging modes as compared with males. Further, it has been hypothesized that differences in foraging between males and females in lizards is a response to the increased energetic demands females incur for reproduction (Andrews & Asato, 1977; Perry, 1996). Geckos have also been shown to display sex-specific foraging behavior (Werner et al., 2006; Wehsener & Noss, 2022), leading to the possibility of dietary differences between the sexes. In fact, sex-specific diet differences have been documented in several Sphaerodactylidae species (Gifford et al., 2000; DeBoer et al., 2018; Steinberg et al., 2007), including the miniaturized gecko *Sphaerodactylus vincenti*. Our work demonstrating sex-specific differences in head shape aligns with these findings, and is consistent with the hypothesis that females of miniaturized species may face proportionally higher energetic demands due to reproduction. Based on this scenario, we posit that the allometric trend in head shape dimorphism observed in sphaerodactylids is the result of differential selection between the sexes, which is stronger in miniaturized species owing to the proportionally greater sex-specific differences in energetic demands. This effect is likely stronger in miniaturized species as a result of proportionally

Downloaded from https://academic.oup.com/evolut/article/80/3/570/8363668 by Iowa State University Library user on 06 March 2026

greater sex-specific energetic demands, potentially selecting for enhanced bite force in females to process harder or more energy-rich prey, or to accommodate larger jaw musculature associated with reproductive metabolic needs (DeBoer et al., 2018; Gifford et al., 2000). Future work should test this hypothesis directly.

Across the tree of life, species vary greatly in the degree of sexual dimorphism that they display, and understanding why such patterns occur remains a major interest to evolutionary biologists. Likewise, deciphering evolutionary trends of body size changes is crucial to untangling the processes that drive phenotypic diversity across species. Our study links these two perennial themes in evolutionary biology, by revealing how interspecific patterns of sexual dimorphism in geckos are affected by body size changes, and miniaturization in particular. Specifically, we found that miniaturized geckos exhibit accentuated patterns of sexual shape dimorphism in functionally-relevant traits, which aligns with patterns observed in other phenotypic attributes. This suggests a broader trend, wherein extreme body size reductions elicit a concomitant increase in selective forces, which results in a suite of coordinated phenotypic changes as species evolve to become smaller. If this hypothesis is correct, identifying whether distinct phenotypic attributes display parallel shifts in lineages undergoing miniaturization would be a fruitful next avenue of future research. Thus, investigations such as these have the capacity to uncover how evolutionary changes in body size may foster phenotypic diversity in multiple dimensions of the organismal phenotype, providing fresh insights into our understanding of the evolutionary forces that shape life's intricate nature.

Data availability

All data are accessible through the Dryad repository (DOI: 10.5061/dryad.ttdz08m9g).

Author contributions

Elizabeth Glynne (Conceptualization [Equal], Data Curation [Equal], Formal Analysis [Equal], Funding Acquisition [Supporting], Investigation [Equal], Methodology [Equal], Software [Equal], Visualization [Equal], Writing—original draft [Equal], Writing—review and editing [Equal]); Dean C. Adams (Conceptualization [Equal], Formal Analysis [Equal], Funding Acquisition [Primary], Methodology [Equal], Software [Equal], Supervision [Primary], Visualization [Equal], Writing—original draft [Equal], Writing—review and editing [Equal])

Funding

This work was sponsored in part by National Science Foundation grant DEB-2140720 (to DCA), and a California Academy of Natural Sciences Michele L. Aldrich Collections Research Grant (to EG).

Conflicts of interest

The authors declare no conflicts of interest.

Acknowledgments

We thank Tracy Heath, Haldre Rogers, Amy Toth, and Nicole Valenzuela for comments on earlier versions of this manuscript. We are deeply indebted to the museum curators and collection managers who gave us access to their collections for this study. The museums enabling with work included: the American Museum of Natural History (AMNH); Herpetology Collection at Brigham Young University (BYU); the Department of Herpetology, California Academy of Sciences (CAS); Amphibians and Reptiles (Herpetology) at Carnegie Museum of Natural History (CM); Amphibians and Reptiles at the Field Museum of Natural History (FMNH); the Biodiversity Institute and Natural History Museum of the University of Kansas (KU); the Natural History Museum of Los Angeles County (LACM); the Museum of Comparative Zoology (MCZ); the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); the Sam Noble Oklahoma Museum of Natural History, University of Oklahoma (OMNH); the San Diego Museum of Natural History (SDNHM); the Biodiversity Research and Teaching Collections, Texas A&M University (TCWC); the University of Michigan Museum of Zoology (UMMZ).

References

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

Adams, D. C. (2014). A method for assessing phylogenetic least squares models for shape and other high-dimensional multivariate data. *Evolution*, *68*, 2675–2688.

Adams, D. C., & Collyer, M. (2018). Phylogenetic ANOVA: Group-clade aggregation, biological challenges, and a refined permutation procedure. *Evolution*, *72*, 1204–1215.

Adams, D. C., & Collyer, M. L. (2024). Extending phylogenetic regression models for comparing within-species patterns across the tree of life. *Methods in Ecology and Evolution*, *15*(12), 2234–2246.

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.

Adams, D. C., Collyer, M. L., Kaliontzopoulou, A., & Baken, E. K. (2025). Geometric Morphometric Analyses of 2D and 3D Landmark Data . R package version 4.0.10. https://doi.org/10.32614/CRAN.package.geomorph

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

Andrews, R. M., & Asato, T. (1977). Energy utilization of a tropical lizard. *Comparative Biochemistry and Physiology Part A: Physiology*, *58*(1), 57–62. https://doi.org/10.1016/0300-9629(77)90015-9

Baken, E. K., Collyer, M. L., Kaliontzopoulou, A., & Adams, D. C. (2021). Geomorph 4.0 and gmshiny: Enhanced analytics and a new graphical interface for a comprehensive morphometric experience. *Methods in Ecology and Evolution*, *12*, 2355–2363.

Berns, C. M., & Adams, D. C. (2013). Becoming different but staying alike: Patterns of sexual size and shape dimorphism in bills of hummingbirds. *Evolutionary Biology*, *40*(2), 246–260. https://doi.org/10.1007/s11692-012-9206-3

Blanckenhorn, W. U., Stillwell, R. C., Young, K. A., Fox, C. W., & Ashton, K. G. (2006). When Rensch meets Bergmann: Does sexual size dimorphism change systematically with latitude?. *Evolution*, *60*(10), 2004–2011. https://doi.org/10.1111/j.0014-3820.2006.tb01838.x

Bonduriansky, R. (2007). Sexual selection and allometry: A critical appraisal of the evidence and ideas. *Evolution*, *61*(4), 838–849. https://doi.org/10.1111/j.1558-5646.2007.00081.x

Bookstein, F. L. (1991). *Morphometric Tools for Landmark Data: Geometry and Biology*, Cambridge University Press, Cambridge.

Downloaded from https://academic.oup.com/evolut/article/80/3/570/8363668 by Iowa State University Library user on 06 March 2026

Bookstein, F. L. (1997). Landmark methods for forms without landmarks: morphometrics of group differences in outline shape. *Medical Image Analysis*, *1*(3), 225–243. https://doi.org/10.1016/s1361-8415(97)85012-8

Bustard, H. (1968). The egg-shell of gekkonid lizards: A taxonomic adjunct. *Copeia*, *1968*, 162–164.

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*, 259–272.

Callieri, M., Ranzuglia, G., Dellepiane, M., Cignoni, P., & Scopigno, R. (2012). Meshlab as a complete open tool for the integration of photos and colour with high-resolution 3d geometry data. *Comput Appl Quant Methods Archaeol*, 1–14.

Carvalho de Oliveira, F. R., Passos, D. C., & Borges-Nojosa, D. M. (2021). Ecology of the lizard *Gonatodes humeralis* (Sphaerodactylidae) in a coastal area of the Brazilian semiarid: What differs from the Amazonian populations?. *Journal of Arid Environments*, *190*, 104506. https://doi.org/10.1016/j.jaridenv.2021.104506

Ceballos, C. P., Adams, D. C., Iverson, J. B., & Valenzuela, N. (2013). Phylogenetic patterns of sexual size dimorphism in turtles and their implications for Rensch's rule. *Evolutionary Biology*, *40*, 194–208.

Collyer, M. L., & Adams, D. C. (2018). RRPP: An R package for fitting linear models to high-dimensional data using residual randomization. *Methods in Ecology and Evolution*, *9*, 1772–1779.

Cox, R., & Kahrl, A. (2014). *Reproductive Biology and Phylogeny of Lizards and Tuatara*, In J. L. Rheubert, D. S. Siegel, & S. E. Trauth (Eds.), pp. 78–108, CRC Press.

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. https://doi.org/10.1111/j.0014-3820.2003.tb00371.x

Cruz-Elizalde, R., Ramirez-Bautista, A., Pacheco, L. F. R., Lozano, A., , & (2020). Sexual dimorphism in size and shape among populations of the lizard sceloporus variabilis (squamata: Phrynosomatidae). *Zoology*, *140*, 125781.

Dale, J., Dunn, P. O., Figuerola, J., Lislevand, T., Székely, T., & 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

Darwin, C. R. (1871). *The Descent of Man, and Selection in Relation to Sex*, J. Murray, London.

Daza, J. D., Abdala, V., Thomas, R., & Bauer, A. M. (2008). Skull anatomy of the miniaturized gecko *sphaerodactylus roosevelti* (squamata: Gekkota). *Journal of Morphology*, *11*(11), 1340–1364. https://doi.org/10.1002/jmor.10664

Daza, J. D., Diogo, R., Johnston, P., & Abdala, V. (2011). Jaw adductor muscles across lepidosaurs: A reappraisal. *The Anatomical Record*, *294*(10), 1765–1782. https://doi.org/10.1002/ar.21467

De Lisle, S. P., & Rowe, L. (2013). Correlated evolution of allometry and sexual dimorphism across higher taxa. *The American Naturalist*, *182*(5), 630–639. https://doi.org/10.1086/673282

De Lisle, S. P., & Rowe, L. (2017). Disruptive natural selection predicts divergence between the sexes during adaptive radiation. *Ecology & Evolution*, *7*, 3590–3601. https://doi.org/10.1002/ece3.2868

DeBoer, J. C., Griffing, A. H., Iyengar, V. K., & Bauer, A. M. (2018). New dietary records for croaking lizards of the genus aristelliger (reptilia: Sphaerodactylidae). *Caribbean Herpetology*, *62*, 1–8.

Dursun, C., Gul, S., & Ozdemir, N. (2022). Sexual size and shape dimorphism in turkish common toads (bufo bufo linnaeus 1758). *The Anatomical Record*, *305*(6), 1548–1558.

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. (2013). *Odd Couples - Extraordinary Differences between the Sexes in the Animal Kingdom*, Princeton University Press.

Fairbairn, D. J., Blanckenhorn, W. U., & Székely, T. (2007). *Sex, Size and Gender Roles*, Oxford University Press.

Fitch, H. (1981). Sexual size differences in reptiles. *Miscellaneous Publications of the Museum of Natural History, University of Kansas*, *70*, 1–72.

Gidaszewski, N. A., Baylac, M., & Klingenberg, C. P. (2009). Evolution of sexual dimorphism of wing shape in the *Drosophila melanogaster* subgroup. *BMC Evolutionary Biology*, *9*(1), 110. https://doi.org/10.1186/1471-2148-9-110

Gifford, M., Powell, R., & Steiner, W. (2000). Relationship of diet and preyavailability in *Aristelliger cochranae*, a gecko from Navassa Island, West Indies. *Caribbean Journal of Science*, *36*, 323–326.

Glynne, E., & Adams, D. C. (2024). The effect of miniaturization on the evolution of sexual size dimorphism in geckos. *Evolution*, *78*, 1275–1286. https://doi.org/10.1093/evolut/qpae046

Griffing, A. H., Daza, J. D., DeBoer, J. C., & Bauer, A. M. (2018). Developmental Osteology of the Parafrontal Bones of the Sphaerodactylidae. *The Anatomical Record*, *301*(4), 581–606 _eprint:. https://doi.org/10.1002/ar.23749

Griwodz, C., Gasparini, S., Calvet, L., Gurdjos, P., Castan, F., Maujean, B., De Lillo, G., & Lanthony, Y. (2021). Alicevision meshroom: An open-source 3d reconstruction pipeline. *in Proceedings of the 12th ACM multimedia systems conference*, 241–247.

Gunz, P., Mitteroecker, P., & Bookstein, F. L. (2005). *Modern Morphometrics in Physical Anthropology*, In D. E. Slice (ed.), pp. 73–98. Kluwer Academic.

Hanken, J., & Wake, D. B. (1993). Miniaturization of body Size: organismal consequences and evolutionary significance. *Annu. Rev. Ecol. Syst.*, *24*, 510–519.

Herrel, A., Vree, F. D., Delheusy, V., & Gans, C. (1999). Cranial kinesis in gekkonid lizards. *Journal of Experimental Biology*, *202*(24), 3687–3698. https://doi.org/10.1242/jeb.202.24.3687

Horne, C. R., Hirst, A. G., & Atkinson, D. (2020). Selection for increased male size predicts variation in sexual size dimorphism among fish species. *Proceedings of the Royal Society B: Biological Sciences*, *287*(1918), 20192640. https://doi.org/10.1098/rspb.2019.2640

Itgen, M. W., Natalie, G. R., Siegel, D. S., Sessions, S. K., & Mueller, R. L. (2022). Genome size drives morphological evolution in organ–specific ways. *Evolution*, *76*, 1453–1468.

Janicke, T., & Fromonteil, S. (2021). Sexual selection and sexual size dimorphism in animals. *Biology Letters*, *17*(9), 20210251.

Johnson, P. J., Noonan, M. J., Kitchener, A. C., Harrington, L. A., Newman, C., & Macdonald, D. W. (2017). Rensching cats and dogs: feeding ecology and fecundity trends explain variation in the allometry of sexual size dimorphism. *Royal Society Open Science*, *4*(6), 170453. https://doi.org/10.1098/rsos.170453

Juarez, B. H., & Adams, D. C. (2022). Evolutionary allometry of sexual dimorphism of jumping performance in anurans. *Evolutionary Ecology*, *36*(4), 717–733. https://doi.org/10.1007/s10682-021-10132-x

Kaliontzopoulou, A., Carretero, M. A., & Adams, D. C. (2015). Ecomorphological 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

Kelly, C. D., Folinsbee, K. E., Adams, D. C., & Jennions, M. D. (2013). Intraspecific sexual size and shape dimorphism in an Australian freshwater fish differs with respect to a biogeographic barrier and latitude. *Evolutionary Biology*, *40*(3), 408–419. https://doi.org/10.1007/s11692-013-9224-9

Klingenberg, C. P., Barluenga, M., & Meyer, A. (2002). Shape analysis of symmetric structures: quantifying variation among individuals and asymmetry. *Evolution*, *56*(10), 1909–1920.

Li, X.-Y., & Kokko, H. (2021). Sexual dimorphism driven by intersexual resource competition: Why is it rare, and where to look for it?. *Journal of Animal Ecology*, *90*(8), 1831–1843.

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*, 787–803. https://doi.org/10.1111/1749-4877.12569

Downloaded from https://academic.oup.com/evolut/article/80/3/570/8363668 by Iowa State University Library user on 06 March 2026

Liao, W. B., Zeng, Y., Zhou, C. Q., & Jehle, R. (2013). Sexual size dimorphism in anurans fails to obey rensch's rule. *Frontiers in Zoology*, *10*(1), 10. https://doi.org/10.1186/1742-9994-10-10

Linke, R., Roth, G., & Rottluff, B. (1986). Comparative studies on the eye morphology of lungless salamanders, family Plethodontidae, and the effect of miniaturization. *Journal of Morphology*, *189*(2), 131–143. https://doi.org/10.1002/jmor.1051890204

Lobón-Rovira, J., Bauer, A. M., Vaz Pinto, P., Trape, J.-F., Conradie, W., Kusamba, C., Júlio, T., Cael, G., Stanley, E. L., Hughes, D. F., Behangana, M., Masudi, F. M., Pauwels, O. S. G., & Greenbaum, E. (2024). Integrative revision of the *Lygodactylus gutturalis* (bocage, 1873) complex unveils extensive cryptic diversity and traces its evolutionary history. *Zoological Journal of the Linnean Society*, *201*(2), 447–492.

Machado, G., Buzatto, B. A., & Samia, D. S. M. (2021). It is not always about body size: evidence of rensch's rule in a male weapon. *Biology Letters*, *17*(6), 20210234. https://doi.org/10.1098/rsbl.2021.0234

McGlothlin, J. W., Cox, R. M., & Brodie III, E. D. (2019). Sex-specific selection and the evolution of between-sex genetic covariance. *Journal of Heredity*, *110*(4), 422–432.

Meiri, S. (2018). Traits of lizards of the world: Variation around a successful evolutionary design. *Global ecology and biogeography*, *27*(10), 1168–1172.

Meiri, S., Feldman, A., & Kratochvíl, L. (2015). Squamate hatchling size and the evolutionary causes of negative offspring size allometry. *Journal of Evolutionary Biology*, *28*, 438–446. https://doi.org/10.1111/jeb.12580

Ocampo, D., Barrantes, G., & Uy, J. A. C. (2018). Morphological adaptations for relatively larger brains in hummingbird skulls. *Ecology and Evolution*, *8*, 10482–10488. https://doi.org/10.1002/ece3.4513

Paradis, E., & Schliep, K. (2019). ape 5.0: an environment for modern phylogenetics and evolutionary analyses in r. *Bioinformatics*, *35*(3), 526–528.

Parmelee, J. R., & Guyer, C. (1995). Sexual differences in foraging behavior of an anoline lizard, norops humilis. *Journal of Herpetology*, *29*(4), 619–621. https://doi.org/10.2307/1564749

Peñalver-Alcázar, M., Galán, P., & Aragón, P. (2019). Assessing Rensch's rule in a newt: Roles of primary productivity and conspecific density in interpopulation variation of sexual size dimorphism. *Journal of Biogeography*, *46*(11), 2558–2569. https://doi.org/10.1111/jbi.13680

Perez-Martinez, C. A., & Leal, M. (2021). Lizards as models to explore the ecological and neuroanatomical correlates of miniaturization. *Behaviour*, *158*, 1121–1168. https://doi.org/10.1163/1568539x-bja10104

Perry, G. (1996). The evolution of sexual dimorphism in the lizard *Anolis polylepis* (Iguania): evidence from intraspecific variation in foraging behavior and diet. *Canadian Journal of Zoology*, *74*(7), 1238–1245. https://doi.org/10.1139/z96-137

Piross, I. S., Harnos, A., & Rózsa, L. (2019). Rensch's rule in avian lice: contradictory allometric trends for sexual size dimorphism. *Scientific Reports*, *9*(1), 7908.

Regis, K. W., & Meik, J. M. (2017). Allometry of sexual size dimorphism in turtles: a comparison of mass and length data. *PeerJ*, *5*, e2914. https://doi.org/10.7717/peerj.2914

Rensch, B. (1950). Die abhangigkeit der relativen sexualdifferenz von der korpergrosse. *Bonner Zoologische Beitraege*, *1*, 58–69.

Rensch, B. (1960). *Evolution Above the Species Level*, Columbia University Press.

Revell, L. J. (2012). Phytools: An r package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, *3*, 217–223.

Reyes-Puig, C., Adams, D. C., Enriquez-Urzelai, U., & Kaliontzopoulou, A. (2023). Rensch's rule: linking intraspecific to evolutionary allometry. *Evolution*, *77*(12), 2576–2589.

Rieppel, O. (1984a). The structure of the skull and jaw adductor musculature in the Gekkota, with comments on the phylogenetic relationships of the Xantusiidae (Reptilia: Lacertilia). *Zoological Journal of the Linnean Society*, *82*(3), 291–318.

Rieppel, O. (1984b). *The Structure, Development and Evolution of Reptiles*., In M. W. J. Ferguson (eds.), pp. 503–520 The Zoological Society of London, Academic Press.

Rieppel, O. (1996). Miniaturization in tetrapods: consequences for skull morphology. *in Symposia of the Zoological Society of London*, 47, London: The Society, 1960-1999.

Rodríguez-Rodríguez, J. D., & Calderón-Espinosa, M. L. (2024). Sexual dimorphism and female ecomorphology in *Anolis* (squamata: Anolidae): knowledge of female morphology increases the understanding of *Anolis* diversification. *Biological Journal of the Linnean Society*, *143*(4), blae019. https://doi.org/10.1093/biolinnean/blae019

Sanger, T. J., Sherratt, E., McGlothlin, J. W., Brodie, E. D. III, Losos, J. B., & Abzhanov, A. (2013). Convergent evolution of sexual dimorphism in skull shape using distinct developmental strategies. *Evolution*, *67*(8), 2180–2193.

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

Schluter, D., Price, T., Mooers, A. O., & Ludwig, D. (1997). Likelihood of ancestor states in adaptive radiation. *Evolution*, *51*, 1699–1711.

Schoener, T. W. (1967). The ecological significance of sexual dimorphism in size in the lizard anolis conspersus. *Science*, *155*(3761), 474–477.

Steinberg, D. S., Powell, S. D., Powell, R., Parmerlee, J. S., & Henderson, R. W. (2007). Population densities, water-loss rates, and diets of *Sphaerodactylus vincenti* on St. Vincent, West Indies. *Journal of Herpetology*, *41*(2), 330–336. https://doi.org/10.1670/0022-1511(2007)41[330:PDWRAD]2.0.CO;2

Székely, T., Reynolds, J. D., & Figuerola, J. (2000). Sexual size dimorphism in shorebirds, gulls, and alcids: the influence of sexual and natural selection. *Evolution*, *54*(4), 1404–1413.

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*, *101*, 12224–12227. https://doi.org/10.1073/pnas.0404503101

Tejero-Cicuéndez, H., Menéndez, I., Talavera, A., Mochales-Riaño, G., Burriel-Carranza, B., Simó-Riudalbas, M., Carranza, S., & Adams, D. C. (2023). Evolution along allometric lines of least resistance: morphological differentiation in *pristurus* geckos. *Evolution*, *77*, 2547–2560. https://doi.org/10.1093/evolut/qpad166

Tonini, J. F. R., Beard, K. H., Ferreira, R. B., Jetz, W., & Pyron, R. A. (2016). Fully-sampled phylogenies of squamates reveal evolutionary patterns in threat status. *Biological Conservation*, *204*, 23–31. https://doi.org/10.1016/j.biocon.2016.03.039

Toyama, K. (2025). Beyond size dimorphism: the past, present, and future of rensch's rule. *The American Naturalist*, *205*, 548–558. https://doi.org/10.1086/735583

Toyama, K. S., Mahler, D. L., & Goodman, R. M. (2023). Climate shapes patterns of sexual size and shape dimorphism across the native range of the green anole lizard, anolis carolinensis (squamata: Dactyloidae). *Biological Journal of the Linnean Society*, *138*(1), 89–102.

Toyama, K. S., Losos, J. B., Herrel, A., & Mahler, D. L. (2025). Sexual size dimorphism as a determinant of biting performance dimorphism in anolis lizards. *Journal of Evolutionary Biology*, *38*(2), 251–260. https://doi.org/10.1093/jeb/voae148

Vallejo-Pareja, M. C. (2018). *Characteristics of Miniaturization in Squamates: A Phylogenetic Perspective from Cranial Morphology. M.S. Thesis*, Sam Houston State University.

Wehsener, J. W., & Noss, C. F. (2022). Disentangling morphological and environmental drivers of foraging activity in an invasive diurnal gecko, phelsuma laticauda. *Journal of Herpetology*, *56*(4), 386–395. https://doi.org/10.1670/21-030

Werner, Y. L., Takahashi, H., Yasukawa, Y., & Ota, H. (2006). Factors affecting foraging behaviour, as seen in a nocturnal ground lizard,goniurosaurus kuroiwae kuroiwae. *Journal of Natural History*, *40*(7–8), 439–459. https://doi.org/10.1080/00222930600681746

Downloaded from https://academic.oup.com/evolut/article/80/3/570/8363668 by Iowa State University Library user on 06 March 2026

Winkler, L., Freckleton, R. P., Székely, T., & Janicke, T. (2024). Pre-copulatory sexual selection predicts sexual size dimorphism: A meta-analysis of comparative studies. *Ecology Letters*, *27*(9), e14515.

Yeh, J. (2002). The effect of miniaturized body size on skeletal morphology in frogs. *Evolution*, *56*(3), 628–641. https://doi.org/10.1111/j.0014-3820.2002.tb01372.x

Downloaded from https://academic.oup.com/evolut/article/80/3/570/8363668 by Iowa State University Library user on 06 March 2026

Received August 7, 2025; revisions received October 21, 2025; accepted November 7, 2025
Associate Editor: Emma Sherratt; Handling Editor: Hélène Morlon
© The Author(s) 2025. Published by Oxford University Press on behalf of The Society for the Study of Evolution (SSE). This is an Open Access article distributed under the terms of the Creative Commons Attribution License (https://creativecommons.org/licenses/by/4.0/), which permits unrestricted reuse, distribution, and reproduction in any medium, provided the original work is properly cited.