Evolution, 2024, **78(7)**, 1275–1286
https://doi.org/10.1093/evolut/qpae046
Advance access publication 05 April 2024
Original Article

OXFORD

The effect of miniaturization on the evolution of sexual size dimorphism in geckos

Elizabeth Glynne and Dean C. Adams

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

Corresponding author: Elizabeth Glynne, Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, IA, United States.
Email: eglynne@iastate.edu

Abstract

The evolution of miniaturization can result in dramatic alterations of morphology, physiology, and behavior; however, the effects of miniaturization on sexual dimorphism remain largely unknown. Here we investigate how miniaturization influences patterns of sexual size dimorphism (SSD) in geckos. Measuring 1,875 individuals from 131 species, we characterized patterns of SSD relative to body size across two families. We found that miniaturized species were more female biased than non-miniaturized species. Additionally, one family that contained many miniaturized species (Sphaerodactylidae) displayed allometric patterns in SSD with body size, where larger species were male biased and smaller species were more female biased. Smaller species in this lineage also produced proportionally larger eggs. By contrast, another family containing few miniaturized species (Phyllodactylidae) displayed a more isometric trend. Together, these observations are consistent with the hypothesis that selection for increased reproductive success in small species of Sphaerodactylidae results in female-biased SSD in these taxa, which in turn drives the positive SSD allometry observed in this lineage. Thus, selection for increased miniaturization in the clade may be offset by selection on maintaining a female size in smaller taxa that ensures reproductive success.

Keywords: macroevolution, Rensch's rule, morphometrics

Introduction

Variation in body size is one of the most striking trends observed across taxa. Biologists have long sought to understand what ecological and evolutionary mechanisms drive the evolution of body size (Acevedo et al., 2022; Maurer et al., 1992; Schmidt-Nielsen, 1975), with particular focus on the causes of extreme body sizes at both large (gigantism) and small (miniaturization) scales (Hanken & Wake, 1993; Van Valen, 1973). Miniaturization, a process that results in extreme body size reduction in comparison with a species' ancestor or close relatives (Carvalho et al., 2021; Hanken & Wake, 1993), is observed in a wide variety of animals including in every major vertebrate lineage (fish, amphibians, reptiles, birds, and mammals). Miniaturized species often encounter physiological and ecological challenges (Glaw et al., 2021), and thus extreme body size reduction is often accompanied by profound structural modifications that maintain functionality and facilitate their survival. For example, miniaturization is often associated with organ reduction, tissue loss, and other structural reorganizations (Daza et al., 2008; Hanken & Wake, 1993; Ocampo et al., 2018; Rieppel, 1996; Strong et al., 2020). Additionally, miniaturization can result in other distinctive features, such as enlarged sensory organs and braincases relative to body size (Hanken, 1983; Perez-Martinez & Leal, 2021; Rieppel, 1996), and changes to the nervous system (Faisal, 2005; Niven & Farris, 2012), which are crucial for navigating in complex microenvironments. Thus, while the anatomical changes associated with miniaturization are quite varied, they often result in common patterns such as structural simplification, novel morphological traits, and an increase in intraspecific disparity (Hanken, 1982, 1984; Hanken & Wake, 1993).

In addition to structural adaptations, the evolution of miniaturization is also commonly associated with alterations in a species' ecological, behavioral, and life history attributes. For instance, in some lineages, miniaturized species utilize terrestrial habitats more frequently than do nonminiaturized species (Perez-Martinez & Leal, 2021). Similarly, in amphibians, there is a paucity of small-bodied species at higher elevations (Womack & Bell, 2020), and thus miniaturized amphibians are found in microhabitats in lower and middle elevational regions. Miniaturization in amphibians is also associated with life history changes, such as an increased incidence of direct development (Blackburn, 2008; Levy & Heald, 2015; Rittmeyer et al., 2012; Womack & Bell, 2020). In lizards and snakes, smaller species tend to produce proportionally larger offspring as compared to those produced by larger species (Bauwens & Diaz-Uriarte, 1997; Kratochvíl & Frynta, 2006; Meiri et al., 2012, 2015; Shine et al., 1998). This pattern suggests that hatchling size in smaller species may be close to the lower limit of absolute size based on physiological considerations (Bauwens & Diaz-Uriarte, 1997). Miniaturization may also confer particular benefits, such as facilitating predator avoidance (Blanckenhorn, 2000; Clarke,

---

Received September 04, 2023; revisions received March 12, 2024; accepted April 03, 2024
Associate Editor: Ian Dworkin; Handling Editor: Miriam Zelditch

1996), enhancing the ability to utilize unique or smaller niches (Clarke, 1996; Zimkus et al., 2012), and aiding in novel resource exploitation (Clarke, 1996). Indeed, there is an increasing body of evidence documenting the potential benefits (and challenges) to exhibiting a miniaturized phenotype, and deciphering the ecological and evolutionary selective forces that drive species to these extreme body sizes remains an active topic of investigation (Blanckenhorn, 2000; Glaw et al., 2021).

Another near ubiquitous pattern observed across the animal tree of life is phenotypic differences between males and females or sexual dimorphism (Fairbairn, 1997, 2013). Within species, it is frequently observed that males and females are not identical, but rather differ to a greater or lesser degree in their phenotypic characteristics. Sexual dimorphism is found in numerous anatomical traits across a diverse set of taxa, but is commonly expressed in body size. Sexual size dimorphism (SSD) is present in many clades and is hypothesized to be the result of various selection pressures related to reproductive demands or to the specific ecological roles that males and females fulfill to survive and reproduce (Cox et al., 2003; Kaliontzopoulou et al., 2015; Littleford-Colquhoun et al., 2019; Stephens & Wiens, 2009; Tarr et al., 2019). For example, intraspecific competition may encourage ecological divergence between the sexes, contributing to the various patterns of sexual dimorphism observed across taxa (Bolnick & Doebeli, 2003; Butler et al., 2000; Kaliontzopoulou et al., 2010; Meiri et al., 2014). Likewise, sexual selection on male body size (Cox et al., 2003; Garcia-Navas, 2015; Horne et al., 2020), and fecundity selection on female body size (Serrano-Meneses & Szekely, 2006; Stuart-Fox & Moussalli, 2007), can accentuate the degree of SSD over time.

When SSD is examined comparatively across taxa, species tend not to display the same patterns, but rather differ in the degree to which that dimorphism is exhibited. For instance, some species may be male biased in SSD (where males are larger than females), others may be female biased, while some may be monomorphic with both sexes exhibiting near-equal sizes. When viewed in a phylogenetic context, these species-specific patterns give rise to macroevolutionary trends of SSD, which can be interrogated to determine the origins and/or maintenance of SSD (Rensch, 1950). Several allometric patterns of SSD in relation to body size have been identified. For instance, species in some clades display consistent levels of SSD across taxa regardless of body size, where one sex remains proportionally larger than the other (Hirst & Kiørboe, 2014). By contrast, many clades display varying levels of SSD across taxa where the larger species become increasingly male biased in SSD, while the smaller species become increasingly female biased in SSD (i.e., positively allometric, Abouheif & Fairbairn, 1997; Blanckenhorn et al., 2007; Rensch, 1950). Conversely, in some clades, larger species become increasingly female biased in SSD, and the smaller species become increasingly male biased in SSD (Liao et al., 2013).

Interestingly, while the effects of reduced body size on many aspects of organismal phenotype and life history have been investigated (e.g., Bauwens & Diaz-Uriarte, 1997; Daza et al., 2008; Hanken, 1983; Kratochvíl & Frynta, 2006; Meiri et al., 2015; Niven & Farris, 2012), to our knowledge, how miniaturization relates to patterns of SSD has not been articulated. In many clades, reproductive output (i.e., offspring size or number) is positively associated with female size (Meiri et al., 2012); thus, we may predict that as a species evolves to be smaller, there may be size-dependent selection on females associated with fecundity and reproductive output (sensu Nali et al., 2014). Indeed, in oviparous lizards, smaller females generally produce proportionally larger offspring (Kratochvíl & Frynta, 2006; Meiri et al., 2015). Thus, we may expect that as a species becomes smaller, females may in turn evolve to be as large as, or larger than, males, as an evolutionary response to selection on reproductive output. From this, we may therefore predict that miniaturized species of lizards will be female biased in their SSD, thereby altering the macroevolutionary trends observed in SSD with body size across taxa.

Determining the size limit below which a species is considered to be miniature is taxon specific and is based on changes in numerous traits. In squamate lizards for example, miniaturization is accompanied by a disproportionate increase in the diameter of the neurocranium, coupled with rearrangements of surrounding skull bones (Scharf & Meiri, 2013). Miniaturized geckos exhibit changes in the ossification patterns of the skull, with a proportionally larger braincase relative to body length, aligning with similar trends observed in other miniaturized vertebrates (see, e.g., Ocampo et al., 2018; Rieppel, 1984; Yeh, 2002). These changes manifest as a loss of complexity in osteological traits, such as a reduction in ossification of bones (e.g., reduced coronoid bone, Vallejo-Pareja, 2018), and rearrangements within the skull. Specifically, miniaturized geckos have been shown to exhibit a fused premaxilla and a fused braincase, and an increased overlap between skull bones (Daza et al., 2008; Vallejo-Pareja, 2018). These alterations are presumed to accommodate neural demands for survival, with larger otic capsules likely maintaining visual requirements and the reinforced braincase accommodating differing ecological and life history demands (Daza et al., 2008, 2009; Gamble, 2011). In terms of body size, such alterations tend to be present in taxa exhibiting skull lengths less than 15 mm and in taxa whose body size is less than 40-mm SVL (Scharf & Meiri, 2013). For this reason, 40-mm snout–vent length (SVL) is generally considered to be the threshold of miniaturization in lizards (see Perez-Martinez & Leal, 2021).

Gekkotan lizards are an ideal clade to investigate the interplay between miniaturization and sexual size dimorphism. Geckos comprise roughly 20% of all squamates (~2,300 species, Uetz et al., 2023), are broadly distributed, occupy a wide range of habitats, and are phenotypically diverse. Geckos also display a large size range among species, including some of the smallest terrestrial vertebrates (*Sphaerodactylus ariasae*: 18-mm average SVL; Hedges and Thomas 2001), as well as species 20 times larger (*Rhacodactylus leachianus*: 360-mm average SVL: Cuvier, 1829). Furthermore, miniaturization in body size is widespread, with nearly 70% of all miniaturized lizard species (340 of 500) belonging to geckos (Perez-Martinez & Leal, 2021). Of particular note is the family Sphaerodactylidae, which contains over 25% of all miniaturized species of lizards (>100; Perez-Martinez & Leal, 2021), including one of the smallest known lizard species (Hedges & Thomas, 2001). Additionally, sexual dimorphism is present in some gekkotan taxa, including sexual dichromatism (Regalado, 2014) and sex-specific habitat use (Miranda & Andrade, 2003). Likewise, sexual size dimorphism (SSD) has been documented in isolated taxa and genera (Johnson et al., 2005; Kratochvíl & Frynta, 2008; Kubička et al., 2016; Massetti et al., 2017; Starostová et al., 2010). However, it remains unclear whether SSD varies systematically across species relative to their body size at broader taxonomic scales.

In this study, we investigated how the evolution of miniaturization influences patterns of SSD in geckos. First, we characterized patterns of SSD in 131 species from two families (Sphaerodactylidae and Phyllodactylidae) that differ greatly in the proportion of miniaturized species in each. We then tested the hypothesis that miniaturized species were more female biased in their SSD relative to non-miniaturized taxa. We also compared size-related patterns of SSD within families to determine whether or not changes in SSD across taxa were isometric. Finally, we examined the relationship between egg size and female body size across taxa to test whether females of smaller species displayed relatively larger eggs.

Methods

We characterized SSD for 46 species of Phyllodactylidae and 85 species of Sphaerodactylidae, including both miniaturized and non-miniaturized taxa. The species used in this study represented those taxa available in Natural History collections that were also represented on a recent molecular phylogeny for the group (see below). Following Perez-Martinez & Leal (2021), any species whose typical adult body size was less than 40-mm SVL (measured from the snout to the cloaca) was considered to be miniaturized. In our sample, 6 of 46 Phyllodactylidae species were classified as miniaturized, while 67 of 85 species in Sphaerodactylidae were determined to be miniaturized species. Thus, between the two clades, the effects of miniaturization were expected to be more prevalent in Sphaerodactylidae. To quantify SSD, we measured SVL from a total of 1,875 adult specimens, with a minimum of 3 males and 3 females per species (mean = 7), obtained from natural history collections (see Supplementary Table S1). All measurements were log-transformed to conform with normality, and the mean $log(SVL)$ for each $species \times sex$ combination was then calculated. Because gekkotans display determinate growth (sensu Frýdlová et al., 2020), it was unlikely that our estimates of species mean sizes were conflated with growth allometry. Additionally, because the number of individuals in each $species \times sex$ combination differed, we calculated the standard deviation for each ($\sigma_{spp \times sex}$) as a measure of within-species variation to be used in some of our analyses (see below). Using the $species \times sex$ means, we calculated the SSD for each species using a size dimorphism index defined as:

$$SSD_I = log(SVL_M) - log(SVL_F)$$

Here, SSD_I was positive for species where males were the larger sex (i.e., *male biased*) and was negative for species where females were the larger sex (i.e., *female biased*). This measure of SSD was used because it is easily interpretable and was appropriate for use in subsequent regression analyses (Smith, 1999). Finally, our data were matched to the phylogeny of Tonini et al. (2016), so that evolutionary relationships could be properly accounted for during our comparative analyses.

Using these data, we conducted a series of analyses to interrogate patterns of SSD across the phylogeny relative to patterns of miniaturization in the group. First, we evaluated whether SSD differed in miniaturized taxa as compared with non-miniaturized species. For this, we used a phylogenetic ANOVA (Adams & Collyer, 2022). Here, and in all subsequent comparative analysis, phylogenetic nonindependence was characterized using a Brownian motion model of evolution. We used the R-package `RRPP` version 2.0.0 (Collyer & Adams, 2018, 2024) to conduct our phylogenetic ANOVA. Additionally, because evaluating macroevolutionary trends using species means alone can result in biased parameter estimates and elevated type I error rates (Felsenstein, 2008; Harmon & Losos, 2005; Ives et al., 2007), we repeated the phylogenetic linear model above via a procedure that accounted for within-species variation (i.e., measurement error), using the R-package `phylolm` (Tung Ho et al., 2014).

Next, a phylogenetic regression between male and female length was conducted to test the allometric relationship between them and to determine the extent to which SSD changed evolutionarily as a function of body size. As above we first performed the analysis of $log(SVL_M)$ versus $log(SVL_F)$ using species means as data (sensu Abouheif & Fairbairn, 1997; Ceballos et al., 2013; Fairbairn, 1997). Phylogenetic regression was performed separately for each family. Then, for each family, we evaluated whether the slope of this relationship (β_{obs}) differed from that of constant SSD across species (i.e., isometry or $\beta = 1.0$). To accomplish this, we used a permutation procedure following that of Tejero-Cicuéndez et al. (2023). Here, the data were fit to a phylogenetic regression where the slope was set to the value representing the null hypothesis (in this case, $\beta = 1.0$), and both predicted values and residuals from this model were obtained. The residuals were then permuted and added to the predicted values, and the original phylogenetic regression was performed using these values, and the slope (β_{rand}) was obtained. This procedure was repeated 1,000 times to generate an empirical sampling distribution of slopes against which the observed value (β_{obs}) was compared (for related procedures, see Adams & Collyer, 2009; Piras et al., 2010). Additionally, to account for within-species measurement error, we repeated the phylogenetic regressions above using procedures that allowed the incorporation of within-species variation for both the dependent and independent variables (Ives et al., 2007). We obtained the slope of the relationship as before and evaluated it relative to the null hypothesis of isometry across species (i.e., $\beta = 1.0$) using a parametric bootstrap procedure with 2,000 simulations (sensu Ives et al., 2007). Here β_{obs} was compared with $\beta = 1.0$ using a t-test whose standard error was the standard error obtained from the 2,000 parametric bootstrap simulations. Additionally, we compared the slope obtained from species means alone to the slope obtained from an analysis that incorporated measurement error using a t-test, to allow us to directly evaluate whether parameter estimates obtained using species means alone were comparable to those obtained when within-species measurement error was included. Finally, we conducted a phylogenetic ANCOVA to compare the allometric slopes between families. Phylogenetic regression and phylogenetic ANCOVA were performed in R using `RRPP` version 2.0.0 (Collyer & Adams, 2018, 2024), and phylogenetic regression incorporating measurement error was accomplished in Matlab, using the PHYSIG program (see Ives et al., 2007).

To characterize the evolution of SSD across the phylogeny, we employed maximum likelihood (ML) methods (Schluter et al., 1997). Using ML, we estimated ancestral states for SSD_I and then mapped these onto the phylogeny to visualize evolutionary shifts in SSD, to determine how patterns of male-biased and female-biased SSD evolved. We also determined whether the ancestral value for each family was monomorphic or dimorphic by determining whether the confidence intervals obtained from the ML analysis bracketed zero. Additionally, we performed Bayesian stochastic character mapping (Bollback, 2006; Huelsenbeck et al., 2003) to evaluate the evolution of miniaturization across the phylogeny. Here we generated 1,000 stochastic character maps on the phylogeny using the Q-matrix calculated using ML under the optimal all rates different model. The resulting stochastic maps were then summarized to obtain estimates of ancestral body size group (miniaturized or non-miniaturized) at each node of the phylogeny. These ancestral state estimates were then used to estimate the number of evolutionary transitions to and from miniaturization across the phylogeny. Both analyses were conducted in R, using `phytools` version 1.9-16 (Revell, 2012). Finally, we determined whether females of smaller species displayed relatively larger eggs using phylogenetic regression. Here egg size data were obtained from the literature (Rosler, 2004) and were matched to corresponding species means for females as described above. A slope significantly lower than $\beta = 1.0$ would imply that smaller species displayed relatively larger eggs as compared to larger taxa, supporting the hypothesis of selection for enhanced reproductive allocation in smaller species (see Kratochvíl & Kubička, 2007). This analysis was performed in R using `RRPP` version 2.0.0 (Collyer & Adams, 2018, 2024).

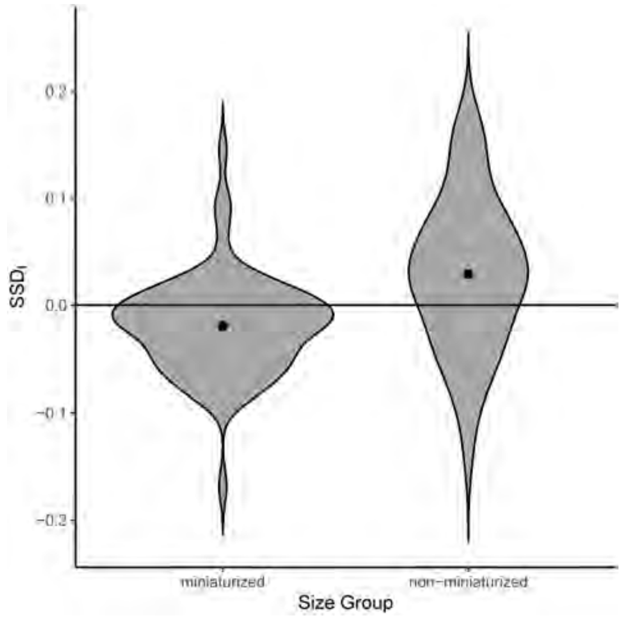

Figure 1. Distribution of sexual size dimorphism (SSD) for miniaturized and non-miniaturized species of geckos, where SSD is represented using the index SSD_I. Monomorphism (i.e., no sexual dimorphism) is denoted by the horizontal line at $SSD_I = 0.0$. The mean value for each group is designated by the black dot. Phylogenetically corrected values display a similar pattern (see Supplementary Figure S1).

Results

Using phylogenetic ANOVA, we found that miniaturized species displayed significantly lower SSD_I values as compared to non-miniaturized species ($F = 4.43$, $Z = 1.66$, $p = 0.04$; $\beta = 0.048$, $SE_\beta = 0.024$, $t = 2.04$, $p = 0.021$). When within-species measurement error was taken into consideration, these results were corroborated ($\beta = 0.033$, $SE_\beta = 0.015$, $t = 2.12$, $p = 0.03$), indicating that estimates from species means were not adversely affected by sampling error. Both miniaturized and non-miniaturized species contained male- and female-biased species (Figure 1), though the greatest concentration of miniaturized species displayed SSD_I values less than zero (i.e., female-biased SSD). Furthermore, the mean value for miniaturized species was less than zero, while that of non-miniaturized species was greater than zero. Thus while there was considerable overlap between the two groups, on average miniaturized species were female biased in their SSD_I, in accordance with our prediction.

Both Sphaerodactylidae and Phyllodactylidae contained species exhibiting male- and female-biased SSD (Figures 2 and 3). Species in Sphaerodactylidae also displayed a much larger range of body sizes than those in Phyllodactylidae, a pattern driven primarily by the presence of miniaturized Sphaerodactylidae species (Figure 2). Phylogenetic regression revealed strong patterns of evolutionary allometry across taxa for both Sphaerodactylidae ($R^2 = 0.96$, $F = 2141.7$, $Z = 10.79$, $p < 0.001$) and Phyllodactylidae ($R^2 = 0.97$, $F = 1209.2$, $Z = 5.63$, $p < 0.001$). A phylogenetic ANCOVA found that the slopes for the two families were not different from one another ($F = 2.93$, $Z = 1.43$, $p = 0.076$), though the pattern did trend towards divergence. Nonetheless, comparing within-family patterns to that of isometry did reveal some differences, with Sphaerodactylidae displaying a positively allometric trend of SSD ($\beta = 1.11$, $SE = 0.067$, $Z = 3.64$, $p < 0.001$), while the evolutionary pattern of SSD across species in Phyllodactylidae was slightly positive, but did not differ significantly from that of isometry ($\beta = 1.05$, $SE = 0.102$, $Z = –0.03$, $p = 0.523$). Thus, in Sphaerodactylidae (Figure 2A), the overall allometric trend was one where larger species displayed male-biased SSD, while smaller species displayed female-biased SSD (a.k.a. Rensch's rule: see also Liang et al., 2021). By contrast, Phyllodactylidae (Figure 2B) showed a modest degree of allometry of SSD, but one that did not differ from isometry. Thus, on average, species were somewhat closer to monomorphic at both small and large sizes. Analyses incorporating measurement error corroborated these findings, where Sphaerodactylidae displayed a slope significantly greater than one ($\beta = 1.08$, $SE = 0.042$, $t = 1.95$, $p = 0.027$), while the slope for Phyllodactylidae did not differ from that of isometry ($\beta = 1.06$, $SE = 0.058$, $t = 1.08$, $p = 0.144$). Finally, the slopes obtained using only species means did not differ from those obtained using models that incorporated measurement error ($t_{Sphaero} = –0.68$, $p = 0.75$; $t_{Phyllo} = 0.27$, $p = 0.39$), implying that for this dataset, within-species variation did not adversely affect statistical inference.

Characterizing the evolution of SSD across the phylogeny (Figure 3), we found that the estimate at the root of the clade was monomorphic with confidence intervals that widely bracketed zero ($SSD_I = 0.006 \pm 0.091$). This implied no difference in size between males and females in the common ancestor of these two gecko families. In addition, the most probable ancestral state of the roots for both the Sphaerodactylidae and Phyllodactylidae clades were also monomorphic, displaying no size differences between males and females ($SSD_{I.Sphaero} = 0.006 \pm 0.086$; $SSD_{I.Phyllo} = 0.006 \pm 0.08$). Visual inspection of SSD among taxa revealed great variation across

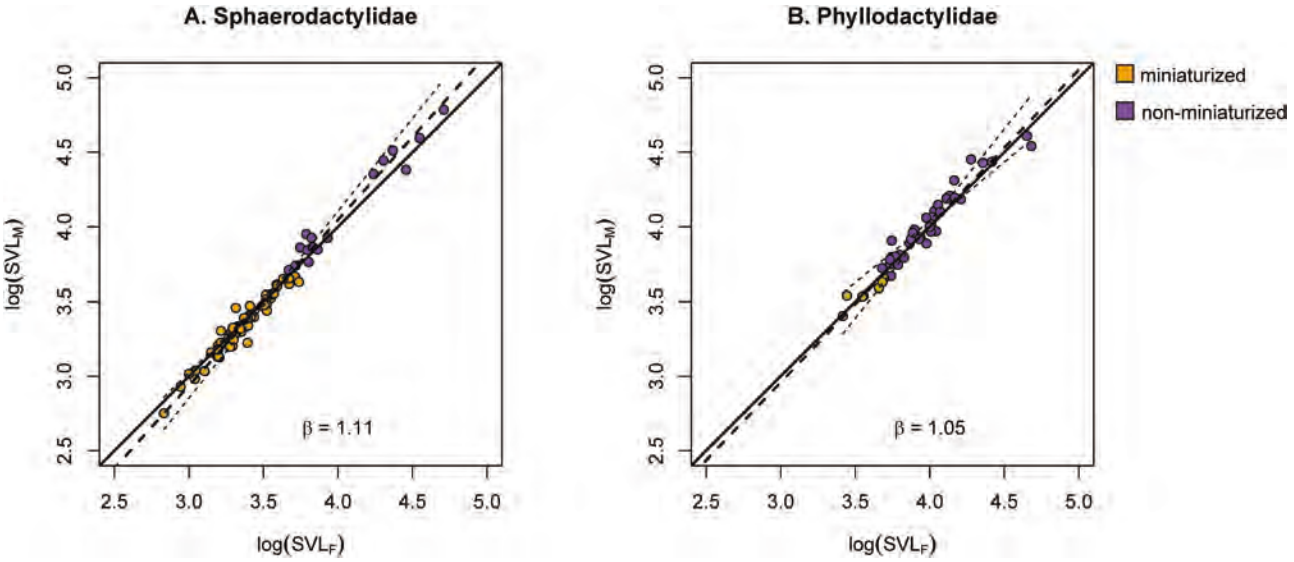

Figure 2. Evolutionary patterns of sexual size dimorphism (SSD) for (A) Sphaerodactylidae and (B) Phyllodactylidae, displaying allometric patterns for the former and isometric patterns for the latter. In each plot, the solid line demarcates a 1:1 relationship between males and females, which designates the case of isometry where species remain monomorphic across a range of body sizes. The observed relationship obtained from phylogenetic regression is shown by the dashed line. Orange designates miniaturized taxa, while purple designates non-miniaturized taxa.

the phylogeny, with no obvious systematic trend toward male-biased SSD or female-biased SSD when moving from the root to the tips (Figure 3). Instead, male- and female-biased taxa were interspersed across the phylogeny, indicating evolutionary liability of this trait over time and implying many recent evolutionary shifts in SSD across taxa (Figure 4). Ancestral reconstruction of body size groups revealed that miniaturization evolved at least six times across the phylogeny, with at least seven reversions from miniaturized to non-miniaturized forms. Not surprisingly, miniaturization was hypothesized to evolve early in the history of the Sphaerodactylidae clade (Figure 4), in accordance with prior results (Perez-Martinez & Leal, 2021).

Finally, we found a strong relationship between egg length and female body size ($R^2 = 0.81$, $F = 64.40$; $Z = 4.66$; $p < 0.001$; Figure 5), with a slope much smaller than one ($\beta_{obs} = 0.58$). Thus, across species, egg size increased more slowly than did female body size, a scaling relationship indicating that females of smaller species displayed relatively larger eggs (Figure 5). Indeed, the smallest four species in our dataset (all miniaturized species) have eggs which were between 24% and 29% of their body length, while the largest four species in our dataset displayed eggs between 18% and 20% of their body length. Thus, these findings were consistent with the hypothesis that in smaller species, egg size could be under selection for increased size to maintain viable offspring size in the smaller species, resulting in miniaturized species with proportionally larger eggs.

Discussion

On nearly every branch of the tree of life, body size differences among taxa are observed, yet it is the evolution of extreme body sizes (such as miniaturization) that represents a particular evolutionary puzzle. In vertebrates, miniaturization results in profound phenotypic, ecological, and physiological changes, but the effects of miniaturization on sexual dimorphism remain underexamined. In this study, we interrogated how miniaturization influences patterns of SSD across species from the families of geckos (Phyllodactylidae and Sphaerodactylidae); the latter of which also displays frequent body size reduction (i.e., miniaturization). We found that SSD differed in miniaturized taxa as compared to non-miniaturized taxa, where miniaturized taxa were more female-biased in their SSD. When compared with the hypothesis of isometry, we also found varying allometric trends of SSD in the two families, with positive allometry of SSD in Sphaerodactylidae, while Phyllodactylidae exhibited a shallower relationship that did not significantly differ from isometry. Additionally, we found evolutionary lability in SSD over time in both families, as the male- and female-biased taxa were distributed across the phylogeny in no predictable manner. Furthermore, in Sphaerodactylidae, we found that small species produced relatively larger eggs, consistent with the prediction that reproductive pressures constrain the lower limit of body size reduction in these taxa. Taken together, our findings further our understanding of the evolution of SSD, and how such sex-specific differences are influenced by the evolution of miniaturization in such lineages.

First, when comparing SSD between miniaturized and non-miniaturized taxa, we found that on average miniaturized species were more female-biased (Figure 1). Thus we can hypothesize that as gecko species become smaller, there is a concomitant trend toward females becoming proportionally larger than males in those lineages. Likewise, when viewed allometrically, we observed that the preponderance of miniaturized species in Sphaerodactylidae were more female biased than were the smallest species of Phyllodactylidae (Figure 2), which is consistent with this interpretation. Additionally, we observed clear allometric trends in SSD among species across all taxa, yet the evolutionary patterns displayed by the two families of geckos differed considerably. In Phyllodactylidae, both male- and female-biased species were observed (Figures 2 and 4), yet differences in SSD among species did not change in

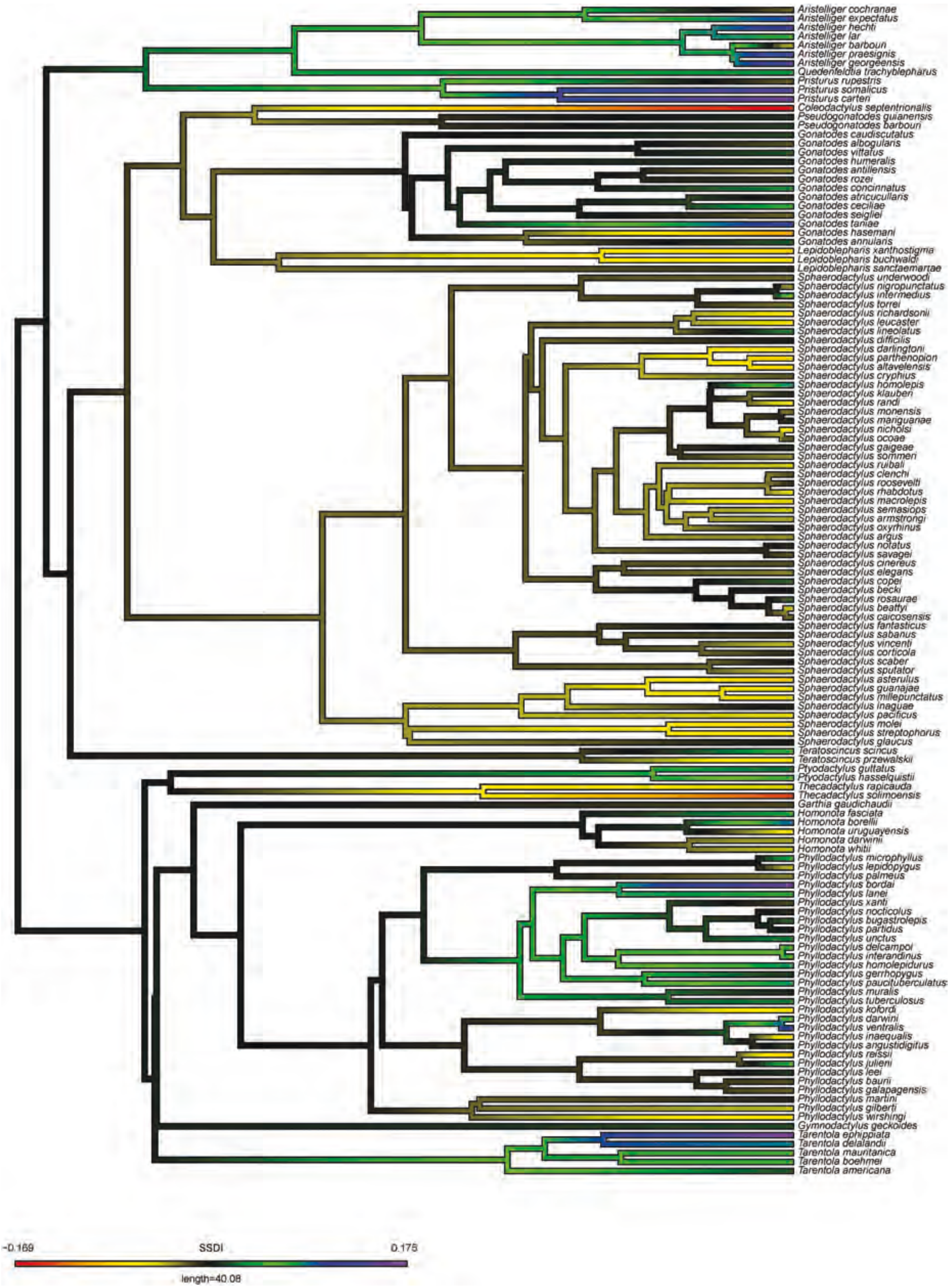

Figure 3. Time-dated phylogeny for reptiles from Tonini et al. (2016) pruned to the 131 species available in this study. Branches display maximum likelihood ancestral estimates for *SSD*$_I$. Warm colors (yellow-red) indicate female-biased SSD, while cooler colors (green-purple) indicate male-biased SSD.

association with species body size. Thus on average, the degree of sexual dimorphism was largely invariant across the range of body sizes observed in the clade, such that Phyllodactylidae displayed a stable isometric pattern of SSD relative to body size at the macroevolutionary level (see also Liang et al., 2021). By contrast, SSD patterns in Sphaerodactylidae varied

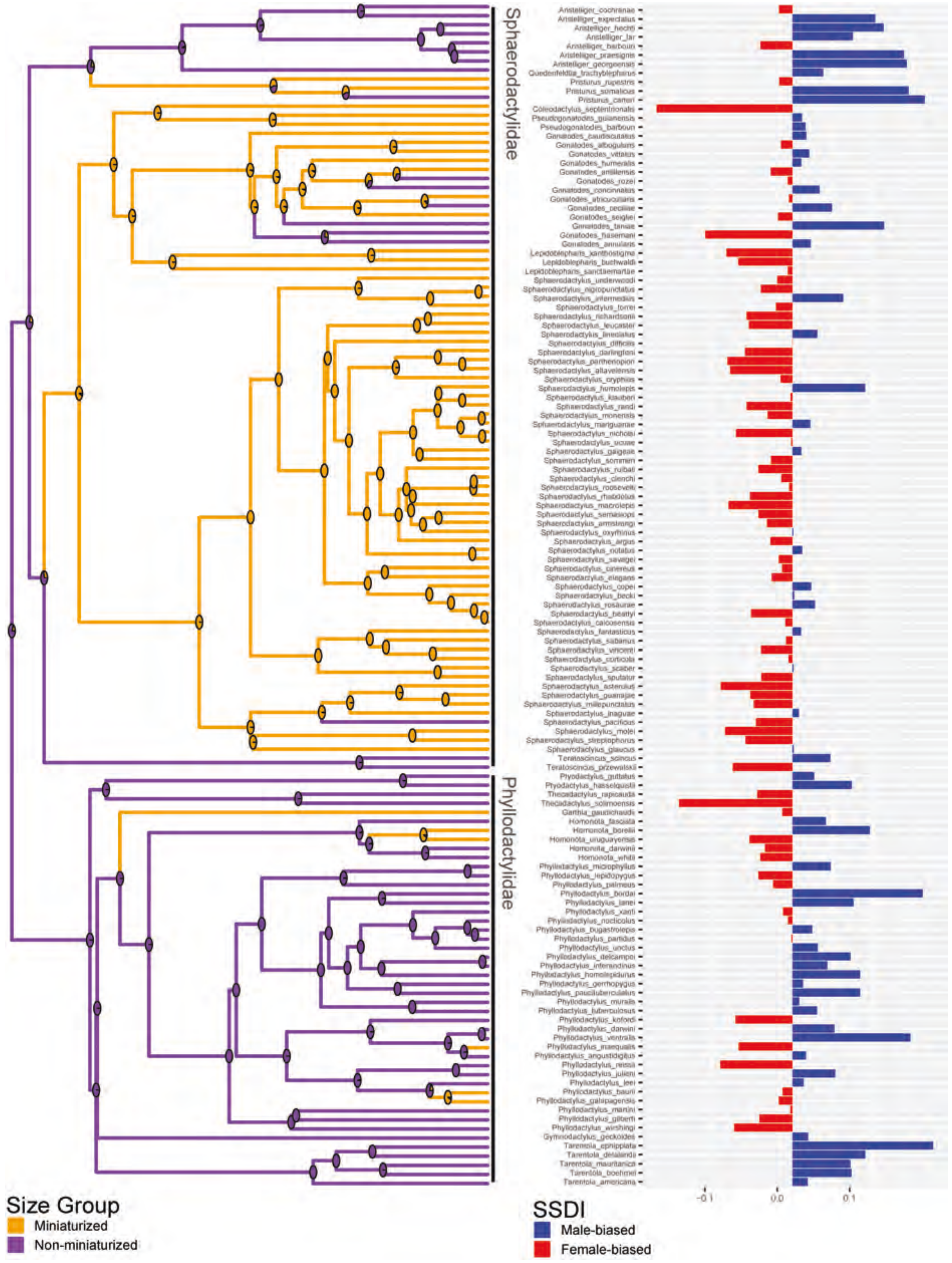

Figure 4. Time-dated phylogeny for reptiles from Tonini et al. (2016) pruned to the 131 species available in this study. Branches display ancestral estimates for size groups (miniaturized or non-miniaturized) based on Bayesian stochastic character mapping, where the color was determined by a 0.51 cutoff. The bar chart to the right of each species displays values of the sexual size dimorphism (SSD) index (SSD_I). Blue designates male-biased species, while red designates female-biased species.

systematically with body size, with larger species becoming more male biased and smaller species becoming more female biased. Furthermore, a greater number of Sphaerodactylidae species displayed female-biased SSD (Figure 4). Thus, unlike the patterns observed in Phyllodactylidae, macroevolutionary changes in SSD across taxa in Sphaerodactylidae were

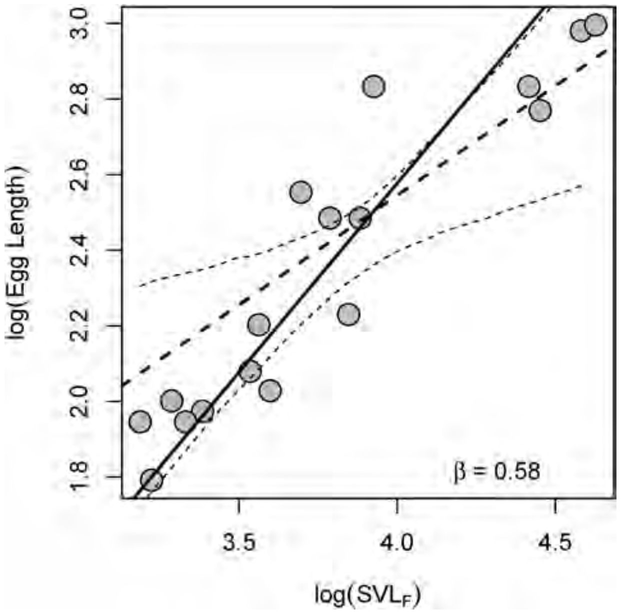

Figure 5. Relationship between egg length and female body size (SVL). The solid line demarcates a 1:1 relationship, where one unit of change in female body size corresponds with one unit change in egg length. The observed relationship obtained from phylogenetic regression is shown by the dashed line.

positively allometric, with small and miniaturized species tending to display more female-biased SSD, adhering to Rensch's rule (1950, 1960).

With respect to Sphaerodactylidae, what mechanisms may have driven the positive allometry of SSD observed in this clade? One likely possibility is that selection on fecundity and/or reproductive output could generate positive SSD allometry. Generally, oviparous reptiles display a positive association between female body size and clutch size (Escalona et al., 2018; Green, 2000; James & Shine, 1988; King, 2000; Meiri et al., 2020; Scharf & Meiri, 2013; Tinkle et al., 1970), which is thought to result from fecundity selection. However, clutch size in geckos is fixed at one or two eggs per reproductive bout (Kratochvíl & Kubička, 2007; Shine & Greer, 1991), and thus fecundity selection (in terms of selection for an increased number of offspring) is unlikely in this group. On the other hand, smaller female lizards tend to produce proportionally larger offspring compared to offspring produced by larger females (Kratochvíl & Frynta, 2006; negative allometry, Meiri et al., 2015). Geckos generally conform with this pattern (Meiri et al., 2015), and in our study, we observed that smaller species of Sphaerodactylidae did in fact lay proportionally larger eggs as compared to those from larger species (Figure 5). Thus, this observation, coupled with our finding that miniaturized species often exhibit female-biased SSD, suggests that miniaturized geckos conform with the lower limit hypothesis of offspring size (sensu Kratochvíl & Frynta, 2006; Meiri et al., 2015) and that selection for increased reproductive success may be responsible for the female-biased size patterns in miniaturized species in this lineage.

On the other hand, our data suggest that while the allometry of SSD in Phyllodactylidae is positive, it does not significantly differ from isometry. Why might this be the case? The macroevolutionary literature on SSD suggests several mechanisms by which an isometric pattern may be maintained. One hypothesis is that isometry would be expected across taxa if the changes in male body size were evolutionarily correlated due to genetic or developmental processes that are concomitant with changes in female body size (Cheng & Kuntner, 2014). Alternatively, a second hypothesis is that if the effects of selection on each sex were of similar effect, an isometric pattern is also expected to evolve (Hirst & Kiørboe, 2014). Despite not being significantly different from isometry, our analysis of the data revealed a slightly positive allometric relationship of SSD in Phyllodactylidae, although not to the extent of that observed in Sphaerodactylidae. Thus, a third potential explanation for the observed pattern is that there is a degree of uncertainty in our estimation due to an artifact of taxonomic sampling and that the inclusion of additional taxa may reveal a more positively allometric relationship in this group. While this remains a possibility, we note that increasing the taxonomic sampling in Phyllodactylidae would largely improve coverage and resolution of the upper portion of the allometry curve (Figure 2B), where non-miniaturized species reside. Given the scarcity of miniaturized Phyllodactylid species, the lower portion of the curve is effectively a region of phenotype space relatively underexplored by evolutionary processes. Thus, understanding how such miniaturized taxa could influence allometric patterns of SSD in this group will remain largely unknown.

Overall, our analyses suggest that on average, miniaturized taxa display more female-biased SSD, while on average non-miniaturized species show the converse. Sphaerodactylidae, which contains many miniaturized species, displays positive allometry of SSD. Phyllodactylidae, which contains few miniaturized species, displays a slightly positive allometric relationship, but one that does not differ significantly from isometry. A comparison of the allometric relationships between the two families found that their slopes were both positive, but trended toward divergence. Females from small Sphaerodactylidae species produced disproportionately larger eggs. When considered together, an argument of consilience suggests that miniaturized species within Sphaerodactylidae may be the driving force behind the allometric patterns of SSD, likely due to constraints associated with reproduction.

Finally and as noted previously, determining the size limit below which a species is considered to be miniature is based on identifying changes in numerous traits required for their functioning and survival. In vertebrates, miniaturization is accompanied by alterations in numerous anatomical traits, including structural simplification, a reduction of bone ossification, and changes to the neurosensory system (Daza et al., 2008; Hanken, 1984; Scharf & Meiri, 2013; Rieppel, 1984). Many of these changes tend to occur in lizard species whose typical body size is less than 40-mm SVL (Scharf & Meiri, 2013), which enables one to define a miniaturization threshold at that size (see Perez-Martinez & Leal, 2021). Clearly however, making such a determination is taxon specific, and identifying the size at which similar changes occur in other organisms would need to be investigated. Nevertheless, our findings contribute to a larger body of work regarding the effects of miniaturization in geckos and demonstrate concomitant changes in patterns of SSD in this group as species become smaller. Indeed, based on our findings, we posit that one understudied consequence of miniaturization in oviparous vertebrates relates to reproduction and its association with SSD. Based on the findings of our study, we hypothesize that miniaturized species in other vertebrate lineages may display a similar female-biased SSD pattern, in part to offset the negative effects of reduced size in females with respect to reproduction. Indeed, another world's smallest lizards, *Brookesia nova*, is also strongly female biased (Glaw et al., 2021), and also displays invariant clutch sizes ($N = 2$). Additionally, miniaturized anurans display female-biased body sexual dimorphism (Gorin et al., 2021), and female-biased SSD is also observed in small species of shorebirds and hummingbirds (Colwell, 2000; Székely et al., 2004). Our findings support the notion that at smaller body sizes, the selective forces driving the evolution of miniaturization are counterbalanced by selection on maintaining female size to ensure reproductive success, thereby resulting in increased female-biased SSD in smaller taxa. We therefore encourage future work to investigate the functional relationship between SSD and miniaturization, in additional clades.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

All data are accessible through the Dryad repository (DOI:10.5061/dryad.kkwh70sb4).

Author contributions

All authors contributed to all aspects of this work.

Funding

This work was sponsored in part by National Science Foundation Grant DBI-1902511 & DEB-2140720 (to DCA), and a California Academy of Natural Sciences Michele L. Aldrich Collections Research Grant (to EG).

Conflict of interest: The authors declare no conflict of interest.

Acknowledgments

We thank Tracy Heath, Haldre Rogers, Amy Toth, and Nicole Valenzuela for comments on earlier versions of this manuscript. We also thank the many museum curators and collection managers who made this work possible, by enabling access to specimens in their collections, including those at 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.

Acevedo, A. A., Palma, R. E., & Olalla-Tárraga, M. Á. (2022). Ecological and evolutionary trends of body size in *Pristimantis* frogs, the world's most diverse vertebrate genus. *Scientific Reports*, *12*, 18106. https://doi.org/10.1038/s41598-022-22181-5

Adams, D. C., & Collyer, M. L. (2009). A general framework for the analysis of phenotypic trajectories in evolutionary studies. *Evolution*, *63*, 1143–1154. https://doi.org/10.1111/j.1558-5646.2009.00649.x

Adams, D. C., & Collyer, M. L. (2022). Consilience of methods for phylogenetic analysis of variance. *Evolution*, *76*, 1406–1419.

Bauwens, D., & R. Diaz-Uriarte. (1997). Covariation of life-history traits in lacertid lizards: A comparative study. *The American Naturalist*, *149*, 91–111. https://doi.org/10.1086/285980

Blackburn, D. (2008). Biogeography and evolution of body size and life history of african frogs: Phylogeny of squeakers (Arthroleptis) and long-fingered frogs (*Cardioglossa*) estimated from mitochondrial data. *Molecular Phylogenetics and Evolution*, *49*, 806–826. https://doi.org/10.1016/j.ympev.2008.08.015

Blanckenhorn, W. U. (2000). The evolution of body size: What keeps organisms small? *The Quarterly Review of Biology*, *75*, 385–407. https://doi.org/10.1086/393620

Blanckenhorn, W. U., Dixon, A. F. G., Fairbairn, D. J., Foellmer, M. W., Gibert, P., van der Linde, K., Meier, R., Nylin, S., Pitnick, S., Schoff, C., Signorelli, M., Teder, T., & Wiklund, C. (2007). Proximate causes of Rensch's rule: Does sexual size dimorphism in arthropods result from sex differences in development time? *The American Naturalist*, *169*, 245–257. https://doi.org/10.1086/510597

Bollback, J. P. (2006). SIMMAP: Stochastic character mapping of discrete traits on phylogenies. *BMC Bioinformatics*, *7*, 1–7. https://doi.org/10.1186/1471-2105-7-88

Bolnick, D. I., & Doebeli, M. (2003). Sexual dimorphism and adaptive speciation: Two sides of the same ecological coin. *Evolution*, *57*, 2433–2449. https://doi.org/10.1111/j.0014-3820.2003.tb01489.x

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.

Carvalho, E. F., Martins, A. R., & Folly, M. (2021). Miniaturization. In J. Vonk, & T. K. Shackelford (Eds.), In *Encyclopedia of animal cognition and behavior* (pp. 1–8). Springer International Publishing. https://doi.org/10.1007/978-3-319-47829-6_2123-1

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.

Cheng, R.-C., & Kuntner, M. (2014). Phylogeny suggests nondirectional and isometric evolution of sexual size dimorphism in argiopine spiders. *Evolution*, *68*, 2861–2872. Wiley. https://doi.org/10.1111/evo.12504

Clarke, B. T. (1996). Small size in amphibians-its ecological and evolutionary implications (pp. 201–224). In *Miniature vertebrates the implications of small body size*. Oxford University Press. https://doi.org/10.1093/oso/9780198577874.003.0011

Collyer, M. L., & Adams, D. C. (2024). *R: RRPP: Linear model evaluation with randomized residuals in a permutation procedure. Vsn. 2.0.0.* R Foundation for Statistical Computing. https://CRAN.R-project.org/package=RRPPhttps://CRAN.R-project.org/package=RRPP

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.

Colwell, R. K. (2000). Rensch's rule crosses the line: Convergent allometry of sexual size dimorphism in hummingbirds and flower mites. *The American Naturalist*, *156*, 495–510. https://doi.org/10.1086/303406

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*, 1653–1669. https://doi.org/10.1111/j.0014-3820.2003.tb00371.x

Cuvier, G. J. L. N. F. D. (1829). Le regne animal distribué, d'apres son organisation, pur servir de base à l'histoire naturelle des animaux et d'introduction à l'anatomie comparé. Nouvelle edition. Vol. 2. Les reptiles (2nd ed.). (pp. 1–406). Déterville, Paris.

Daza, J. A., Herrera, A., Thomas, R., & Claudio, H. J. (2009). Are you what you eat? A geometric morphometric and analysis of gekkotan skull shape. *Biological Journal of the Linnean Society*, *97*, 677–707.

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*, 1340–1364. https://doi.org/10.1002/jmor.10664

Escalona, T., Adams, D. C., & Valenzuela, N. (2018). A lengthy solution to the optimal propagule size problem in the large-bodied south American freshwater turtle, *Podocnemis unifilis*. *Evolutionary Ecology*, *32*, 29–41. https://doi.org/10.1007/s10682-017-9922-3

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*, 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.

Faisal, A. A., White, J. A., & Laughlin, S. B. (2005). Ion-channel noise places limits on the miniaturization of the brain's wiring. *Current Biology*, *15*, 1143–1149. https://doi.org/10.1016/j.cub.2005.05.056

Felsenstein, J. (2008). Comparative methods with sampling error and within-species variation: Contrasts revisited and revised. *The American Naturalist*, *171*, 713–725.https://doi.org/10.1086/587525

Frýdlová, P., Mrzilková, J., Šeremeta, M., Křemen, J., Dudák, J., Žemlička, J., Minnich, B., Kverková, K., Němec, P., Zach, P., & Frynta, D. (2020). Determinate growth is predominant and likely ancestral in squamate reptiles. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *287*, 20202737. https://doi.org/10.1098/rspb.2020.2737

Gamble, T., Bauer, A. M., Colli, G. R., Greenbaum, E., Jackman, T. R., Vitt, L. J., & Simons, A. M. (2011). Coming to america: Multiple origins of new world geckos. *Journal of Evolutionary Biology*, *24*, 231–244. https://doi.org/10.1111/j.1420-9101.2010.02184.x

Garcia-Navas, V., Bonnet, T., Bonal, R., & Postma, E. (2015). The role of fecundity and sexual selection in the evolution of size and sexual size dimorphism in New World and Old World voles (Rodentia: Arvicolinae). *Oikos*, *125*, 1250–1260. https://doi.org/10.1111/oik.03026

Glaw, F., Köhler, J., Hawlitschek, O., Ratsoavina, F. M., Rakotoarison, A., Scherz, M. D., & Vences, M. (2021). Extreme miniaturization of a new amniote vertebrate and insights into the evolution of genital size in chameleons. *Scientific Reports*, *11*, 2522. https://doi.org/10.1038/s41598-020-80955-1

Gorin, V. A., Scherz, M. D., Korost, D. V., & Poyarkov, N. A. (2021). Consequences of parallel miniaturisation in microhylinae (Anura, Microhylidae), with the description of a new genus of diminutive south east Asian frogs. *Zoosystematics and Evolution*, *97*, 21–54. Pensoft Publishers. https://doi.org/10.3897/zse.97.57968

Green, A. J. (2000). The scaling and selection of sexually dimorphic characters: An example using the marbled teal. *Journal of Avian Biology*, *31*, 345–350. https://doi.org/10.1034/j.1600-048x.2000.310310.x

Hanken, J. (1982). Appendicular skeletal morphology in minute salamanders, genus *Thorius* (Amphibia: Plethodontidae): Growth regulation, adult size determination, and natural variation. *Journal of Morphology*, *174*, 57–77. https://doi.org/10.1002/jmor.1051740106

Hanken, J. (1983). Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia, Plethodontidae): II. The fate of the brain and sense organs and their role in skull morphogenesis and evolution. *Journal of Morphology*, *177*, 255–268. https://doi.org/10.1002/jmor.1051770304

Hanken, J. (1984). Miniaturization and its effects on cranial morphology in plethodontid salamanders, genus *Thorius* (Amphibia: Plethodontidae). I. Osteological variation. *Biological Journal of the Linnean Society*, *23*, 55–75. https://doi.org/10.1111/j.1095-8312.1984.tb00806.x

Hanken, J., & Wake, D. B. (1993). Miniaturization of body size: Organismal consequences and evolutionary significance. *Annual Review of Ecology and Systematics*, *24*, 501–519. https://doi.org/10.1146/annurev.es.24.110193.002441

Harmon, L. J., & Losos, J. B. (2005). The effect of intraspecific sample size on type I and type II error rates in comparative studies. *Evolution*, *59*, 2705–2710. https://doi.org/10.1554/05-224.1

Hedges, S. B., & Thomas, R. (2001). At the lower size limit in amniote vertebrates: A new diminutive lizard from the West Indies. *Caribbean Journal of Science*, *37*, 168–173.

Hirst, A. G., & Kiørboe, T. (2014). Macroevolutionary patterns of sexual size dimorphism in copepods. *Proceedings of the Royal Society of London, Series B: Biological Sciences*, *281*, 20140739. https://doi.org/10.1098/rspb.2014.0739

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 of London, Series B: Biological Sciences*, *287*, 20192640. https://doi.org/10.1098/rspb.2019.2640

Huelsenbeck, J. P., Nielsen, R., & Bollback, J. P. (2003). Stochastic mapping of morphological characters. *Systematic Biology*, *52*, 131–158. https://doi.org/10.1080/10635150390192780

Ives, A. R., Midford, P. E., & Garland, T. (2007). Within-species variation and measurement error in phylogenetic comparative methods. *Systematic Biology*, *56*, 252–270. https://doi.org/10.1080/10635150701313830

James, C., & Shine, R. (1988). Life-history strategies of Australian lizards: A comparison between the tropics and the temperate zone. *Oecologia*, *75*, 307–316. https://doi.org/10.1007/bf00378615

Johnson, J. B., McBrayer, L. D., & Saenz, D. (2005). Allometry, sexual size dimorphism, and niche partitioning in the Mediterranean gecko *Hemidactylus turcicus*. *The Southwestern Naturalist*, *50*, 435–439. https://doi.org/10.1894/0038-4909(2005)050%5B0435:assdan%5D2.0.co;2

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*, 80–94. https://doi.org/10.1111/jeb.12540

Kaliontzopoulou, A., Carretero, M. A., & Llorente, G. A. (2010). Intraspecific ecomorphological variation: Linear and geometric morphometrics reveal habitat-related patterns within *Podarcis bocagei* wall lizards. *Journal of Evolutionary Biology*, *23*, 1234–1244.

King, R. B. (2000). Analyzing the relationship between clutch size and female body size in reptiles. *Journal of Herpetology*, *34*, 148. https://doi.org/10.2307/1565253

Kratochvíl, L., & Frynta, D. (2008). Body size, male combat and the evolution of sexual dimorphism in eublepharid geckos (Squamata: Eublepharidae). *Biological Journal of the Linnean Society*, *76*, 303–314. https://doi.org/10.1111/j.1095-8312.2002.tb02089.x

Kratochvíl, L., & Frynta, D. (2006). Body-size effect on egg size in eublepharid geckos (Squamata: Eublepharidae), lizards with invariant clutch size: Negative allometry for egg size in ectotherms is not universal. *Biological Journal of the Linnean Society*, *88*, 527–532. https://doi.org/10.1111/j.1095-8312.2006.00627.x

Kratochvíl, L., & Kubička, L. (2007). Why reduce clutch size to one or two eggs? Reproductive allometries reveal different evolutionary causes of invariant clutch size in lizards. *Functional*

Ecology, *21*, 171–177. https://doi.org/10.1111/j.1365-2435.2006.01202.x

Kubička, L., Golinski, A., John-Alder, H., & Kratochvíl, L. (2013). Ontogeny of pronounced female-biased sexual size dimorphism in the Malaysian cat gecko (*Aeluroscalabotes felinus*: Squamata: Eublepharidae): A test of the role of testosterone in growth regulation. *General and Comparative Endocrinology*, *188*, 183–188.

Levy, D. L., & Heald, R. (2015). Biological scaling problems and solutions in amphibians. *Cold Spring Harbor Perspectives in Biology*, *8*, a019166. https://doi.org/10.1101/cshperspect.a019166

Liang, T., Meiri, S., & Shi, L. (2021). 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

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*, 10. https://doi.org/10.1186/1742-9994-10-10

Littleford-Colquhoun, B. L., Clemente, C., Thompson, G., Cristescu, R. H., Peterson, N., Strickland, K., Stuart-Fox, D., & Frere, C. H. (2019). How sexual and natural selection shape sexual size dimorphism: Evidence from multiple evolutionary scales. *Functional Ecology*, *33*, 1446–1458. https://doi.org/10.1111/1365-2435.13337

Massetti, F., Gomes, V., Perera, A., Rato, C., & Kaliontzopoulou, A. (2017). Morphological and functional implications of sexual size dimorphism in the moorish gecko, *Tarentola mauritanica*. *Biological Journal of the Linnean Society*, *122*, 197–209. https://doi.org/10.1093/biolinnean/blx060

Maurer, B. A., Brown, J. H., & Rusler, R. D. (1992). The micro and macro in body size evolution. *Evolution*, *46*, 939–953. https://doi.org/10.1111/j.1558-5646.1992.tb00611.x

Meiri, S., Avila, L., Bauer, A. M., Chapple, D. G., Das, I., Doan, T. M., Doughty, P., Ellis, R., Grismer, L., Kraus, F., Morando, M., Oliver, P., Pincheira-Donoso, D., Ribeiro-Junior, M. A., Shea, G., Torres-Carvajal, O., Slavenko, A., & Roll, U. (2020). The global diversity and distribution of lizard clutch sizes. *Global Ecology and Biogeography*, *29*, 1515–1530. https://doi.org/10.1111/geb.13124

Meiri, S., Brown, J. H., & Sibly, R. M. (2012). The ecology of lizard reproductive output. *Global Ecology and Biogeography*, *21*, 592–602. https://doi.org/10.1111/j.1466-8238.2011.00700.x

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

Meiri, S., Kadison, A. E., Novosolov, M., Pafilis, P., Foufopoulos, J., Itescu, Y., Raia, P., & Pincheira-Donoso, D. (2014). The number of competitor species is unlinked to sexual dimorphism. *Journal of Animal Ecology*, *83*, 1302–1312. https://doi.org/10.1111/1365-2656.12248

Miranda, J. P., & Andrade, G. V. (2003). Seasonality in diet, perch use, and reproduction of the gecko *Gonatodes humeralis* from eastern Brazilian Amazon. *Journal of Herpetology*, *37*, 433–438. https://doi.org/10.1670/0022-1511(2003)037%5B0433:sidpua%5D2.0.co;2

Nali, R. C., Zamudio, K. R., Haddad, C. F. B., & Prado, C. P. A. (2014). Size-dependent selective mechanisms on males and females and the evolution of sexual size dimorphism in frogs. *The American Naturalist*, *184*, 727–740. https://doi.org/10.1086/678455

Niven, J. E., & Farris, S. M. (2012). Miniaturization of nervous systems and neurons. *Current Biology*, *22*, R323–R329. https://doi.org/10.1016/j.cub.2012.04.002

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

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

Piras, P., Colangelo, P., Adams, D. C., Buscalioni, A., Cubo, J., Kotsakis, T., Meloro, C., & Raia, P. (2010). The gavialis-tomistoma debate: The contribution of skull ontogenetic allometry and growth trajectories to the study of crocodylian relationships. *Evolution and Development*, *12*, 568–579. https://doi.org/10.1111/j.1525-142x.2010.00442.x

Regalado, R. (2014). Does dichromatism variation affect sex recognition in dwarf geckos? *Ethology Ecology and Evolution*, *27*, 56–73. https://doi.org/10.1080/03949370.2014.885465

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.

Rieppel, O. (1996). Miniaturization in tetrapods: consequences for skull morphology. In P/J. Miller (Ed.), *Miniature Vertebrates: The Implications of Small Body Size. Symposia of the Zoological Society of London* (pp. 47–61). Claredon Press, Oxford.

Rieppel, O. (1984). 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*, 291–318.

Rittmeyer, E. N., Allison, A., Gründler, M. C., Thompson, D. K., & Austin, C. C. (2012). Ecological guild evolution and the discovery of the world's smallest vertebrate. *PLoS ONE*, *7*, e29797. https://doi.org/10.1371/journal.pone.0029797

Rosler, H. (2004). *Vermehrung von geckos: Grundlagen, anleitungen, erfahrungen*. Herpeton Verlag.

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*, 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.

Schmidt-Nielsen, K. (1975). Scaling in biology: The consequences of size. *Journal of Experimental Zoology*, *194*, 287–307. https://doi.org/10.1002/jez.1401940120

Serrano-Meneses, M.-A., & Szekely, T. (2006). Sexual size dimorphism in seabirds: Sexual selection, fecundity selection and differential niche-utilisation. *Oikos*, *113*, 385–394. https://doi.org/10.1111/j.0030-1299.2006.14246.x

Shine, R., & Greer, A. E. (1991). Why are clutch sizes more variable in some species than in others? *Evolution*, *45*, 1696–1706. https://doi.org/10.1111/j.1558-5646.1991.tb02675.x

Shine, R., Harlow, P. S., Keogh, J. S., & Boeadi. 1998. The allometry of life-history traits: Insights from a study of giant snakes (*Python reticulatus*). *Journal of Zoology*, *244*, 405–414. https://doi.org/10.1111/j.1469-7998.1998.tb00045.x

Smith, R. J. (1999). Statistics of sexual size dimorphism. *Journal of Human Evolution*, *36*, 423–458. https://doi.org/10.1006/jhev.1998.0281

Starostová, Z., Kubička, L., & Kratochvíl, L. (2010). Macroevolutionary pattern of sexual size dimorphism in geckos corresponds to intraspecific temperature-induced variation. *Journal of Evolutionary Biology*, *23*, 670–677. https://doi.org/10.1111/j.1420-9101.2010.01933.x

Stephens, P. R., & Wiens, J. J. (2009). Evolution of sexual size dimorphisms in emydid turtles: Ecological dimorphism, Rensch's rule, and sympatric divergence. *Evolution*, *63*, 910–925. https://doi.org/10.1111/j.1558-5646.2008.00597.x

Strong, C. R. C., Palci, A., & Caldwell, M. W. (2020). Insights into skull evolution in fossorial snakes, as revealed by the cranial morphology of *Atractaspis irregularis* (Serpentes: Colubroidea). *Journal of Anatomy*, *238*, 146–172. https://doi.org/10.1111/joa.13295

Stuart-Fox, D., & Moussalli, A. (2007). Sex-specific ecomorphological variation and the evolution of sexual dimorphism in dwarf chameleons (*Bradypodion* spp.). *Journal of Evolutionary Biology*, *20*, 1073–1081. https://doi.org/10.1111/j.1420-9101.2007.01295.x

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

Tarr, S., Meiri, S., Hicks, J. J., & Algar, A. C. (2019). A biogeographic reversal in sexual size dimorphism along a continental temperature gradient. *Ecography*, *42*, 706–716. https://doi.org/10.1111/ecog.03593

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

Tinkle, D. W., Wilbur, H. M., & Tilley, S. G. (1970). Evolutionary strategies in lizard reproduction. *Evolution*, *24*, 55–74. https://doi.org/10.2307/2406714

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

Tung Ho, L. si, & Ané, C. (2014). A linear-time algorithm for Gaussian and non-Gaussian trait evolution models. *Systematic Biology*, *63*, 397–408. https://doi.org/10.1093/sysbio/syu005

Uetz, P., Freed, P, Aguilar, R., Reyes, F., & Hošek, J. (2023). *The reptile database*. http://www.reptile-database.org

Vallejo-Pareja, M. C. (2018). *Characteristics of miniaturization in squamates: A phylogenetic perspective from cranial morphology* [MS thesis]. Sam Houston State University.

Van Valen, L. (1973). Patterns and the balance of nature. *Evolutionary Theory*, *1*, 31–49.

Womack, M. C., & Bell, R. C. (2020). Two-hundred million years of anuran body-size evolution in relation to geography, ecology and life history. *Journal of Evolutionary Biology*, *33*, 1417–1432. https://doi.org/10.1111/jeb.13679

Yeh, J. (2002). The effect of miniaturized body size on skeletal morphology in frogs. *Evolution*, *56*, 628–641.

Zimkus, B. M., Lawson, L., Loader, S. P., & Hanken, J. (2012). Terrestrialization, miniaturization and rates of diversification in African puddle frogs (Anura: Phrynobatrachidae). *PLoS ONE*, *7*, e35118. https://doi.org/10.1371/journal.pone.0035118