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Original Article

Rensch's rule: linking intraspecific to evolutionary allometry

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Abstract

Sexual dimorphism describes phenotypic differences between the sexes; the most prominent of which is sexual size dimorphism (SSD). Rensch's rule (RR) is an allometric trend in which SSD increases in male-larger taxa and decreases in female-larger ones. Covariation between a trait and overall size within and across species can both be affected by sexual and natural selection. Thus, intraspecific allometric variation could influence the expression of RR. Here we used computer simulations to dissect how RR emerges under specific allometric patterns of intraspecific sexual differentiation in a trait. We found that sexual differentiation in static allometric slopes is the main determinant of RR. Based on our findings, RR and its converse can manifest in both body size and other traits. As a realistic showcase, we also examined RR and static allometry of different body parts in Mediterranean green lizards to establish whether intraspecific and evolutionary allometry are linked. Here, we identified RR and its converse for different traits, where the amount of sexual differentiation in static allometric slopes within species had a significant contribution to RR. Integrating the simulations and the empirical case we corroborate that sexual differentiation in static allometric slopes is a major parameter affecting evolutionary allometry.

Keywords: body size, trait evolution, allometric slope, allometric intercept, simulations, sexual dimorphism

Introduction

Sexual dimorphism (SD) refers to the difference in phenotypic traits between the sexes of a species (Casselman & Schulte-Hostedde, 2004; Ralls & Mesnick, 2009). One of the most conspicuous patterns of SD in animals relates to differences in body size, although many other traits, such as coloration, shape, sound, behavior, or appendage development, are also frequently dimorphic (Mori et al., 2017; Ralls & Mesnick, 2009). Sexual size dimorphism (SSD) is the pattern of significant differences in size between males and females of a species or population (Cox & Calsbeek, 2010; Fairbairn et al., 2007). SSD may vary in directionality, being expressed with the presence of larger males (male-biased) or larger females (female-biased). This directionality, as well as the magnitude of SSD, exhibits variation across taxa associated with differences in mating system, reproductive mode, or the fitness of a population (e.g., high fitness in larger males as a consequence of competitive behavior) (Blanckenhorn et al., 2007; Nali et al., 2014).

The study of evolutionary allometry can provide useful insights into the evolution of SD in size and other phenotypic traits. Evolutionary allometry describes variation in trait size concerning to body size across species or evolutionarily closely related groups (Figure 1) (Gayon, 2000; Pélabon et al., 2014; Voje et al., 2014). Likewise, the degree of SD may vary across species or populations (Tubaro & Bertelli, 2003; Cox & Calsbeek, 2010). Such variation in the degree of dimorphism is often examined in light of its covariation with body size, and considerable attention has been devoted to determining whether there are allometric patterns of SSD in a macroevolutionary context (Dale et al., 2007; Fairbairn, 2005). Indeed, numerous studies have found that SSD increases with species body size in male-biased groups (Abouheif & Fairbairn, 1997; Fairbairn, 2005; Frýdlová & Frynta, 2010; Frynta et al., 2012; Rensch, 1959), while others have shown that it increases with species body size in female-biased groups (Jannot & Kerans, 2003; Peñalver-Alcázar et al., 2019), a trend known as Rensch's rule (RR)

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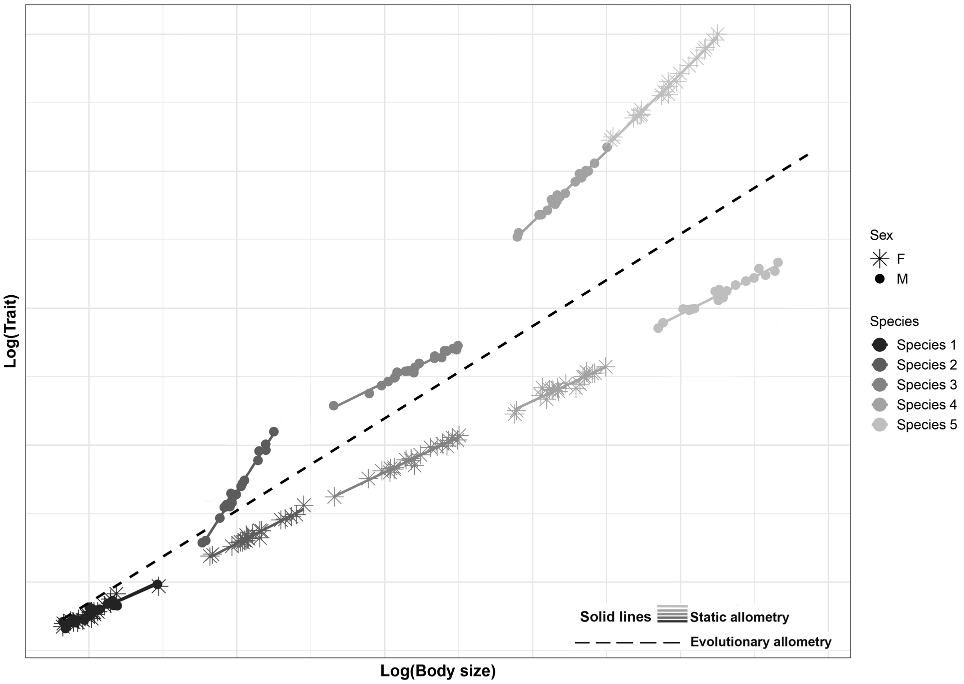

Figure 1. Hypothetical scenarios of sexual differentiation in static allometry within species and the emerging evolutionary allometric relationship.

and its converse, respectively. RR proposes that "*the relative sexual difference is generally more important in larger species than in small species of the same kind of group*" (Rensch, 1950, 1959). Rensch (1950) examined the allometric relationship between male and female traits in several biological groups. His revisions concentrated on size dimorphism, but he also considered dimorphism in other traits (e.g., the head, brain, and eyes), and he proposed the "rule of proportioning" (Rensch, 1950, 1959). Currently, RR is defined as the increase or decrease in SD with body size in independent male-biased or female-biased evolutionary groups, respectively (Abouheif & Fairbairn, 1997; Adams et al., 2020; Dale et al., 2007; Fairbairn, 2005).

Several hypotheses have been proposed as possible evolutionary drivers of SSD and of the macroevolutionary allometric trends in its occurrence; namely, those that conform with RR and its converse (see Fairbairn, 1997). Of these, many are selection-based, where natural or sexual selection on one sex drives body size changes. For instance: (a) sexual selection favors positive evolutionary allometry in males (RR pattern) mainly when they show male-male competition and do not have displays with agility, so males do not have to exhibit attraction maneuvers for females (Cox et al., 2003; Dale et al., 2007; Fairbairn, 2005; Fairbairn et al., 2007; Szekely et al., 2004); (b) sexual selection may favor the decrease of body size in males if they exhibit displays with agility (i.e., converse RR), so the maneuverability in stunts is enhanced with smaller body size (Dale et al., 2007; Szekely et al., 2004); (c) natural selection may select for increased body sizes in females to produce large number of offspring, so that females present larger trunk lengths compared to males (i.e., converse RR) (Cox et al., 2003; Pincheira-Donoso & Hunt, 2017) or bodies of equal size as males (i.e., isometry for RR), depending on the balance with sexual selection also acting on males; (d) natural selection may act on the body size of one of the sexes and its relationship with the surrounding habitat, favoring either larger males (RR pattern) or females (converse RR) (Cox, 1981; Pearson et al., 2002). Genetic-based hypotheses have also been explored, where there is evidence of greater phenotypic plasticity of body size in males compared to females (Fairbairn, 1997). Thus, these hypotheses (one of them or a combination thereof) could act on one of the sexes directionally, maintaining an RR pattern. However, sexual selection has been the most widely accepted and supported hypothesis for explaining RR and differences in the degree of SSD across taxa (Ceballos et al., 2013; Cox et al., 2003; Dale et al., 2007; Fairbairn, 2005; Fairbairn & Preziosi, 1994; Szekely et al., 2004). Some evidence suggests that, under sexual selection, female body size evolves in concert with male body size. If natural selection decreases for females, it could reverse this effect, leading to males stabilizing at a size balanced by sexual selection (Andersson, 1994; Fairbairn, 1997).

Complementary to evolutionary allometry, intraspecific allometry describes the rate of change between trait size and overall size in individuals of the same species at the same ontogenetic stage (i.e., static allometry), or throughout growth (i.e., ontogenetic allometry) (Eberhard et al., 2018; Freidline et al., 2015; Gould, 1966a, 2000; Pélabon et al., 2013). Variation in intraspecific allometry has been explored in several taxonomic groups, providing information regarding the potential association between allometric trends within and among species (Klingenberg & Zimmermann, 1992; Voje et al., 2014). For instance, differentiation between the sexes in static allometry has been frequently linked to sexual selection, and the evolvability of sexually selected traits with respect to body size has been the focal point for understanding morphological functionality (Eberhard et al., 2018). Here, positive static allometry has been interpreted as an indication of sexual selection. However, this will only occur if the combined influence of sexual and natural selection on the size of a trait and body size leads to a comparatively greater benefit of larger trait size in larger individuals (Bonduriansky & Day, 2003; Bonduriansky, 2007). Nonetheless, sexual selection is not the only explanation that may result in this pattern. Merely focusing on the selection of either the absolute or relative size of a trait in isolation is insufficient to generate a trait that exhibits positive allometry (Bertin & Fairbairn, 2007; Bonduriansky, 2007).

Given the shared research foci on how sexual and natural selection affect intraspecific and evolutionary trends of SD, investigating possible links between them seems paramount to better comprehend how the interplay between trait and body size coevolution shapes SD patterns. Some studies have analyzed the effects of intraspecific on evolutionary allometry, suggesting that the former acts mainly as a constraint to the latter, possibly by shaping genetic lines of least resistance (Brombacher et al., 2017; Schluter, 1996; Tejero-Cicuéndez et al., 2022; Voje et al., 2022). However, this association between levels of allometry has been poorly explored from the perspective of SD evolution and the trend expressed as RR. This connection becomes particularly relevant when considering that RR may or may not occur in traits other than body size (Colleoni et al., 2014; Liang & Shi, 2017). Thus, both types of allometries (i.e., intraspecific and evolutionary) can occur in a clade, and investigating them in concert may provide insights into the mechanisms of selection operating within and across species (Firmat et al., 2014; Tejero-Cicuéndez et al., 2022; Voje et al., 2014).

From the perspective of understanding SD, we may characterize sexual differentiation within species in trait size–body size allometry expressed through linear relationships (on a log-log scale) (Figure 1). Here, the two sexes may exhibit the exact same allometric trend and no differences in their intercept and slope (e.g., species 1 in Figure 1). By contrast, there may be differences in both the intercept and the slope (species 4 and 5), in the intercept but not in the slope (species 3), or vice versa (species 2) (Figure 1). Then changes in these parameters could affect the evolutionary allometric slope in light of RR. The static or intraspecific slope, being one of the most studied parameters, has garnered significant attention from numerous researchers who have explored its relationship with species' size (Gould, 1966a; Voje & Hansen, 2013). Gould (1966a, b) suggested that larger species tend to exhibit shallower intraspecific slopes. However, subsequent investigations have yielded inconclusive results to find evidence supporting this relationship (Kawano, 2002; Voje & Hansen, 2013; Voje et al., 2013). Therefore, delving into the connections between intraspecific allometry and species size could also offer valuable insights into the effect of within-species allometric slope on the evolutionary slope in the context of SD.

Here we examined intraspecific and evolutionary allometry through the implementation of a series of computer simulations. We first used these simulations to establish when RR in body size is identified given different degrees of SSD. Then, we explored the interplay between intraspecific and evolutionary allometry of SD (RR) in a trait by simulating differences between the sexes in intraspecific slope and intercept and then assessing their effect on the evolutionary slope of RR. To illustrate how the results of the simulations can be reflected in a real-life example, we examined intraspecific and evolutionary allometry in several morphological traits in Mediterranean green lizards as an empirical case. First, we tested whether RR occurred in body size and in four other morphological traits, and then we explored whether differences between the sexes in intraspecific allometric slope and intercept contributed to determining RR patterns.

Simulations

Methods

Rensch's rule in body size

To set up a hypothetical interspecific dataset that encompassed RR in body size, we performed a series of computational simulations across different degrees of SSD. For this, we first generated a pure-birth phylogenetic tree of 50 species and simulated mean values for the body size of females (Y_F) under a Brownian motion model of evolution. From these, we then obtained male body sizes (Y_M) through the allometric equation of Huxley (1924) and Huxley and Tessier (1936) as: $Y_M = \beta_0 Y_F^{\beta 1} + \varepsilon$, where β_1 is a uniform factor with value 1 + SSD and ε represents small random error drown from a normal distribution with $\mu = 0$ and $\sigma = 0.01$. We defined SSD to range from −0.05 to 0.05 in intervals of 0.001 to simulate different evolutionary patterns for SSD. These scenarios included an isometric relationship between Y_M and Y_F (i.e., a lack of RR) when SSD = 0 ($Y_M = Y_F$) and all species are monomorphic. On the other hand, our simulations encompassed male-biased SSD when SSD > 1 (e.g., when SSD = 0.05, $Y_M = Y_F^{1.05}$), and female-biased SSD when SSD < 1 (e.g., with SSD = −0.05, $Y_M = Y_F^{0.95}$).

Once female and male species means for body size were generated, we simulated body size for 50 individuals per sex, by drawing 50 random values from a normal distribution with a standard deviation of 0.1, around each of the species-mean elements (Y_F and Y_M). This provided a database containing simulated values of body size for 50 individuals per sex, for each of 50 species on a random phylogeny. These individual values were later used to explore the association between within-species allometric patterns and the emergence of RR in body traits other than body size. We repeated these simulations 1,000 times.

From each of these matrices of 5,000 individual male and female values for 50 species, we explored RR for body size. We first calculated means by sex and by lineage. Then, we performed a phylogenetic generalized least-squares regression (PGLS) regression between the SD ratio (i.e., $\log(Y_M/Y_F)$) and log-transformed species body size, following the equivalence between the later and the standard regression for testing for RR (Abouheif & Fairbairn, 1997) as shown by Adams et al. (2020) (see details in page 1911) and tested whether the slope of this regression was significantly different from 0 through a *t*-test.

Rensch's rule in other traits and linking of intraspecific allometry to evolutionary allometry

We explored how the occurrence of RR in a trait other than body size is linked to its occurrence in body size and investigated whether variation in sexual differentiation of intraspecific allometric intercept and slope influences RR in the trait. To obtain simulated data expressing variation in a second trait, we used the empirically observed values of intercept and slope between a morphological trait (head size) and body size in our dataset of green lizards (see further on), ensuring realistic relationships that may allow us to abstract the results to an organism of interest. We ran a set of 1,000 trait simulations for each of the SSD variation scenarios previously considered: (a) isometry (no dimorphism in body size), (b) male-biased

SSD, and (c) female-biased SSD. To evaluate the effect of sexual differentiation in intraspecific allometric intercepts on the emergence of RR in the trait, we kept the static slope of both sexes constant and generated trait values under variable intraspecific intercepts. Based on female and male body sizes simulated before (Y_F and Y_M), we generated trait values as $Z_F = \beta_0 * Y_F^{\beta 1} + \varepsilon$ and $Z_M = \beta_0{}' * Y_M^{\beta 1'} + \varepsilon$, where $\beta_0{}' = \beta_0 + \text{ID}$. Here, ID (intercept difference) is the simulated intercept difference between the sexes, ranging from −1 to 1 at intervals of 0.02 in our simulations, and ε random error $N(\mu = 0, \sigma = 0.001)$.

Similarly, to evaluate the effect of sexual differences in intraspecific allometric slope on the emergence of RR in the trait, we kept the intraspecific intercept (β_0) constant and generated traits with varying differences between the sexes in intraspecific slopes (β_1 for females and $\beta_1{}'$ for males, with $\beta_1{}' = \beta_1 + \text{SLD}$), the slope difference (SLD) taking values between −1 and 1 (in intervals of 0.02). A matrix with 50 individuals per sex and species with two variables (i.e., body size and a second trait) was created for each value of simulated body size, ID, and SLD. To evaluate the effect of sexual differentiation in intraspecific allometric intercept and slope on RR we followed the same procedure mentioned above. To test whether RR was identifiable in the simulated trait, we first standardized individual trait values over body size (i.e., trait/size). Then we calculated means by sex and lineage for the size-corrected, log-transformed trait values, and performed a PGLS regression in the same way as for body size (i.e., SD ratio ~ log(mean species size)).

Finally, to assess the stability of the simulation results with smaller sample sizes we performed a rarefaction analysis. For this, we chose 40, 30, 20, and 10 random individuals of each sex from the 50 originally simulated individuals per lineage. Using these data, we ran the RR tests mentioned above with these sample sizes.

We performed all analyses in R (R Core Team, 2020) using the packages ape (Paradis et al., 2019), phytools (phytools. Revell, 2014), geiger (Harmon et al., 2015), RRPP (Collyer & Adams, 2018), and tidyverse (Wickham & Wickham, 2017).

Results

Based on the simulations of RR in body size we identified that RR emerges at SSD values greater than 0.025 in male-biased groups and lower than −0.025 in female-biased groups (Figure 2A–C; Supplementary Figure S1.1). Importantly, this SSD value follows Huxley's allometric power law and therefore increases when species body size does. So, the minimum value for RR to be detected was |SSD| = 0.025. That is, if the increase in SSD was greater than 0.025, the slope resulted in a pattern of RR according to the regression of SD ratio on log mean species size ($\beta_1 > 0$). Conversely, for SSD values lower than −0.25 the converse RR pattern emerged ($\beta_1 < 0$; Figure 2; Supplementary Figure S1.1).

Rensch's rule in traits when there is no SSD

The simulations conducted to examine how RR in body size and sexual differences in intraspecific allometry influence the occurrence of RR in other traits showed that, in the absence of RR in body size (i.e., $\beta_1 = 0$), intercept differences between the sexes do not affect RR in the trait. Thus, the RR pattern in the trait would resemble that observed for body size regardless of any sexual variation in intraspecific allometric intercept (Figure 2A.1; Supplementary Figure S1.2). Instead, it is possible to observe RR in a trait other than body size if there are differences between the sexes in intraspecific allometric slope (Figure 2A.2; Supplementary Figure S1.3). If the slope difference is negative (i.e., the trait slope is steeper in females than in males), RR could be observed (that is, in female-biased groups SD decreases as the species body size increases); if the slope difference is positive then converse RR would be detected. If no differences exist in the intraspecific slope, RR is not observed in the trait (Figure 2A.2).

Rensch's rule in traits when there is SSD and RR in body size ($\beta_1 > 0$) and converse of RR ($\beta_1 < 0$)

Simulations introducing variation in intraspecific intercept difference show the inverse pattern of RR than that observed in body size. That is, for trait data simulated on a pattern of body size RR under varying values of intercept differentiation between the sexes, the resulting value of the allometric evolutionary slope for RR for the trait is the inverse of that observed for body size (Figure 2B.1 and C.1; Supplementary Figures S1.4–S1.6). Complicating things further, if a difference in static slope between the sexes is introduced when simulating trait variation, both RR and the converse of RR may appear, and also the lack of RR ($\beta_1 = 0$) in the trait (Figure 2B.2 and C.2; Supplementary Figures S1.6 and S1.7). It is important to mention that based on our simulations the static intercept difference alone has little effect on the expression of RR (when the static slope is uniform between the sexes).

Finally, the rarefaction procedures showed that the patterns and trends of RR were the same as those mentioned above, even with sample sizes as low as 10–20 individuals per sex per lineage (Supplementary Figures S1.8–S1.13). However, as expected, the variance increased with smaller sample sizes.

Real-life empirical example

Methods

To explore how the aforementioned links between intraspecific sexual differentiation in allometric trajectories and evolutionary allometry of SD (i.e., Rench's rule) may occur and be interpreted in a real-life situation, we explored their occurrence in several body traits in a group of Mediterranean green lizards. Green lizards of the genera *Timon* and *Lacerta* (Squamata: Lacertidae) represent a monophyletic clade of species distributed in a variety of ecosystems and habitats in the Mediterranean basin (Ahmadzadeh et al., 2016; Verwaijen & Van Damme, 2007). They exhibit a remarkable diversity of body sizes and the relative size of other morphological traits (e.g., head size) between species (Enriquez-Urzelai et al., 2022), as well as between sexes of the same species (Adams et al., 2020; Arnold et al., 2007; Braña, 1996). Together, these features make them an excellent model system for linking micro- and macroevolutionary patterns of static vs. evolutionary allometry in the context of SD and RR.

We examined 1,097 preserved individuals from 24 lineages of green lizards from natural history museum collections (see Acknowledgments), an initial dataset that fully overlapped that of Adams et al. (2020). We based our taxon sampling on a phylogenetic criterion, and we considered each lineage as an independent and divergent group, so we used the same criteria as Adams et al. (2020) and Enriquez-Urzelai et al. (2022). To avoid any effects of growth and because our objectives are not related to ontogenetic allometry, all measured individuals were adults, whereas juveniles and neonates were excluded from data collection. The specimens measured were

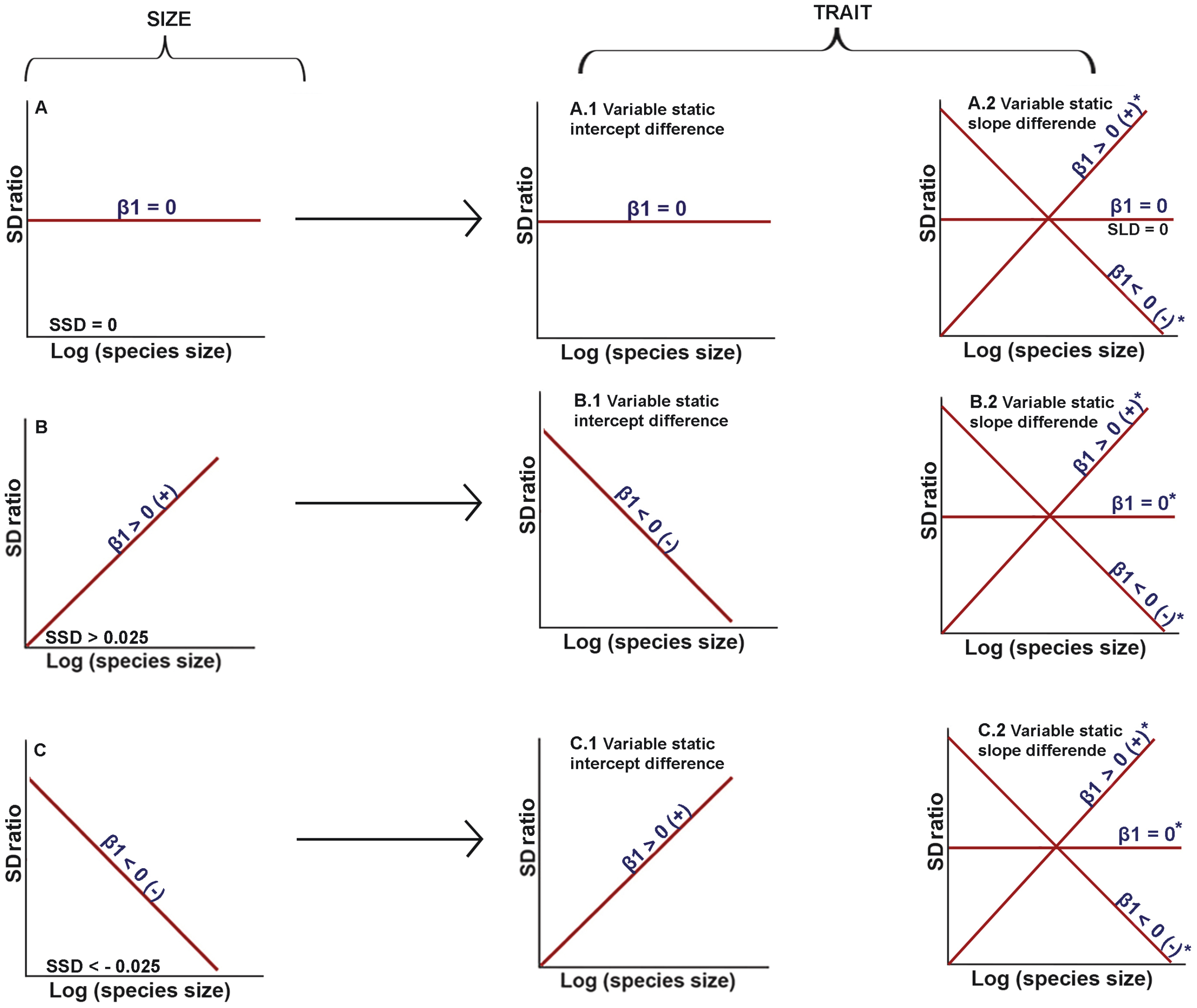

Figure 2. Summary of results obtained from RR test simulations, SD ratio = log(Y_M/Y_F) vs. log(mean species size), β_1: estimated evolutionary slope. RR pattern is equivalent to $\beta_1 > 0$, converse RR pattern is equivalent to $\beta_1 < 0$. (A) Isometric relationship of body size between males and females, so absence of RR in size. (B) Allometric relationship of body size between males and females following a male-biased pattern. (C) Allometric relationship of body size between males and females following a female-biased pattern. (A.1, B.1, C.1) RR simulations in trait with variable static intercept difference between sexes. (A.2, B.2, C.2) RR simulations in trait with variable static slope difference between sexes. *Asterisks correspond to thresholds within the simulations, in which the static slope can stabilize its value with body size and the trait could lack RR. For details, see Supplementary material S1. SLD = slope difference, so in scenario (A) lack of RR in the trait is due to no differences in the static slope. (+) means that the evolutionary slope of the regression is different from 0 and positive and (–) means that the evolutionary slope of the regression is different from 0 and negative.

chosen to adequately cover morphological variation across the distribution range of each lineage. To take into account variation in traits that exhibit SD in adult individuals and to avoid sampling bias due to unequal sample size in each lineage, we selected the 15 largest individuals per sex and lineage. This decision is based (a) on the fact that the samples were obtained from scientific collections of natural history museums, therefore, larger individuals have less preservation effects and measurements can be easily taken, (b) our study is focused on SD and body size, so we assume that larger individuals represent more visible and more expressive maturation features, and (c) to reduce the bias introduced by non-random sampling, this is an approach to standardize the sampling. In addition, similar approaches have been proposed for comparative studies (Martínez-Gil et al., 2022; Stamps & Andrews, 1992). Lineages with a small sample size ($n < 10$) were removed from analyses (i.e., *Lacerta boemica*, *Lacerta bosnica*, *Lacerta ciliciensis*, *Lacerta guentherpetersi*, and *Lacerta pamphylica*). This provided a final database of 515 individuals from 19 lineages. A set of linear measurements were taken on each individual with a digital caliper, rounded to the nearest 0.01 mm, always recorded by the same observer to reduce measurement error. These measurements were: (a) snout to vent length, SVL, as a proxy for body size; (b) trunk length, TRL; (c) head length, HL; (d) head width, HL; (e) head height, HH; (f) forelimb length, FLL; and (g) hindlimb length, HLL (Supplementary Figure S2.1). To summarize head size (HS), we calculated the geometric mean of HL, HW, and HH, so finally we analyzed five traits: SVL, TRL, HS, FLL, and HLL.

Intraspecific and evolutionary (Rensch's rule) allometry

To examine variation in static allometric relationships between trait size (TRL, HS, FLL, and HLL) and body size

(SVL), and test whether allometric slopes and intercepts varied between the sexes and across lineages, we fit general linear models (GLMs) between each linear measurement and body size (all log-transformed). We also included sex, lineage, and all interactions in GLMs. We performed analysis of variance tests on those models to determine whether males and females differed in their allometric slopes and intercepts and whether the degree of sexual differentiation in allometric parameters varied evolutionarily (i.e., across lineages), as can be inferred through the interaction terms of the aforementioned models. Next, to quantify the amount of allometric differentiation between the sexes in each individual lineage, we fit separate within-lineage GLMs including body size and sex to explain variation in body size. From these models, we extracted the difference in static allometric slopes and intercepts between sexes to subsequently link intraspecific allometries with RR (see further on).

To perform all analyses across lineages accounting for evolutionary relationships, we used the updated green lizard phylogeny presented in Adams et al. (2020), which included all initial 24 lineages mentioned above. We calculated the mean of each morphological trait by lineage and sex. In addition, to consider the effect of body size on the other traits, we standardized these measurements as Y/SVL (following Mosimann, 1970). With these values, we evaluated whether RR occurred in body size and the other four size-standardized traits. For this, we first performed a PGLS between the SD ratio (i.e., $\log(Y_M/Y_F)$) and log-transformed species body size, following the same reasoning of the simulations explained above. This procedure was implemented for both body size dimorphism and dimorphism in size-corrected traits. Then, we used a PGLS to test whether the difference in static (i.e., intraspecific) allometric slopes and intercepts between males and females had an effect on the general pattern of RR. For this, we included the difference between the sexes in static slopes (slope_diff) and intercepts (intercept_diff) for each lineage extracted from the previous within-species allometry analyses (see above) together with average lineage body size in the model used to evaluate RR. Because the contribution of the parameters to trait variance is not additive (Voje et al., 2014), one has to consider all interaction terms to link them in an evolutionary context. Thus, we evaluated the model: $\log(Y_M/Y_F)$ ~ log(species size) * slope_diff * intercept_diff | phylo. This allowed us to investigate how sexual differences in body size, allometric intercept, and allometric slope may conjointly determine evolutionary patterns of RR-in traits other than body size.

We also included a static allometry approach in which we considered two levels: the difference in static allometry between the sexes and the static allometry per species. So, the difference in slope and static intercept (as mentioned in the model above) and the slope and static intercept of the species (including males and females in the same dataset). To relate these parameters to species sizes, we performed a PGLS with the following models: slope_diff ~ log(species size) | phylo, intercept_diff ~ log(species size) | phylo, species_static_slope ~ log(species size) | phylo, and species_static_intercept ~ log(species size) | phylo.

As the simulations showed that the static allometric slope is a key factor influencing RR we performed a rarefaction analysis on empirical data with a sample size of 10 individuals per sex per lineage to evaluate if the estimates of the static allometric slopes and their effect on the emergence of RR change considerably if smaller sample sizes are used. With these data, we estimated the static allometric intercept and slope and their contribution to the evolutionary allometry of RR.

We evaluated the significance of all models using RRPP (Collyer & Adams, 2018) and 1,000 permutations.

Results

Intraspecific allometry

We found significant effects of body size, sex, and lineage on explaining variation in all investigated morphological traits (Supplementary Table S3.1). The interactions of body size and lineage, and body size and sex, were significant for all traits except for forelimb length, so static allometric slopes varied significantly across species and between the sexes (Supplementary Table S3.1). By contrast, the three-way interaction between body size, sex, and lineage was not significant for any trait, suggesting that sexual differences in allometric slopes were similar across lineages. As a general trend, we detected that, in all analyzed traits, species of larger body sizes (*Timon* species) exhibited smaller intercept differences between the sexes, while the opposite was true for smaller species (*Lacerta* species) (Figure 3). The examination of static allometries unveiled contrasting patterns of allometric slope variation between different body traits and body size. When examining the relationship between trunk length and body size, larger species generally presented flatter slopes than smaller species (Supplementary material S4). By contrast, for head size the static allometric slopes tended to be steeper for larger than for smaller species (Supplementary material S4).

When evaluating SD in static allometries within each species separately, trunk length only exhibited significant differences in allometric slopes between sexes in *Lacerta media israelica* ($F = 8.608$, $Z = 2.248$, $p = .008$) and *Lacerta trilineata trilineata* ($F = 5.817$, $Z = 1.856$, $p = .032$) (Supplementary Table S5.1; Figure 3A). For head size only *Timon nevadensis* ($F = 13.226$, $Z = 2.637$, $p = .003$) and *Timon princeps* ($F = 4.350$, $Z = 1.592$, $p = .046$) showed sexual differences in allometric slopes (Figure 3D; Supplementary Table S5.2). On the other hand, all lineages presented significant differences between the sexes in allometric intercepts (details of the individual statistics of each trait per species can be found in Supplementary Tables S5.1–S5.4). In addition to differences in trait size caused by sexual differences in intercepts, some species also exhibited sexual differences in body size which further amplified sexual trait differentiation. This is, for example, the case in *Timon lepidus* (Figure 3D, G, and J) and *L. trilineata trilineata* (Figure 3E, H, and K; Supplementary Tables S5.1 and S5.2).

Evolutionary allometry (Rensch's rule)

Tests for RR revealed that the body size of males and females varied in a congruent way with this macroevolutionary pattern (SD ratio ~ mean species size, $F = 20.222$, $p < .001$) (Table 1; Figure 4). Regarding tests for RR in other body traits, we found a significant relationship between the SD ratio of head size and mean species size, a pattern consistent with RR (Table 1; Figure 4). We did not find a significant relationship between the SD ratio of trunk length and mean species size. SD ratio of hindlimb length and forelimb length exhibited the converse pattern of RR with negative slope values different from 0 (Table 1; Figure 4).

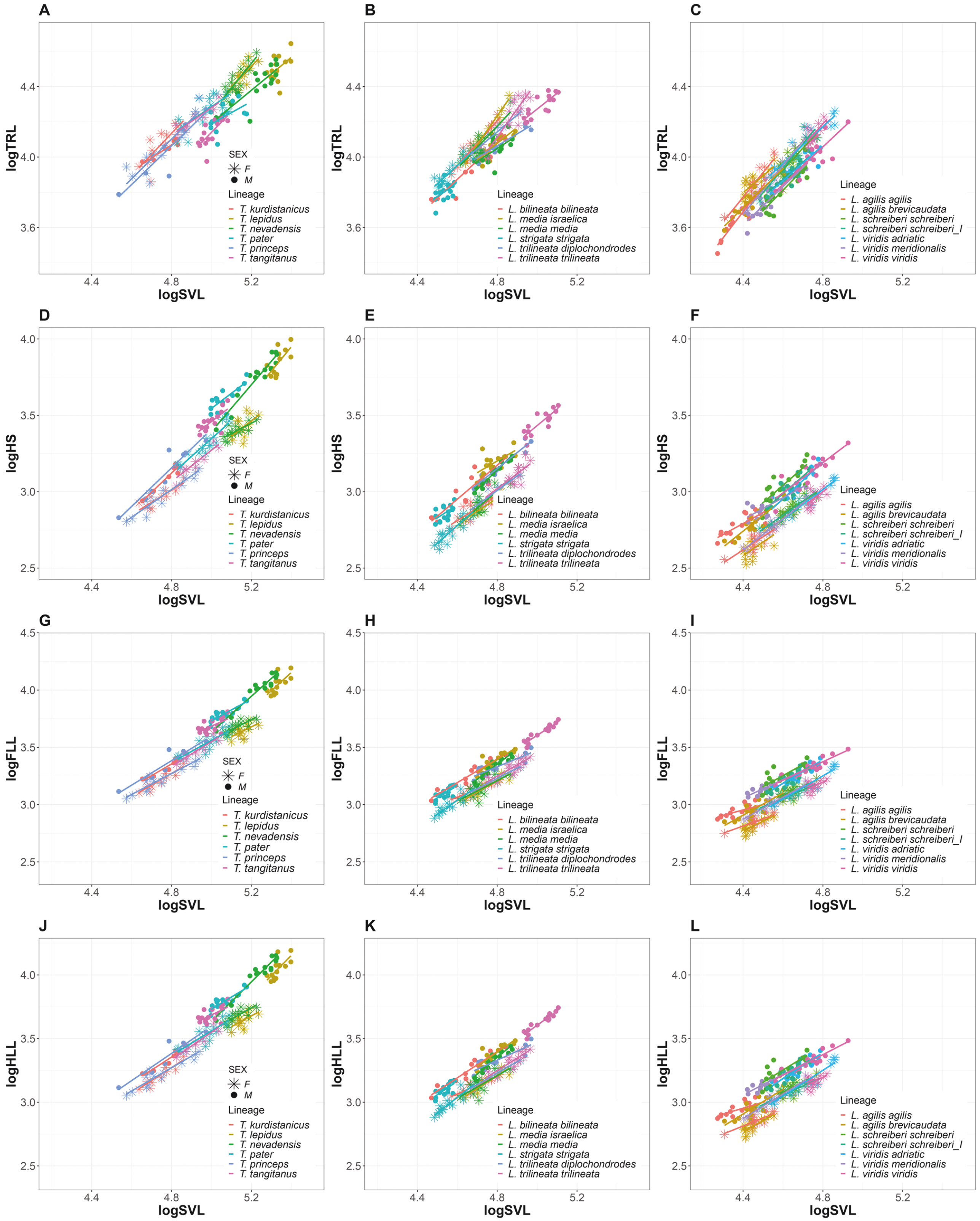

Figure 3. Static allometries of studied morphological traits with body size (SVL) within green lizard species. (A)–(C) Trunk length; (D)–(F) head size; (G)–(I) forelimb length; and (J)–(L) hindlimb length.

Contribution of intraspecific allometry to Rensch's rule

The degree of sexual differentiation in static allometric slopes contributed to explaining RR for most traits (Table 2). The interaction between static allometric intercept, slope, and body size had a significant effect on the display of the converse pattern of RR in forelimb length (Table 2). In general, static intercepts had no effect on evolutionary allometry (RR) in other traits. Rarefaction analysis with the smaller dataset

Table 1. Statistics of tests for Rensch's rule with sexual dimorphism ratio (SD ratio) approach. β_1: estimated allometric slope, SE: standard error of the slope estimate, *t* and *p* value: corresponding *t* and *p* values of significance testing for slope estimates ($\beta_1 \neq 0$). Significant patterns (using a threshold of $\alpha = 0.05$) are highlighted with asterisks.

Trait	β_1	SE	*t* value	*p* value
SVL	0.290	0.064	4.478	**<0.001*****
TRL	0.044	0.067	0.663	0.520
HS	0.194	0.069	2.794	**<0.05***
FLL	−0.065	0.016	−3.946	**<0.05***
HLL	−0.125	0.038	−3.298	**<0.05***

showed the same trends as the main dataset, including the influence of the static allometric slope on the RR pattern (Supplementary Tables S5.5 and S5.6). In this dataset the results of trunk length were the only ones that varied, showing a significant negative relationship between trunk length and mean species size (i.e., converse RR) (Supplementary Table S5.5).

The species static allometric slope and intercept showed a highly significant relationship with mean species size in all traits. Specifically, the static allometric slope increased and the static allometric intercept decreased for head size as the mean species size increased (Figure 5; Supplementary Tables S6.1 and S6.2). By contrast, for trunk length, as mean species size increased its static allometric slope decreased and static allometric intercept increased (Figure 5; Supplementary Tables S6.3 and S6.4). Static allometric slopes and intercepts alone had no relationship with mean species size for hindlimb length and forelimb length (Supplementary Tables S6.5–S6.8). However, when we considered the interaction of the static intercept with the static allometric slope we did detect a highly significant positive relationship between the static allometric slope and mean species size (Figure 5; Supplementary Tables S6.9 and S6.10). We found the same pattern when analyzing the static slope and intercept difference against body size, although *p* values for regression significance ranged from 0.06 to 0.07. Thus, we found a significant relationship between the species static allometry and mean species size rather than with the difference of static intercepts and slopes between the sexes (i.e., intercept_diff and slope_diff) (Supplementary Table S6).

Discussion

Two of the most common phenotypic patterns are changes in trait values that scale with body size (allometry), and systematic differences between the sexes (SD) (Mori et al., 2017; Ralls & Mesnick, 2009). At macroevolutionary scales, SD may also display allometric variation, that is, systematic differences across species of different sizes, a pattern known as *Rensch's rule*. Interestingly, how intraspecific allometry relates to macroevolutionary trends of SD allometry had not been previously investigated. We filled this gap through a thorough exploration of the links between sexual differentiation in intraspecific trait allometry and evolutionary allometry of SD (RR) using computer simulations and examined a real-life example considering several morphological traits in empirical data. Through computer simulations, we found that RR and converse RR can emerge in a trait depending on whether there are differences in intraspecific allometric slope, but not intercept, between the sexes. In the empirical data, we found that intraspecific allometry varies considerably in Mediterranean green lizards, mainly depending on the body size of the species. Furthermore, we detected RR patterns that varied across traits, following the classic pattern of positive evolutionary allometry in body and head size, but the converse RR pattern in limb length. Our results provide several important insights for the study of allometric effects on SD across levels of biological organization.

The thorough simulations conducted here highlighted the importance of the intraspecific allometric slope in shaping evolutionary trends of SD allometry (i.e., RR). Indeed, we identified that sexual differences in static allometric slopes affect RR in a second trait, under different scenarios for RR in body size. Indeed, our simulations revealed that RR may occur in the trait if intraspecific slopes differ between the sexes, even if RR does not occur in body size. In the absence of body size RR, the emerging pattern of RR in a second trait (i.e., following the classic definition of the rule or its converse) will mainly depend on the differences in intraspecific slope between the sexes: if the difference in slope between the sexes is simulated as positive (i.e., the largest sex exhibits also higher intraspecific allometric slope), then the classical RR pattern will occur in the trait. Instead, if the difference in allometric slope between the sexes is negative (i.e., the largest sex exhibits a shallower slope) a reverse RR pattern will be observed. When there is RR or its converse in body size, the pattern may or may not be maintained for a second trait. For instance, slope differences between the sexes may cancel out the effects of body size causing the RR pattern to disappear in the trait (Supplementary material S1): This is exactly what we can see in the case of trunk length in the empirical example (see Tables 1 and 2).

In this context, we found that body size and head size followed RR, and the limbs followed its converse in green lizards of the genera *Timon* and *Lacerta*. Linking the simulations with the empirical example, we detected that a trait can also exhibit RR or its converse and that this pattern can be affected by the static allometric slope (Figure 2). The traits in which we detected RR (i.e., head size) and its converse (i.e., forelimb length and hindlimb length) suggest that the static slope difference between the sexes acted as an interaction factor for the emergence of RR in that trait (Table 2), an example consistent with our simulations (Figure 2). We identified a significant relationship between static slope and mean species size. So, from an RR perspective, our results suggest that the effect of larger species exhibiting steeper static slopes shapes this macroevolutionary pattern and its converse trend. That is, species with larger body sizes tend to exhibit either amplification or reduction of the phenotypic characteristic through the static slope (Figure 5), resulting in positive or negative evolutionary allometry between the SD ratio and mean species size in that particular trait (Figure 4). The outcome of this combination is the classical RR pattern in some traits, such as head size, or its converse in others, such as limb length, or pattern elimination, as is the case for trunk length. All these scenarios are possible and consistent with our simulations (Figure 2).

It is important to note that these, as any, simulations are framed in a hypothetical scenario where the intraspecific slope varies between the sexes while the intercept remains constant and *vice versa*, which may differ somewhat from biological reality (Voje & Hansen, 2013). However, they provide insights

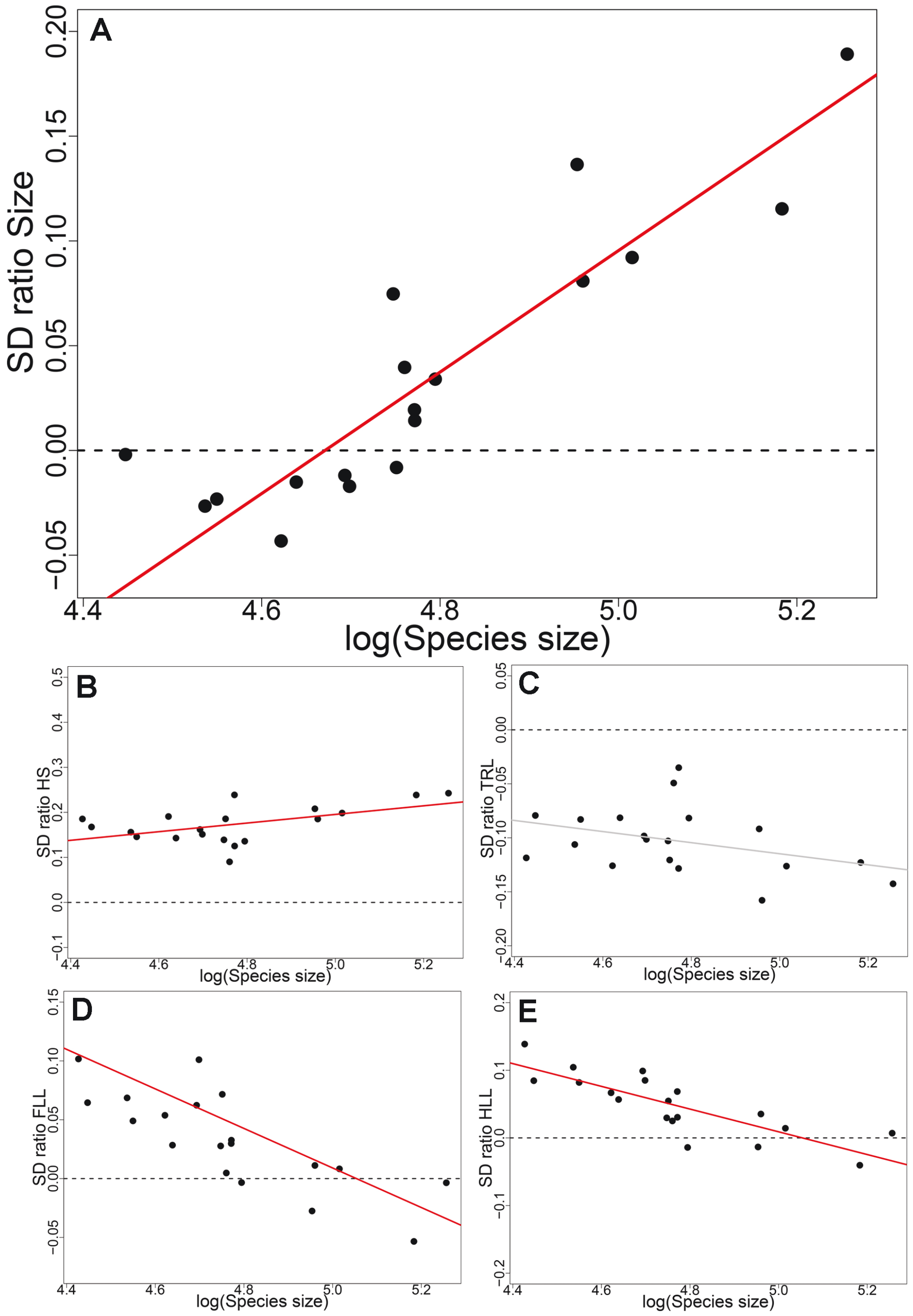

Figure 4. Rensch's rule (RR) pattern for five morphological traits in green lizards. (A) Body size (SVL); (B) head size; (C) trunk length; (D) forelimb length; and (E) hindlimb length. The gray line (in C) represents a non-significant relationship, and the dashed line depicts isometry (lack of RR).

into the relative importance of these two parameters, showing that sexual differences in intraspecific allometric slope are the main source of variation in the occurrence of RR and its converse. Further simulations encompassing additional parameters, such as the covariation of intraspecific allometric slope and intercept, or variation in body size SD, may help to better understand how all these intraspecific parameters interact to shape evolutionary allometry of SD in traits other than

Table 2. Analysis of variance (ANOVA) table for the linear model used to test for the effect of intersexual differences in static allometric intercept and slope on the trait Rensch's rule pattern with the SD ratio approach. β_1: estimated allometric slope, β_0: estimated allometric intercept. Interaction factors of the model are depicted with an asterisk. *F* value and *p* values of significance. Significant patterns (using a threshold of $\alpha = 0.05$) are highlighted with bold asterisks.

SD ratio Source of variation	TRL		HS		FLL		HLL	
	F value	*p* value	*F* value	*p* value	*F* value	*p* value	*F* value	*p* value
(Intercept)	51.395	<0.001***	397.2168	<0.001***	17.450	0.001*	9.910	<0.05*
Species size (SVL)	0.638	0.441	58.354	<0.001***	100.669	<0.001***	42.164	<0.001***
β_1	2.313	0.156	14.478	<0.05*	22.131	<0.001***	0.015	0.903
β_0	10.159	<0.05*	5.628	0.037	0.704	0.419	0.175	0.686
sp.sz* β_1	24.388	<0.001***	212.966	<0.001***	138.146	<0.001***	44.083	<0.001***
sp.sz* β_0	0.635	0.442	0.998	0.339	0.014	0.906	0.629	0.444
β_0* β_1	5.065	<0.05*	5.041	<0.05*	8.825	0.127	2.546	0.138
sp.sz* β_0* β_1	0.264	0.617	0.448	0.516	34.150	<0.001***	0.0001	0.992

body size. Other authors have highlighted the importance of the intraspecific allometric slope and its effect on evolutionary allometry in contexts other than SD evolution (Cheverud, 1982; Pélabon et al., 2014; Voje et al., 2022), although some results are inconclusive. For example, Voje et al. (2022) found a strong relationship between static and evolutionary allometry for certain traits and not for others, suggesting that this relationship depends on strong selection over ancient times. Although we found through simulations that sexual differences in intraspecific slope are related to RR, it is important to consider that, evolutionarily, the intraspecific allometric slope is considered a constraint for evolutionary allometry (Pélabon et al., 2014). As such, strong selection may limit the evolutionary potential of intraspecific slopes (Pélabon et al., 2014; Voje et al., 2022), but there is still a lack of available data in this regard.

Following our empirical case and to exemplify the results obtained in the simulations, most species of green lizards exhibited similar static allometric slopes between the sexes except for certain species in some traits (e.g., *L. trilineata trilineata* in trunk length and *T. nevadensis* in head size). This contrasts with the results of Voje and Hansen (2013), who found that static allometric slopes of eye span differed between the sexes in 60% of the species of stalk-eyed flies. Such discordance could be due to the fact that closely related species tend to retain the ancestral static allometric slopes, which have been reported to be evolvable over at least 2-million-year time scales (Pélabon et al., 2014; Voje & Hansen, 2013; Voje et al., 2014). On the other hand, our findings coincide with those of Voje and Hansen (2013) in that static allometric intercepts differed between the sexes in more than 90% of the species studied. This reinforces the observation that evolutionary changes in the static allometric intercept are probably faster than changes in the static slope (Hansen & Houle, 2008; Pélabon et al., 2014). Along the same lines, results regarding the evolution of allometric trajectories across different scales seem to lend support to the constraint hypothesis, which holds that the evolution of morphological characters is more constrained within than across species and that evolutionary allometries are limited by static allometries so that both should be similar (Hansen & Houle, 2008; Pélabon et al., 2014; Voje et al., 2014).

Strikingly, variation in static allometric slopes follows a pattern related to species' body size. This relationship has already been referred to as Gould's hypothesis (Gould, 1966a, b; Voje & Hansen, 2013), where shallower allometric slopes in larger species would prevent anatomically non-functional trait sizes. Indeed, our analyses showed that variation in trait static allometric slopes is tightly linked to species' body size (Figure 5; Supplementary Tables S6.9 and S6.10). For trunk length, we found shallower static allometric slopes with increasing body size. Instead, for head size, forelimb length, and hindlimb length the relationship was inverse, that is, the larger the species body size, the steeper the static slope (Figure 5; Supplementary Tables S6.9 and S6.10). However, our findings for fore- and hind-limb lengths showed that the association between static slope and body size was only significant if the interaction of the static intercept was also considered as a factor within the model. This reinforces the importance of considering both allometric parameters in concert, as the intercept is mathematically dependent on the slope (Anzai et al., 2017). As such, important patterns might be missed when examining a single parameter in isolation, whereas identifying significant effects of explanatory variables becomes more efficient by considering both parameters together. In a sexual selection context, several authors have detected that allometric slopes are evolvable at macroevolutionary scales and that mainly species that have sexual selection toward specific traits can evolve steeper slopes (Voje & Hansen, 2013; Voje et al., 2014; Pélabon et al., 2014; Voje et al., 2022).

Our simulation and empirical results allowed us to confirm that the main source of contribution for RR is the static allometric slope and, in some cases, its interaction with the static intercept. Trying to understand the two levels of allometry—within and between species—and their relationship is complex and the theoretical framework does not yield a straightforward answer as to whether allometry is adaptive or not (Ganyon, 2000). However, the available information suggests that allometric static slopes play an important role in the evolution of traits (Pélabon et al., 2014; Voje & Hansen, 2013; Voje et al., 2014; Voje et al., 2022), although their evolvability might be slower than that of static intercepts (Pélabon et al., 2014; Voje et al., 2014). Furthermore, if static allometric slopes evolve, it is mainly due to selective pressure on sexually selected traits (Voje & Hansen, 2013).

Our study stands out as one of the few investigations that not only focus on examining RR in body size but also extends its exploration to other traits. Since the work of Abouheif

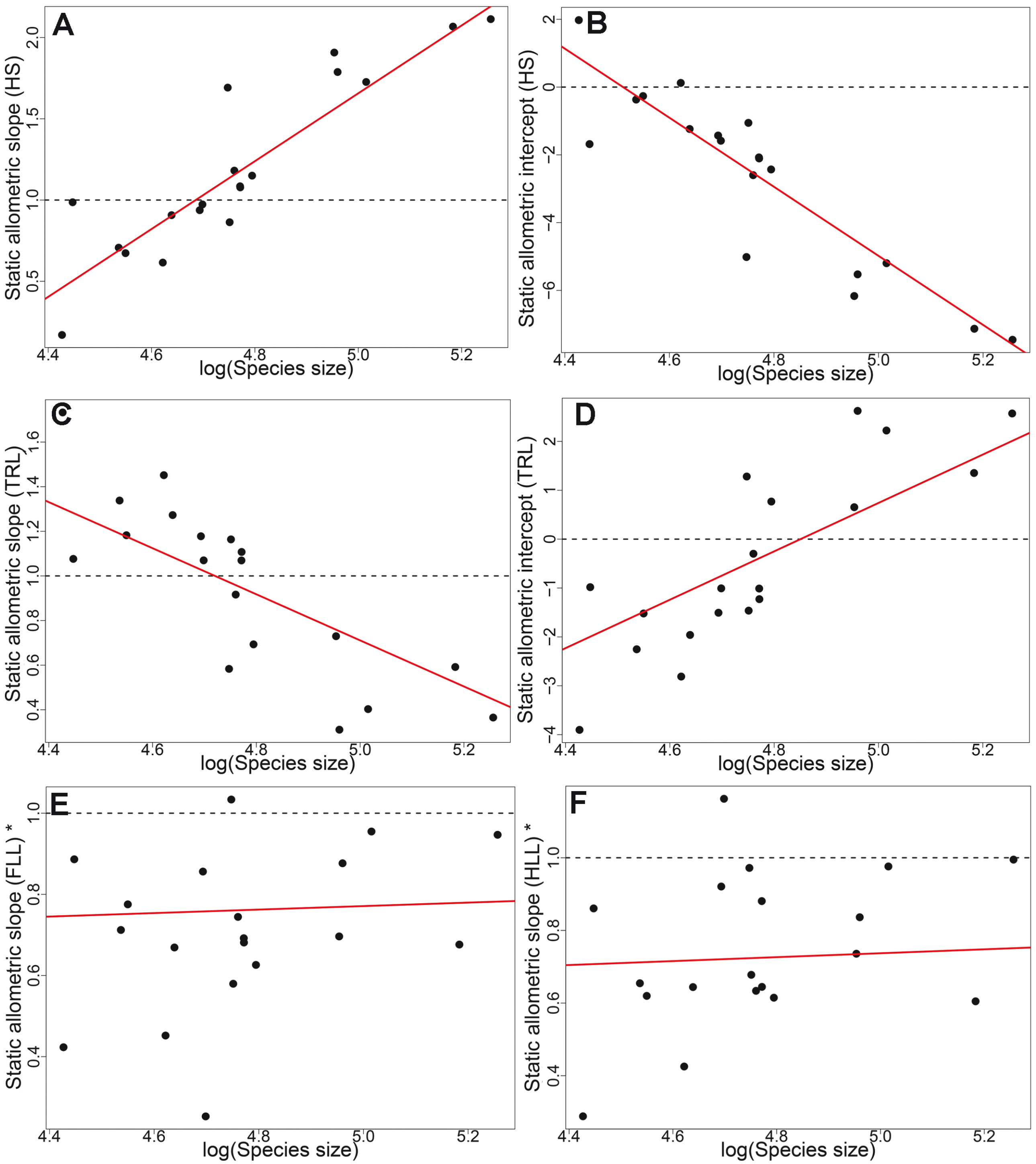

Figure 5. Relationship between static allometric parameters and mean species size in green lizards. (A) Slope vs. size in head size (HS). (B) Intercept vs. size in HS. (C) Slope vs. size in trunk length (TRL). (D) Intercept vs. size in TRL. (E) Slope vs. size in forelimb length (FLL). (F) Slope vs. size in hindlimb length (HLL). The asterisk represents the interaction with the static allometric intercept in the model for FLL and HLL.

and Fairbairn (1997) assessments of RR have mainly focused on body size (Blanckenhorn et al., 2007; Ceballos et al., 2013; Frýdlová & Frynta, 2010; Liang et al., 2021; Remeš & SzéKely, 2010) and not on other traits as initially examined by Rensch himself (1950, 1959), with a few remarkable exceptions (Adams et al., 2020; Bidau & Martinez, 2016; Colleoni et al., 2014; Liang & Shi, 2017; Machado et al., 2021; Szekely et al., 2004). Our results from both simulations and an empirical case have allowed us to explore RR in body size and in other traits considering important parameters such as static intercept and slope. We delved into static allometry, finding a link between static allometry and body size, mainly in the relationship between the static allometric slope and the species size, confirming some previous research (Gould, 1966a; Pélabon et al., 2014; Voje et al., 2022). Importantly, we have found concordance between our numerical simulations and the empirical real-life example, in that static allometry can determine the occurrence of RR or its converse in a trait through the allometric slope. The complex linkage between SD in body and trait size, static allometry, and evolutionary allometry of SD (i.e., RR) is a challenge for current studies. The combination of sexual selection, natural selection, and genetic-based hypothesis may be a possible explanation to understand these intricate patterns. By considering the interplay of these mechanisms, we may gain insights into the underlying explanations for RR. Sexual selection, driven by mate choice and competition for reproductive success, could play a role in shaping certain traits or exaggerating their expression. Natural selection, on the other hand, influences traits that enhance fitness in specific environments, favoring specific features over others. In addition, genetic-based hypotheses highlight the role of genetic factors and mechanisms in configuring trait variation and inheritance patterns. By integrating these factors, we can potentially unravel the complex dynamics behind the observed RR patterns.

The intricate links that connect intraspecific allometry, SD, and RR in body size and other traits established through simulations are exemplified with more realism through the empirical case of green lizards. The analyses focusing on *Lacerta* and *Timon* lineages revealed a strong relationship between intraspecific allometric parameters (slope and intercept) and body size. Traits such as trunk length exhibited steeper static slopes and lower static intercepts in smaller species, and traits such as head size exhibited steeper static slopes and lower static intercepts as species increased in size. Our results support Gould's hypothesis only for trunk length, while not for the other three traits. Interestingly trunk length is the only trait that does not show RR or its converse. This could be linked to physical and anatomical constraints between trait and body size. In conclusion, our results confirm that patterns consistent with Rench's rule can appear in body size and traits and that they can do so consistently with the rule or conversely to it. We provide strong evidence that intraspecific allometry is linked to evolutionary allometry for RR through variations in slope and sometimes through the interaction between slope and intercept. As such, we conclude that the intraspecific allometric slope is a major parameter influencing the evolutionary allometry of sexual differences.

Supplementary material

Supplementary material is available online at *Evolution*.

Data availability

All the files necessary to reproduce analyses are available at GitHub at the following link https://github.com/Pristimantis2016/RR_Evolution

Author contributions

C.R.P. was responsible for conceiving and designing the research, conducting the experiments, analyzing the data, creating figures and tables, writing, or reviewing drafts of the article, and approving the final version. A.K. was responsible for conceiving and designing the research, conducting the experiments, analyzing the data, writing, or reviewing drafts of the article, and approving the final version. D.C.A. was responsible for conceiving and designing the research, analyzing the data, writing, or reviewing drafts of the article, and approving the final version. U.E.U. was responsible for conceiving and designing the research, writing, or reviewing drafts of the article, and approving the final version.

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