

Allometry, sexual dimorphism, and Rensch's rule in pygmy and marbled newts

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Abstract

Allometry, the relationship between body size and the size of other body parts, explains a significant portion of morphological variation across biological levels, at the individual level, within and between species. We used external morphology measurements of 6 *Triturus* (sub)species, focussing on the *T. marmoratus* species group, to explore allometric parameters within and between taxa. We tested for allometry of sexual size dimorphism in body, head, and limb dimensions and examined whether intraspecific allometry directed evolutionary allometry, as described by Rensch's rule. Our findings indicated that female-biased trunk and head dimensions exhibited positive allometry, whereas male-biased limb dimensions showed isometric relationships or weak correlations with body size. Morphological divergences between sexes occurred along common allometric slopes, most often through changes in the intercepts. Among taxon, comparisons revealed that (sub)species diverged in the direction of the allometric slopes. In line with Rensch's rule, sexual size dimorphism in female-biased traits significantly decreased as overall body size increased. However, the observed intraspecific allometric parameters deviated from theoretical expectations because the steepest allometric slopes for female-biased traits were recorded in the larger species. Our results contribute to understanding the dynamics of allometric relationships and sexual dimorphism in amphibians and provide a robust baseline for future comparative analyses.

Keywords: sexual selection, sexual size dimorphism, standardized major axes, *Triturus*

Introduction

The study of size and its biological consequences, known as allometry, has fascinated biologists for centuries (e.g., Snell, 1892; Thompson, 1917; Huxley, 1932; Gould, 1966; see also Stevens 2009). Allometry refers to the covariation between body size and the size of other body parts, capturing a crucial aspect of phenotypic variation across biological levels—from ontogeny and within individuals to variation among individuals, populations, and species. During ontogeny, organisms grow and change in shape following specific phenotypic trajectories, which are directed by species-specific developmental programs (Alberch, 1980). These changes are described by ontogenetic allometry, which captures the relationship between size and shape as organisms develop. Variations in individual phenotypic trajectories result in differences in size and shape among individuals within a population or species, including size-related shape changes, a pattern known as static allometry. In contrast, size-related changes in shape among phylogenetically related species are referred to as evolutionary allometry (Klingenberg, 1998).

Due to its developmental origins and hierarchical nature, static allometry is expected to mirror ontogenetic allometry and, in turn, shape evolutionary allometry (e.g., Klingenberg, 1998, 2005; Pélabon et al., 2013). Additionally, the directions of size-related shape changes—allometric slopes—are often considered evolutionary stable among phylogenetically

related species (e.g., Voje et al., 2014). This stability can be attributed, at least in part, to shared developmental programs inherited from a common ancestor. As a result, allometric slopes are frequently regarded as phylogenetical constraints (Gould, 1966, 1977; Klingenberg, 1998, 2005; Lande, 1979; Niklas, 1994; Pélabon et al., 2013). However, despite this conservatism, allometric slopes are also subject to natural and sexual selection and are thus evolvable (Bolstad et al., 2015; Bonduriansky & Day, 2003; Reyes-Puig et al., 2023).

Sexual size dimorphism (SSD) is a significant source of phenotypic variation in many species, driven by a combination of sexual selection, fecundity selection, and ecological factors, which leads to niche divergences between the sexes (Andersson, 1994; Arnold & Wade, 1984; Bro-Jørgensen, 2007; Herrel et al., 2012; Shine, 1989). SSD refers to both the direction of intersexual differences and the magnitude of the divergence (Lovich & Gibbons, 1992). If females are the larger sex, SSD is referred to as female-biased; if males are the larger sex, SSD is referred to as male-biased. SSD is most often associated with differences in overall body size (Fairbairn et al., 2007; Lovich & Gibbons, 1992). However, different body parts may be subject to different selection pressures and may vary in the direction and intensity of SSD in relation to each other and to overall body size. For instance, trunk size in newts may be influenced by fecundity selection, which favours a larger trunk and body size in females, whereas other

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traits, such as a dorsal crest or leg size, may be shaped by sexual selection, resulting in crest proliferation and larger leg size in males (Reinhard & Kupfer, 2015; Wiens et al., 2011). Therefore, SSD is not limited to body size but also manifests in the size of other traits and the relative proportions of different body parts (e.g., Machado et al., 2021; Petrović et al., 2017). These differences may arise through changes in allometric relationships between the sexes. The divergences in static allometry parameters therefore reflect SSD (Adams et al. 2020; Kalezić et al., 2000; Kaliontzopoulou et al. 2015; Reyes-Puig et al., 2023; Sanger et al., 2013).

At the evolutionary level, an allometric pattern of change in the magnitude of SSD relative to species size, known as Rensch's rule (RR), has been observed in many taxa (Abouheif & Fairbairn, 1997; Fairbairn, 1997; Fairbairn et al., 2007). Specifically, RR states that as species size increases, SSD tends to increase for male-biased traits and decrease for female-biased traits (Rensch, 1950, 1959). To distinguish between the two patterns described by RR, an increase in SSD of male-biased traits with increasing species size is here designated as RR+, while a decrease in SSD for female-biased traits with increasing species size is designated RR-. Despite numerous studies, there is no generally accepted explanation for RR, with sexual selection, natural selection and developmental constraints frequently mentioned as causative factors (Colleoni et al., 2014; Dale et al., 2007; Fairbairn, 1997; Fairbairn et al., 2007; Reyes-Puig et al., 2023). The same holds for the proximate mechanisms leading to RR (e.g., Blanckenhorn et al., 2007), though it has been proposed that sexual differentiation of static allometric slopes at the species level is underlying and directing RR (Reyes-Puig et al., 2023). According to this hypothesis, for male-biased sexually dimorphic traits, steeper allometric slopes at the static level would lead to an increase in SSD in larger taxa (RR+), whereas a shallower slope for female-biased sexually dimorphic traits would result in a decrease in SSD in larger taxa (RR-). Empirical data are crucial for assessing the evolvability of allometric slopes, particularly robust datasets that allow comparisons of allometric slopes at different biological levels (e.g., Klingenberg & Zimmermann, 1992; Voje & Hansen, 2013; Voje et al., 2022).

One animal group with great research potential in the study of allometry is the genus *Triturus*, also known as "large-bodied newts." These newts display an eco-morphological gradient, from the less aquatic, stout and short-bodied marbled newts to the more aquatic and elongated and slender crested newts. Allometric changes in limb size (Ivanović et al., 2008) and skull shape (Ivanović & Arntzen, 2014) have been shown to drive morphological differences across species. Also, the phylogenetic relationships of *Triturus* species are well-documented, with two main clades, the *T. marmoratus* and *T. cristatus* species groups, which separated from one another approximately between 24 and 16 million years ago (Marjanović & Laurin, 2014; Steinfartz et al., 2007; Wielstra et al., 2014). Our study focuses on the *T. marmoratus* species group, which includes marbled and pygmy newts. Their diversification occurred approximately five to two million years ago (Arntzen, 2024b; Kazilas et al., 2024), with distributions limited to the Iberian Peninsula and France (Arntzen, 2024c, 2024d).

Triturus newts have a basic tetrapod body plan, biphasic life cycle, and fascinating courtship rituals, which take place underwater. Males often exhibit specific postures or swim in distinct patterns to catch the female's attention (Green,

1989; Hidalgo-Vila et al., 2002; Sparreboom & Teunis, 1990; Zuiderwijk & Sparreboom, 1986). The male deposits a packet of sperm (spermatophore) on the substrate at the bottom of the water body. The female is then guided over the spermatophore by the male, and she picks it up with her cloaca. Fertilization is internal, and the female newt lays about 400 fertilized eggs (Arntzen & Hedlund, 1990) one by one, attaching them to aquatic plants and folding leaves around the embryo (Díaz-Paniagua, 1989; Miaud, 1995).

Females are the larger sex, whereas males have longer limbs (Colleoni et al., 2014; Malmgren & Thollessen, 1999; Reinhard & Kupfer, 2015). To date, two studies on European newts, which included *Triturus* species, have not found clear support for RR (Colleoni et al., 2014; Ivanović et al., 2008). While most attention has so far been given to members of the *T. cristatus* species group (Ivanović & Kalezić, 2012; Ivanović et al., 2008; Malmgren & Thollessen, 1999), the counterpart *T. marmoratus* species group may be more promising because size variation between taxa is more pronounced, with a ca. 20% (females) to 30% (males) difference in body size among the smallest and largest species. It must be noted that pygmy newts (as the name implies) are of relatively small size and that they show substantial size variation as affected by environmental conditions (Díaz-Paniagua et al., 1996) and possibly representing a latitudinal geographical cline (Arntzen, 2018).

The aims of the study are to quantify sexual dimorphism using standard SSD indices and allometry and to explore and compare allometric relationships between the sexes and taxa. We analyze data on seven measurements of the body, head, and limbs of five taxa in the *T. marmoratus* species group as obtained earlier (Arntzen, 2018, 2024b) to which we include the northern crested newt, *T. cristatus*, for comparison. We selected snout-vent length as a measure of overall body size, along with one trunk dimension and two measurements each for the head, forelimbs, and hind limbs. Using these measurements, we aimed to examine sex-based divergences and to infer potential ultimate and proximate mechanisms driving SSD, focussing on the allometric relationships between trait sizes and body size and on shifts in these relationships between sexes and across species. Based on RR and a hypothesis suggesting that differences in allometric slopes at the species level underlie and direct RR (Reyes-Puig et al., 2023), we expect the following: for female-biased traits, we anticipate a decrease in the magnitude of sexual dimorphism in larger taxa (denoted as RR-), with these traits exhibiting shallower allometric slopes, whereas for male-biased traits, we expect the opposite trend, where the magnitude of sexual dimorphism increases in larger taxa (denoted as RR+), with these traits showing steeper allometric slopes.

Materials and methods

Samples and measurements

Five (sub)species of *T. marmoratus* species group were analyzed: two subspecies of the marbled newts—*T. marmoratus harmannii* (338 females and 247 males from 46 populations) and *T. m. marmoratus* (80 females and 70 males from five populations), and three taxa of pygmy newts namely *T. p. pygmaeus* (26 males and 24 females from five populations), *T. pygmaeus lusitanicus* (317 females and 254 males from 38 populations) and *T. rudolfi* (126 females and 125 males from six populations). Hybrid populations were excluded

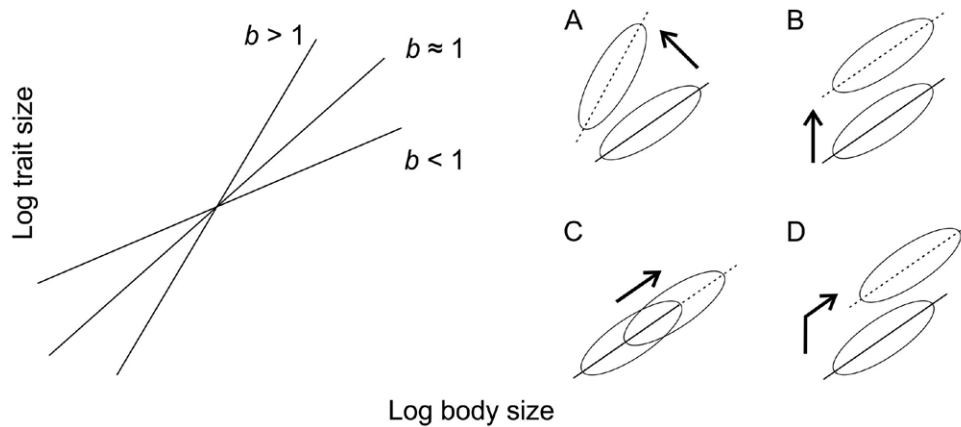


Figure 1. Schematic representation of patterns of change in allometric parameters after Warton et al. (2006), with log body size on the horizontal axis and log trait size on the vertical axis. Left panel—lines showing isometry ($b \approx 1$) versus positive ($b > 1$) and negative ($b < 1$) allometry. Right panel—changes in allometric relationships between groups, such as here females and males. Ellipses represent the bivariate cloud of data points for both sexes in morphological space defined by body size and the size of the morphometric trait of interest. (Un)interrupted lines are the allometric slopes for one sex or the other. The direction of change in allometric parameters is assigned randomly.

from suppressing the admixture of morphological trait data (Arntzen, 2018, 2024a, 2024b). In the further text, the (sub)species are arranged by size, from the smallest, *T. p. pygmaeus*, to the largest, *T. m. marmoratus*, along with a sample of *T. cristatus* (15 males, 30 females from one population). All measured individuals were adults. The following eight morphometric traits were analyzed: snout-vent length (SVL), as representative of overall body size, was measured from the tip of the snout up to and including the insertion of hind limbs, interlimb distance (ILD), head width (Hw), head length (HL), forelimb length (FLI), third finger length (TFL), hindlimb length (HLL) and fourth toe length (FTL). SVL as here measured purposely excludes the cloaca, the size of which is season-dependent. That measure largely corresponds to the more commonly used measure up to the cloacal slit (e.g., Reinhard & Kupfer, 2015). The analyzed dataset is compilation of published (Arntzen, 2018, 2024b, 2024c) and newly collected data and covers the entire distribution range (Arntzen, 2024c, 2024d). All animals were measured on the field by the senior author under relevant licenses (France—Prefecture de la Mayenne, by permit number 2003-A-2007; Spain—various provinces by permits numbers CN0010/12/ACA, CN03/0085, CN04/0269, CN10/0030, DGMEN/SEN/avp_12_015_aut, DNP 27/2008, E.P-107/04 (MG), IS/pa/EPCYL/129/2012 and SGYB/FOA/AFR/CFS, Consejerías de Medio Ambiente de Castilla la Mancha, Castilla y León, Comunidad de Madrid (Grant PID2020-116289GB-I00, FEDER/Ministerio de Ciencia, Innovación y Universidades-Agencia Estatal de Investigación, Spain), and Portugal—Instituto da Conservação da Natureza, by letters dated 26/10/1998, 19/4/2000 and 19/3/2002 and by permit numbers 397/2007/CAPT, 102/2010/CAPT, 103/2010/CAPT and 107/2012/CAPT; sampling in the Doñana National Park was carried out under permit number 27/2008).

SSD index and allometric parameters

SSD was extensively studied across animal taxa, and the most frequently used estimates of intersexual differentiation are indices of SSD that relate to size in females and males (Lovich & Gibbons, 1992). To quantify SSD for each trait separately we used the standard index [(trait size of the larger sex/trait size of the smaller sex) – 1] (Lovich & Gibbons,

1992), arbitrarily defined as positive when the trait is larger in females and vice versa.

The allometric relationship is described by the power law $y = a x^b$ (Huxley, 1932). On a log–log scale, the relationship between traits is linear, with x representing body size, y representing trait size, a as the intercept of the allometric line on the y -axis, and b as the slope exponent that describes how trait size (y) changes relative to body size (x). If the allometric slope does not significantly depart from unity ($b \approx 1$), trait size increases proportionally with an increase in body size (isometry), whereas $b \neq 1$ indicates positive or negative allometry (Figure 1). Differentiation in body proportions between groups, such as females and males, can be achieved through a change in the direction of the allometric slope (Figure 1, pattern A), a lateral shift (elevation), where sexes share the same allometric slope but differ in the intercept (pattern B), or a shift in position along a shared allometric slope (pattern C), also the combination of the latter two is possible, with changes in elevation as well as shift along a common slope (pattern D).

To estimate trait-specific allometry for each sex and sub-(species) separately and to estimate patterns of change in allometric parameters between sexes and (sub)species (Figure 1), we used standardized major axis (SMA) analysis. This procedure estimates the allometric slope between log values of body size and trait size, accounting for measurement error in both variables and without assuming a distinction between independent and dependent variables and has been proposed as an appropriate approach for the study of allometry (Warton et al., 2006; but see Meiri & Liang, 2021, for an opposing view). Rensch's Rule (RR) was also tested by estimating the allometric slope. Unlike static allometry, where the slope describes the relationship between body size and trait size, the RR allometric slopes were fitted between the mean trait values of males and females, calculated separately for each (sub)species. A slope value of $b > 1$ indicates that SSD increases with an increase in male size, whereas $b < 1$ suggests that SSD decreases as the size of females increases.

Statistical analyses

All statistical analyses were conducted using R (R Core Team, 2022). The significance of differences in mean trait size

Table 1. Allometric relationships and changes in allometric parameters between females and males in five (sub)species in the *Triturus marmoratus* species group and *T. cristatus*.

(Sub)species	Females				Males				Slope (<i>b</i>)	Elevation	Shift	Pattern
	<i>r</i> ²	<i>b</i>	CI 2.5%	CI 97.5%	<i>r</i> ²	<i>b</i>	CI 2.5%	CI 97.5%				
<i>T. p. pygmaeus</i>												
ILd	0.025	0.688	-0.884	0.910	0.333	0.883	0.621	1.563	NA			None
HI	0.623	1.093	0.866	1.358	0.705	0.958	0.818	1.299	NS	NS	*	C
Hw	0.596	0.788	0.628	0.949	0.752	0.808	0.697	1.027	NS	NS	*	C
FLI	0.561	0.991	0.707	1.282	0.491	1.234	0.899	2.033	NS	*	*	D
TFl	0.459	1.287	0.928	1.655	0.242	1.364	0.932	2.564	NS	*	*	D
HLI	0.698	1.012	0.806	1.229	0.651	1.285	1.024	1.933	NS	*	*	D
FTI	0.583	1.719	1.271	2.178	0.556	1.807	1.405	3.000	NS	*	*	D
<i>T. p. lusitanicus</i>												
ILd	0.615	1.361	1.267	1.446	0.494	1.432	1.306	1.566	NS	*	*	D
HI	0.451	0.973	0.888	1.068	0.333	1.123	0.998	1.270	NS	*	*	D
Hw	0.549	0.974	0.900	1.051	0.470	0.938	0.851	1.030	NS	*	*	D
FLI	0.408	0.939	0.859	1.022	0.332	1.026	0.911	1.160	NS	*	*	D
TFl	0.119	1.805	1.638	1.976	0.005	2.086	-2.210	2.358	NS	*	*	D
HLI	0.389	1.020	0.936	1.106	0.275	1.101	0.983	1.247	NS	*	*	D
FTI	0.088	1.828	1.638	2.056	0.001	1.869	-2.013	2.053	NS	*	NS	B
<i>T. rudolfi</i>												
ILd	0.757	1.316	1.203	1.431	0.714	1.313	1.194	1.440	NS	NS	*	C
HI	0.340	1.055	0.927	1.191	0.319	1.026	0.871	1.200	NS	*	*	D
Hw	0.645	1.082	0.987	1.183	0.518	1.011	0.888	1.144	NS	*	*	D
FLI	0.661	1.037	0.918	1.154	0.550	1.110	0.986	1.230	NS	*	*	D
TFl	0.147	1.446	1.173	1.751	0.151	1.687	1.320	2.075	NS	*	*	D
HLI	0.618	1.106	0.984	1.24	0.471	1.157	1.007	1.317	NS	*	*	D
FTI	0.044	1.601	1.239	1.936	0.131	1.708	1.479	1.994	NS	*	NS	B
<i>T. m. harmannis</i>												
ILd	0.517	1.337	1.250	1.436	0.471	1.203	1.087	1.341	NS	NS	*	C
HI	0.435	1.304	1.209	1.413	0.391	1.243	1.117	1.396	NS	*	*	D
Hw	0.589	1.086	1.007	1.166	0.588	0.985	0.908	1.071	NS	*	*	D
FLI	0.503	0.994	0.904	1.083	0.505	1.156	1.058	1.276	NS	*	NS	B
TFl	0.121	1.859	1.685	2.049	0.228	1.678	1.459	1.932	NS	*	NS	B
HLI	0.450	1.057	0.967	1.147	0.484	1.081	0.978	1.195	NS	*	NS	B
FTI	0.026	2.128	1.912	2.380	0.165	1.704	1.485	1.957	*	NA	NA	A
<i>T. m. marmoratus</i>												
ILd	0.556	1.719	1.493	1.971	0.423	1.325	1.085	1.629	NS	NS	NS	None
HI	0.665	1.304	1.152	1.494	0.024	1.144	NA	NA	NS	NS	NS	None
Hw	0.705	1.218	1.077	1.406	0.196	0.939	0.781	1.153	NS	NS	NS	None
FLI	0.524	1.087	0.193	1.281	0.108	1.192	0.942	1.496	NS	*	NS	B
TFl	0.268	2.286	1.913	2.779	0.136	-2.811	-3.611	-2.264	NS	*	NS	B
HLI	0.270	0.944	0.794	1.114	0.125	1.156	0.918	1.498	NS	*	NS	B
FTI	0.136	2.553	2.090	3.114	0.157	-3.485	-4.556	-2.781	NA			None
<i>T. cristatus</i>												
ILd	0.593	1.507	1.159	1.621	0.783	1.742	1.263	2.456	NS	NS	NS	None
HI	0.054	1.377	-1.356	1.711	0.266	1.223	0.634	2.290	NA			None
Hw	0.299	1.483	1.081	1.716	0.124	1.301	0.446	2.532	NA			None
FLI	0.263	1.081	0.769	1.211	0.301	1.139	0.654	1.824	NA			None
TFl	0.179	2.913	1.816	3.769	0.007	-1.360	-2.284	2.454	NA			None
HLI	0.065	1.234	0.657	1.695	0.462	0.984	0.648	1.640	NA			None
FTI	0.029	-2.376	-3.103	2.181	0.434	2.401	-1.939	4.204	NA			None

Note. The strength of the association between snout-vent length and the specified trait is expressed by the square of Pearson's correlation coefficient (r^2). The value of the allometric slope (b) was given along with the CI with a 95% confidence level. Statistically significant results are shown in boldface type. Values not relevant because of the lack of significant support for the presence of an axis (i.e., r^2 is not significant) are shown in italics. Significances of values for the intercept (elevation) and shift along a common slope are shown at the right, along with the inferred pattern of allometric change (A, B, C, D or none, see Figure 1).

Bonferroni's corrected significances are: * $p < 0.05$; NS = not significant; NA = not applicable.

between the sexes was tested by t-tests using the *t.test* function. The allometric relationships between females and males within (sub)species and among (sub)species, as well as RR was explored using SMA with the *smatr* package (Warton et al., 2012, 2018). First, we plotted trait measures versus SVI (all log-transformed) for each (sub)species and sex separately using *sma* function. The strength of the association between SVI and the specified trait was estimated by the square of Pearson's correlation coefficient (r^2). The statistical significance of the fitted allometric slope for each sex and (sub)species was estimated by the sample correlation between residuals and fitted values. We subsequently tested whether the allometric slope is nonisometric ($b \neq 1$). Differentiation of the sexes was explored by testing for differences in the direction of allometric slopes (Figure 1, pattern A). When no differences were found, we tested for lateral shifts that led to a change in elevation (pattern B), shifts along the common allometric slope (pattern C), or both (pattern D).

We tested for RR using again the *sma* function. The log-transformed mean values for specific traits in females versus males for each (sub)species were plotted and tested for isometry ($b = 1$). To test for common slopes across taxa and between pairs of taxa, we used the *slope.com* function. First, we calculated the common slope for each of the traits for all six taxa with pooled males and females as these have common slopes (Table 1) and estimated its statistical significance based on the (Bartlett-corrected) likelihood ratio statistic testing for common slope (Taskinen & Warton, 2013; Warton & Weber, 2002; Warton et al., 2006). We did post hoc multiple comparisons of slopes by calculating the common slope for pairs of taxa for each trait. Interpretation of all statistical tests was done using the standard Bonferroni correction for multiple comparisons.

To calculate 95% CIs for the values of allometric slopes in all aforementioned tests, we used *boot* package (Canty & Ripley, 2024; Davidson & Hinkle, 1997). We defined bootstrap function and then used *replicate* function to create bootstrap samples. CIs were calculated by using the *quantile* function. All R scripts and data used are available as Supplementary Material on the Dryad database: <https://doi.org/10.5061/dryad.w6m905qzm>.

Results

Females were, on average, larger than males, with the differences between sexes decreasing as overall size increased (Figure 2). Females had longer bodies (SVI, ILd) and wider heads (Hw) than males, as indicated by significantly positive SSD values, across all taxa except *T. marmoratus* and *T. cristatus* (Figure 2; see Supplementary Table 1 for details). Positive SSD was observed for head length (HL) in pygmy newts but not in marbled and crested newts. In contrast, male-biased SSD was more pronounced in digit lengths (TFL, FTI) compared to limb lengths (FLI, HLI).

The amount of variation explained by body size varied across traits. Interlimb distance (ILd) and head width (Hw) showed the strongest covariation with SVI, while limb measurements, particularly digit lengths (TFL, FTI), showed weak covariation with SVI (Table 1). In all taxa except *T. p. pygmaeus*, ILd showed positive allometry ($b > 1$), whereas head width (Hw) and limb lengths (FLI and HLI) were largely isometric ($b \approx 1$) or uncorrelated with SVI (*T. marmoratus*, *T. cristatus*). The 95% CIs for allometric slopes (CI) reflected

the strength of association between traits and SVI (r^2). The CI ranges were broader for traits with weak covariation with SVI (Table 1), especially digits (TFL, FTI). However, CI also increased in larger species represented by smaller sample sizes (*T. marmoratus* and *T. cristatus*).

Changes in elevation (pattern B) and shifts along a common allometric slope (pattern C) were frequently observed, either independently (pattern B eight times, pattern C four times) or in combination (pattern D seventeen times). A significant difference aligning with the allometric slope (pattern A) was observed only once for toe length, which showed weak or no correlation with SVI. Support for RR- was found in female-biased traits (SVI, ILd, and Hw; Table 2). Male-biased traits were either isometric ($b \approx 1$) or could not be estimated, providing no support for RR.

Comparisons among taxa revealed divergences in allometric slopes, represented by pattern A (Table 3). Post hoc comparisons of slopes showed that pygmy newts (*T. p. pygmaeus*, *T. p. lusitanicus*, and *T. rudolfi*) had significantly shallower allometric slopes for female-biased traits (ILd, HL, and Hw) than marbled and crested newts, especially *T. marmoratus*. The highest number of significant directional differences in allometric slopes was observed for finger and toe lengths. However, the model explained only a small amount of variation (Table 1), and the data supported neither RR+ nor RR-.

Discussion

By analyzing a large dataset that covers morphological variation in five (sub)species, we provided evidence for patterns of sexual dimorphism and the underlying allometry of sexual differences in marbled newts. Their close phylogenetic relatedness (Kazilas et al., 2024; Pincheira-Donoso et al., 2021), overall similar ecological preferences when compared to crested newts (Arntzen & Espregueira Themudo, 2008; Wielstra et al., 2019), and the robustness of the dataset allowed us to obtain reliable estimates of allometric divergences between the sexes and changes in SSD. In all taxa, the direction and pattern of SSD largely corresponded to those observed in a population of *T. marmoratus* (Reinhard & Kupfer, 2015) we . We found that trunk and head dimensions (ILd, HL, Hw) were female-biased and that the larger dimensions in females were achieved through positive allometric growth without changes in the direction of sex-specific allometric slopes. A female-biased sexual dimorphism in newts is often explained by fecundity selection toward longer body and trunk sizes, which are directly related to reproductive output (Malmgren & Thollessen, 1999; Kupfer, 2007; but see Monroe et al., 2015). Egg size in *Triturus* newts is species-specific, with larger species producing larger eggs (Furtula et al. 2008). Additionally, there is variation in the number of eggs between females both within and between species (Vučić et al., 2020). However, to our knowledge, no empirical data currently support the relationship between female fecundity and trunk size in newts.

Another possible explanation for SSD is the “niche divergence hypothesis” (Van Valen, 1965) stating that intersexual competition drives divergence between males and females (Bolnick & Doebeli, 2003; Ivanović & Kalezić, 2012; Peñalver-Alcázar et al., 2019), which also remains to be empirically tested. Sex-specific mortality was invoked as a possible proximate source of sexual dimorphism in amphibians (Kupfer, 2007; Shine, 1989), but it has been documented

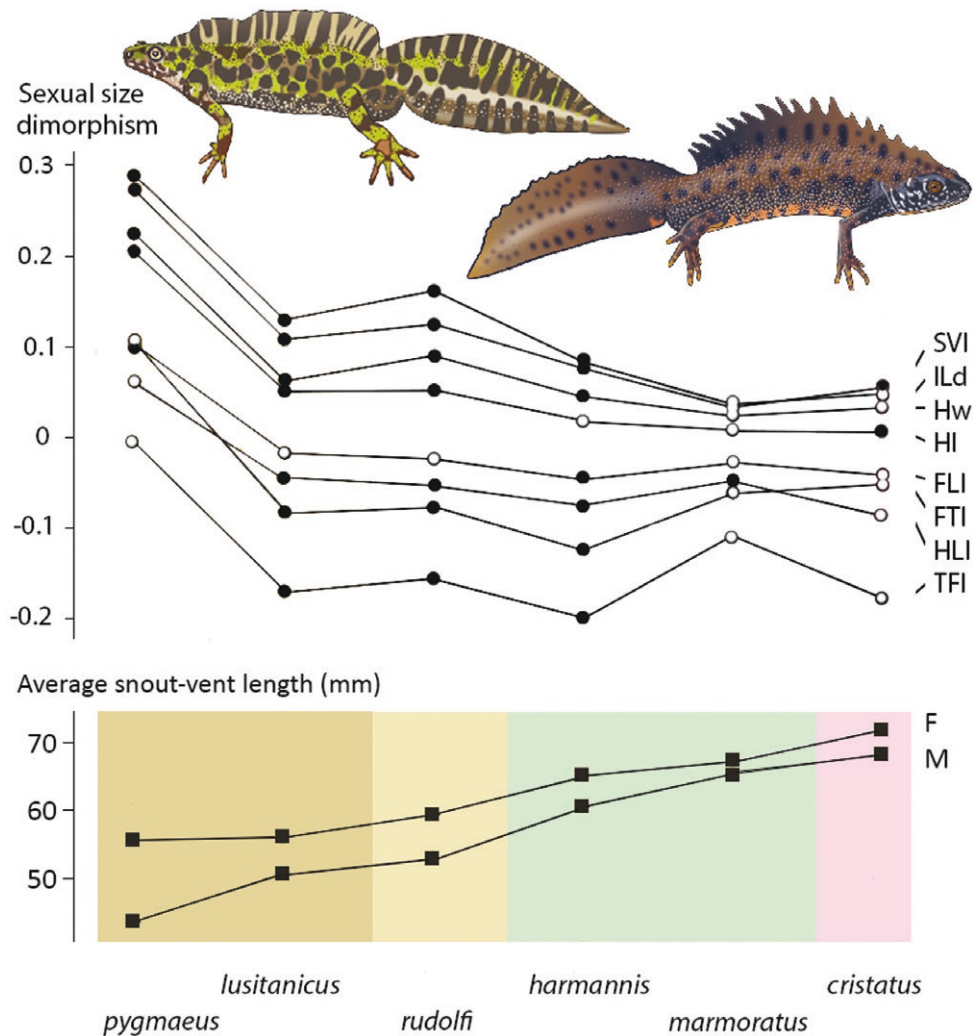


Figure 2. Sexual size dimorphism (SSD) in eight morphometric traits across five taxa within the *Triturus marmoratus* species group, including *T. cristatus*. For details on the SSD index and character abbreviations, refer to the text. Solid round symbols represent statistically significant results, while open round symbols indicate insignificant results. The middle panel displays the average snout-vent length for females (F) and males (M). The background shading corresponds to species in the following order from left to right: *T. pygmaeus* (brown), *T. rudolfi* (yellow), *T. marmoratus* (green) and *T. cristatus* (red). The animal illustrations in the bottom panel depict *T. marmoratus* (left) and *T. cristatus* (right), courtesy of Bas Blankevoort, Naturalis Biodiversity Center.

Table 2. Test for differentiation of allometric slopes in the *Triturus marmoratus* species group and *T. cristatus*.

	r^2	b	CI 2.5%	CI 97.5%
SVI	0.934	0.666	0.476	0.831
ILd	0.935	0.584	0.448	0.768
HI	0.891	1.271	0.459	1.560
Hw	0.984	0.781	0.539	0.850
FLI	0.927	0.804	0.569	0.951
TFI	0.899	1.047	0.429	1.277
HLI	0.920	0.756	0.564	1.026
FTI	<i>0.595</i>	<i>0.891</i>	<i>0.350</i>	<i>1.580</i>

Note. Squared correlation coefficients (r^2) and common slopes (b) were obtained by fitting mean log female and mean log male trait sizes for six taxa by standardized major axis analysis. The value of the common slope (b) was given along with the CI with a 95% confidence level. Statistically significant results are shown in boldface type. Note that Rensch's rule (RR-) is supported for three traits with $b < 1$. One value not relevant because of the lack of significant support for the presence of an axis (i.e., r^2 not significant) is shown in italics.

that in large-bodied newts sexual dimorphism in body size arises through divergences in the growth rate of females and males after reaching sexual maturity, generally with unity sex ratio (Arntzen, 2000; Bugarčić et al., 2022; Cogălniceanu et al., 2020; Francillon-Viellet et al., 1990).

Limb sizes (FLI and HLI) and digit sizes (TFI and FTI) were male-biased. The change in limb size was proportional to the change in body size. The observed isometry of the fore- and hind limbs may result from stabilizing selection that maintains the body and limb proportions, not just for movement and body support but also for reproductive output, as females use their hind limbs and toes to handle eggs and wrap them in submerged vegetation (Miaud, 1995). These highly adaptive functional requirements, along with the integration between the limbs, support isometry (Tomašević Kolarov et al., 2011). However, digit lengths were at best weakly correlated with body size. Larger legs and digits (and smaller body size) in males may be attributed to sexual selection and related to males' acrobatic mating performances, as observed in birds (Székely et al., 2004). In *Triturus* newts, males use their long legs and toes to enhance their posture (Zuiderwijk &

Table 3. Comparisons among taxon-specific allometric slopes with statistically significant results in boldface type ($p < 0.05$).

Trait	Common slope (b)	CI 2.5%	CI 97.5%	Pairwise comparisons with taxon			
				pygmaeus	lusitanicus	rudolfi	harmannis
Ild	1.311	1.271	1.352	<l,r,m,c			<m
HI	1.023	0.978	1.065	<h,m	<h,m	<h,m	
Hw	0.945	0.914	0.974	<m	<h,m		
FLI	0.937	0.895	0.978	<m	<h,m		
TFl	1.702	1.616	1.788	<l,r,h,m,c	<m	<l,h,m	<m
HLI	0.995	0.952	1.043	<h,m			
FTI	-1.978	-2.072	-1.866	>l,h,m,c	>m	>h,m	>m

Note. Because no differences in the direction of allometric slopes were found between sexes (Table 1), slopes were calculated from pooled data. The value of the common slope (b) was given along with the CI with a 95% CI. Taxa diverge in the direction of the slopes (pattern A, Figure 1). Taxon abbreviations are p—*Triturus p. pygmaeus*, l—*T. p. lusitanicus*, r—*T. rudolfi*, h—*T. m. harmannis*, m—*T. m. marmoratus* and c—*T. cristatus*. The symbols < and > stand for significantly shallower or steeper allometric slopes, respectively.

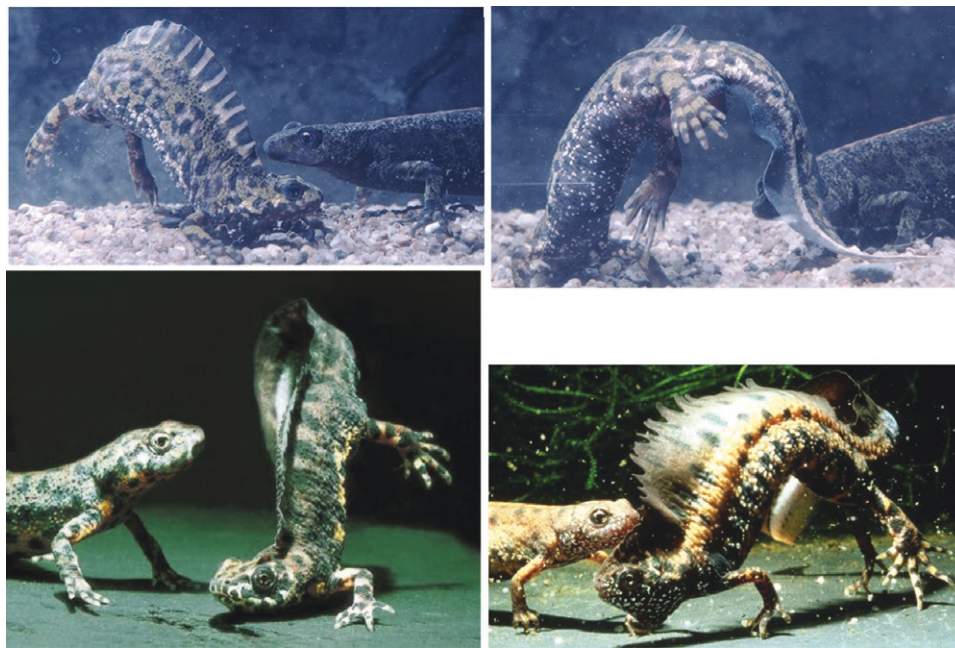


Figure 3. “Handstand” breeding postures in *Triturus marmoratus* (top). For comparison, the “handstand” and “cat-buckle” displays are shown in the sturdy *T. karelinii* (bottom left) and the slender *T. dobrogicus* (bottom right), both members of the *T. cristatus* species group. Note that body flexing as in *T. dobrogicus* is not an option in species of stocky built such as *T. marmoratus*. For courtship displays in *T. cristatus* and *T. pygmaeus* see Green (1989) and Hidalgo et al. (2002). Photography by Max Sparreboom.

Sparreboom, 1986), perhaps even more so in the *T. marmoratus* species group than in *T. cristatus*, which has a higher crest (Wiens et al., 2011). For example, the acrobatic “cat-buckle” display, where the male’s body is kinked and often rests only on the forelegs, may be more difficult or impossible to perform for the sturdy *T. marmoratus* than for the slender *T. cristatus* (cf. Figure 3). The weak correlation between digit size and SVI indicates that strong selection pressure breaks developmental constraints on these traits, allowing them to change independently (Andersson, 1994; Young & Hallgrímsson, 2005). Accordingly, the observed pattern of SSD in newts results from both natural and sexual selection, which jointly operate on complex phenotypes (Lande, 1979; Lande & Arnold, 1983).

Most of the observed differences in body measurements between the sexes resulted from changes in allometric

parameters, regardless of whether SSD was female- or male-biased. These changes were primarily due to shifts in the intercept (pattern B, Figure 1; Table 1), increases in size along a shared allometric slope (pattern C), or a combination of both (pattern D). These findings align with empirical estimates suggesting low evolvability of allometric slopes within taxa (Voje et al., 2014), while the allometric intercept (elevation) is more evolvable. Similar results were reported for lizard species with more pronounced male-biased SSD, where the majority of interspecific changes were related to a change in intercept (Reyes-Puig et al., 2023).

On the other hand, the divergence in allometric slopes among taxa indicates that, in marbled newts, allometric slopes may be considered highly evolvable. According to theoretical expectations, the allometric slope among closely related taxa should be conserved (Gould, 1966, 1977; Huxley,

1932; Klingenberg, 2005; Pélabon et al., 2013; Voje et al., 2022). Studies estimate that substantial changes in allometric slopes and evolutionary divergence generally require millions of years (Bolstad et al., 2015; Voje & Hansen, 2013; Voje et al., 2022). Our study system allows for such a temporal window because the most recent common ancestor of pygmy and marbled newts is estimated to have lived approximately five million years ago, while basal splits within *T. marmoratus* (leading to *T. m. marmoratus* and *T. m. harmanni*) and pygmy newts (yielding *T. pygmaeus* and *T. rudolfi*) are estimated to have occurred in the early Pleistocene, around two million years ago (Kazilas et al., 2024).

Although the number of taxa was at the lower limit for statistical testing, the substantial divergence in size among taxa—ranging from 45 to 68 mm in SVI for males and 65 to 72 mm for females (Figure 2)—along with a significant trend of decreasing SSD along this axis (e.g., for SVI from 0.30 to 0.05), provided evidence that SSD for female-biased traits decreases with increasing species size (RR−). Conversely, for male-biased limb traits, no statistical support was found for an increase in SSD with increasing species size (RR+). According to theoretical expectations, there is a link between variation in intraspecific allometric slopes and RR (Reyes-Puig et al., 2023). In the case of RR− female-biased traits should exhibit a shallower slope. However, we did not detect such a pattern of divergences in allometric slopes between sexes or species. Contrary to expectations, the steepest allometric slopes for female-biased traits were recorded in the larger species, particularly in *T. marmoratus*. The observed isometry in limb size and the low correlation between digit size and body size may explain why RR does not apply to these traits.

In ectothermic vertebrates with indeterminate growth, such as *Triturus* newts, various factors—such as resource-mediated growth and population age structure—can affect variation in body size and the magnitude of SSD among populations (Cvetković et al., 2009; Liao et al., 2015; Peñalver-Alcázar et al., 2019; Vale et al., 2024). The dwarf pygmy newts from Doñana National Park in southern Spain serve as an extraordinary example of this variation (Díaz-Paniagua et al., 1996). Our results contribute to the understanding of allometric relationships and sexual dimorphism in a group of amphibians where sexual dimorphism is present but not strongly pronounced. This study highlights the importance of static, sex- and species-specific allometric patterns, providing a robust baseline for future comparative analyses.

Supplementary material

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

Data availability

All R scripts and data used are available as Supplementary Material on the Dryad database: <https://doi.org/10.5061/dryad.w6m905qzm>

Author contributions

Ana Ivanovic (Conceptualization [equal], Formal analysis [lead], Methodology [lead], Validation [equal], Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal]), Tijana Vucic (Formal analysis [equal],

Validation [supporting], Visualization [supporting], Writing—original draft [supporting], Writing—review & editing [equal]), and Jan Arntzen (Conceptualization [equal], Formal analysis [supporting], Funding acquisition [lead], Methodology [supporting], Project administration [lead], Supervision [lead], Validation [equal], Visualization [equal], Writing—original draft [equal], Writing—review & editing [equal])

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Conflicts of interest

None declared.

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