Patterns and allometries of sexual size dimorphism in salamanders and the rejection of Rensch's Rule

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Abstract. Sexual size dimorphism (SSD) is a result of selective pressures acting differently on size in each sex. SSD is examined in salamanders by analysing data from 356 species representative of all major lineages to identify which sex is more frequently larger and test the validity of the Rensch's Rule. Most species of salamanders exhibit a female-biased SSD (66.9% of species analysed). The overall mean SSD index was 0.061, indicating that sex-linked differences in SVL were not large. Standard major axis regression using species data and phylogenetically independent contrasts indicated a general lack of fit of Rensch's Rule to the allometric patterns found for the whole data set and the analysis restricted to major families. Fecundity selection is more influential on female SSD than sexual selection associated with inter-male competition for mating partners. However, this selective pressure could be less forceful in females to produce a departure from isometry of biometric relationships between sex-linked sizes, thus leading to the rejection of Rensch's Rule.

Key words. Amphibia, Urodela, morphology, size, sexual dimorphism, Rensch's Rule.

Introduction

Sexual dimorphism is believed to be determined by the confrontation between opposite evolutionary forces, particularly natural and sexual selection (Fairbairn 1997, Shine 2000). Natural selection affects traits subjected to sexual dimorphism by balancing survivorship and reproductive success favouring either sex depending on biotic and abiotic characteristics of the environment (e.g., predation, trophic resources, microhabitat availability, parasitism: Slatkin 1984, Shine 1989). Thus, natural selection can reduce the competition between sexes for food, space and other resources by selecting different traits and thus adapting each one to different regimes in the available ecological niches (e.g., Earhart & Johnson 1970, Martin & Badyaev 1996, Wikelski & Trillmich 1997, Mysterud 2000). When these environmental selective pressures act on males and females in different ways based on the characteristics of habitats they may produce habitat-specific sexual dimorphism (e.g., Geist & Bayer 1988, Spoljaric & Reimchen 2008).

Sexual selection acts on traits that will optimise the chances of success during behavioural interactions between opponents or reproductive partners by making individuals who have those traits more attractive, or improve their ability to defeat rivals, or better protect their descendants (Arnold & Duvall 1994, Andersson & Simmons 2006). This kind of selection commonly produces larger males or positively affects allometric traits in this sex (Emlen 2008, Warren et al. 2013) and may lead to the development of sexual shape and size dimorphism. Thus, male-biased SSD is found mainly in birds and mammals and has been explained by a selective advantage of larger males during their contest for females (Selander 1972, Clutton-Brock et al. 1977). In contrast, it has been proposed that sexual selection favouring female-biased SSD enables females to store more energy for reproductive purposes and thus lets them produce more or larger young (selection for fecundity, Andersson 1994).

Patterns of sexual dimorphism have been explored in various vertebrates, revealing a general pattern of female-biased size in amphibians and reptiles (e.g., Shine 1978, Shine 1979, Kupfer 2007). Salamanders have been subjected to studies of body shape and size to elucidate intraspecific patterns of sexual dimorphism (see for example Hasumi, 2000, Kalezić et al. 2000). To date, large-scale interspecific comparative analyses of sexual dimorphism have been focused only on size to test whether there is a link between SSD and male combat (Shine 1979). Research has also been undertaken to test the validity of Rensch's Rule in the case of salamanders (De Lisle & Rowe 2013, Colleoni at al. 2014). This rule predicts an increase of SSD with size when SSD is positively biased towards males and to the reverse, a decrease of SSD when females are larger (Rensch 1950). Nevertheless, Rensch's Rule has been found to be not applicable to various taxonomic groups in-

cluding amphibians (De Lisle & Rowe 2013, Liao & Chen 2013). Salamanders exhibit a huge size disparity, ranging from giant fully aquatic species of cryptobranchids, amphiumids and sirenids to several miniaturized lineages of tropical lungless salamanders adapted to arboreal or terrestrial habitats (e.g., Raffaëlli 2013). Therefore, salamanders are potentially good models to evaluate the validity of Rensch's Rule given it is expected to find male-biased SSD in lineages of larger species and the opposite pattern in the extremely small-sized species.

The main goal of this study is to evaluate whether there may be a widespread female- or male-biased pattern of SSD in salamanders. Specifically, two issues are addressed: a) characterising the patterns of sexual size dimorphism in salamanders by measuring their interspecific variation; b) testing the applicability of Rensch's Rule to salamanders in the light of the size disparity existing in this group.

Materials and methods

Mean female and male sizes (snout–vent length, SVL) from salamander species were collected from literature with the exception of *Taricha torosa* of which SVLs were obtained by measuring individuals from a museum collection (Supplementary data S1). Some critics have argued against the use of mean size in studies of sexual dimorphism and suggested that maximum size should be used instead in the case of organisms with indeterminate growth (Stamps 1993). Nonetheless, in the case of the dataset used in this study these two measurements were found to be highly and positively correlated (Pearson correlation n = 318; males: R = 0.985, P < 0.001, females: R = 0.986, P < 0.001). To optimise SSD estimation when several studies were available for the same species, the one using the largest sample size was selected. While in some cases mean values were available straightaway, these had to be calculated from individual data in other publications. In total, our dataset included SVL data from 356 species belonging to all families of salamanders. In order to assess the statistical significance of SSD, a t-test was performed when sample sizes and standard deviations were available from literature (Supplementary data S1). A total of 200 species were analysed thus, although in 25% of the cases, sample sizes for at least one of the sexes were low, less than five specimens.

An SSD index was calculated based on Lovich & Gibbons (1992), where SSDI is (Mean SVL of larger sex / Mean SVL of smaller sex) -1, supposing that positive SSDI values indicate females to be the larger sex and negative ones that males are larger. This index is widely used in studies of sexual dimorphism and is intuitively and easily interpretable.

To check the phylogenetic signal on the SSDI and perform phylogenetic comparative analyses, a time-calibrated phylogenetic tree was used. Information about the phylogenetic relationships among the species of our dataset was compiled from bibliographic sources. Thus, the phylogenetic tree was not estimated, but built based on the combined information from several available phylogenies

Table 1. Results for test of phylogenetic signal performed on male and female SVL and the Lovich & Gibbons index of sexual size dimorphism.

	λ	P	K	P
Male SVL	0.975	<0.0001	0.696	0.001
Female SVL	0.972	<0.0001	0.598	0.001
SSD Index	0.331	<0.0001	0.096	0.007

(mainly from Pyron & Wiens 2011: Supplementary data S2). Branch lengths were estimated using mitochondrial cytochrome b, 16sRNA and ND2, and nuclear RAG1 genes from Genbank (Supplementary data S2) by means of maximum likelihood estimations performed upon the HKY 86 model using this phylogeny and was dated by means of a molecular clock based on four palaeontological reference points (Supplementary data S2) using the RelTime method. All our analyses were performed using Mega 7 (Kumar et al. 2016).

The phylogenetic signal on SSD was first assessed by means of Pagel's λ and Blomberg's K measures using Picante R software (Kembel et al. 2010). Lambda values can oscillate between zero (lack of correlation between species) to one, indicating a strong correlation of a trait between species through the phylogenetic tree upon a Brownian model of evolution. K is a ratio of the variance between species over the variance of phylogenetically independent contrast and has an expected value of one under a perfect Brownian motion. The significance of K is assessed by randomly placing the species data at the tips.

Rensch's Rule was tested by performing a regression of male SVL against female SVL, after log-10 transformations of these variables. Thus, departures from isometry (slope equal to one) should be interpreted as congruent with the Rensch's Rule when the slope is greater than one. Given that it is likely that SVLs do not have different errors between sexes, a standardised major axis (SMA) was preferred over an ordinary least-squared regression. SMA regression on species data was performed using R smatr (Warton et al. 2012), considering that a lower limit of the 95% confidence intervals > 1 is consistent with Rensch's Rule.

Analysis was performed on the species data and phylogenetically independent contrasts obtained from the phylogenetic tree using PDAP 1.1 incorporated in Mesquite 2.2 (Maddison & Maddison 2018) using whole species data and separately for each of the most speciose salamander families (Plethodontidae, Salamandridae and Hynobiidae).

Results

Most salamanders were found to be small-sized, with females having larger SVLs (mean ± SD: 62.5 mm ± 44.9) than males (59.7 mm ± 48.6). However, the existence of a few giant species resulted in a large disparity of sizes within the group: females (17.2 – 545.0 mm); males (16.0–555.0 mm). Thus, SSD biased towards females (66.9% of species) was

Table 2. Standard reduced major axis relationships between male and female SVL for the 346 species analysed and main salamander families, using raw species data and PICs.

	Slope	CI	Intercept	CI	R^2	P
Species data	1.018	0.994–1.042	-0.056	-0.098– -0.014	0.948	<0.0001
PIC	0.998	0.996–1.034			0.893	<0.0001
Plethodontidae	0.977	0.939–1.017	0.008	-0.056–0.939	0.917	<0.0001
PIC	0.999	0.966–1.034			0.893	<0.0001
Hynobiidae	1.017	0920–1.125	-0.041	-0.231–0.148	0.894	<0.0001
PIC	1.059	0.976–1.149			0.929	<0.0001
Salamandridae	1.012	0.945–1.085	-0.049	-0.178–0.079	0.897	<0.0001
PIC	1.029	0.953–1.111			0.857	<0.0001

the most common pattern among salamanders, although apparently perceptual increases of size in relation to the smaller sex was not large (mean ± SD: 9.2% ± 9.5). T-tests for male vs female differences in SVL were performed on 56.1% of the species of our dataset, exhibiting significant differences in 55.5% of the analyses. Smaller sample sizes had a strong influence on the statistical power of the tests, as was revealed by an ANOVA test of the pooled sample size per sex ($F_{1\ 200}$ = 11.588; P < 0.01; mean sample size of significant test = 105.3; non-significant = 30.5). Therefore, it is likely that smaller sample sizes have precluded the detection of significant sexual differences in most species. When a test showed a significant result, 82.5% of these detected that females were the larger sex, indicating the existence of a widespread pattern of female-biased sexual size dimorphism in salamanders. The mean SSD index was 0.061 ± 0.119, ranging from -0.390 to 0.751 (Fig. 1), thus reinforcing the idea of a general pattern of sexual dimorphism characterised by females being larger than males.

Male and female SVLs exhibited a strong and significant phylogenetic signal on all the traits based on λ and K values, but were weak for the SSD index in the second parameter (Table 1). All SMA regressions showed significant and positive slopes close to one (Table 2) with the high variability being explained by the models. Minimum val-
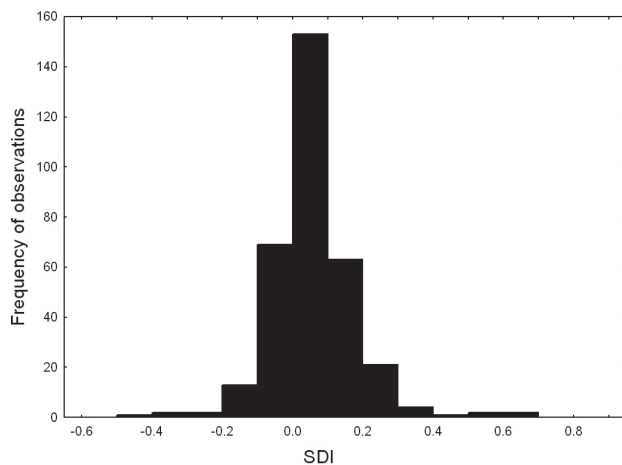

Figure 1. Distribution of the SSD index of 356 species of salamanders analysed herein.

ues for the 95% confidence intervals of slopes were lower than this value (Fig. 2). Nevertheless, SMA regressions using PICs obtained from the same dataset were bounded by minimum values lower than one (Fig. 3). Indeed, analyses produced an isometric pattern of relationships between male and female SVLs, indicating that salamanders do not adhere to Rensch's Rule.

Discussion

The scope of this study, including 356 species, renders the most extensive taxonomically representative analysis of SSD in salamanders to date. As expected in ectothermic organisms such salamanders, female-biased SSD is clearly the most common and taxonomically widespread pattern, as has also been found in previous studies (e.g., De Lisle & Rowe 2013). However, our results indicate that size differences between males and females are small in most species. This might be the result of a strong co-evolution between male and female SVLs, congruent with the high percentage of the explained variance in allometric relationships found by this study. This parallel evolution of SVLs between the sexes could be influenced by mechanistic constraints or a weakness of selective forces promoting SSD. Many species of salamanders have developed complex courtship rituals involving physical interactions between sexes, for example in salamandrids or plethodontids (e.g., Arntzen & Spar-reboom 1989, Verrell & Mabry 2000). Large differences in SVL between males and females could compromise the efficiency of these elaborate behaviours. Nonetheless, species with little behavioural interaction between sexes during reproduction, as for example those employing external fertilisation, likely show the same tight co-evolution of size. On the other hand, given that genes affecting size are presumably the same in males and females (Poissant et al. 2010), this shared genetic mechanism probably promotes small divergence of this trait between sexes. However, attenuation of adaptive forces that influence each sex differently might also drive the development of small sexual divergence of size.

SSD in salamanders is a result of the sexes maturing at different ages rather than different growth rates during the immature phase of life after metamorphosis (Zhang & Lu 2013). Thus, female-biased SSD may be the result of delayed

sexual maturation in this sex, thus making provision for a longer period of immature growth. It is likely that the most straightforward explanation of this evolutionary adaptive pattern is that female fecundity will increase with size, as has been found in interspecific studies (e.g., Salthe 1969). The availability of more space in the body cavity of a female for holding more eggs or greater fat reserves that can be invested into reproduction might be the main causes driving the development of a larger size in this sex. Although it is possible that males may also become more fertile by increased testis size, few studies have indicated a positive correlation between this and size (Stanton 2013). Despite the evidence of fecundity selection as a promoter of female SSD, intraspecific studies have revealed that major variation in fecundity is apparently not related to SVL (Tilley 1977, Bruce 1996, Bruce 1997). This suggests that in reality female fecundity could be primarily constrained by the quantity of energy expended on reproduction and that size imposes a theoretical limit that will hardly be achieved under natural conditions. If this is true, it could lead to a relaxed fecundity selection, reducing the scope of female-biased SSD in salamanders.

Our study indicates that male-biased SSD is an infrequent phenomenon in salamanders and scattered throughout the phylogeny of this group (Pyron & Wiens 2011). Therefore, it is likely that female-biased SSD has evolved several times independently from various ancestral species. Amphibians display a vast variety of strategies devoted to achieving optimal reproductive success, including, for example, the maintenance of territories, scramble competition in mating aggregations, clutch attendance and aggressive displays and fights between males, among others (Nussbaum 1985). In some species of frogs, the allocation of resources to behavioural interactions between males can

lead to male-biased SSD, because larger individuals will be more successful, as some studies indicate (e.g., Liao & Xu 2011, Reichert & Gerhardt 2011, Rausch et al. 2014).

Few studies have been undertaken to examine whether salamanders follow the same pattern. Shine (1979) found a significant correlation between male combat and SSD biased towards this sex, but the behavioural data used in this study was not accurate enough and analyses were performed without using phylogenetic methods (Halliday & Verrell 1986). Current knowledge of antagonistic behaviour between males competing for mating partners or clutch fertilisation is incomplete for most species of salamanders and in most cases limited to anecdotal observations. For example, results showed male-biased SSD in many Desmognathinae salamanders, a lineage in which aggressive interactions between males are common (Houck 1988, Bruce 1993). Fierce defence of oviposition territories by males has been reported in cryptobranchid salamanders (Hillis & Bellis 1971), and this study suggested that males were larger than females in the Japanese species *Andrias japonicus*, but the opposite pattern was true for the North American salamander *Cryptobranchus alleganiensis*. On the other hand, the development of male ornamentation in newt males and complex courtship behaviours (Salthe 1967, Houck & Arnold 2003; Wiens et al. 2011) have independently appeared several times in salamandrids, but are not clearly associated with the development of unidirectional SSD. Tyrrhenian newts of the genus *Euproctus* have a SSD biased towards males, enabling them to immobilise their females with a holding bite
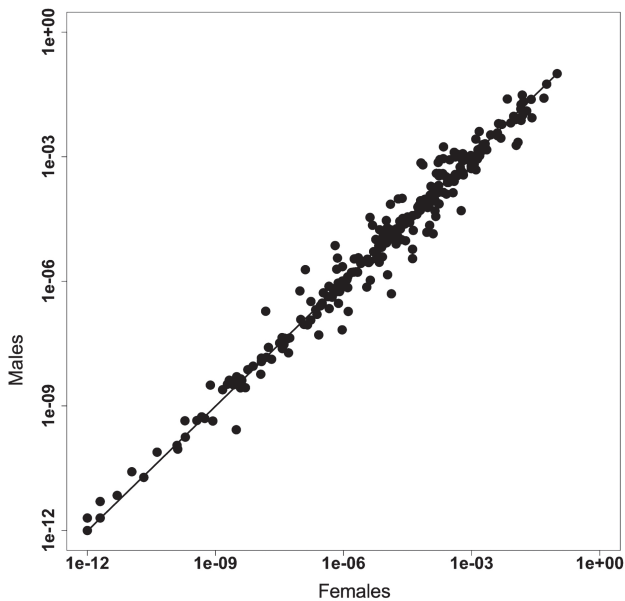

Figure 2. SMA regression of male and female SVLs using the whole dataset of 356 salamander species.
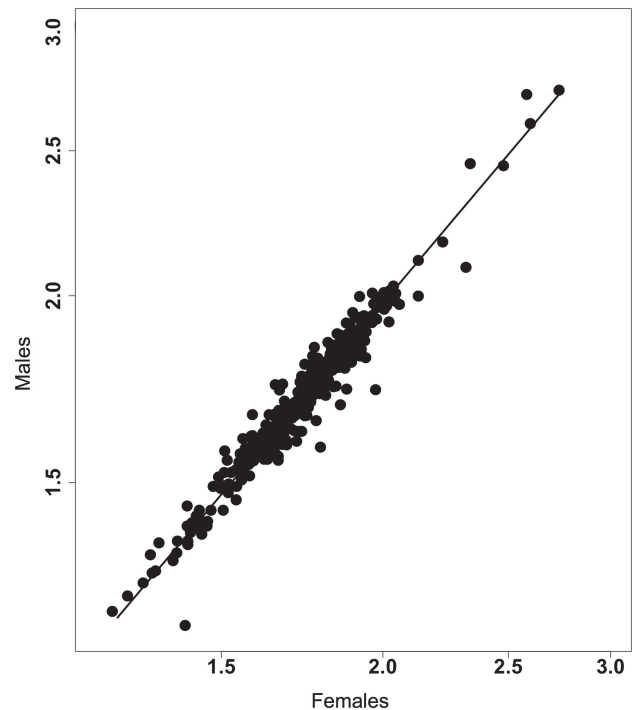

Figure 3. SMA regression of male and female SVLs using PICs from whole dataset of 356 salamander species.

during courtship (e.g., Thiesmeier & Hornberg 1990). In contrast, males of Iberian *Calotriton* newts will bite other males during aggressive interactions, which could be related to the defence of mating sites (Parzefall et al. 2000), and females are larger than males. Thus, the association between mating system or male contest and the development of male-biased SSD in salamanders does not offer a straightforward explanation.

Rensch's Rule predicts hyperallometry when males are the larger sex, but hypoallometry in the opposite situation (Fairbairn 2005). The first scenario holds true for male-biased SSD taxa, while Rensch's Rule does not apply when SSD favours larger females (Abouheif & Fairbairn 1997). In the case of salamanders and in accordance with a previous analysis (De Lisle & Rowe 2013), the allometric pattern found is inconsistent with Rensch's Rule and rather supports the converse situation. The only evidence of validity of Rensch's Rule in salamanders was provided by a study focused on salamandrids (Colleoni et al. 2014) and only when species with male-biased SSD were analysed separately. Herein the isometric relationship between male and female SVLs remained unchanged when analysing the most speciose families of salamanders by using standard and comparative methods, indicating the strength of the results. Rensch's Rule might be an oversimplification of the expected patterns of sexual dimorphism, only describing lineages in which sexual selection is extremely strongly expressed. For example, mammals exhibit social behaviours and mating strategies that are more complex and richer than in other vertebrates, combining intense male competition for mates with female fecundity weakly shaped by size (Lindenfors et al. 2007). In the case of salamanders, the diversity of competitive behaviours among males appears in many cases decoupled from size differences from females. It suggests the selection for fecundity in females to be the main selective pressure driving SSD in salamanders, leaving open the possibility of allometric size relationships between sexes. Thus, the inconsistency of Rensch's Rule in a lineage dominated by species that develop female-biased SSD might be evidence of a relaxed selection for female fecundity in salamanders.

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Supplementary data

Supplementary data S1. Species data used in this study and references list.

Supplementary data S2. Accession numbers of the DNA sequences, bibliographic references, points of reference used to build the time-calibrated tree and phylogenetic tree depicting phylogenetic relationships among the salamander species analysed.

Supplementary Figure S1. Phylogenetic tree depicting phylogenetic relationships among the salamander species analysed.