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Correlated Evolution of Allometry and Sexual Dimorphism across Higher Taxa

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abstract: Empirical evidence suggests that Rensch's rule of allometric scaling of male and female body size, which states that body size divergence is greater across males than across females of a clade, is not universal. In fact, quantitative genetic theory indicates that the sex under historically stronger directional selection will exhibit greater interspecific variance in size. Thus, the pattern of covariance between allometry of male and female body size and sexual size dimorphism (SSD) across related clades allows a test of this causal hypothesis for macroevolutionary trends in SSD. We compiled a data set of published body size estimates from the amphibians, a class with predominantly female-biased SSD, to examine variation in allometry and SSD among clades. Our results indicate that females become the more size-variant sex across species in a family as the magnitude of SSD in that family increases. This rejects Rensch's rule and implicates selection on females as a driver of both amphibian allometry and SSD. Further, when we combine our data into a single analysis of allometry for the class, we find a significant nonlinear allometric relationship between female body size and male body size. These data suggest that allometry changes significantly as a function of size. Our results illustrate that the relationship between female size and male size varies with both the degree of sexual dimorphism and the body size of a clade.

Keywords: amphibian, evolutionary allometry, phenotypic variation, macroevolution, phylogenetic comparative methods, Rensch's rule, sex-specific selection, sexual size dimorphism.

Introduction

Dimorphism between the sexes in form and function is ubiquitous in nature, and its extent varies widely, even within closely related groups. In many cases, males are the more variable sex, exhibiting greater phenotypic divergence than females across related taxa (Darwin 1871). Body size is a trait that has received a great deal of attention in this regard. Rensch (1950, 1960) was the first to observe a common pattern of interspecific covariance between body size and sexual size dimorphism (SSD), noting that SSD increases with increasing average body size in clades where males are the larger sex and decreases where females are the larger sex. Fairbairn and Preziosi (1994) pointed out that Rensch's two observations represent a common pattern of greater evolutionary divergence in male than in female size, resulting in a slope of less than 1 in a regression of log female size on log male size ("Rensch's rule," hereafter "male-divergent allometry"; fig. 1*A*). This pattern represents a special type of interspecific allometry (Gould 1966) that is of interest because it indicates that one general mechanism may account for the evolution of both body size and sexual dimorphism (Fairbairn and Preziosi 1994; Fairbairn 1997).

In their analysis of mostly birds, mammals, and reptiles, Abouheif and Fairbairn (1997) found strong support for Rensch's rule. Since then, a burst of analyses have suggested that male-divergent allometry may be commonplace (e.g., Colwell 2000; Székely et al. 2004; Cox et al. 2007; Stephens and Wiens 2009), even in dioecious plants (Kavanagh et al. 2011). However, a growing number of examples highlight taxa exhibiting no general pattern of allometry or, in some cases, an opposite pattern of female-divergent allometry (fig. 1*B*; i.e., a situation opposite of Rensch's rule, where females are the more variant sex; Blanckenhorn et al. 2007; Webb and Freckleton 2007; Herczeg et al. 2010; Ceballos et al. 2013; Halamkova et al. 2013; Liao et al. 2013). Thus, both whether male-divergent allometry is general and why patterns of allometry vary across taxa are unclear. In fact, there is no theoretical expectation for Rensch's rule to be general, a somewhat underappreciated point that we elaborate below. In addition, an overrepresentation of amniote vertebrates, the clade with the highest proportion of male-biased SSD (Fairbairn 1997), in studies of allometry of male and female size makes assessment of the generality of patterns of allometry difficult.

Although many models explain male-divergent allometry in specific taxa (e.g., Sibly et al. 2012), the quantitative

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genetic models of Zeng (1988) provide a general explanation for the evolution of allometry that can account for both male- and female-divergent allometry. Zeng's models indicate that shifts in directional selection (during species divergence) on body size in one sex and correlated shifts in selection on body size in the other sex can lead to the evolution of interspecific allometry. Correlation between selection on male body size and selection on female body size may arise, for example, through shared ecology or the mechanics of reproduction. Key features of this model are its prediction that the sex under more intense direct selection will be the more phenotypically divergent and that the response in the second sex will be weaker, depending on correlational selection and only transiently on the intersexual genetic correlation. Thus, the model predicts male-divergent allometry in cases where there is stronger direct selection on male size and female-divergent allometry where there is stronger direct selection on female size (Fairbairn 1997). If selection on male size and female size has been of equal importance in the history of a lineage, then the clade would exhibit isometry (fig. 1). Selection does not have to act in the same direction through time for allometry to evolve (see Ceballos et al. 2013 for an illustration).

Because sexual size dimorphism and the allometry in a clade both represent a history characterized by different intensities of selection on male and female body size in Zeng's model, the strength of the allometric relationship may be expected to covary in a predictable manner with the average value of SSD among related clades (fig. 1*A*, 1*B*). The sign of this expected covariance between SSD and allometry across related clades allows inference into the causality of SSD in a taxon (fig. 1*C*). For example,

Figure 1: *A*, *B*, Interspecific allometry of male and female body size. The slope of a model II regression of log female size on log male size (species as data points) quantifies how male and female body sizes scale across related species. Hypothetical dashed regression lines in *A* and *B* represent allometry of different related lineages (labeled a–c and d–f). The solid line indicates isometry (slope = 1) and a lack of sexual size dimorphism (SSD). *A*, If selection on male size has been more intense than selection on female size, slopes would be generally <1 (male divergent [Rensch's rule]: males have higher body size variance) and covary negatively with sexual dimorphism across clades. *B*, If selection on female size as been more intense than selection on males through evolutionary time, allometric slopes would be generally >1 (female divergent: females have higher body size variance) and would covary positively with sexual dimorphism across related clades. In *C*, the patterns illustrated in *A* and *B* are plotted as the relationship between allometry and SSD across clades. If Rensch's rule is general and selection on males is a main driver of the evolution of SSD, as in *A*, then the allometric slope decreases across related clades as the magnitude of SSD increases (dashed line). Alternatively, if the evolution of SSD is driven primarily by selection on female size, as in *B*, allometry will become female divergent (the allometric slope will increase) as the magnitude of SSD increases (solid line) across related clades. Although sexual dimorphism in *A* and *B* is illustrated as female biased, a key point is that these predictions hold regardless of the direction of sexual dimorphism (i.e., male or female biased).

female-biased SSD may evolve primarily through negative directional selection on male body size or positive directional selection on female body size. In the first case, we would expect a negative association between allometric slopes and SSD among related clades, because direct selection on males is driving both; selection on males that effects a decrease in SSD will also effect an increase in the allometric slope. In the second case, we would expect a positive association between allometric slopes and SSD, because direct selection on females is driving both; selection on females that effects an increase in SSD will also result in an increase in the allometric slope (fig. 1). Thus, although allometry may shed light on patterns of sex-specific selection within a single clade, the covariance between allometry and sexual dimorphism across related clades allows broader tests of the hypothesis of sex-specific selection in generating macroevolutionary patterns in both allometry and SSD.

Most empirical assessments of allometry have focused on amniote vertebrates or invertebrates with male-biased SSD (Webster 1992; Abouheif and Fairbairn 1997; Székely et al. 2004; Cox et al. 2007; Webb and Freckleton 2007; Serrano-Meneses et al. 2008; Stephens and Wiens 2009). The results of these studies indicate that the allometric slope within clades often decreases as the magnitude of SSD increases (see, e.g., fig. 2*A* in Fairbairn 1997), supporting the hypothesis that selection on male size is a common cause for the evolution of both allometry and male-biased SSD. The few comprehensive analyses of allometry of male and female size in major clades that exhibit predominantly female-biased SSD indicate less clear patterns of allometry (e.g., in turtles: Ceballos et al. 2013; Halamkova et al. 2013; and frogs: Han and Fu 2013). If Rensch's rule is general, as has been suggested (Abouheif and Fairbairn 1997), the implication is that selection on males is the primary cause of both male-biased and female-biased SSD. Some examples do exist of female-biased SSD driven predominantly by selection on males (Zamudio 1998; Stuart-Fox 2009). Yet natural history suggests that this may not be the case in many clades where females are larger than males and under apparently intense directional (e.g., fecundity) selection, for example, in many anamniotes (Darwin 1871; Williams 1966; Crump 1974; Kaplan and Salthe 1979; Andersson 1994). Further, negative directional selection on body size is rare in the wild (Kingsolver and Pfennig 2004), indicating that negative directional selection on male size may not be a general explanation for the evolution of female-biased SSD. This suggests the intuitively appealing hypothesis that the evolution of female-biased SSD is often driven, at least in part, by strong positive selection on female size. This hypothesis predicts a reversal of Rensch's rule in clades with female-biased SSD (fig. 1*B*, 1*C*).

We compiled a data set of published body size estimates from the amphibians, a diverse vertebrate class exhibiting predominantly female-biased SSD (Shine 1979; Kupfer 2007). Past work in anurans indicates that both male-divergent allometry and female-divergent allometry are present in six families (Han and Fu 2013) and that overall allometry of the order may be either weakly female divergent (Liao et al. 2013) or weakly male divergent (Han and Fu 2013). Our aim was to use patterns of variation in allometry across clades to test two alternative hypotheses for the macroevolutionary trend of female-biased SSD (fig. 1*C*). We also estimate allometry for amphibians as a group, compare this to our analysis at lower taxonomic levels, and discuss future directions in the study of the allometry of male and female body size.

Material and Methods

Data Collection

We compiled sex-specific body size estimates (mean snout-vent length) for amphibian species haphazardly from the published literature; the wide variety of studies that may include summary statistics for body size measurements limits the utility of a systematic literature search, as in formal meta-analysis. For the caecilians (Gymnophiona), we used total length as a body size estimate, as snout-vent lengths are rarely reported for this group. We included only estimates that were calculated from more than one individual from each sex and included only studies that reported estimates from both sexes of a species. Our analytical approach follows figure 1. First, we calculated the allometric slope across species in a clade (as in fig. 1*A*, 1*B*). Next, we used these estimates to examine the correlation between the allometric slope and SSD across clades (fig. 1*C*).

Our initial search yielded estimates from 1,139 species. The full data set is archived on the Dryad Digital Repository (http://dx.doi.org/10.5061/dryad.24251; De Lisle and Rowe 2013). Most of the species in our data set could be assigned to a family whose phylogenetic placement was known with high confidence (Pyron and Wiens 2011); phylogenetic information at lower taxonomic levels was not available for many of the species in our data set (i.e., within-family relationships were often unknown). After dropping species from families with uncertain phylogenetic placement and those from families with fewer than 8 representative species, our final data set consisted of 1,083 species from 32 families or subfamilies across the three orders in the class (table 1). We chose $N = 8$ as our cutoff because this allowed us to use most of our data set. We retained the identification of some monophyletic sub-

Table 1: Summary statistics of amphibian allometry

					b_1			b_{1p}			
Order, family, subfamily	*n*	SSD	SSD%	*r*	Slope	SE	95% CI	Slope	SE	95% CI	*n*
Anura:											
Arthroleptidae	11	.12	82	.94	1.17	.13	.87–1.46				
Brachycephalidae	13	.20	100	.99	1.08	.04	.99–1.17				
Bufonidae	64	.19	92	.96	1.00	.04	.93–1.07	1.01	.06	.89–1.13	41
Centrolenidae	9	.10	89	.87	.97	.18	.54–1.41				
Craugastoridae	133	.39	100	.93	**1.14**	.04	1.06–1.21	1.12	.07	.98–1.25	72
Dendrobatidae:											
Aromobatinae	9	.06	100	.99	1.10	.05	.97–1.22				
Colostethinae	10	.12	100	1.00	1.05	.02	1.00–1.10				
Dendrobatinae	23	.06	83	.99	1.04	.03	.98–1.10	1.01	.03	.95–1.08	18
Hyloxalinae	10	.15	90	.95	**1.41**	.16	1.04–1.78	**1.38**	.08	1.18–1.58	9
Dicroglossidae	58	.06	67	.95	**.89**	.04	.82–.97	.91	.05	.81–1.01	41
Eleutherodacylidae	39	.29	97	.94	**1.20**	.07	1.07–1.33	1.14	.09	.96–1.31	32
Hemiphractidae	19	.18	84	.61	1.25	.24	.74–1.76	1.14	.20	.70–1.58	15
Hylidae:											
Hylinae	128	.16	91	.96	.97	.02	.92–1.01	.95	.04	.87–1.03	90
Phyllomedusinae	12	.24	100	.94	.96	.1	.72–1.19	.99	.18	.58–1.41	10
Hyperoliidae	8	.12	100	.98	1.09	.09	.88–1.31				
Leptodactylidae:											
Leiuperinae	9	.12	100	.95	1.10	.13	.79–1.41				
Leptodactylinae	34	.07	82	.99	.96	.03	.90–1.02	.98	.06	.85–1.11	17
Megophryidae	37	.21	81	.78	.92	.10	.72–1.11	.81	.11	.57–1.05	18
Microhylidae	32	.16	91	.97	.93	.04	.84–1.02	.96	.09	.77–1.15	12
Myobatrachidae	12	.04	75	.97	.88	.07	.72–1.03				
Petropedetidae	9	.04	56	.98	.91	.06	.77–1.05				
Phrynobatrachidae	13	.14	77	.96	**.85**	.07	.70–.99				
Ranidae	97	.32	97	.78	1.00	.06	.88–1.13	.95	.05	.85–1.04	77
Rhacophoridae	43	.27	100	.98	**1.12**	.04	1.04–1.19	1.03	.09	.85–1.21	20
Telmatobiidae	10	.05	70	.95	1.20	.13	.90–1.51				
Caudata:											
Ambystomatidae	13	.07	100	.99	1.03	.04	.93–1.13	1.05	.04	.95–1.15	10
Hynobiidae	15	.02	60	.92	.97	.10	.75–1.19	.80	.11	.56–1.04	13
Plethodontidae:											
Bolitoglossinae	115	.11	89	.96	**1.12**	.03	1.06–1.18	1.01	.05	.92–1.11	65
Plethodontinae	44	.03	59	.97	1.08	.04	.99–1.16	1.06	.04	.99–1.14	44
Spelerpinae	9	.03	67	.96	.87	.09	.65–1.09	.98	.11	.74–1.23	10
Salamandridae	36	.04	75	.96	.92	.05	.83–1.02	.94	.05	.83–1.05	28
Gymnophiona:											
Caeciliidae	9	.12	67	.95	**1.48**	.18	1.05–1.91				
Total or mean	1,083	.13	85	.94	1.05			1.01			642

Note: SSD = sexual size dimorphism; SSD% = % of species with female-biased SSD; CI = confidence interval; b_1 = reduced major axis (RMA) slope (log female on log male size); b_{1p} = phylogenetic RMA slope. Boldface indicates slopes significantly different from 1 ($\alpha = 0.05$).

families dropped by Pyron and Wiens (i.e., those in family Dendrobatidae) because our sample size allowed us to estimate allometric slopes separately for them. We used the Lovich and Gibbons estimator to characterize SSD (size of larger sex/size of smaller sex − 1, arbitrarily set negative for male-larger species; Lovich and Gibbons 1992) and used mean values for families. We chose family and subfamily (when we had suitable sample sizes for multiple subfamilies in a family) as our lowest taxonomic level of analysis because this level generally identifies major divergence in ecology, life history, and mating system (Wells 2007). In addition, phylogenetic information suggests that many amphibian genera are not monophyletic (e.g., *Rana*; Pyron and Wiens 2011), making it difficult to identify monophyletic groups below the family or subfamily level in the absence of a phylogeny with 100% coverage.

Allometry

Empirical assessments of allometry typically use model II regression of the logarithm of female size on log male size (H_0: $b_1 = 1$; fig. 1*A*; Fairbairn 1997; Blanckenhorn et al. 2007). We calculated the allometric slope as the reduced major axis regression of $\log_{10}$(female size) on $\log_{10}$(male size) for families and subfamilies. For comparative purposes, we present standard errors from ordinary least squares regressions to approximate standard errors for our allometric slopes (Sokal and Rohlf 1995), as well as Pearson correlation coefficients for log male size and log female size. We also performed phylogenetic reduced major axis regressions (Revell 2012) to estimate phylogenetically informed allometric slopes for the 20 clades that had suitable species-level phylogenetic information (table 1). We indicate statistically significant departures from isometry in table 1, although we note that power for any one test is often low.

Many past studies of allometry of male and female size have estimated allometric regressions across large species groups composed of many aggregate clades. In order to compare our family-level analyses to a pooled estimate of allometry for all amphibians, we performed a single phylogenetic reduced major axis regression of log female size on log male size across the 731 species of frogs and salamanders in our initial data set for which species-level phylogenetic information was available. We excluded the caecilians because the measurement of body size was not entirely comparable to that used for frogs and salamanders. We first fitted alternative models of body size evolution and proceeded with a "speciational" model (equal branch lengths), because this model fitted the data better than alternatives (see appendix). Inspection of residuals from the phylogenetic reduced major axis (RMA) regression suggested a quadratic deviation from linearity. To explore this, we proceeded to fit a phylogenetic generalized least squares (PGLS) linear model with a quadratic term to assess the strength and form of nonlinearity. This least squares model assumes no error in the independent variable, which will lead to systematic underestimation of the functional relationship between female size and male size; however, fitting a polynomial model by minimizing orthogonal distances while incorporating a known covariance matrix (e.g., a phylogeny) is a statistically nontrivial task.

Correlated Evolution across Clades

We used PGLS to estimate correlated evolution of allometric slope and SSD across clades while accounting for common ancestry of related families (Felsenstein 1985; Martins and Hansen 1997; Rohlf 2001). We set branch lengths equal when calculating the phylogenetic correlation matrix because this model of evolution was a better fit to the data than alternatives. We log-transformed our estimates of allometric slope and SSD before performing PGLS to better meet assumptions of regression/correlation, and we applied the correction for small sample size to our estimate of the correlation coefficient (Sokal and Rohlf 1995; Rohlf 2006). We repeated this same analysis for both our full data set of 32 clades and our reduced data set of 20 clades.

All statistical analyses were performed either in R, using the "phytools" (Revell 2012) and APE (Paradis et al. 2004) packages, or in SAS/IML (for nonphylogenetic RMA regressions and for calculating PGLS correlation coefficients; ver. 9.3; SAS Institute, Cary, NC). SAS/IML code to calculate the PGLS correlation coefficient (see Rohlf 2001, 2006) is available from the first author upon request.

Results

Our data suggest that SSD in the amphibians as a group is generally female biased, consistent with past studies of sexual dimorphism in amphibians (Shine 1979; Kupfer 2007; Han and Fu 2013), and that allometry is variable (table 1). Although SSD varies widely among clades and includes species with male-biased SSD from families with mixed SSD, the average SSD for all families and subfamilies was greater than 0 (i.e., female biased). Pearson product-moment correlations between log female size and log male size were generally high but variable ($r = 0.61$–1.00; table 1). Allometric slope was also variable, ranging from weakly male divergent to strongly female divergent ($b_1 = 0.85$–1.48; table 1); however, the mean was slightly female divergent ($b_1 = 1.05$) across all 32 clades. The average slope of the 20 clades for which we calculated a phylogenetic allometric slope was $b_1 = 1.01$ (table 1). The phylogenetically informed slope estimates generally matched those that ignored phylogeny (Pearson correlation $r = 0.88$, $n = 20$).

Correlated Evolution of SSD and Allometry

Allometric slope transitions from male divergent or isometric to female divergent across families and subfamilies as SSD becomes more female biased (fig. 2*A*); this positive correlation is statistically significant (PGLS: $r = 0.37$, df = 30, $P = .035$). The same relationship is found when the phylogenetic RMA slope is treated as the dependent variable (fig. 2*B*; PGLS: $r = 0.49$, df = 18, $P = .027$).

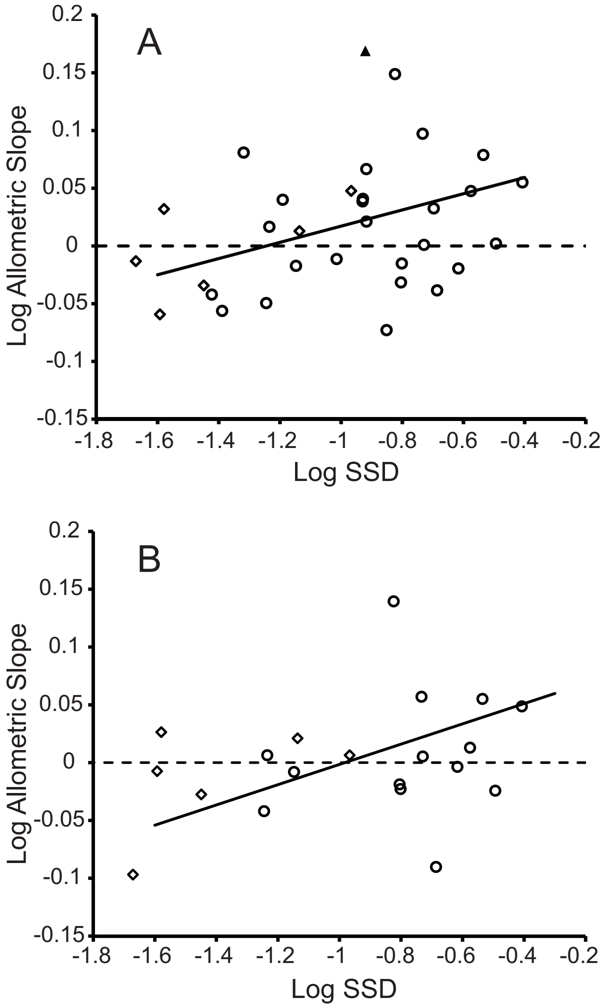

Figure 2: Relationship between log-transformed allometric slope (*A*, reduced major axis [RMA] regression of log female size on log male size; *B*, phylogenetic RMA of log female size on log male size) and sexual size dimorphism (SSD) across amphibian clades. Data points represent families and subfamilies: circles are for anurans, diamonds are for caudates, and the triangle is for caecilians. The dashed line represents isometry (slope = 1). The correlation between log slope and log SSD is positive and significantly different from 0 (phylogenetic generalized least squares: *A*, $r = 0.37$, $P = .035$; *B*, $r = 0.49$, $P = .027$).

Species-Level Analysis

For comparative purposes, we also examined allometry across all species of frogs and salamanders pooled into a single phylogenetic allometric regression. The linear phylogenetic reduced major axis regression indicated no significant departure from isometry (fig. 3; $b_1 = 0.98$, 95% confidence interval [CI] = 0.96–1.01, $P = .22$), consistent with a recent similar pooled analysis of frogs (Han and Fu 2013). Because of an observed relationship between residuals from this linear regression and species body size, we also proceeded to fit a quadratic model. The quadratic term in the PGLS regression of log female size on log male size was significant (PGLS: $b_2 = -0.096$, 95% CI = -0.17 to -0.03, $F_{1,728} = 7.31$, $P = .007$; $b_1 = 1.24$, 95% CI = 1.00–1.47; fig. 3). We obtained the same results (significant quadratic term) in a regression across species using our full data set (i.e., not accounting for phylogeny).

Discussion

Our data from 32 amphibian clades demonstrate that females become the more size-variant sex within clades as the magnitude of sexual dimorphism of that clade increases, breaking Rensch's rule (fig. 2). This correlation between allometric slope and SSD supports the hypothesis that selection on female body size has played a key role in generating variation in both allometry and sexual dimorphism across the class (fig. 1). On average, however, allometry of the class as whole was close to isometric and significantly nonlinear (table 1; fig. 3). Although past work has indicated that Rensch's rule may break down in some

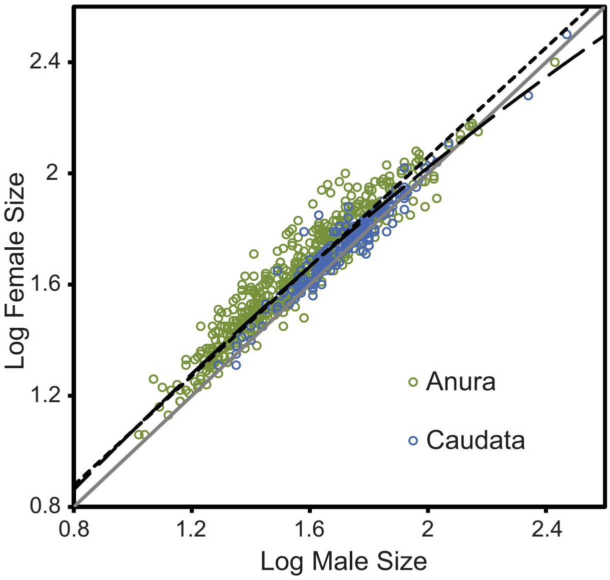

Figure 3: Allometry of sexual size dimorphism across 731 species of frogs (anurans) and salamanders (caudates) pooled in a single analysis. The short-dashed line represents the phylogenetic reduced major axis (RMA) regression; the long-dashed line represents the quadratic relationship fitted by phylogenetic generalized least squares (PGLS). The linear RMA relationship was not significantly different from isometry ($b_1 = 0.98$, 95% confidence interval [CI] = 0.96–1.01, $P = .22$). The quadratic term was significant in the PGLS model (PGLS: $b_2 = -0.096$, 95% CI = -0.17 to -0.03, $F_{1,728} = 7.31$, $P = .007$). The solid gray line represents isometry and a lack of sexual size dimorphism, as a reference.

taxa (Blanckenhorn et al. 2007; Webb and Freckleton 2007; Herczeg et al. 2010; Ceballos et al. 2013; Halamkova et al. 2013; Han and Fu 2013; Liao et al. 2013), our work illustrates that partitioning variation in allometry among closely related clades can be informative even if the net allometry of the group is close to isometric. An important implication of our results is that selection on female body size or correlated traits may be a prominent driver of both sexual dimorphism and body size diversity in amphibians. This is contrary to past suggestions that the diversity of SSD in amphibians is primarily driven by variation in the strength of sexual selection on males (Shine 1979; Woolbright 1983). Our results suggest that selection on males may play a critical role in body size evolution only in the clades that approach sexual monomorphism (fig. 2).

In amphibians, selection on female body size may often occur indirectly through selection on fecundity. The relationship between female body size and clutch size is strongly positive both within and among species in a number of amphibians (Crump 1974; Kaplan and Salthe 1979; Wells 2007). In addition, amphibians exhibit the greatest diversity of reproductive strategies among vertebrates (Wells 2007). This diversity of reproductive modes creates a degree of variation in female life history that may translate into variation in the strength of selection on female body size across clades. For males of many species of frogs and salamanders, reproduction entails physically grasping the female; thus, correlated selection on male size, in response to direct selection on female size, would be expected. The observed pattern of covariance between allometric slopes and SSD across amphibian clades is, in many ways, not surprising if one accepts that selection on female size may differ among clades.

The association between SSD and allometric slopes also rejects the unlikely null hypothesis of the evolution of interspecific allometry through random drift or randomly fluctuating selection. It is theoretically possible for interspecific allometry to evolve through drift in cases where there are differences in the additive genetic variance in male and female body sizes and a genetic correlation between them (Lande 1979). Theory (Rowe and Houle 1996) and data (Wyman 2013) suggest that sexual differences in additive genetic variance may be commonplace. In such a case, an allometric relationship between male size and female size could exist across species, but there is no reason to expect the direction of divergence (i.e., male- vs. female-divergent allometry) to associate with the direction of SSD (male vs. female biased) across clades. A drift hypothesis seems highly unlikely in the case of male and female body sizes, at least one of which is presumably under directional or stabilizing selection.

Many comparative studies of the allometry of male and female size have aimed to estimate a single allometric slope for large, often ecologically disparate aggregations of related clades. In our study, we performed such a regression, using 731 species of frogs and salamanders, and found a relationship between log female size and log male size that is significantly quadratic. By eye, this deviation from linearity appears trivial (fig. 3), yet examining the line tangent to this curve across a range of body sizes suggests that it may be biologically significant. At small body sizes, allometry is female divergent (i.e., at log male size $= 1$, $b_1 = 1.05$), while at larger body sizes, allometry is male divergent (i.e., at log male size $= 2$, $b_1 = 0.86$). We emphasize that this least squares estimate is an underestimate of the true functional relationship between male size and female size.

There is a danger in placing emphasis on power laws that are built on limited theoretical justification or empirical support (Stumpf and Porter 2012). Although the log-linear allometric equation may be grounded in first principles of biomechanics for many types of evolutionary, ontogenetic, and static allometry (Gould 1966), there is no a priori reason to expect a specific form of the functional relationship between male size and female size across species. Our data suggest that even slight deviations from linearity can be biologically meaningful, because they represent changes in the relationship between body size and SSD across the body size spectrum. It is likely that such deviations from linearity may be common in large analyses or in those of taxa that span a large range of body sizes, if the strength or form of selection on male or female size changes with body size. Although large-scale analyses of allometry typically incorporate phylogenetic information, this does not circumvent the issue. In fact, phylogenetic independent contrasts (Felsenstein 1985), a popular way to analyze such data, mask nonlinear evolutionary relationships between traits (Quader et al. 2004).

Females of small-bodied species of frogs and salamanders have proportionally larger clutch volumes than females of larger-bodied species, regardless of reproductive mode (Crump 1974; Kaplan and Salthe 1979; Wells 2007). If relative lifetime reproductive effort is roughly equal across taxa (Charnov et al. 2007), then selection on female size at maturity may necessarily be stronger in these small-bodied groups than in larger-bodied clades because of body size–clutch volume allometry (but see Shine 1988). In addition, Shine (1979) found, in his survey of amphibian SSD, that male combat was most prevalent in large-bodied taxa. He speculated that large body size may release species from some predation pressure and thereby reduce the mortality costs associated with combat, although neither our data nor Shine's can exclude the equally likely alternative that sexual selection itself is the cause of large body size in these combative groups. Both of these ideas relating body size to unique patterns of selection on male and female size have been cited in the past as a potential explanation of Rensch's rule (Clutton-Brock 1985; Andersson 1994; Fairbairn 1997). Our results indicate that such size-specific patterns of selection, regardless of their causality, may interact to produce complex allometric relationships between male size and female size.

Many studies of allometry have focused on uncovering the mechanisms responsible for generating male-divergent allometry in taxa with male-biased SSD or female-divergent allometry in taxa with female-biased SSD (Clutton-Brock et al. 1977; Webster 1992; Székely et al. 2004; Dale et al. 2007; Sibly et al. 2012). These studies have proven useful for furthering our understanding of how allometry evolves and for confirming predictions from theory. Future studies that determine how allometry opposite of these patterns (e.g., male-divergent allometry in taxa with female-biased SSD) can evolve may be enlightening. For example, if a history of negative directional selection on body size in one sex can produce allometry such that the smaller sex is more variant in size than the larger sex (Zeng 1988; Fairbairn 1997; see, e.g., Zamudio 1998), then taxa exhibiting such allometry may be a good starting point for empirical assessments of the prevalence of negative directional selection on body size. Such allometry could also be caused by a shift in selection regime (i.e., a transition in a lineage to direct selection on one sex after a history of strong direct selection on the other sex; Fairbairn 1990; Fairbairn and Preziosi 1994); the conditions that would promote such a shift in selection regime are unclear. Assessing the trajectory of correlated evolution of allometry and SSD in a group (figs. 1*B*, 2) is a necessary first step in identifying such biological outliers.

Finally, if allometry of male and female size is a signature of direct selection on one sex and a correlated response in the other, allometry may be of interest in understanding the role of sex-specific selection in ecological diversification (e.g., Bonduriansky 2011). Theory indicates that sex-specific selection may facilitate ecological divergence by promoting a correlated peak shift in the sex under indirect selection (Lande and Kirkpatrick 1988; Price et al. 1993). Given that body size is so closely related to ecological niche, extreme allometries may be associated with particularly high speciation rates if strong direct selection on body size in one sex facilitates correlated ecological divergence in the other sex.

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APPENDIX

Models of Evolution

We based relationships among species and families on the phylogeny of Pyron and Wiens (2011). In order to find the best-fit model of body size evolution for use in our comparative analyses, we first had to transform the molecular divergence branch lengths of Pyron and Wiens's tree to units of time. Where available, we used the crown age estimates from Pyron (2011). These divergence-time estimates are from a Bayesian analysis combining fossil and molecular data. After imposing these crown age constraints, we used penalized likelihood (Sanderson 2002) to estimate divergence times for the rest of the nodes in the tree, using APE in R (Paradis et al. 2004). We chose the value of the smoothing parameter that minimized the cross-validation criterion (Sanderson 2002; Paradis 2012).

We then pruned the tree to coincide with our data and proceeded to fit evolutionary models of species log average (male and female) body size, using the GEIGER package in R (Harmon et al. 2008). Candidate evolutionary models are listed in table A1, ranked by Akaike Information Criterion. We fitted a speciational model (branch lengths raised to the power of 0) after first estimating a "kappa" model in which the maximum likelihood estimate of kappa was clearly approaching 0. This speciational model fitted the data best, and we treated branch lengths as equal for all comparative analyses. We note that adding biological interpretation to these models of body size evolution is tenuous because of the incompleteness of our data and the phylogeny (many speciation events are not represented).

Table A1: Comparison of models of body size evolution in amphibians

Model	Unique parameter (estimate)	Log likelihood	AIC	ΔAIC	K
Speciational[a]		375.85	−747.69	0	2
Kappa[b]	κ (2.32×10^{-6})	375.85	−745.70	2.00	3
Relaxed Brownian[c]	λ (.95637)	351.39	−696.77	50.92	3
Ornstein-Uhlenbeck[d]	α (.412201)	253.85	−501.70	245.99	3
Brownian motion		27.35	−50.71	696.99	2

Note: AIC = Akaike Information Criterion; ΔAIC = deviation in AIC from that of best model; K = number of parameters in model.

[a] Branch lengths raised to the power of κ. A speciational model assumes $\kappa = 0$ (branch lengths equal).

[b] The "kappa" model fits the maximum likelihood value of κ.

[c] Brownian motion (random walk), where off-diagonal elements in the phylogenetic covariance matrix are weighted by λ, which is fitted by maximum likelihood in the "lambda" model. Brownian motion assumes $\lambda = 1$.

[d] Brownian motion with a tendency toward some optimum, the strength of which is denoted by α.

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