CHICAGO JOURNALS

The University of Chicago

Size-Dependent Selective Mechanisms on Males and Females and the Evolution of Sexual Size Dimorphism in Frogs

Renato C. Nali,[1,*] Kelly R. Zamudio,[2] Célio F. B. Haddad,[3] and Cynthia P. A. Prado[4]

1. Programa de Pós-Graduação em Ciências Biológicas (Zoologia), Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista, 13506-900 Rio Claro, São Paulo, Brazil; 2. Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, New York; 3. Departamento de Zoologia, Instituto de Biociências, Universidade Estadual Paulista, 13506-900 Rio Claro, São Paulo, Brazil; 4. Departamento de Morfologia e Fisiologia Animal, Faculdade de Ciências Agrárias e Veterinárias, Universidade Estadual Paulista, 14884-900 Jaboticabal, São Paulo, Brazil

ABSTRACT: Sexual size dimorphism (SSD) varies in animals from male biased to female biased. The evolution of SSD is potentially influenced by a number of factors, such as territoriality, fecundity, and temporal breeding patterns (explosive vs. prolonged). In general, frogs show female-biased SSD with broad variance among species. Using comparative methods, we examine how different selective forces affect male and female sizes, and we test hypotheses about size-dependent mechanisms shaping SSD in frogs. Male size was weakly associated with SSD in all size classes, and we found no significant association among SSD, male size, temporal breeding pattern, and male territoriality. In contrast, female size best explained SSD variation across all size classes but especially for small-bodied species. We found a stronger evolutionary association between female body size and fecundity, and this fecundity advantage was highest in explosively breeding species. Our data indicate that the fecundity advantage associated with female body size may not be linear, such that intermediate and large females benefit less with body size increases. Therefore, size-dependent selection in females associated with fecundity and breeding patterns is an important mechanism driving SSD evolution in frogs. Our study underscores the fact that lineage-specific ecology and behavior should be incorporated in comparative analyses of animal SSD.

Keywords: temporal breeding pattern, male territoriality, female fecundity, sexual selection, Rensch's rule, phylogenetic comparative methods.

Introduction

Sexual size dimorphism (SSD)—the difference in body size between adult males and adult females—varies in animals from male biased, as in most mammals and birds (Andersson 1994; Abouheif and Fairbairn 1997; Isaac 2005), to female biased, as in most invertebrates (Fairbairn 1997),

* Corresponding author; e-mail: r_nali@yahoo.com.br.

frogs (Kupfer 2007), and snakes (Shine 1994), with some cases of extreme female-biased SSD in fishes (Ota et al. 2010). Typically, differences in SSD have been attributed to selective regimes in which larger males gain direct reproductive benefit because of male-male competition or as a result of female choice (leading to male-biased SSD) or in which larger females are favored because of increased fecundity (leading to female-biased SSD; Reeve and Fairbairn 1999; Dale et al. 2007; Kupfer 2009). However, many studies examining SSD in a phylogenetic context show that in most cases, the degree and direction of SSD within lineages result from a complex combination of evolutionary processes acting on both males and females (Zamudio 1998; Serrano-Meneses et al. 2008; Pincheira-Donoso and Tregenza 2011). Differences in mating systems and sex-specific behaviors contribute to selection on male and female body sizes and therefore shape the macroevolutionary distribution of SSD across animals (Ralls 1977; Shine 1989; Abouheif and Fairbairn 1997; Kupfer 2007).

Rensch's rule summarizes a macroevolutionary pattern in the distribution of SSD (Rensch 1950) and states that SSD decreases with body size when females are the larger sex and increases with body size when males are the larger sex. Rensch's rule has been investigated primarily for terrestrial vertebrates (Fairbairn 1997; Davis and Roth 2008; Stuart-Fox 2009; but see other examples in Fairbairn 1997). Allometric relationships consistent with Rensch's rule occur most often in lineages in which males are the larger sex (Fairbairn 1997). This pattern has led to the proposal that Rensch's rule is a product of sexual selection on male size, because of the fact that selection pressures on males (e.g., male-male competition and female choice for larger males) are expected to be strongest in taxa with male-biased SSD (Abouheif and Fairbairn 1997). Inconsistencies with Rensch's rule have been reported primarily in lineages with female-biased SSD, likely related to se-

lective pressures for increased fecundity (e.g., Ralls 1977; Fairbairn 1997; Dale et al. 2007). Recent studies on an increasing number of taxa have investigated the evolution of SSD using a phylogenetic framework (e.g., Cox et al. 2003; Székely et al. 2004; De Lisle and Rowe 2013; Colleoni et al. 2014). However, these do not yet capture taxonomic diversity and lineage-specific selective mechanisms, precluding inference of the evolutionary complexities leading to SSD divergences among species. Recent studies in various frog lineages have shown that Rensch's rule does not hold true (De Lisle and Rowe 2013; Han and Fu 2013; Liao et al. 2013), despite broad variance in SSD among species. Therefore, frogs are particularly interesting for the study of selective mechanisms driving SSD.

SSD in frogs ranges from female biased to male biased. Female frogs are larger than males in 90% of the species (Shine 1979), a pattern that has been attributed to fecundity selection favoring larger female body size (the fecundity advantage hypothesis; Darwin 1874; Shine 1989). However, male territoriality is common in frogs of all body sizes: males emit aggressive calls to compete for mates, chase invaders, and even engage in physical combats to defend breeding territories (Wells 2007; Nali and Prado 2012). These agonistic interactions should favor larger males with increased fighting ability (Shine 1989; Katsikaros and Shine 1997). In addition, male body size is often used as advertisement (Lips 2005) and in some cases may be a phenotype selected by females. Thus, among frogs, male-male competition (intrasexual selection) and female choice for males (intersexual selection) can operate either independently or together to select for larger male body size (Wells 1979; Tejedo 1988; Lips 2005). Therefore, we expect that sex-specific selective pressures will depend on traits of the mating system and other ecological and behavioral factors mediating breeding dynamics (Kupfer 2007; Wells 2007) and contribute differentially to the evolution of SSD in this group.

Considering these selective mechanisms, Shine (1979) stated that in larger species, males might reach or overcome female size because of higher selective advantage for male territoriality compared with female fecundity. This framework is useful (fig. 1A) but likely an oversimplification and does not account for many possible mechanisms that could explain the full continuum of SSD in frogs, which ranges from highly dimorphic female-biased to male-biased SSD (fig. 2). A recent comparative review of SSD in frogs showed that female fecundity is an important selective pressure driving SSD evolution whereas male territoriality apparently fails to explain body size variation, despite the fact that some species (~10%) show male-biased SSD (Han and Fu 2013). However, the relative strength of selection on body sizes of males and females under these sex-specific regimes probably differs among
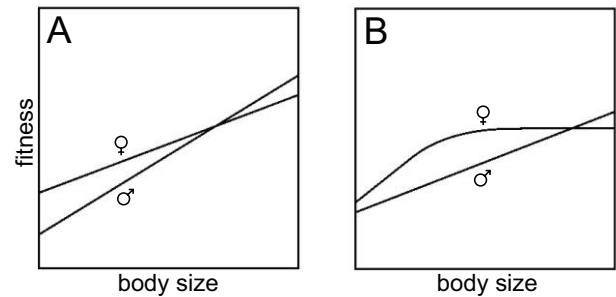

Figure 1: *A,* Classical model for the evolution of sexual size dimorphism (SSD) in frogs (based on Shine 1979). Female body size increases as a result of strong selective pressure for fecundity increase. Male body size increases as a result of high fitness of larger males due to territorial defense and fighting ability. The intersection of the curves represents the body size beyond which male territoriality becomes more important than female fecundity increase, leading to male-biased SSD. *B,* Model for the evolution of SSD in frogs proposed in this study, considering body size classes and different temporal breeding strategies. Size-based fecundity for females may not be linear, such that intermediate and large females receive diminished fitness advantages with increased body size. Males may also have increased fitness as they become larger due to fighting ability and female choice. The intersection of the curves represents the body size beyond which male-biased SSD is likely. However, this is primarily driven by diminished fecundity advantage for larger females and not by high selective advantage for large territorial males. For details, see "Discussion."

body size categories. Thus, size-dependent selective mechanisms within sexes warrant further analyses (De Lisle and Rowe 2013).

Temporal breeding pattern (explosive vs. prolonged) is one ecological trait that likely differentially influences the occurrence and intensity of selection on body sizes of both sexes. Explosively breeding frogs have short reproductive periods. Females arrive synchronously at high-density breeding sites, where males generally actively search for females and displace other males in amplexus but do not defend territories or guard individual females (Wells 1977). In prolonged-breeding species, females arrive at reproductive sites asynchronously and are typically less numerous than males, males benefit from defending territories and/or oviposition sites from which they call to attract females, and females often inspect territories and choose among available males (Wells 1977; Martins and Haddad 1988; Nali and Prado 2012). Therefore, the degree of male-male competition and the opportunity for mate selection by females are strongly influenced by these breeding patterns (Bourne 1993; Bastos and Haddad 1996; Wells 2007). In turn, they will influence the strength of natural selection on traits important for reproduction, such as male territoriality, clutch size, gonad investment, and male
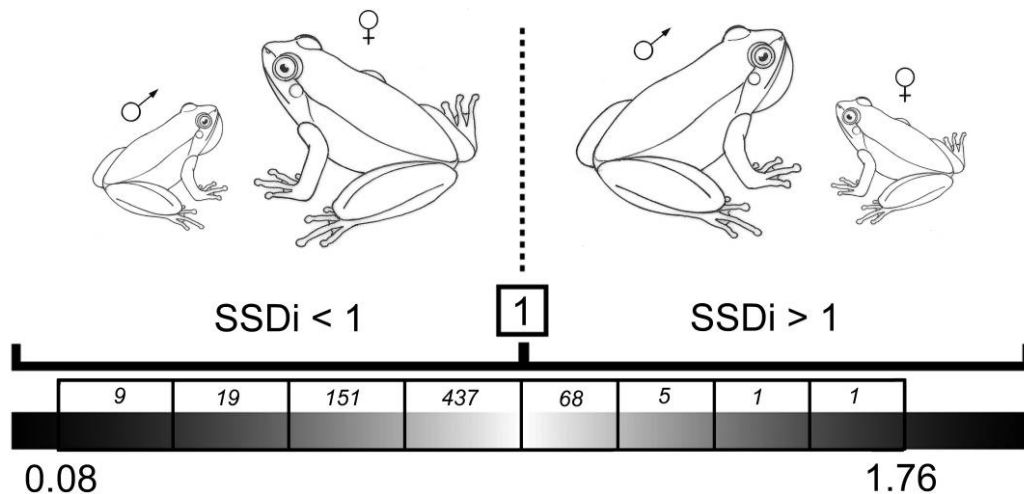
Figure 2: Properties of the sexual size dimorphism index (SSDi) used in this study. SSDi is symmetrical around 1; the grayscale bar represents the extent of SSD (white, nondimorphic species; black, highly dimorphic species). The rectangle represents the empirical range of SSDi (0.08–1.76) in our data set, divided into four equal classes for female-biased (left) and male-biased (right) SSD. The number of species distributed in each SSDi class is listed in italics.

and female body sizes (Praderio and Robinson 1990; Prado and Haddad 2005).

Independent selective pressures on the sexes, which can be either opposing or concordant, have resulted in a complex distribution of body sizes in many animal lineages, making the study of SSD particularly challenging. However, enhanced availability of reproductive and behavioral data now makes it possible to perform fine-scale phylogenetic comparative analyses that reveal mechanisms shaping male and female body sizes. Here we quantify patterns of SSD evolution in frogs, using data on 718 species from 38 families. First, we test whether frogs follow Rensch's rule to examine the distribution of SSD in this female-biased lineage. We then examine size- and behavior-dependent selective mechanisms on males and females that may drive the evolution of SSD in frogs. We tested four main hypotheses: (1) evolutionary changes in male size associated with territoriality predict variation in SSD among species, and this effect will be most pronounced in species with large body sizes; (2) evolutionary changes in female size associated with fecundity predict variation in SSD among species, and this effect will be most pronounced in species with small body sizes; (3) explosively breeding females show stronger size-based selective advantage for fecundity because of limited breeding opportunities; and (4) prolonged-breeding males show stronger selective pressure for territoriality because of the fitness advantage of this behavior and female choice, potentially increasing selection for large male body sizes. We considered body size categories within each sex and temporal aspects of reproductive activity associated with fecundity

and territoriality to test whether selective mechanisms act differentially in species along a size continuum and/or among reproductive categories (explosive vs. prolonged).

Material and Methods

Comparative Species Data and Analyses

We gathered from the literature the following data on 718 frogs from 38 families: (1) average male snout-vent length (SVL); (2) average female SVL; (3) temporal breeding pattern (prolonged or explosive); (4) clutch size (number of eggs/clutch), estimated by either egg counts in the field or number of mature oocytes in preserved specimens; and (5) evidence of male territoriality, such as aggressive calls, combat scars, or male-male physical combat. Analyses for each hypothesis test used subsets of these data, according to their availability in our data set. The full data set is deposited in the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.270sf (Nali et al. 2014).

We conducted phylogenetic independent contrast (PIC) analyses (Felsenstein 1985) using an amphibian phylogeny with original branch lengths (Pyron and Wiens 2011). We placed additional species not included in the original tree according to proposed phylogenetic relationships in other studies (Faivovich et al. 2005; Nascimento et al. 2005; Frost et al. 2006; Wiens et al. 2010; Clemente-Carvalho et al. 2011; Orrico 2012; Peloso et al. 2014). For these additional species, branch lengths were estimated as the arithmetic means of adjacent branches. All PIC analyses were per-
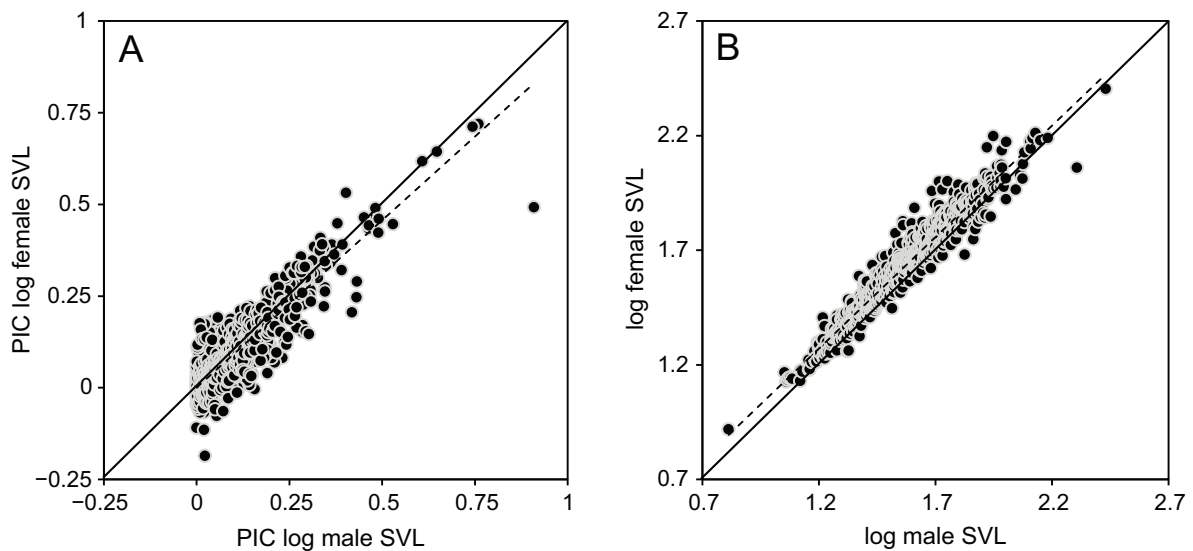
Figure 3: Allometric relationships between male and female body sizes in frogs, using data corrected (*A*) and noncorrected (*B*) for phylogeny (phylogenetic independent contrasts [PICs]). Solid lines represent isometric axes ($\beta = 1$), and dashed lines represent reduced major axis regressions with β statistically similar to 1. SVL, snout-vent length.

formed in Mesquite (ver. 2.75; Maddison and Maddison 2011).

As a measurement of SSD for each species, we calculated an SSD index (SSDi) based on a two-step ratio, in which *M* is male SVL and *F* is female SVL (Lovich and Gibbons 1992; revised by Smith 1999). Step 1: for species in which $M \geq F$, SSDi $= M/F$. Step 2: for species in which $F > M$, SSDi $= 2 - (F/M)$.

SSDi is the best possible ratio on a linear scale if the data set exhibits a range of SSD where both sexes can be the larger sex (Smith 1999). SSDi is symmetrical around 1, such that when SSDi > 1, males are the larger sex, and when SSDi < 1, females are the larger sex. In frogs, cases of male-biased SSD are fewer than cases of female-biased SSD; thus, in the majority of cases, SSDi < 1, and sexual dimorphism decreases as SSDi approaches 1 (fig. 2).

We applied branch length standardization to avoid linear correlation between independent contrasts and their standard deviations (Garland et al. 1992). We log transformed the data set and adopted the exponential transformation of branch lengths, which removed these correlations in all cases. The only exception occurred in the analysis of male and female sizes versus SSD in small species (see below), for which we used the branch lengths method of Nee (Purvis 1995). For each analysis, degrees of freedom were subtracted according to the number of polytomies in the topology (Purvis and Garland 1993), all of which were considered soft (i.e., because of lack of data).

Tests of Predictions and Hypotheses

Rensch's Rule. To assess Rensch's rule, we performed a reduced major axis (RMA) regression between log male SVL and log female SVL for both phylogenetically corrected and noncorrected data for 691 species (Bohonak and van der Linde 2004), with male size assigned to the *X*-axis (Abouheif and Fairbairn 1997). RMA assesses Rensch's rule by checking whether β (regression slope) is statistically different from 1, as judged by 95% confidence intervals (CIs; Fairbairn 1997; Fairbairn 2005; Frýdlová and Frynta 2010); if yes, there is an allometric relationship between male and female sizes. On the other hand, if $\beta = 1$, the data do not conform to this allometry (Rensch 1950; Fairbairn 1997), indicating that male and female sizes are isometric.

The Targets of Selection: Male and Female Body Sizes and SSD. Using PICs, we conducted ordinary least squares (OLS) regressions between (1) log male SVL versus log SSDi and (2) log female SVL versus log SSDi to test for an evolutionary association between SSD and male and female body sizes. OLS regression was used because it is appropriate when one variable is a ratio (SSDi) and the other is a direct measurement (male and female sizes; Smith 1999; Davis and Roth 2008; Astúa 2010). Given our a priori expectations for size-dependent selective mechanisms, we also tested for evolutionary correlations for species in three body size categories; the PIC regressions were

Table 1: Ordinary least squares regression analyses of phylogenetic independent contrasts (PICs) for male body size, female body size, and sexual size dimorphism (SSD) for three species size categories

Species	N	PIC log male size vs. PIC log SSDi				PIC log female size vs. PIC log SSDi			
		P	R^2	Slope	SSD direction	P	R^2	Slope	SSD direction
All	690	**<.001**	**.04**	**.13**	Decreases with increased male body size	**.002**	**.014**	**−.08**	Increases with increased female body size
Small	113	**.036**	**.037**	**.17**	Decreases with increased male body size	**<.001**	**.12**	**−.29**	Increases with increased female body size
Intermediate	471	.10	.006	...	Not correlated with male body size	**<.001**	**.12**	**−.32**	Increases with increased female body size
Large	104	**.039**	**.04**	**.19**	Decreases with increased male body size	**<.001**	**.11**	**−.32**	Increases with increased female body size

Note: Statistically significant results shown in bold. *N*, sample size; SSDi, sexual size dimorphism index.

conducted independently for (1) small species, (2) intermediate-sized species, and (3) large species by considering species below or above 1 SD of the mean log male SVL as small and large species, respectively. Body sizes in our data set are normally distributed (Shapiro-Wilk = 0.97; $P = .07$). Therefore, using 1 SD from the mean to delimit large and small body size categories will result in a larger number of species of intermediate sizes, as expected for animal lineages (Gaston and Blackburn 2000), but still with significant sample sizes in the large and small body size categories (approximately 16% each). We tested whether differences in the number of species in each size category could potentially bias our results by randomly subsampling 110 intermediate-sized species and repeating the OLS regression analyses for both male and female sizes versus SSD. We used male size to assign species to the three size classes because, in general, males are more frequently sampled in the field; thus, the average male size for each species will be more accurate.
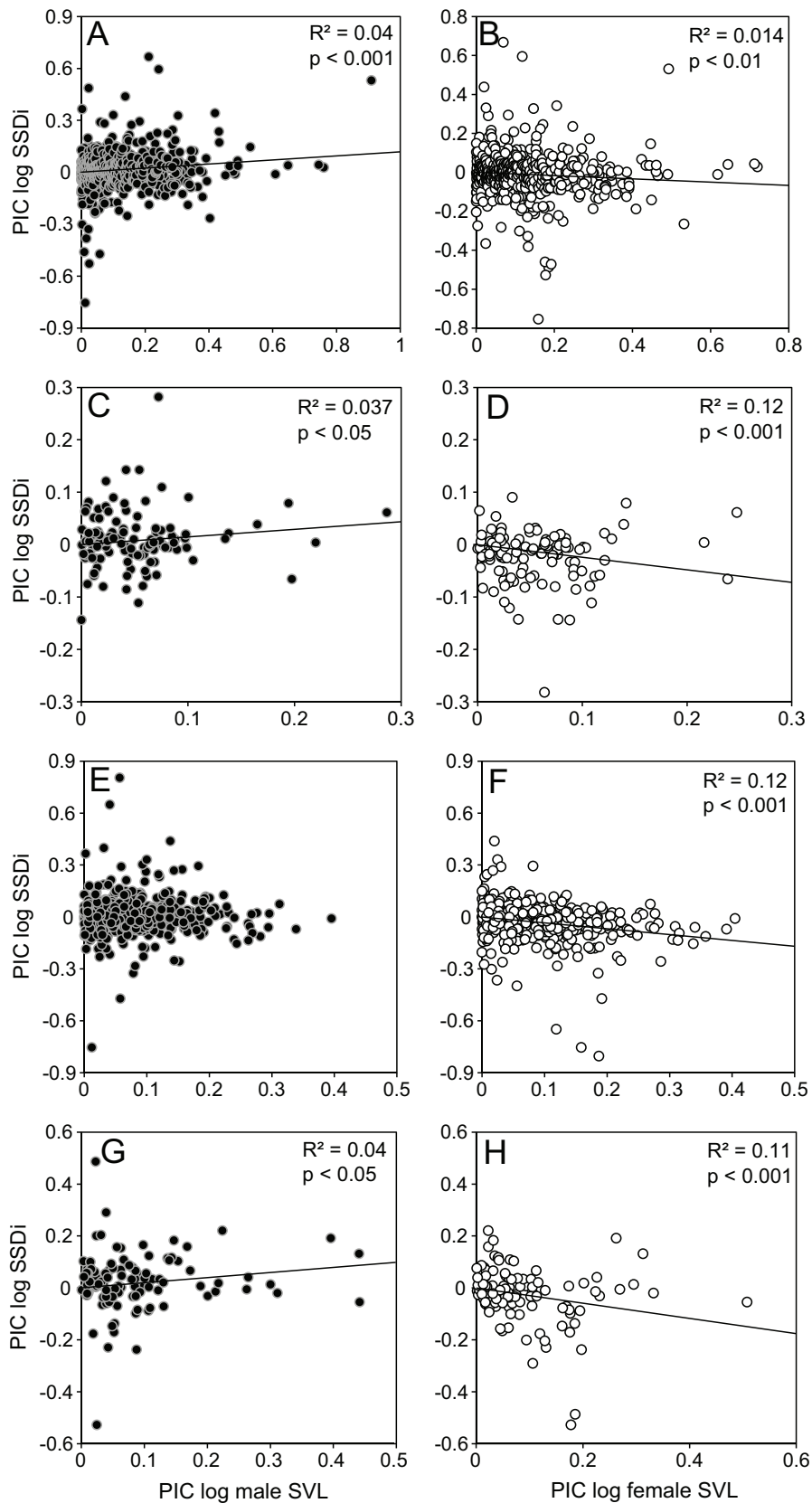
Adaptive Mechanisms for Male and Female Body Sizes. To test whether female size is positively correlated with fecundity, we conducted regression analyses through the origin between PICs of female size and number of eggs/clutch for those species for which we had fecundity data. Here we considered two potential biases in our data set. First, we excluded frogs with terrestrial and/or highly specialized reproductive modes from our size-fecundity analysis ($N = 103$), because they often have larger and fewer eggs per clutch (Salthe and Duellman 1973), and their specialized reproductive modes impose additional selective pressures on clutch characteristics. Therefore, we retained in the size-fecundity analysis 294 species of frogs with aquatic reproduction typical of most frogs (Haddad and Prado 2005). A second possible source of bias is that our estimates of fecundity include both number of mature oocytes in preserved specimens and number of eggs from clutches collected in the field, and these two measures may

not correspond. To account for this possibility, we used a smaller data set for which we had specific information on the origin of fecundity estimates (oocytes or clutch) and performed independent size-fecundity regression analyses, with the first including fecundity estimates independent of their origin and a second one excluding the records obtained from preserved specimens (Nali et al. 2014). These two regressions did not differ; thus, we included all fecundity data in subsequent analyses.

To test male territoriality as a potential mechanism shaping SSD evolution, we compared PIC regressions for log male size versus log SSDi for territorial and nonterritorial species. Slopes of the two independent regressions were compared using ANCOVA in GraphPad Prism 6 (GraphPad Software).

Breeding Patterns and Strength of Selection. To test our hypothesis that females of explosively breeding species show greater strength in selection for fecundity, we conducted size-fecundity PIC regressions for prolonged and explosive breeders separately and compared regression slopes with ANCOVA. We then tested for evolutionary associations between female body sizes and SSD according to the breeding pattern and size class, by conducting OLS regressions for PICs of log female SVL versus log SSDi for females in three body size classes (small, intermediate, and large species) and explosive or prolonged breeding categories.

For males, to test whether prolonged breeding pattern is correlated with male territoriality across the phylogeny, we used the test of correlated character evolution (Pagel 1994) using 100 randomizations of characters on the tree, implemented in Mesquite (ver. 2.75; Maddison and Maddison 2011).

Results

Rensch's Rule

Our data confirmed that Rensch's rule does not hold in frogs ($N = 691$ species). With or without phylogenetic correction, the slopes of the RMA regressions were not significantly different from 1 (independent contrasts: slope $= 1.008 \pm 0.018$; 95% CI $= 0.972$–1.043; $R^2 = 0.78$; non-corrected data: slope $= 1.007 \pm 0.010$; 95% CI $= 0.988$–1.027; $R^2 = 0.93$; intercept $= 0.049 \pm 0.016$; fig. 3).

The Targets of Selection: Male and Female Body Sizes and SSD

The OLS regression analyses between PICs of log male SVL and log female SVL versus log SSDi showed significant results for all but one comparison (table 1; fig. 4). Male body size predicted SSD for all species together and for small- and for large-sized species, such that species with larger males have less pronounced SSD (or tend toward male-biased SSD), but correlations had low coefficients of determination ($R^2 \leq 0.04$). Male size did not predict SSD among intermediate-sized species. For females, our results showed that SSD increases with increased female size for all species, with low coefficient of determination ($R^2 = 0.014$). However, when females were analyzed separately by body size category, increased female size better explained SSD increases (R^2 ranging from 0.11 to 0.12; table 1; fig. 4). Our analyses of randomly subsampled intermediate-sized species showed statistically identical results (males: $P = .70$, $R^2 = 0.001$; females: $P < .001$, $R^2 = 0.13$) when compared with the full data set (table 1).

Adaptive Mechanisms for Male and Female Body Sizes

Female size-fecundity regression analyses including and excluding mature oocyte estimates yielded identical results (mature oocytes and actual clutch sizes: $R^2 = 0.68$, $P < .001$, $N = 64$; actual clutch sizes only: $R^2 = 0.65$, $P < .001$, $N = 48$); thus, the origin of fecundity estimates do not bias our downstream analyses. Female size correlated positively with fecundity (fig. 5A; $R^2 = 0.32$, $P < .001$, $N = 293$) across all frogs with aquatic reproduction; larger females produce more eggs, even after controlling for phylogeny.

We also compared the relationship between PICs of male body size and SSDi for territorial and nonterritorial species and found significant results for both categories (territorial: $R^2 = 0.11$, $P < .001$, $N = 157$, slope $= 0.143$; non-territorial: $R^2 = 0.024$, $P < .001$, $N = 534$, slope $= 0.098$). Slopes for both PIC correlations were positive, showing that species with larger male body sizes have less pronounced SSD. However, the regression slopes were statistically similar (ANCOVA: $F_{1, 689} = 0.73$, $P = .39$), indicating that the potential fitness benefit of large body size holds for all species, and male territoriality is not the sole explanation for the evolution of SSD in frogs.

Breeding Patterns and Strength of Selection

In females, both explosive ($R^2 = 0.63$, $P < .001$, $N = 64$) and prolonged ($R^2 = 0.42$, $P < .001$, $N = 77$) breeders showed significant positive size-fecundity relationships (fig. 5B). The slope for explosive breeders (2.55) was higher—although marginally not significant—than that for prolonged breeders (1.92; ANCOVA: $F_{1, 140} = 2.998$, $P = .08$); in addition, female body size in explosive breeders better explained variation in clutch size ($R^2 = 0.63$) when compared with prolonged breeders ($R^2 = 0.42$). We then compared the relationship of female size versus SSD for prolonged and explosive breeders, considering all species and separately by size categories (table 2; fig. 6). We found that (1) for all species together, increases in female body size poorly explained variation in SSD for both explosive and prolonged breeders ($R^2 = 0.043$ and 0.065, respectively); (2) for small-sized species, increases in female body sizes best explained variation in SSD for both explosive and prolonged breeders ($R^2 = 0.57$ and 0.41, respectively); (3) for intermediate-sized species, increases in female sizes poorly explained variation in SSD for both explosive and prolonged breeders; and (4) for large-bodied species, female size did not predict SSD variation for species with either breeding pattern (table 2). Therefore, the advantages of female size increases are not linear across size categories and are most important for small-bodied female frogs independent of breeding pattern.

For males, the test of phylogenetically correlated character evolution showed that prolonged breeding pattern is not associated with male territoriality (likelihood difference $= 4.90$; $P = .11$), despite the fact that in our data set territorial behaviors were more commonly observed in prolonged-breeding species (50%) than in explosively breeding ones (33%).

Figure 4: Regression analyses between independent contrasts of male (filled circles) and female (open circles) sizes and sexual size dimorphism (SSD) in frogs. Solid lines are shown for significant results only. Positive slopes represent SSD decreases, and negative slopes represent SSD increases (see table 1). *A, B,* All species. *C, D,* Small species. *E, F,* Intermediate species. *G, H,* Large species. PIC, phylogenetic independent contrast; SSDi, sexual size dimorphism index; SVL, snout-vent length.
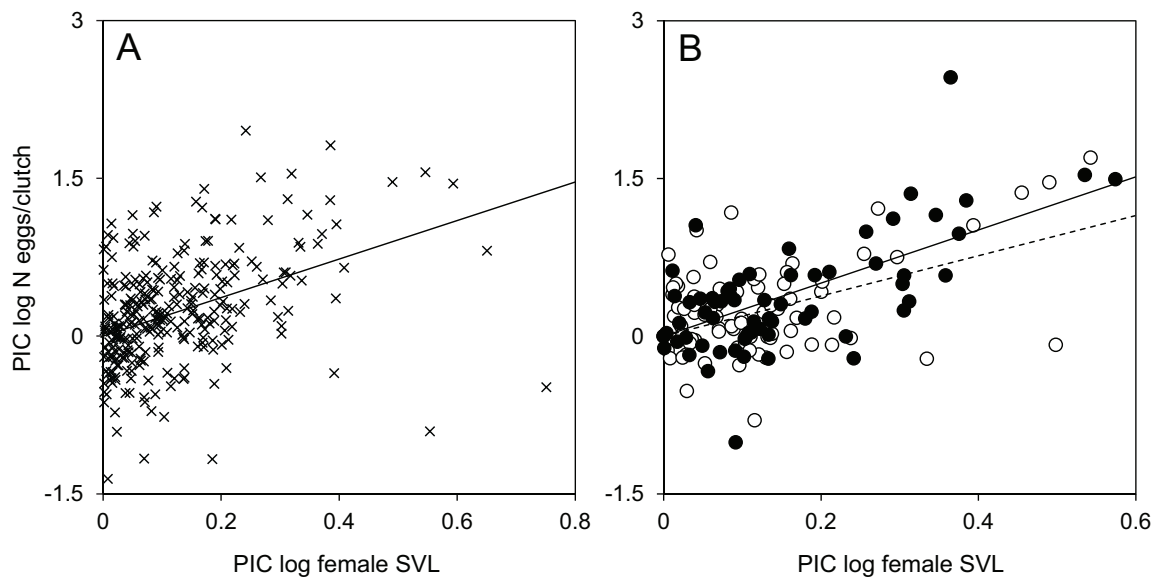
Figure 5: Size-fecundity relationships between independent contrasts of female body size and clutch size for all frogs included here (*A*) and species with explosive breeding pattern (filled circles, solid line) and prolonged breeding pattern (open circles, dashed line; *B*). PIC, phylogenetic independent contrast; SVL, snout-vent length.

Discussion

Macroevolutionary patterns reflect selective pressures and processes that occur over long time periods, manifested among species within lineages (Brooks and McLennan 1991). Comparative studies, which take into account the phylogenetic relationships among taxa, are key to comprehending mechanisms underlying biological diversity and phenotypes (Harvey and Pagel 1991). In this study, we found that in 616 of 691 frogs (89%), females were larger than males, corroborating earlier surveys of SSD in this group (Shine 1979; De Lisle and Rowe 2013; Han and Fu 2013). We showed that frogs do not follow Rensch's rule, showing isometry in the evolution of male and female body sizes (De Lisle and Rowe 2013; Liao et al. 2013) and corroborating the prediction that Rensch's rule might not hold in lineages where 80% or more of the included species exhibit female-biased SSD (Fairbarn 1997). Allometry consistent with Rensch's rule is expected in lineages where male body sizes respond to environmental variables or selective pressures more strongly than those of females (Fairbairn 2005; Colleoni et al. 2014). Although some recent studies have identified highly female-biased lineages that follow Rensch's rule (e.g., Davis and Roth 2008; Stuart-Fox 2009), we did not observe that pattern in frogs, likely because females are under stronger selective pressures for increased body size compared to males. Our analyses also reveal that males and females experience different size-dependent selection because of differential fitness benefits of reproductive strategies between sexes (Carranza 2009). The explanation of SSD in female-biased lineages, therefore, depends specifically on which sex is the main target of selection on body size.

We found a significant positive correlation between male size and SSDi, indicating that species with larger males show less-pronounced SSD, tending to male-biased SSD. However, male size explained little of the observed variation in SSD in all body size categories, indicating a biologically weak correlation (table 1; fig. 4). The relationship between male size and SSD held for territorial and nonterritorial males, but the slopes for the two groups were statistically identical, indicating that selection on territorial males does not contribute disproportionately to SSD in frogs. The idea that larger frogs generally exhibit more intense physical male-male combats has been widespread (Wells 1977; Shine 1979); indeed, studies of some species have shown that larger male frogs can achieve higher reproductive success by defeating younger and smaller males (Howard 1984; Katsikaros and Shine 1997). However, male-male combats are common even in small-bodied species with female-biased SSD (Haddad 1991; Costa et al. 2010). Although larger male size may be advantageous in intrasexual contests (male-male competition), male frogs also rely on other fitness-related traits that may be body size independent, such as forearm thickness for male displacement, time at reproductive site, energy expenditure in calling activity, or early sexual maturity (e.g., Howard and Kluge 1985; Howard et al. 1994;

Table 2: Ordinary least squares regression analyses between phylogenetic independent contrasts (PICs) for female body size and sexual size dimorphism (SSD) in explosively and prolonged-breeding species in three species size categories

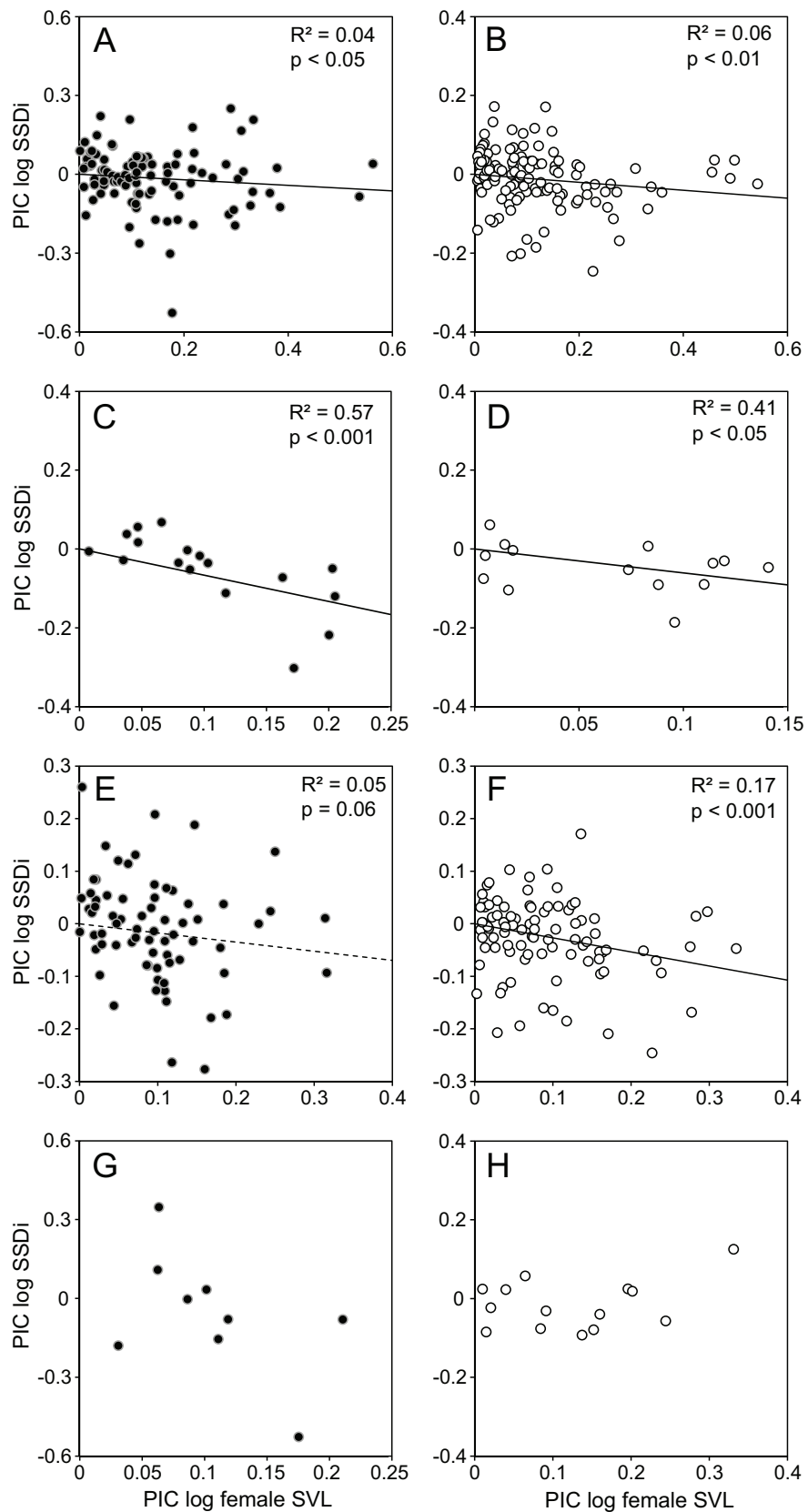| Species	N	Explosive: PIC log female size vs. PIC log SSDi				Prolonged: PIC log female size vs. PIC log SSDi			
		P	R^2	Slope	SSD direction	P	R^2	Slope	SSD direction
All	98/121	**.038**	**.043**	−.13	Increases with increased female body size	**.004**	**.065**	−.11	Increases with increased female body size
Small	17/14	**<.001**	**.57**	−.67	Increases with increased female body size	**.01**	**.41**	−.57	Increases with increased female body size
Intermediate	70/91	.06	.05	...	Not correlated with female body size	**<.001**	**.17**	−.27	Increases with increased female body size
Large	9/14	.12	.28	...	Not correlated with female body size	.98	.0003	...	Not correlated with female body size

Note: Statistically significant results shown in bold. *N*, respective sample size; SSDi, sexual size dimorphism index.

Byrne 2008; Zhang and Lu 2013). Furthermore, even in species with male-male combat, small males can attain reproductive success through alternative breeding tactics, such as female interception, satellite behavior, sneaked fertilizations, or postmating clutch piracy (Howard 1984; Haddad 1991; Prado and Haddad 2003; Vieites et al. 2004; Zamudio and Chan 2008). Combined, these multidirectional selective forces on male body size in frogs may explain the weak evolutionary correlation between SSD and male body size and the similar relationship of male sizes versus SSD between territorial and nonterritorial species. Thus, our first hypothesis was rejected. This same pattern was found in eublepharid geckos, where territoriality was not correlated to SSD, but other traits such as head size dimorphism and presence of precloacal pores were under strong selection for increased male fitness (Kratochvíl and Frynta 2002).

In contrast to males, we found a stronger correlation between female size and SSD, especially when analyzing body size categories independently (table 1; fig. 4). This corroborates our hypothesis that females are the main target of selection driving patterns of SSD in frogs. Cases in which selection strongly favors larger females might occur because of a size-based fecundity advantage (Darwin 1874). In frogs, a positive relationship between female size and number and/ or size of eggs is a common pattern (Crump 1974; Prado and Haddad 2005; Pupin et al. 2010), even when controlling for phylogeny (Han and Fu 2013; this study). However, previous studies have not taken into account how temporal breeding patterns might influence the strength of both natural and sexual selections on body sizes of both sexes. Woolbright (1983) proposed a model of frog SSD evolution comparing prolonged and explosively breeding species but assuming that the strength of selection for size-based fecundity was strong and constant for females independent of their breeding pattern. In our study, however, we found that fecundity in explosive breeders increases more rapidly with female body size; that is, selection for larger female body size may be stronger for explosive breeders (slope =

2.55) when compared with prolonged breeders (slope = 1.92). This trend is marginally not significant ($P = .08$), so it lends some support to our hypothesis that explosively breeding females show stronger size-based selective advantage for fecundity. One possible mechanism is that explosive breeders have few opportunities to breed in a season (Wells 1977, 1979); thus, higher fecundity per clutch might be more advantageous to ensure maximum production of offspring in a single bout. In fact, our data showed that changes in female body size better explained changes in fecundity for explosive ($R^2 = 0.63$) than for prolonged breeders ($R^2 = 0.42$), indicating that factors other than body size may affect the evolution of clutch size, especially in prolonged-breeding species. Explosive breeders typically show generalized aquatic reproduction, while prolonged breeders exhibit a high diversity of reproductive modes (Haddad and Prado 2005; Prado et al. 2005). Explosive breeders tend to use ponds at the beginning of the breeding season to avoid larval predation and competition (Prado et al. 2005), whereas prolonged breeders use a large variety of microhabitats throughout the season. Therefore, in addition to the effects of body size, prolonged breeders might experience a wider range of external factors during the longer breeding season (e.g., larval predation and competition pressures, number of clutches per breeding season, food availability) affecting clutch size (Kaplan 1987; Reading and Clarke 1988; Girish and Saidapur 2000; Prado et al. 2005).

Because (1) prolonged and explosively breeding females tend to have different size-based fecundity advantages and (2) female body size versus fecundity varies among species with different breeding patterns, we reanalyzed the PIC regressions for female size versus SSD for these breeding categories separately. We found that the phylogenetic correlation between increased female body size and increased SSD is much more evident for small species independent of breeding category (fig. 6), suggesting that size-based fecundity advantage is strongest in small-bodied species. One could argue that increased fecundity should select for

larger females independent of body size classes, but trade-offs with other traits could limit this advantage. For example, in some frogs, size-assortative mating occurs because cloacal juxtaposition is necessary to assure maximum fertilization efficiency during spawning, promoting an optimum male size/female size ratio (Bastos and Haddad 1996; Wogel and Pombal 2007; Lu et al. 2010). This mechanical limitation has also been observed in garter snakes (Shine et al. 2001). On the other hand, the fitness cost of small body size should be highest for small females, because their capacity for egg production is limited compared with larger species (Prado and Haddad 2005; Pupin et al. 2010; this study). For explosive breeders, few reproductive events increase selective pressures for fecundity increase. Prolonged breeders, in contrast, have more reproductive opportunities, but small animals tend to have shorter life spans (Berube et al. 1999; Ricklefs and Scheuerlein 2001; Voituron et al. 2011); thus, small prolonged-breeding species might also experience strong pressures for fecundity increase. Our data support the fact that the fecundity advantage of female body size may not be linear (small females benefit more with body size increase), decreasing the overall correlation between female body size and SSD in pooled analyses (fig. 1*B*). Our findings underscore that size-dependent mechanisms may explain the high degree of variation in frog SSD (fig. 2) and corroborate our hypothesis that evolutionary changes in female size associated with fecundity predict variation in SSD among species and that this relationship is strongest for small-bodied species.

Temporal breeding patterns could also differentially affect males because of the fitness consequences of territorial behaviors and male body size. Compared with explosive breeders, prolonged-breeding males should benefit more from defending territories and oviposition sites that are selected by females (Wells 1977). Thus, we predicted that prolonged-breeding males should show higher rates of territoriality, potentially leading to stronger selective pressure for larger male body sizes. However, we did not find an evolutionary association between male territoriality and prolonged breeding pattern, despite the fact that territoriality was more common among prolonged breeders (50%) when compared with explosive ones (33%) in our data set (Nali et al. 2014). One possible limitation of our data is that territorial behaviors are not systematically reported in the literature; therefore, lack of evidence does

not necessarily mean that a given species is not territorial but only that such behaviors have not been observed. As we accumulate further natural history data on reproductive behaviors, our inferences of the complex associations between male breeding patterns and territoriality may become clearer. Currently, our data refute the fourth hypothesis and emphasize that the association between body size, territoriality, and breeding patterns in male frogs is not obvious, likely due to a variety of additional male traits that increase fitness, as previously discussed (Howard et al. 1994; Byrne 2008; Zhang and Lu 2013).

A number of studies of SSD in other animal groups have been recently published, allowing for comparisons beyond frogs. In mammals, male-biased SSD is a common pattern, and female-biased dimorphism is generally explained by reduced male-male competition and concomitant evolutionary decreases in male size (Isaac 2005). A study of small mammals with a lack of SSD further showed that this pattern was not driven by size-based fecundity selection (Lu et al. 2014). These findings in mammals are contradictory to our results and likely stem from the different reproductive strategies adopted by mammals and frogs (Pianka 1970). On the other hand, a study on primates showed that length of female sexual receptivity was associated with the evolution of copulatory plugs in males (passive mate guarding), which in turn could alter the strength of sexual selection on male size (Dunham and Rudolf 2009). Similarly, we found that temporal breeding patterns in frogs, which also determine the period of sexual receptivity, may affect size-fecundity relationships in females, thus shaping the evolution of SSD. Dale et al. (2007) argued that social mating system is a key life-history variable that predicts size allometry and SSD in birds because of differential selection on males and females. Likewise, we found that social dynamics during breeding, which are influenced by temporal breeding patterns, imposed selective mechanisms that differ between the sexes in frogs. Among ectotherms, strong sexual selection on male size drives SSD evolution in New World pit vipers, but fecundity selection on female size in this clade is less evident (Hendry et al. 2014). A fine-scale analysis revealed, though, that arboreal lineages showed higher rates of SSD evolution and a pronounced shift to female-biased dimorphism (Hendry et al. 2014). Habitat types have also influenced the evolution of male body size and SSD in turtles, in which terrestrial males are proportionally larger than

Figure 6: Regression analyses between independent contrasts of female body size and sexual size dimorphism (SSD) in frogs with explosive breeding pattern (filled circles) and prolonged breeding pattern (open circles). Solid regression lines represent significant results, the dashed line represents the marginally not significant result, and negative slopes represent SSD increases (see table 2). *A, B,* All species. *C, D,* Small species. *E, F,* Intermediate species. *G, H,* Large species. PIC, phylogenetic independent contrast; SSDi, sexual size dimorphism index; SVL, snout-vent length.

aquatic ones (Ceballos et al. 2013). These examples clearly demonstrate that lineage-specific ecology and behavior should be incorporated in analyses of SSD evolution.

Sexual size dimorphism is a composite character resulting from different selective pressures on the sexes (Carranza 2009). Many factors can affect male and female body sizes, such as temporal availability of breeding sites, male and female density, mortality rates, diet variation, competition, growth rates, population age structure, and age at maturity (e.g., Shine 1989; Monnet and Cherry 2002; Lu et al. 2008; Zhang and Lu 2013). We found evidence that selection leading to variation in SSD may operate differently among body size classes, and we recommend that future analyses account for size-dependent selection, behavior, and ecology to better capture mechanisms leading to SSD. Literature records allowed us to analyze SSD patterns and targets of selection in frogs; however, data on reproductive patterns, territorial behaviors, and fitness consequences of specific phenotypes are generally scarce when compared with data on body size itself. Future studies should focus on documenting specific ecological traits—especially for poorly studied taxa—for further investigation of mechanisms involved in the evolution of SSD in frogs.

Acknowledgments

Literature Cited

Abouheif, E., and D. J. Fairbairn. 1997. A comparative analysis of allometry for sexual size dimorphism: assessing Rensch's rule. American Naturalist 14:540–562.

Andersson, M. 1994. Sexual selection. Princeton University Press, Princeton, NJ.

Astúa, D. 2010. Cranial sexual dimorphism in New World marsupials and a test of Rensch's rule in Didelphidae. Journal of Mammalogy 91:1011–1024.

Bastos, R. P., and C. F. B. Haddad. 1996. Breeding activity of the Neotropical treefrog *Hyla elegans* (Anura, Hylidae). Journal of Herpetology 30:355–360.

Berube, C. H., M. Festa-Bianchet, and J. T. Jorgenson. 1999. Individual differences, longevity, and reproductive senescence in bighorn ewes. Ecology 80:2555–2565.

Bohonak, A. J., and K. van der Linde. 2004. RMA: software for reduced major axis regression, Java version. http://www.kimvdlinde.com/professional/rma.html.

Bourne, G. R. 1993. Proximate costs and benefits of mate acquisition at leks of the frog *Ololygon rubra*. Animal Behaviour 45:1051–1059.

Brooks, D. R., and D. A. McLennan. 1991. Phylogeny, ecology, and behavior: a research program in comparative biology. University of Chicago Press, Chicago.

Byrne, P. G. 2008. Strategic male calling behavior in an Australian terrestrial toadlet (*Pseudophryne bibronii*). Copeia 1:57–63.

Carranza, J. 2009. Defining sexual selection as sex-dependent selection. Animal Behaviour 77:749–751.

Ceballos, C. P., D. C. Adams, J. B. Iverson, and N. Valenzuela. 2013. Phylogenetic patterns of sexual size dimorphism in turtles and their implications for Rensch's rule. Evolutionary Biology 40:194–208.

Clemente-Carvalho, R. B. G., J. Klaczko, S. I. Perez, A. C. R. Alves, C. F. B. Haddad, and S. F. dos Reis. 2011. Molecular phylogenetic relationships and phenotypic diversity in miniaturized toadlets, genus *Brachycephalus* (Amphibia: Anura: Brachycephalidae). Molecular Phylogenetics and Evolution 61:79–89.

Colleoni, E., M. Denoël, E. Padoa-Schioppa, S. Scali, and G. F. Ficetola. 2014. Rensch's rule and sexual dimorphism in salamanders: patterns and potential processes. Journal of Zoology 293:143–151.

Costa, T. B., L. D. A. Guimarães, and R. P. Bastos. 2010. Territorial and mating behavior in *Phyllomedusa azurea* (Anura: Hylidae) at a temporary pond in west-central Brazil. Phyllomedusa 9:99–108.

Cox, R. M., S. L. Skelly, and H. B. John-Alder. 2003. A comparative test of adaptive hypotheses for sexual size dimorphism in lizards. Evolution 57:1653–1669.

Crump, M. L. 1974. Reproductive strategies in a tropical community. Miscellaneous Publications of the Museum of Natural History, University of Kansas 61:1–68.

Dale, J., P. O., Dunn, J. Figuerola, T. Lislevand, T. Székely, and L. A. Whittingham. 2007. Sexual selection explains Rensch's rule of allometry for sexual size dimorphism. Proceedings of the Royal Society B: Biological Sciences 274:2971–2979.

Darwin, C. R. 1874. The descent of man, and selection in relation to sex. 2nd ed. Appleton, New York.

Davis, C. M., and V. L. Roth. 2008. The evolution of sexual size dimorphism in cottontail rabbits (*Sylvilagus*, Leporidae). Biological Journal of the Linnean Society 95:141–156.

De Lisle, S. P., and L. Rowe. 2013. Correlated evolution of allometry and sexual dimorphism across higher taxa. American Naturalist 182:630–639.

Dunham, A. E., and V. H. W. Rudolf. 2009. Evolution of sexual size monomorphism: the influence of passive mate guarding. Journal of Evolutionary Biology 22:1376–1386.

Fairbairn, D. J. 1997. Allometry for sexual size dimorphism: pattern and process in the coevolution of body size in males and females. Annual Review of Ecology and Systematics 28:659–687.

———. 2005. Allometry for sexual size dimorphism: testing two

hypotheses for Rensch's rule in the water strider, *Aquarius remigis.* American Naturalist 166(suppl.):S69–S84.

Faivovich, J., C. F. B. Haddad, P. C. A. Garcia, D. R. Frost, J. A. Campbell, and W. C. Weeler. 2005. Systematic review of the frog family Hylidae, with special reference to Hylinae: phylogenetic analysis and taxonomic revision. Bulletin of the American Museum of Natural History 294:1–240.

Felsenstein, J. 1985. Phylogenies and the comparative method. American Naturalist 125:1–15.

Frost, D. R., T. Grant, J. Faivovich, R. Bain, A. Haas, C. F. B. Haddad, R. O. De Sá, et al. 2006. The amphibian tree of life. Bulletin of the American Museum of Natural History 297:1–370.

Frýdlová, P., and D. Frynta. 2010. A test of Rensch's rule in varanid lizards. Biological Journal of the Linnean Society 100:293–306.

Garland, T., P. H. Harvey, and A. R. Ives. 1992. Procedures for the analysis of comparative data using phylogenetically independent contrasts. Systematic Biology 41:18–32.

Gaston, K., and T. Blackburn. 2000. Pattern and process in macroecology. Wiley, Hoboken, NJ.

Girish, S., and S. K. Saidapur. 2000. Interrelationship between food availability, fat body, and ovarian cycles in the frog, *Rana tigrina,* with a discussion on the role of fat body in anuran reproduction. Journal of Experimental Zoology 286:487–493.

Haddad, C. F. B. 1991. Satellite behavior in the Neotropical treefrog *Hyla minuta.* Journal of Herpetology 25:226–229.

Haddad, C. F. B., and C. P. A. Prado. 2005. Reproductive modes in frogs and their unexpected diversity in the Atlantic forest of Brazil. BioScience 55:207–217.

Han, X., and J. Fu. 2013. Does life history shape sexual size dimorphism in anurans? a comparative analysis. BMC Evolutionary Biology 13:27.

Harvey, P. H., and M. D. Pagel. 1991. The comparative method in evolutionary biology. Oxford University Press, Oxford.

Hendry, C. R., T. J. Guiher, and R. A. Pyron. 2014. Ecological divergence and sexual selection drive sexual size dimorphism in New World pitvipers (Serpentes: Viperidae). Journal of Evolutionary Biology 27:760–771.

Howard, R. D. 1984. Alternative mating behaviors of young male bullfrogs. American Zoologist 24:397–406.

Howard, R. D., and A. G. Kluge. 1985. Proximate mechanisms of sexual selection in wood frogs. Evolution 39:260–277.

Howard, R. D., H. H. Whiteman, and T. I. Schueller. 1994. Sexual selection in American toads: a test of a good-genes hypothesis. Evolution 48:1286–1300.

Isaac, J. L. 2005. Potential causes and life-history consequences of sexual size dimorphism in mammals. Mammal Review 35:101–115.

Kaplan, R. H. 1987. Developmental plasticity and maternal effects of reproductive characteristics in the frog, *Bombina orientalis.* Oecologia (Berlin) 71:273–279.

Katsikaros, K., and R. Shine. 1997. Sexual dimorphism in the tusked frog, *Adelotus brevis* (Anura: Myobatrachidae): the roles of natural and sexual selection. Biological Journal of the Linnean Society 60: 39–51.

Kratochvíl, L., and D. Frynta. 2002. Body size, male combat and the evolution of sexual dimorphism in eublepharid geckos (Squamata: Eublepharidae). Biological Journal of the Linnean Society 76:303–314.

Kupfer, A. 2007. Sexual size dimorphism in amphibians: an overview. Pages 50–59 *in* D. J. Fairbairn, W. Blanckenhorn, and T. Székely,

eds. Sex, size and gender roles: evolutionary studies of sexual size dimorphism. Oxford University Press, Oxford.

———. 2009. Sexual size dimorphism in caecilian amphibians: analysis, review and directions for future research. Zoology 112:362–369.

Liao, W. B., Y. Zeng, C. Q. Zhou, and R. Jehle. 2013. Sexual size dimorphism in anurans fails to obey Rensch's rule. Frontiers in Zoology 10:10.

Lips, K. R. 2005. Quantification of selection and male reproductive success in *Hyla calypsa,* a Neotropical treefrog. Pages 215–226 *in* M. A. Donnelly, B. I. Crother, C. Guyer, M. H. Wake, and M. E. White, eds. Ecology and evolution in the tropics. University of Chicago Press, Chicago.

Lovich, J. E., and J. W. Gibbons. 1992. A review of techniques for quantifying sexual size dimorphism. Growth Development and Aging 56:269–281.

Lu, D., C. Q. Zhou, and W. B. Liao. 2014. Sexual size dimorphism lacking in small mammals. North-Western Journal of Zoology 10: 53–59.

Lu, X., W. Chen, L. X. Zhang, and X. Y. Ma. 2010. Mechanical constraint on size-assortative paring success in a temperate frog: an experimental approach. Behavioural Processes 85:181–184.

Lu, X., X. Ma, Y. Li, and L. Fan. 2008. Breeding behavior and mating system in relation to body size in *Rana chensinensis,* a temperate frog endemic to northern China. Journal of Ethology 27:391–400.

Maddison, W. P., and D. R. Maddison. 2011. Mesquite: a modular system for evolutionary analysis. Version 2.75. http://mesquiteproject.org.

Martins, M., and C. F. B. Haddad. 1988. Vocalizations and reproductive behaviour in the smith frog, *Hyla faber* Wied (Amphibia: Hylidae). Amphibia-Reptilia 9:49–60.

Monnet, J.-M., and M. I. Cherry. 2002. Sexual size dimorphism in anurans. Proceedings of the Royal Society B: Biological Sciences 269:2301–2307.

Nali, R. C., and C. P. A. Prado. 2012. Habitat use, reproductive traits and social interactions in a stream-dweller treefrog endemic to the Brazilian Cerrado. Amphibia-Reptilia 33:337–347.

Nali, R. C., K. R. Zamudio, C. F. B. Haddad, and C. P. A. Prado. 2014. Data from: Size-dependent selective mechanisms on males and females and the evolution of sexual size dimorphism in frogs. American Naturalist, Dryad Digital Repository, http://dx.doi.org/10.5061/dryad.270sf.

Nascimento, L. B, U. Caramaschi, and C. A. Gonçalves-Cruz. 2005. Taxonomic review of the species groups of the genus *Physalaemus* Fitzinger, 1826 with revalidation of the genera *Engystomops* Jiménez-de-la-Espada, 1872 and *Eupemphix* Steindachner, 1863 (Amphibia, Anura, Leptodactylidae). Arquivos do Museu Nacional 63:297–320.

Orrico, V. G. D. 2012. The phylogeny of *Dendropsophus* Fitzinger, 1843. PhD diss. Instituto de Biociências, Universidade Estadual Paulista, Rio Claro, São Paulo, Brazil.

Ota, K., M. Kohda, and T. Sato. 2010. Why are reproductively parasitic fish males so small? influence of tactic-specific selection. Naturwissenschaften 97:1113–1116.

Pagel, M. 1994. Detecting correlated evolution on phylogenies: a general method for the comparative analysis of discrete characters. Proceedings of the Royal Society B: Biological Sciences 255:37–45.

Peloso, P. L., M. J. Sturaro, M. C. Forlani, P. Gaucher, A. P. Motta, and W. C. Wheeler. 2014. Phylogeny, taxonomic revision, and character evolution of the genera Chiasmocleis and Syncope (An-

ura, Microhylidae) in Amazonia, with descriptions of three new species. Bulletin of the American Museum of Natural History 386: 1–112.

Pianka, E. R. 1970. On *r*- and *K*-selection. American Naturalist 102: 592–597.

Pincheira-Donoso, D., and T. Tregenza. 2011. Fecundity selection and the evolution of reproductive output and sex-specific body size in the *Liolaemus* lizard adaptive radiation. Evolutionary Biology 38:197–207.

Praderio, M. J., and M. D. Robinson. 1990. Reproduction in the toad *Colostethus trinitatus* (Anura: Dendrobatidae) in a northern Venezuela seasonal environment. Journal of Tropical Ecology 6:333–341.

Prado, C. P. A., and C. F. B. Haddad. 2003. Testes size in leptodactylid frogs and occurrence of multimale spawning in the genus *Leptodactylus* in Brazil. Journal of Herpetology 37:354–362.

———. 2005. Size-fecundity relationships and reproductive investment in female frogs in the Pantanal, South-Western Brazil. Herpetological Journal 15:181–189.

Prado, C. P. A., M. Uetanabaro, and C. F. B. Haddad. 2005. Breeding activity patterns, reproductive modes, and habitat use by anurans (Amphibia) in a seasonal environment in the Pantanal, Brazil. Amphibia-Reptilia 26:211–221.

Pupin, N. C., J. L. Gasparini, R. P. Bastos, C. F. B., and C. P. A. Prado. 2010. Reproductive biology of an endemic *Physalaemus* of the Brazilian Atlantic forest and the trade-off between clutch and egg size in terrestrial breeders of the *P. signifer* group. Herpetological Journal 20:147–156.

Purvis, A. 1995. A composite estimate of primate phylogeny. Philosophical Transactions of the Royal Society B: Biological Sciences 348:405–421.

Purvis, A., and T. Garland. 1993. Polytomies in comparative analyses of continuous characters. Systematic Biology 42:569–575.

Pyron, R. A, and J. J. Wiens. 2011. A large-scale phylogeny of Amphibia including over 2800 species, and a revised classification of extant frogs, salamanders and caecilians. Molecular Phylogenetics and Evolution 61:543–583.

Ralls, K. 1977. Sexual dimorphism in mammals: avian models and unanswered questions. American Naturalist 111:917–938.

Reading, C. J., and R. T. Clarke. 1988. Multiple clutches, egg mortality and mate choice in the mid-wife toad, *Alytes obstetricans*. Amphibia-Reptilia 9:357–364.

Reeve, J. P., and D. J. Fairbairn. 1999. Change in sexual size dimorphism as a correlated response to selection on fecundity. Heredity 83:697–706.

Rensch, B. 1950. Die Abhangigkeit der relativen sexualdifferenz von der Korpergrole. Bonner Zoologische Beitrage 1:58–69

Ricklefs, R. E., and A. Scheuerlein. 2001. Comparison of aging-related mortality among birds and mammals. Experimental Gerontology 36:845–857.

Salthe, S. N., and W. E. Duellman. 1973. Qualitative constraints associated with reproductive mode in anurans. Pages 229–249 *in* J. Vial, ed. Evolutionary biology of the anurans: contemporary research on major problems. University of Missouri Press, Columbia.

Serrano-Meneses, M. A., A. Córdoba-Aguilar, M. Azpilicueta-Amorín, E. González-Soriano, and T. Székely. 2008. Sexual selection, sexual size dimorphism and Rensch's rule in Odonata. Journal of Evolutionary Biology 21:1259–1273.

Shine, R. 1979. Sexual selection and sexual dimorphism in the Amphibia. Copeia 1979:297–306.

———. 1989. Ecological causes for the evolution of sexual dimorphism: a review of the evidence. Quarterly Review of Biology 64: 419–461.

———. 1994. Sexual size dimorphism in snakes revisited. Copeia 1994:326–346.

Shine, R., D. O'Connor, M. P. Lemaster, and R. T. Mason. 2001. Pick on someone your own size: ontogenetic shifts in mate choice by male garter snakes result in size-assortative mating. Animal Behaviour 61:1133–1141.

Smith, R. J. 1999. Statistics of sexual size dimorphism. Journal of Human Evolution 36:423–459.

Stuart-Fox, D. 2009. A test of Rensch's rule in dwarf chameleons (*Bradypodion* spp.), a group with female-biased sexual size dimorphism. Evolutionary Ecology 23:425–433.

Székely, T., R. P. Freckleton, and J. D. Reynolds. 2004. Sexual selection explains Rensch's rule of size dimorphism in shorebirds. Proceedings of the National Academy of Sciences of the USA 101: 12224–12227.

Tejedo, M. 1988. Fighting for females in the toad *Bufo calamita* is affected by the operational sex ratio. Animal Behaviour 36:1765–1769.

Vieites, D. R., S. Nieto-Roma, M. Barluenga, A. Palanca, M. Vences, and A. Meyer. 2004. Post-mating clutch piracy in an amphibian. Nature 431:305–308.

Voituron, Y., M. de Fraipont, J. Issartel, O. Guillaume, and J. Clobert. 2011. Extreme lifespan of the human fish (*Proteus anguinus*): a challenge for ageing mechanisms. Biology Letters 7:105–107.

Wells, K. D. 1977. The social behaviour of anuran amphibians. Animal Behaviour 25:666–693.

———. 1979. Reproductive behavior and male mating success in a Neotropical toad, *Bufo typhonius*. Biotropica 11:301–307.

———. 2007. The ecology and behavior of amphibians. University of Chicago Press, Chicago.

Wiens, J. J., C. A. Kuczynski, X. Hua, and D. Moen. 2010. An expanded phylogeny of treefrogs (Hylidae) based on nuclear and mitochondrial sequence data. Molecular Phylogenetics and Evolution 55:871–882.

Wogel, H., and J. P. Pombal Jr. 2007. Comportamento reprodutivo e seleção sexual em *Dendropsophus bipunctatus* (Spix, 1824) (Anura, Hylidae). Papéis Avulsos de Zoologia 47:165–174.

Woolbright, L. L. 1983. Sexual selection and size dimorphism in anuran amphibia. American Naturalist 121:110–119.

Zamudio, K. R. 1998. The evolution of female-biased sexual size dimorphism: a population-level comparative study in horned lizards (*Phrynosoma*). Evolution 52:1821–1833.

Zamudio, K. R., and L. M. Chan. 2008. Alternative reproductive tactics in amphibians. Pages 300–331 *in* R. F. Oliveira, M. Taborsky, and H. J. Brockmann, ed. Alternative reproductive tactics. University of Cambridge Press, Cambridge.

Zhang, L., and X. Lu. 2013. Sexual size dimorphism in anurans: ontogenetic determination revealed by an across-species comparison. Evolutionary Biology 40:84–91.