Evolutionary allometry of sexual dimorphism of jumping performance in anurans

Running Title: Allometry of jumping dimorphism in anurans

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Abstract

Sexual dimorphism is a common feature in animals, yet the degree of sexual dimorphism is not constant across taxa. Sometimes the magnitude of sexual dimorphism varies systematically with body size, resulting in evolutionary allometry of sexual dimorphism. While such patterns are commonly investigated for traits such as overall size, allometric variation in sexual dimorphism of other traits remains underexplored. Here, we characterize the evolutionary allometry of sexual dimorphism in a functional phenotypic trait (jumping performance) in anurans. Using morphology and anatomical approximations of jumping performance across 146 species, we test for evidence of the correlated selection model of sexual dimorphism evolution. We analyze patterns of evolutionary allometry of sexual dimorphism in key phenotypic traits, including: body size (snout-vent length and mass), relative leg length, relative leg muscle volume, mass-specific peak jumping energy, and peak jumping velocity. We find that as previously reported, sexual size dimorphism scales isometrically between species and is independent of sexual dimorphism in jumping performance. Notably, however, we found significant trends in the evolutionary allometry of sexual dimorphism in relative limb length, and in two components of jumping performance. Additionally, we found greater rates of evolution for females versus males in relative limb length, but not jumping performance. We also observed that the allometric trends in limb length dimorphism were related to performance allometry. Sexual dimorphism in jumping performance increased in species with high performance while females in high performance species displayed increased relative limb length. Thus, we hypothesize that selection acting on functional performance explains allometric patterns of sexual dimorphism in morphology. We discuss biological implications of our findings in relation to natural and sexual selection. This study highlights the types of insights one may gain by studying the allometry of sexual dimorphism from a functional perspective to learn about both patterns and processes in evolution.

Introduction

Sexual dimorphism is a common feature in animals and is documented across a variety of groups. Instances of sexual dimorphism may include sexual differences in traits such as color (Bell and Zamudio 2012), ornamentation (Stuart–Fox and Ord 2004), body size (Cox et al. 2007), or even shape (Kaliontzopoulou et al. 2007). Some traits tend to be exaggerated in males, while others tend to be exaggerated in females (Berry and Shine 1980; Emlen et al. 2005). Often, the evolution of sexual dimorphism is the result of differential selection pressures exerted on males and females, stemming from both natural and sexual selection. For example, male-male competition (Baeza and Asorey 2012) and mate choice (Hunt et al. 2009) can each lead to the evolution of sexual dimorphism, by applying greater directional selection on traits in males as compared with females. Conversely, forces such as fecundity selection may exert a greater pressure on female size as compared with male size, resulting in female-biased sexual size dimorphism (Pincheira-Donoso and Hunt 2017). Indeed, numerous selection-based scenarios can lead to the evolution of sexual dimorphism (e.g., differences in mortality rate, selection pressures due to habitat use, etc.), provided that there exists differential selection between males and females of the same species (Anderson and Vitt 1990; Kaliontzopoulou et al. 2015).

Microevolutionary studies of sexual dimorphism commonly focus on characterizing the extent of sexual dimorphism in particular taxa and elucidating the selective forces that may have generated sex-specific differences (Lovich and Gibbons 1992; Fairbairn and Preziosi 1996; Blanckenhorn 2005). However, when comparisons among taxa are made, it is often observed that the degree of sexual dimorphism is not consistent, but rather varies across species and clades (Selander 1966; Berry and Shine 1980; Owens and Hartley 1998; Blanckenhorn et al. 2006; De Lisle and Rowe 2013; Kaliontzopoulou et al. 2015). Sometimes, this diversity of sexual dimorphism may reflect variation in intraspecific allometry. This scenario posits that the intraspecific relationship between body size and sex-specific differences is reflective of trends across taxa in the degree of sexual dimorphism relative to a species' body size; resulting in evolutionary allometry of the degree of sexual dimorphism across taxa (Reiss 1986; Bonduriansky 2007; De Lisle and Rowe 2013). Alternatively, differences in the intensity of natural or sexual selection among taxa may result in differing degrees of sexual dimorphism across species (Blanckenhorn et al. 2006; Kaliontzopoulou et al. 2015), which may also vary with a species' body size and explain interspecific variation. Thus, an important macroevolutionary question is to identify the extent to which patterns of sexual dimorphism vary across taxa, and why allometric trends in the magnitude of sexual dimorphism are observed (e.g., Rensch 1960).

To this end, numerous studies have investigated interspecific trends in sexual dimorphism. In some lineages, the magnitude of sexual dimorphism does not vary with overall species' body size, suggesting that the degree of sexual dimorphism is isometric (Astúa 2010; Liao et al. 2013; Hirst and Kiørboe 2014; Nali et al. 2014; Johnson et al.

2017; Portik et al. 2020). Such patterns may result when males and females respond similarly to selection, such that their phenotypic proportions scale evenly with respect to each other (isometry). In other cases, the magnitude of sexual dimorphism covaries systematically with overall body size, resulting in allometric trends at the interspecific level. Two patterns are possible. First, when male size varies more across taxa than does female size (Fairbairn 1997), the degree of sexual dimorphism changes allometrically with overall size. This hyperallometry of sexual dimorphism (Abouheif and Fairbairn 1997; Fairbairn 1997; also Rensch 1960) describes cases where the degree of male-biased sexual dimorphism increases with increasing body size across male-biased species, and where female-biased sexual dimorphism increases with decreasing body size in female-biased species (see Fig. 1). Examples of hyperallometry of sexual dimorphism are found in, for example, insects, birds, mammals, and turtles (Abouheif and Fairbairn 1997; Dale et al. 2007; Ceballos et al. 2013; Johnson et al. 2017). Alternatively, hypoallometry describes the opposite pattern (Burbrink and Futterman 2019; Peñalver-Alcázar et al. 2019); where variation in females is greater than in males, resulting in the allometry of sexual dimorphism that runs counter to hyperallometry (i.e., female-biased sexual dimorphism increases with increasing size, and male-biased sexual dimorphism increases with decreasing size: see Fig. 1). Many hypotheses have been proposed to explain the evolution of allometry of sexual dimorphism, including various types of sexual selection, differential natural selection (e.g., reproductive roles or resource utilization), and genetic correlations among the sexes (Colwell 2000; Dale et al. 2007; Serrano-Meneses et al. 2008; Cabrera et al. 2013).

Correlational selection (Zeng 1988; Fairbairn 1997) is a quantitative genetic model that describes the evolution of allometry of sexual dimorphism, independent of genetic correlations among the sexes. Generally, this model predicts the evolution of interspecific allometry of sexual dimorphism following correlated male-female responses to selective pressures. Such a correlation implies that the optimal trait value in one sex is affected by the mean trait value in the other sex. Therefore, changes in one sex result in a correlated change in the other. The correlational selection model predicts hyperallometry as a result of diversifying selection on males with high trait values or females with low trait values. Conversely, the model predicts hypoallometry if diversifying selection acts on females with high trait values, or males with low trait values. Importantly, this model also predicts greater interspecific variance of one sex over the other. This is equivalent to diversifying selection acting on the trait variance generated through a higher rate of phenotypic evolution in one sex compared to the other. The evolution of sexual dimorphism arising from sexual differences in rates of phenotypic evolution have been identified empirically, as predicted from theory (see Lande 1980; Reeve and Fairbairn 2001; Ceballos et al. 2013; Cheng and Houle 2020).

Much of the literature linking allometry and sexual dimorphism overwhelmingly documents patterns of sexual dimorphism in body size. However, natural and sexual selection may result in sexual dimorphism in traits other than body size. These include, for example, coloration, behavioral, physiological traits, or shape (Endler 1984; Price and Birch 1996; Adams et al. 2020; Logan et al. 2021). Importantly, behavioral or functional traits, such as climbing or jumping, which are typically characterized as measures of maximum or ‘peak’ performance, will respond directly to selection (Arnold

1983). This is because in many situations, organismal performance is the substrate upon which selection acts (Arnold 1983). Unfortunately, although such performance traits serve a clear functional role in organismal survival, and frequently covary with body size, patterns of evolutionary allometry of sexual dimorphism in performance traits have generally been unexamined. This, then, provides the opportunity to understand how selection on both body size and functional behaviors have resulted in diverse patterns of sexual dimorphism. Investigating the relationship between allometry and sexual dimorphism in traits other than body size is crucial for unveiling how selection can produce diverse forms, some of which have evolved repeatedly across the animal tree of life.

Anurans are one ideal system for studying the drivers of interspecific allometry of sexual dimorphism. Anuran amphibians comprise >7,000 species (AmphibiaWeb 2021) split between several major superfamilies with great morphological and ecological diversity. At a coarse level, two major groups of anurans include the Hyloidea and Ranoidea. The group Hyloidea is globally distributed and generally encompasses arboreal (though there are many exceptions) treefrogs with long legs. Included within Hyloidea are true toads of the family Bufonidae which are generally terrestrial, stout, and apt hoppers. Ranoid frogs generally include microhylid and ranid frogs which tend to have rounded bodies with short limbs and streamlined bodies with long muscular legs, respectively. Notably, Ranoidea includes some of the largest frogs in the world (e.g., *Conraua*). Anurans are comprised of many other superfamilies with relatively fewer species in each when compared to Hyloidea and Ranoidea. Included in these other group are species which have strong aquatic or terrestrial habits (e.g., Pipoidea and Pelobatoidea) or unique reproductive modes as seen in Midwife Toads and Tailed Frogs (Discoglossoidea and Leiopelmatoidea). Importantly, patterns of sexual size dimorphism, ecology, life history, and behavior are well documented in anurans. >90% of species exhibit sexual size dimorphism (De Lisle and Rowe 2013; Han and Fu 2013; Nali et al. 2014). Furthermore, fecundity selection has been linked to the evolution of sexual size dimorphism in some species (Han and Fu 2013) and this may be important in the evolution of interspecific allometry. Furthermore, the biomechanics of jumping performance is well-studied in this group, including recent advancements that allow the approximation of jumping performance from anatomical information (Juarez et al. 2020).

In this study, we evaluate the evolution of jumping performance allometry in anurans. First, we revisit patterns of sexual size dimorphism, confirming isometric scaling between males and females across species. Next, we test whether patterns of sexual dimorphism in jumping simply covary with size and reflect patterns of sexual size dimorphism. Furthermore, we characterize patterns of sexual dimorphism in jumping-related morphology and jumping performance using novel jumping approximation methods to characterize two aspects of peak jumping performance (velocity and energy) and examine interspecific allometric trends in each. Two alternative evolutionary hypotheses were evaluated: 1) jumping performance displays isometry, and 2) jumping performance displays allometry, potentially associated with increased evolutionary rates in one sex. We test the hypothesis that allometric patterns of sexual dimorphism are the result of diversifying selection linked to increased rates of evolution as predicted under the correlational selection model of interspecific allometry.

Materials and Methods

Data Collection

We characterized evolutionary trends of the allometry of sexual dimorphism for several morphological and functional traits, including two measures of body size (snout-vent length and body mass), two morphological traits associated with jumping (limb muscle volume and limb length) and two functional performance estimates (mass-specific peak jumping energy and peak jumping velocity). Data analyzed here represented male and female mean values from 146 species obtained from 2,592 individual museum specimens (complete details of all measurement procedures are found in the Appendix). Anatomical approximations of peak jumping performance (velocity and energy) at take-off were obtained using equations 1 and 3 of Juarez et al. (2020), based upon a series of anatomical measurements, as per below. To obtain these estimates, we measured body mass, snout-vent length, muscle volume, and limb length (L_{com}) from each individual. Briefly, L_{com}, the distance from the toes to the center of mass, was found as the summation of the sacral length and hindlimb length (Peplowski and Marsh 1997; Juarez et al. 2020), and limb muscle volume was obtained as the bilateral sum of the muscle volume of the fore and hind limbs: $v_{muscle} = 2(\frac{2}{3}\pi r_1 r_2 H_1 + \frac{2}{3}\pi r_3 r_4 H_2)$, where r_1 and r_2 are the radii represented by half the muscle depth and width of the thigh, r_3 and r_4 are half the muscle depth and width of the calf, and H_1 and H_2 are cone heights represented by half the femur and tibiofibula lengths, respectively (for additional details see Appendix).

From these measures, approximations of jumping velocity and jumping energy were then obtained (see Juarez et al. 2020). Specifically, the anatomical approximation for peak jumping velocity ($v_{Appx.}$) was obtained as follows:

$$v_{Appx.} = \sqrt{\frac{2L_{com}F_{PCSA}}{m}}, \tag{1}$$

where L_{com} is as above, F_{PCSA} is muscle force, here estimated as the muscle volume (v_{muscle}), and m is body mass. Likewise, the anatomical approximation for peak jumping energy ($E_{Appx.}$) was obtained as:

$$E_{Appx.} = L_{com}F_{PCSA}. \tag{2}$$

Since several of these traits covary strongly with body size (Moen 2019; Juarez et al. 2020), interpretations of sex-specific patterns are compromised. Thus, as is common in the field (e.g., Astley 2016), we size-standardized L_{com} using snout-vent length, and muscle volume and jumping energy using body mass; the resulting relative muscle volume, relative L_{com}, and mass-specific jumping energy were used in subsequent analyses. Finally, all traits were natural log transformed before estimating species means for each sex. All data may be found in Dryad (XXX upon manuscript acceptance).

Data Analysis and Visualization

To evaluate interspecific trends in sexual dimorphism, we used a series of phylogenetic comparative analyses. First, morphological and functional performance data were matched to a time-dated molecular phylogeny for anurans (Fig. 2; Feng et al. 2017). The phylogeny was pruned to match the dataset using the *treedata* function in the *geiger* package version 2.0.7 (Harmon et al. 2008) and plotted using the *phytools* package version 0.7-70 (Revell 2012). We estimated phylogenetic signal (K) for jumping performance and relevant morphological traits using the *physignal* function, with 10,000 random permutations of the data to estimate significance level, in the *geomorph* package version 4.0.0.99 (Adams 2014; Adams et al. 2021). We tested whether sexual dimorphism of jumping performance covaries with sexual size dimorphism by regressing the natural log of jumping energy and velocity against the natural log of sexual size dimorphism. We estimated sexual size dimorphism using the appropriate measure of body size (Astley 2016): mass and snout-vent length for each of jumping energy and velocity, respectively. Next, interspecific patterns in the allometry of sexual dimorphism were evaluated for each trait by regressing natural log male values onto natural log female values (see Fig. 1). We incorporated phylogenetic covariance in these models through phylogenetic generalized least squares (PGLS), implemented using the *gls* function in the R package *nlme* version 3.1-152 (R Core Team 2020; Pinheiro et al. 2021). Here, phylogenetic non-independence was estimated using a phylogenetic covariance matrix (Felsenstein 1985; Martins and Hansen 1997) obtained under Brownian motion, based on the phylogeny of Feng et al. (2017). Upon estimation of model parameters, we then used a slope test (t-test) to determine whether trends in sexual dimorphism differed from isometry ($\beta_0 = 1.0$). The test statistic in these models is $t = \frac{\beta - \beta_0}{SE}$, where β is the estimated slope, β_0 is the null hypothesis, and SE is the standard error of β. For tests where the null hypothesis is isometry, $\beta_0 = 1.0$.

Statistical evaluation of allometric patterns involves phylogenetic regression and a slope test to determine if the true slope differs from $\beta_0 = 1$. There has been considerable discussion in the allometric literature as to whether model I or model II regression is more appropriate, in part because species values for both males and females are measured with error (see e.g., Wharton et al. 2006; Bonduriansky 2007; Ives et al. 2007; Hansen and Bartoszek 2012; Killmer and Rodríguez 2017; Adams et al. 2020). However, as pointed out by Kilmer and Rodríguez (2017), when measurement error variance is small in proportion to total variance, slope attenuation is limited, and slopes from model I regression are robust. Additionally, when biological variation and measurement error is present in interspecific data, slope estimates from model II regression are strongly biased (Hansen and Bartoszek 2012). For these reasons, we performed model I PGLS regression here, assigning the larger sex (females) as the independent variable (following Liao et al 2013 and Portik et al 2020). Additionally, we implemented phylogenetic regressions with intraspecific sampling error (see Appendix), to evaluate the robustness of our findings while incorporating intraspecific variation. Finally, we compared male and female rates of evolution for jumping performance (analyzed multivariately) and relevant morphological variables using the *compare.multi.evol.rates* function (see Adams 2013; Denton and Adams 2015) in *geomorph*. We used 10,000 random permutations to evaluate significance. All analyses were accomplished in R version 4.0.3 (R Core Team 2020). All code associated with this manuscript may be found at https://github.com/bhjuarez/allometry-dimorphism-jumping (upon manuscript acceptance).

Results

General trends of sexual dimorphism (the log ratio of males to females), for each trait are found in Fig. 3. Here the distribution of traits indicated female-biased dimorphism in most morphological traits: body size (snout-vent length: mean ± standard error = -0.14 ± 0.01, median = -0.14), body mass (mean = -0.44 ± 0.04; median = -0.43), relative muscle volume (mean = -0.37 ± 0.05, median = -0.32), with the exception of relative L_{com} (mean = 0.01 ± 0.00, median = 0.01). However, when functional performance traits were examined, both exhibited male-biased dimorphism in jumping performance; including mass-specific peak jumping energy (mean = 0.06 ± 0.01, median = 0.08) and peak jumping velocity (mean = 0.03 ± 0.01, median = 0.04). Additionally, we found that male and female morphological and performance traits all featured significant and similar levels of phylogenetic signal including body mass ($\mathrm{K}_{Male} = 0.32, P = 0.0002$; $\mathrm{K}_{Female} = 0.35, P < 0.0001$), snout-vent length ($\mathrm{K}_{Male} = 0.32, P = 0.0002$; $\mathrm{K}_{Female} = 0.35, P < 0.0001$), relative L_{com} ($\mathrm{K}_{Male} = 0.33, P = 0.0003$; $\mathrm{K}_{Female} = 0.40, P < 0.0001$), relative muscle volume ($\mathrm{K}_{Male} = 0.34, P < 0.0001$; $\mathrm{K}_{Female} = 0.35, P < 0.0001$), and jumping performance ($\mathrm{K}_{Male} = 0.29, P = 0.0016$; $\mathrm{K}_{Female} = 0.34, P = 0.0003$). Finally, we found that sexual size dimorphism is not significantly related to sexual dimorphism of jumping performance (mass-specific energy: F = 2.20, r^2 = 0.02, df = 144, P = 0.1406; velocity: F = 0.02, r^2 = 0.00, df = 144, P = 0.8896).

When allometric trends were evaluated (Fig. 4), all traits displayed significant associations between male and female values: snout-vent length (F = 585.02, r^2 = 0.80, df = 144, P < 0.0001), body mass (F = 556.52, r^2 = 0.79, df = 144, P < 0.0001), relative muscle volume (F = 590.38, r^2 = 0.80, df = 144, P < 0.0001), relative L_{com} (F = 882.16, r^2 = 0.86, df = 144, P < 0.0001), mass-specific peak jumping energy (F = 497.18, r^2 = 0.78, df = 144, $P < 0.0001$), and peak jumping velocity ($F = 2531.75$, $r^2 = 0.78$, df = 144, $P < 0.0001$). As with previous studies, evolutionary patterns of body size dimorphism were isometric, implying that the degree of sexual size dimorphism did not differ systematically with overall organismal size (snout-vent length: $\beta = 0.96$ (95% Confidence Interval = 0.88, 1.03), $t = -1.09$, $P < 0.220$; body mass: $\beta = 0.95$ (0.87, 1.03), $t = -1.16$, $P < 0.203$). Additionally, relative muscle volume exhibited isometry (muscle volume: $\beta = 0.928$ (0.85, 1.00), $t = -1.88$, $P < 0.069$). However, relative limb length displayed an allometric trend of sexual dimorphism with a slope of less than 1.0 (L_{com}: $\beta = 0.843$ (0.79, 0.90), $t = -5.51$, $P < 0.0001$). Species that seem to be driving this pattern include the ranoid frogs *Sylvirana guentheri* and *Strongylopus grayii*, and the hyloid frogs *Litoria caerulea* and *Pseudis paradoxa* in which females tend to have an L_{com} 7–20% greater than males at a given body size. Likewise, both mass-specific jumping energy and jumping velocity displayed significant allometry, with slopes less than 1.0 (energy: $\beta = 0.87$ (0.79, 0.94), $t = -3.38$, $P < 0.002$; velocity: $\beta = 0.87$ (0.79, 0.94), $t = -3.38$, $P < 0.001$). Notable species include *Astylosternus diadematus*, *Rana draytonii*, and *Heleophryne purcelli* whose females exhibit velocity approximation values that are 2–5% greater than males. Comparisons of these results with models incorporating intraspecific sampling error yielded identical interpretations and biological conclusions (see Appendix for detailed results). We determined through tests of evolutionary rate that female L_{com} evolves faster than male L_{com} (σ_F^2 = 0.026, σ_M^2 = 0.022, P = 0.0032). However, we found that male and female jumping performance evolves at statistically similar rates between the sexes (σ_F^2 = 0.142, σ_M^2 = 0.138, P = 0.7295).

Discussion

The evolutionary allometry of sexual dimorphism is important for understanding the ways in which patterns of sexual dimorphism are generated and maintained in different groups. However, the vast majority of studies on the allometry of sexual dimorphism focus on body size. In this study, we examined such interspecific trends in anurans, corroborating previous findings that anurans generally display female-biased size distributions (Shine 1979; Monnet and Cherry 2002; Silva et al. 2020). Our findings also provide the first evidence of allometry in the sexual dimorphism of jumping traits in anurans. We found support for the correlated selection model of evolutionary allometry of sexual dimorphism. These findings are inconsistent with a model of sexual dimorphism evolution which predicts allometry of sexual dimorphism simply through genetic correlations among the sexes. Histograms of sexual dimorphism in body size and key jumping-related traits showed clear dimorphic patterns consistent with the findings in this study. Here, we also corroborate previous findings of isometry of sexual dimorphism in body size (Liao et al. 2013; Nali et al. 2014; Portik et al. 2020). Likewise, we found the same isometric pattern of sexual dimorphism in leg muscle volume. However, we discovered a hypoallometric pattern of limb length (L_{com}), mass-specific peak jumping energy, and peak jumping velocity, with significant differences in the rate of L_{com} evolution between males and females. L_{com} evolved faster in females relative to males. We rejected the hypothesis that patterns of sexual dimorphism in jumping performance simply reflect patterns of sexual size dimorphism.

Anurans generally exhibit female-biased sexual size dimorphism (Nali et al. 2014), and our finding of evolutionary isometry of sexual size dimorphism is consistent with an interpretation that although females tend to be larger, this pattern does not vary across the range of sizes among species. Thus, our findings are consistent with those of Nali et al. (2014) and Liao et al. (2013), who also found isometric patterns of size dimorphism in anurans. Other studies (Han and Fu 2013) have reported mixed results, with weak evidence of hyperallometry of sexual size dimorphism when some data are excluded, but isometry of body dimorphism when all species are included (Portik et al. 2020). Thus, our results contribute to the growing body of evidence suggesting that sexual size dimorphism is generally consistent with isometry in anurans.

By contrast, we found patterns of evolutionary allometry in L_{com} and jumping performance (Fig. 4), suggesting that the degree of sexual dimorphism in jumping differs systematically across the range of L_{com} and jumping ability. Furthermore, tests of evolutionary rate, under the expectation of the correlational selection model that the sexes differ in trait variance, reveal that diversifying selection on female L_{com} drives the evolutionary allometry of L_{com} and jumping performance. These patterns were significantly hypoallometric and suggested that males and females of species with generally longer legs (relative to other species) are under natural or sexual selection for possessing disproportionately longer legs. This may be the case if females are evolving longer legs to overcome increases in body size. Corroborating evidence for this hypothesis is manifested in the research showing that longer limbs lead to increased jumping performance (Peplowski and Marsh 1997; Juarez et al. 2020). Furthermore, the evolution of L_{com} might also be related to the evolution of size and overcoming the biomechanical cost of carrying large egg masses, as fecundity selection has been linked to sexual size dimorphism in some species (Han and Fu 2013) and carrying large egg masses have been shown to decrease overall jumping performance in lizards (Kuo et al. 2011). Continuing the logic of the correlational selection model, species with low values of L_{com} do not seem to be under selection for possessing shorter or longer limbs, relative to body size. Visually, this trend is not obvious from the allometry plots (Fig. 4), since there do not seem to be many species at higher trait values that are below the 1:1 line of isometry. This is explained by the fact that these traits show significant phylogenetic signal, thus a plot of the logged data (versus interpretation of phylogenetic models) is insufficient for explaining evolutionary patterns under the correlational selection model. The hypoallometric pattern describing jumping performance also reveals that species with overall higher jumping performance are associated with females with greater performance than males, and the converse is true in species with overall lower jumping performance.

Interestingly, we did not find differences in rate of evolution of jumping performance between the sexes and this pattern is inconsistent with diversifying selection driving the evolution of the allometry of sexual dimorphism under the correlational selection model. This results from the lack of greater interspecific variation in one sex over the other as determined through evolutionary rate analyses. Thus, another mechanism might be driving the evolution of allometry of sexual dimorphism of jumping. Alternatively, the correlated selection model assumes that diversifying selection acts only on one sex and not the other, leaving the other sex to evolve by indirect (correlated) selection alone (see Fairbairn 1997). It is unlikely that female jumping performance but not male jumping performance is under selection in nature given that jumping is a behavior with many uses including locomotion, escaping predation, and prey capture. For example, males are known to face increased predation risks relative to females, especially while calling to attract mates, and this has been documented extensively (Ryan et al. 1982; Rand 1985; Bastos and Haddad 1997). Male jumping performance would be under especially strong selection if calling was energetically costly, resulting in a net metabolic cost to the calling animal as found in male anurans (Taigen and Wells 1985; Prestwich 1994). Increased jumping performance in this case would limit costs associated with predator evasion. Thus, it should be expected that jumping performance is under the influence of several distinct selective forces (which might vary between species), resulting in a 'many-to-one' mapping of selective forces to fitness (sensu Wainwright et al. 2005) that shape its evolution. Future research should aim to develop an understanding of selective pressures on male jumping performance at the interspecific level, and an understanding of the role of life history or ecological traits (e.g., reproductive traits, microhabitats) in the evolution of sexual dimorphism.

Our findings are consistent with the hypothesis that selection acting on functional performance influences patterns of morphological evolution. This, in turn, would suggest that jumping behavior evolved prior to morphological specializations for increased jumping performance. Many authors have stressed the importance of behavior as a "pacemaker" in evolution (Mayr 1963; Grant 1963), where behavior partly determines the tempo of evolution by allowing organisms to overcome challenging situations or environments and potentially facilitating speciation. Specifically, the alternative adaptation hypothesis (West-Eberhard 1986, 1989) describes how plastic behaviors (such as jumping) may precede morphological specialization through the facultative use and possible fixation of the focal behavior, followed by sympatric speciation and morphological changes (e.g., longer legs or larger muscles) specifically matched to the environment that elicits the behavior. In this study, we found evidence of selection for increased jumping performance on weak jumpers. Such a pattern would in fact be consistent with the alternative adaptation hypothesis (sensu West-Eberhard 1986), if early-diverging anurans were poor jumpers with morphological specialization for high jumping performance evolving later, if high-performance jumps evolved rapidly after the initial evolution of jumping in anurans (indicating an increase in the evolutionary rate; West-Eberhard 1986), and if high-performance jumping evolved convergently many times (indicating many instances of morphological specialization for increased performance). These predictions are supported by the findings of Reilly and Jorgensen (2010) where: 1) pelvic morphology typical of early-diverging anurans implies that they were not great jumpers, and 2) that morphology associated with high performance (long distance) jumping evolved convergently multiple times. However, their findings do not support the prediction that high-performance jumps evolved early in the history of anura (at least relative to extant species). Wcislo (1989) describes behavior as allowing organisms to effectively “modify” their environment and as being important in promoting divergence in relation to sexual behaviors, feeding behaviors, and habitat selection. Thus, jumping performance may be important in each of these and may potentially link patterns of allometry of sexual dimorphism with patterns of speciation.

Interpreting the precise mechanism of allometric patterns of sexual dimorphism in traits other than body size may be difficult since most of the proposed mechanisms rely on body size being the focal trait (Fairbairn 1997). However, we use patterns of sexual dimorphism to propose a clear mechanism for the evolution of allometry of sexual dimorphism in jumping performance. This study shows that future research on the evolutionary allometry of sexual dimorphism in traits other than body size would benefit from using a functional approach to understand which traits, and their dimorphism, might be relevant in a particular study system. Using a functional approach would allow researchers to more accurately identify which traits selection is targeting, particularly when studying complex functional systems. Lastly, this study underscores the diverse insights gained from, and importance, of studying the evolutionary allometry of sexual dimorphism in traits other than body size.

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Code availability (software application or custom code): All code associated with this manuscript may be found at https://github.com/bhjuarez/allometry-dimorphism-jumping (upon manuscript acceptance).

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Figure Legend

Figure 1. Possible interspecific allometry relationships between male and female sizes across species. Figure *sensu*: Abouheif and Fairbairn 1997. Isometry is represented as the 1:1 line. In this construction, hyperallometry ($\beta > 1.0$) describes scenarios where male-biased sexual dimorphism increases with increasing body size, while female-biased sexual dimorphism increases with decreasing body size. Hypoallometry ($\beta > 1.0$) describes the converse relationship.

Figure 2. Phylogeny of the 146 anuran species included in this study. Tree pruned from Feng et al. (2017). Myobatrachidae and Heleophrynidae are not assigned to a superfamily. Images taken from PhyloPic. Images used under a Public Domain Dedication 1.0 license. The tailed frog image is used with credit to Sarah Werning under a Creative Commons Attribution 3.0 Unported license; https://creativecommons.org/licenses/by/3.0/.

Figure 3. Sexual dimorphism of morphology and jumping performance in 146 species of anurans. Red vertical lines denote the 95% Confidence Interval of the mean. Log ratios representing sexual dimorphism are unitless. Black vertical line denotes a ratio of 0 indicating lack of dimorphism. A. SVL is snout-vent length (mean ± standard error = -0.14 ± 0.01, median = -0.14). B. Mass is body mass (mean = -0.44 ± 0.04; median = -0.43). C. Muscle volume reflects bilateral limb muscle volume (mean = -0.37 ± 0.05, median = -0.32). D. L_{com} is the distance from the tip of the toes to the center of mass

(see text; mean = 0.01 ± 0.00, median = 0.01). E. Peak jumping energy estimated using anatomical approximation (mean = 0.06 ± 0.01, median = 0.08). F. Peak jumping velocity estimated using anatomical approximation (mean = 0.03 ± 0.01, median = 0.04).

Figure 4. Evolutionary allometry of sexual dimorphism in 146 species of anurans. Logs are natural logs. Solid black lines are phylogenetic least squares regression lines. Dashed red line is 1:1 line. A. Isometry of snout-vent length (SVL) in anurans ($y = 0.957x - 0.252$). B. Isometry of body mass in anurans ($y = 0.953x - 0.514$). C. Isometry of relative muscle volume ($y = 0.928x - 1.183$). D. Hypoallometry of relative L_{com} ($y = 0.843x + 0.131$). E. Hypoallometry of mass-specific peak jumping energy ($y = 0.861x - 0.868$). F. Hypoallometry of peak jumping velocity ($y = 0.866x - 0.388$). Slope of regressions are not significantly different from one in A, B, C, but are significantly less than one in D, E, and F. 95% Confidence Intervals of the slope methods to approximate jumping performance are given in the main text.