

RESEARCH ARTICLE

Ecology, sexual dimorphism, and jumping evolution in anurans

 Bryan H. Juárez^{1,2}  | Daniel S. Moen³  | Dean C. Adams¹

¹Department of Ecology, Evolution, and Organismal Biology, Iowa State University, Ames, Iowa, USA

²Departments of Biology and Earth System Science, Stanford University, Stanford, California, USA

³Department of Integrative Biology, Oklahoma State University, Stillwater, Oklahoma, USA

Correspondence

Bryan H. Juárez, Departments of Biology and Earth System Science; Stanford University; Stanford, CA 94305, USA.
Email: bryanhjuarez@gmail.com

Dean C. Adams, Department of Ecology, Evolution, and Organismal Biology; Iowa State University; Ames, IA 50010, USA.
Email: dcadams@iastate.edu

Funding information

California Academy of Sciences, Michele L. Aldrich Collections Research Grant; National Science Foundation, Grant/Award Number: DBI-1902511, DEB-1655812, Graduate Research Fellowship, IOS-1942893 and NSF PRFB/2109850

Abstract

Sexual dimorphism (SD) is a common feature of animals, and selection for sexually dimorphic traits may affect both functional morphological traits and organismal performance. Trait evolution through natural selection can also vary across environments. However, whether the evolution of organismal performance is distinct between the sexes is rarely tested in a phylogenetic comparative context. Anurans commonly exhibit sexual size dimorphism, which may affect jumping performance given the effects of body size on locomotion. They also live in a wide variety of microhabitats. Yet the relationships among dimorphism, performance, and ecology remain underexamined in anurans. Here, we explore relationships between microhabitat use, body size, and jumping performance in males and females to determine the drivers of dimorphic patterns in jumping performance. Using methods for predicting jumping performance through anatomical measurements, we describe how fecundity selection and natural selection associated with body size and microhabitat have likely shaped female jumping performance. We found that the magnitude of sexual size dimorphism (where females are about 14% larger than males) was much lower than dimorphism in muscle volume, where females had 42% more muscle than males (after accounting for body size). Despite these sometimes-large averages, phylogenetic *t*-tests failed to show the statistical significance of SD for any variable, indicating sexually dimorphic species tend to be closely related. While SD of jumping performance did not vary among microhabitats, we found female jumping velocity and energy differed across microhabitats. Overall, our findings indicate that differences in sex-specific reproductive roles, size, jumping-related morphology, and performance are all important determinants in how selection has led to the incredible ecophenotypic diversity of anurans.

KEYWORDS

frogs, morphology, phylogenetic comparative method, regression

1 | INTRODUCTION

Arnold's (1983) ecomorphological paradigm describes the relationships among morphology, performance, and fitness. In evolutionary biology, these three factors are often studied through the lens of

ecological morphology (Wainwright & Reilly, 1994), which stresses the importance of the environment in studies of organismal form and function. For example, ecomorphological approaches have been used to decipher how the environment relates to the evolution of morphology, performance, and lineage diversification (e.g.,

This is an open access article under the terms of the [Creative Commons Attribution-NonCommercial](https://creativecommons.org/licenses/by-nc/4.0/) License, which permits use, distribution and reproduction in any medium, provided the original work is properly cited and is not used for commercial purposes.

© 2023 The Authors. *Journal of Evolutionary Biology* published by John Wiley & Sons Ltd on behalf of European Society for Evolutionary Biology.

Blackburn et al., 2013; Collar et al., 2010; Goodman et al., 2008). Different selective forces may affect ecological morphology, including natural and sexual selection (Lailvaux & Irschick, 2006). Furthermore, sexual selection may play a key role in diversification through its effect on functional morphology in the context of habitat use (Butler et al., 2000; Cox et al., 2007; Kaliontzopoulou et al., 2010, 2015).

A prevalent feature of animals is sexual dimorphism (SD), wherein sexes exhibit extravagant differences in colour (Endler, 1984), ornamentation (Whiting et al., 2015), shape (Adams et al., 2020), and other phenotypic attributes. Of particular interest in the ecomorphological paradigm is body size, which is known to correlate with a wide variety of other traits, including functional morphological traits and performance. Males and females under distinct evolutionary pressures may evolve sexual size dimorphism (SSD), which can result in SD of functional performance (e.g., Huey & Hertz, 1982; Losos, 1990; Samejima & Tsubaki, 2010; Simon et al., 2022). However, since performance does not depend on size alone, SD of performance may be independent of dimorphism in size. If true, an underlying morphological component of performance other than body size would be expected to display SD. Thus, understanding the evolution of performance, size and related morphological traits in each sex is key to understanding the ways through which SD might arise (Kaliontzopoulou et al., 2015).

Theory predicts that SD evolves through three general mechanisms. First, SD may evolve due to anisogamy, where the sexes exhibit different energetic investments in reproduction (Connallon & Hall, 2018; Olsson et al., 2007). Such sex-specific differences are sometimes related to environmental differences through trade-offs between growth and reproduction (Cox et al., 2007; García-Navas et al., 2016; Shine, 2005). Second, SD may also evolve through differences in how each sex interacts with its environment (Lande, 1980; Shine, 1989; Slatkin, 1984). Empirical evidence suggests that sex-specific ecological demands resulting in SD are common (Bonnet et al., 2001; Butler et al., 2007; Butler & Losos, 2002; da Silva et al., 2014; Simon et al., 2022; Temeles et al., 2010). Additionally, De Lisle and Rowe (2017) found that the degree of separation in sex-specific ecological demands may differ by habitat use, as indicated by increased SD of gape size and other traits in salamander species that were more aquatic than others. Third, SD may evolve through resource competition between the sexes (De Lisle, 2019). While all three of these mechanisms include (to varying extents) sex-based differences in environments or resource use, less well-understood is how SD in body size and other traits is related to the evolution of ecological morphology across vertebrate groups.

Anurans (frogs and toads) are a diverse group of >7400 species (Amphibia Web, 2022). They inhabit a wide variety of environments and make an excellent study system to investigate the relationships between SD, ecological morphology, and locomotor performance (especially jumping; Gans & Parsons, 1966; Jenkins Jr & Shubin, 1998; Juarez et al., 2020; Mendoza et al., 2020; Moen, 2019). Jumping performance is essential for obtaining prey items or escaping from predators (Emerson, 1978; Gomes et al., 2002; Zug, 1972). Furthermore,

over 90% of anuran species have SSD (De Lisle & Rowe, 2013; Han & Fu, 2013; Nali et al., 2014). For example, *Strabomantis sulcatus* from Ecuador displays one of the greatest degrees of SSD, where males (28 mm) are about half as large as females (51 mm; Frenkel & Guayasamin, 2022). Notably, size-dependent selection associated with fecundity (egg size and clutch size) drives SSD evolution in frogs (Han & Fu, 2013; Nali et al., 2014). Larger female body sizes are generally associated with larger clutches and eggs, though the latter relationship is weaker than the former (Furness et al., 2022; Gomez-Mestre et al., 2012). Moreover, Silva et al. (2020) reported an association between fecundity and oviposition site (aquatic vs. arboreal), suggesting effects of microhabitats on SSD. Finally, a rich literature describes the relationship between morphology, jumping performance, and microhabitat use in male anurans (Astley, 2016; Citadini et al., 2018; Gomes et al., 2009; Mendoza et al., 2020; Moen, 2019; Moen et al., 2013; Rebelo & Measey, 2019; Vidal-García & Keogh, 2015). Thus, anurans offer a great opportunity to determine how SD of jumping performance, size, and relevant functional traits (e.g., leg length and muscle mass) have evolved in an ecological context.

To date, most comparative studies on anurans have focused on males (e.g., Moen et al., 2016), given their higher availability in the field (i.e., males call for reproduction) and thus in museum collections. Performance data for females and performance-associated measures of SD are thus lacking at a broad macroevolutionary scale. Nonetheless, sexual differences in jumping performance may exist due to two non-mutually exclusive reasons. First, fecundity selection due to anisogamy may result in a larger female body size (i.e., related to clutch mass). In frogs, SSD is driven by fecundity selection associated with larger females (Han & Fu, 2013; Nali et al., 2014). Female jumping performance may be reduced if females increase in body mass (e.g., due to increased clutch mass) without changing another aspect of their anatomy (e.g., leg muscle mass or leg length) to compensate (i.e., a trade-off; Jagnandan & Higham, 2018; Kuo et al., 2011; Marsh, 1994; Moen et al., 2013). For example, Juarez and Adams (2021) found that females have evolved longer legs at a given body length, possibly to compensate for decreased jumping performance associated with heavier bodies for carrying eggs. Thus, in species that compensate for fecundity-related decreases in jumping performance, we can expect (1) females to be larger than males (female-biased SSD), (2) no SD of jumping performance, and (3) a correlation between SSD and SD of jumping-related morphology. Alternatively, if females do not compensate for reduced jumping performance associated with heavier clutches, we may expect (1) female-biased SSD, (2) male-biased SD of jumping performance, and (3) no correlation between SSD and SD of jumping-related morphology.

Second, natural selection on reproductive traits may lead to SD of jumping performance that varies in degree or occurrence across particular microhabitats. This variation may occur if selection has resulted in greater male or female body sizes in some microhabitats but not in others, which could be related to reproductive traits, such as in species with aquatic lifestyles and relatively larger clutches compared to arboreal

species (Wells, 2007). Other reproductive traits that could lead to differences in SSD between microhabitats include egg-laying site or the presence of parental care. Laying clutches out of the water and parental care are associated with larger eggs and smaller clutch sizes (Furness et al., 2022; Gomez-Mestre et al., 2012) and such reproductive strategies are most common in arboreal and terrestrial species (e.g., dendrobatids, hylids or leptodactylids; Wells, 2007). Additionally, a greater degree of SD of jumping performance might occur in species associated with water. Species with aquatic lifestyles include those living in aquatic, semi-aquatic, and torrential microhabitats. Since females with aquatic lifestyles are associated with heavy egg clutches, this may substantially weigh them down during jumping, resulting in lower jumping performance. Therefore, ecology and egg mass may be related to SD of jumping performance. Given the various ways in which microhabitat is related to SSD, leg length and leg muscle mass, one unresolved question is whether microhabitat has a similar role in driving sexual differences in jumping performance and related morphological traits in anurans.

In this study, we aim to identify the evolutionary factors that drive SD in anurans. As we described above, factors such as fecundity selection, natural selection, and associations with microhabitats may each lead to distinct patterns of sexual differences in jumping performance and jumping-related morphology. We consider two aspects of jumping performance: peak velocity and peak energy. These traits are evolutionarily important because jumping velocity is related to jumping distance (Marsh, 1994), which helps anurans escape predation (Emerson, 1978; James et al., 2007). Moreover, energy used during jumping may yield net metabolic costs limiting the proportion of energy available for reproduction (e.g., calling in males and egg production in females). Specifically, we (1) test for SD in body size, jumping-related morphology and estimated jumping performance, (2) test for correlations between SD in body size (SSD), jumping-related morphology and estimated jumping performance (sexual jumping dimorphism or SJD), (3) test whether SJD differs based on microhabitat use and (4) determine how intrasexual variation in jumping performance, morphology and microhabitat might explain the observed variation in SJD.

2 | MATERIALS AND METHODS

2.1 | Data collection

We gathered data from 3738 individual museum specimens and analysed data for 3444 individuals representing 146 species, including 43 of 54 families of anurans. See Appendix S1 for further details of specimens included in this study and Supporting Information 2 for specimen references and catalogue numbers. We based our sampling on inclusion in a recent phylogenetic study of all 54 frog families (Feng et al., 2017). We obtained museum specimens across collections in the United States (see Acknowledgements), choosing collections that had large samples of males and females for our sampled species.

We estimated jumping performance via anatomy-based approximations of peak velocity and energy at take-off, as described in detail

by Juarez et al. (2020) and Juarez and Adams (2021). Briefly, these methods use body mass, leg muscle volume and L_{com} (0.67 times the distance from the sacral joint to the tip of the toes; Peplowski & Marsh, 1997) to approximate peak jumping performance. Total muscle volumes (the sum of thigh and calf muscle volume) were estimated using the geometric equation for the volume of a bicone, as described in Juarez and Adams (2021). See Appendix S2 for a comparison of using leg muscle volume instead of muscle mass to approximate jumping performance. The relationships between jumping performance measured in vivo and anatomical approximations showed an r^2 of 0.87 and 0.67, respectively for take-off velocity and peak energy, as determined from 96 individuals across 16 species for which necessary data were available (see Appendix S3 for details). Following Juarez et al. (2020), anatomical approximations described in vivo jumping performance better than any single input variable when compared using AIC and r^2 (Appendix S3). We used raw values of muscle volume and L_{com} for performance estimates. However, for including muscle volume and L_{com} in linear models, we standardized each by individual body mass and snout-vent length, respectively, to account for the fact that both traits scale (isometrically) with body size (Moen, 2019). We calculated the natural log values before estimating species means for males and females for all traits in this study: peak jumping velocity, peak jumping energy, relative leg length, relative muscle volume, body mass, and snout-vent length. Species means were estimated from 3 to 18 males (median = 14) and 3 to 17 females (median = 14) per species. Finally, we pruned the time-calibrated molecular phylogeny of Feng et al. (2017) to match the species-mean dataset using the *treedata* function in the R (version 4.1.2; R Core Team, 2022) package *geiger*, version 2.0.7 (Harmon et al., 2008).

We classified each species by microhabitat use following previous literature (Moen et al., 2013; Moen & Wiens, 2017). As in those studies, our classification emphasized non-breeding microhabitats, including arboreal, terrestrial, burrowing, semi-aquatic, aquatic, and torrential microhabitats. Importantly, species in all of these microhabitats jump when moving on land (Citadini et al., 2018; Gomes et al., 2009; Moen et al., 2013, 2021), including nearly all aquatic species when moving between water bodies (e.g., De Villiers & Measey, 2017). We also included a leaf-litter classification, whose members' jumping performance has not been considered previously in a phylogenetic comparative context. This latter classification groups all frogs that are found in leaf litter, typically in forests near wetlands or streambeds (e.g., Dugo-Cota et al., 2019; Jongasma et al., 2017). We obtained microhabitat data from the primary literature, online databases (e.g., Amphibia Web, 2022) and other published studies (Moen et al., 2013; Moen & Wiens, 2017). We list microhabitat classifications and sources in Table S1 of the SI.

2.2 | Statistical analyses and data visualization

We used phylogenetic paired t-tests to test for SD in body size (snout-vent length), relative L_{com} , relative muscle volume, peak

jumping energy and peak jumping velocity. Phylogenetic paired *t*-tests were based on the method of Lindenfors et al. (2010), as implemented in the *phyl.pairedttest* function in *phytools* package version 1.0-1 (Revell, 2012) in R. Each aspect of dimorphism was calculated as the difference in natural log values between males and females (e.g., $SD_{\text{velocity}} = \log\left(\frac{M_{\text{vel}}}{F_{\text{vel}}}\right) = \log(M_{\text{vel}}) - \log(F_{\text{vel}})$) for use in phylogenetic models (Smith, 1998). To visualize the evolution of differences in male and female anatomical approximations of jumping performance, we used maximum likelihood to map ancestral trait estimates of SJD in peak jumping velocity and energy onto the phylogeny of Feng et al. (2017) using *contMap* in *phytools*. We then used phylogenetic multiple regression to determine relationships between SJD and sexual differences in body size (snout-vent length), relative L_{com} and relative leg muscle mass. Additionally, we tested for interactions between microhabitat and sexual differences in body size, relative L_{com} and relative leg muscle mass. We also evaluated levels of phylogenetic signal (Adams, 2014a; Blomberg et al., 2003) for estimates of jumping velocity and energy using the *physignal* function in the *geomorph* package version 4.0.3 (Adams et al., 2021).

To determine how sexual jumping dimorphism was related to microhabitat use and SSD, we evaluated the fit of two separate phylogenetic multiple regression models for peak jumping velocity and peak jumping energy. In accordance with previous studies (e.g., Moen, 2019), we included a covariate in our models to account for the role of size in the context of jumping performance. When modelling SJD of velocity, our covariate was SD of snout-vent length (SVL). In contrast, our covariate was SD of body mass when modelling SJD in jumping energy (see Astley, 2016).

Next, since SD differences emerge from evolutionary factors individually affecting males and females (Butler et al., 2000; Butler & Losos, 2002; Kaliontzopoulou et al., 2015), we fit phylogenetic analysis of variance (ANOVA) models to test for microhabitat effects on the natural log of peak jumping performance (velocity and energy) for both males and females treated separately (i.e., two sets of analyses). We then used phylogenetic ANOVA to test for morphological differences across microhabitats for relative L_{com} , relative muscle volume and body mass to determine how each variable may uniquely contribute to differences in jumping performance in each sex. These latter microhabitat analyses included only female data, given we used them to explain our findings of the relationship between female jumping velocity and microhabitat (with no such relationship found in males). For these phylogenetic multiple regressions, we estimated model coefficients and calculated pairwise statistics and least-squares means for each microhabitat using the *lm.rppp* and *pairwise* functions in the R package *RRPP* version 1.2.3 (Collyer & Adams, 2018). We used 10 000 residual permutations to obtain effect sizes (Z-scores) and to evaluate the model significance and pairwise differences (Adams & Collyer, 2018a, 2018b; Collyer et al., 2015). To account for multiple comparisons in pairwise tests, we used the Sidak-like step-down procedure (*mutoss* library version 0.1-12; MuToss Coding Team, 2017) to obtain adjusted *p*-values after setting the family-wise error rate to $\alpha = 0.05$. To aid in the visualization of pairwise results, we

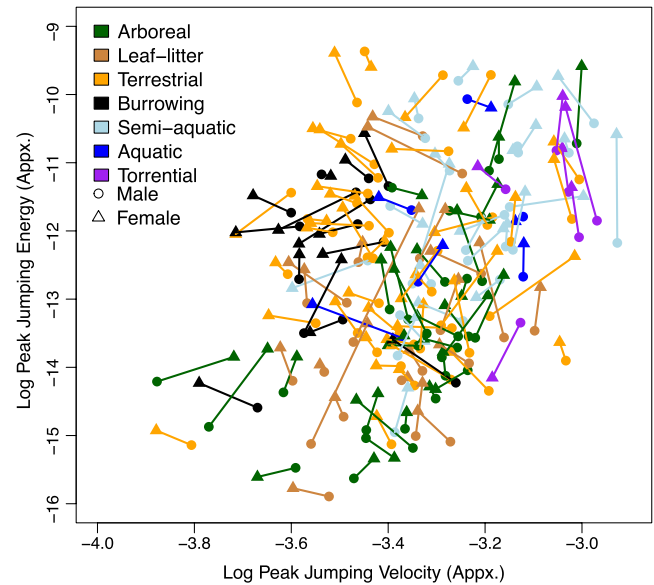


FIGURE 1 Diversity of male and female differences in jumping velocity and energy. Males are represented as circles and females as triangles, with lines linking the sexes of each species. Shape colours indicate species' microhabitat use. Data were natural log-transformed. Approximate (unlogged) units for velocity and energy are $\text{m}^{1/2}\text{kg}^{-1/2}$ and m^3kg^{-1} , respectively. These units differ from those typical of velocity and energy due to parameter substitutions in our approximations (see Supporting Information).

estimated probability densities using the *ggirdges* package version 0.5.3 (Wilke, 2021) for trait data after applying a phylogenetic transformation, rendering the data independent of phylogenetic covariance (Garland Jr. & Ives, 2000; Adams, 2014b). We plotted least-squares means obtained from microhabitat models onto these densities to aid interpretation.

3 | RESULTS

3.1 | Sexual dimorphism is prevalent in anurans

We summarized estimates of SD in several ways. A scatterplot of velocity and energy (Figure 1) shows pairs of male and female species means. Here, the length and direction of these vectors represent SD in jumping performance for each species (e.g., see Adams et al., 2020; Herler et al., 2010; O'Higgins & Collard, 2002) and demonstrate how the magnitude and direction of SJD varied substantially across taxa. Additionally, since energy is defined as proportional to the square of velocity ($E = \frac{1}{2}mv^2$), we may have reasonably expected a correlation between species means of jumping velocity and energy after log transformation; these correlations were $r = 0.33$ in males and $r = 0.37$ in females. We also visualized how SJD diversity has evolved by plotting tip estimates of SJD and ancestral-state estimations on a phylogeny (Figure 2). The estimates of phylogenetic signal for SJD of velocity and energy were statistically significant but low ($K_{\text{velocity}} = 0.287, p = 0.0015; K_{\text{energy}} = 0.244, p = 0.0125$).

Anatomical approximations of jumping performance indicated males jump an average of 1.03 times as fast (median = 1.03, range = 0.84–1.22) as females (Figure 3a), using an average of 0.70 times as much energy (median = 0.73, range = 0.14–2.24; Figure 3b). As an extreme example of a male-biased jumping velocity difference, *Ceratophrys cornuta* males should jump about 22%

faster than females. Unlike estimates of jumping velocity, sexual differences in jumping energy were more typical in *C. cornuta* (relative to other species in this study), with males expected to use about half as much energy to jump relative to females. Notably, male *C. cornuta* are about half as large as females (mass = 60g vs. 120g, respectively; Amphibia Web, 2022). While we found SJD in

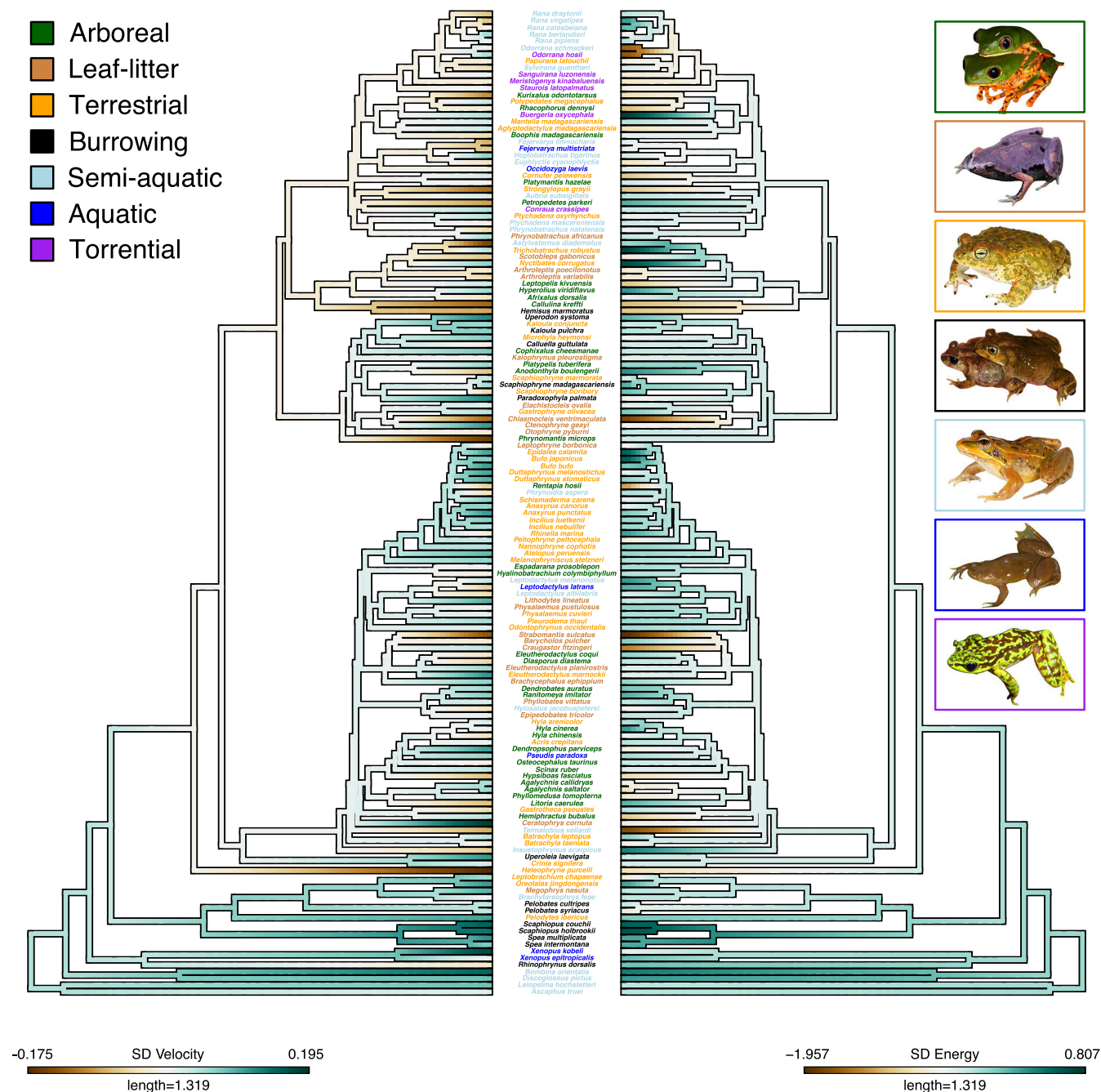


FIGURE 2 Ancestral-state estimates of sexual dimorphism (SD) in peak jumping velocity and energy. SD was estimated as natural log (M/F). Branch colours indicate SD estimates. Root estimates for velocity and energy are 0.06 and -0.32, respectively, which include 0 within their 95% confidence intervals. Tip label colours represent microhabitat classifications. Frog images represent microhabitats, in the same order as the legend (from top to bottom): arboreal (*Phyllomedusa tomopterna*), leaf-litter (*Chiasmocleis bassleri*), terrestrial (*Epidalea calamita*), burrowing (*Scaphiopus hurterii*), semi-aquatic (*Ptychadena mascareniensis*), aquatic (*Xenopus tropicalis*) and torrential (*Amolops tuberodepressus*). The top photo (*Phyllomedusa*) shows a case of sexual size dimorphism (smaller male on top), whereas the middle photo (*Scaphiopus*) shows a species without size dimorphism (male behind female). All photos by DS Moen.

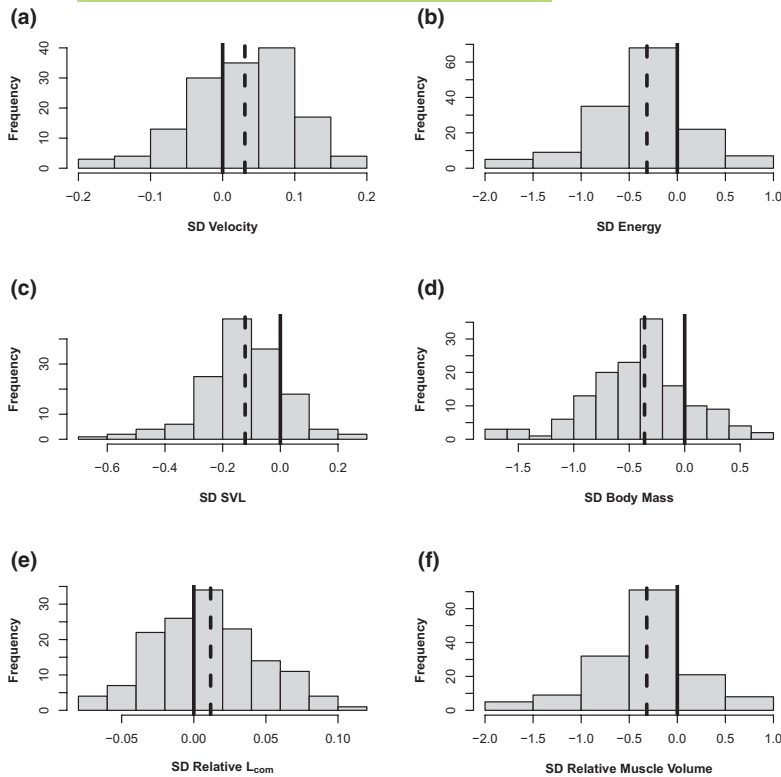


FIGURE 3 Histograms showing the degree of sexual dimorphism (SD; natural log(M/F) values) in anurans. (a) peak jumping velocity, (b) peak jumping energy, (c) snout-vent length (SVL), (d) body mass, (e) relative L_{com} (see text) and (f) relative muscle volume. Vertical solid lines at SD = 0 denote a lack of dimorphism (M = F values). Vertical dashed lines denote the median of each distribution. Jumping performance is based on anatomical approximations (see text).

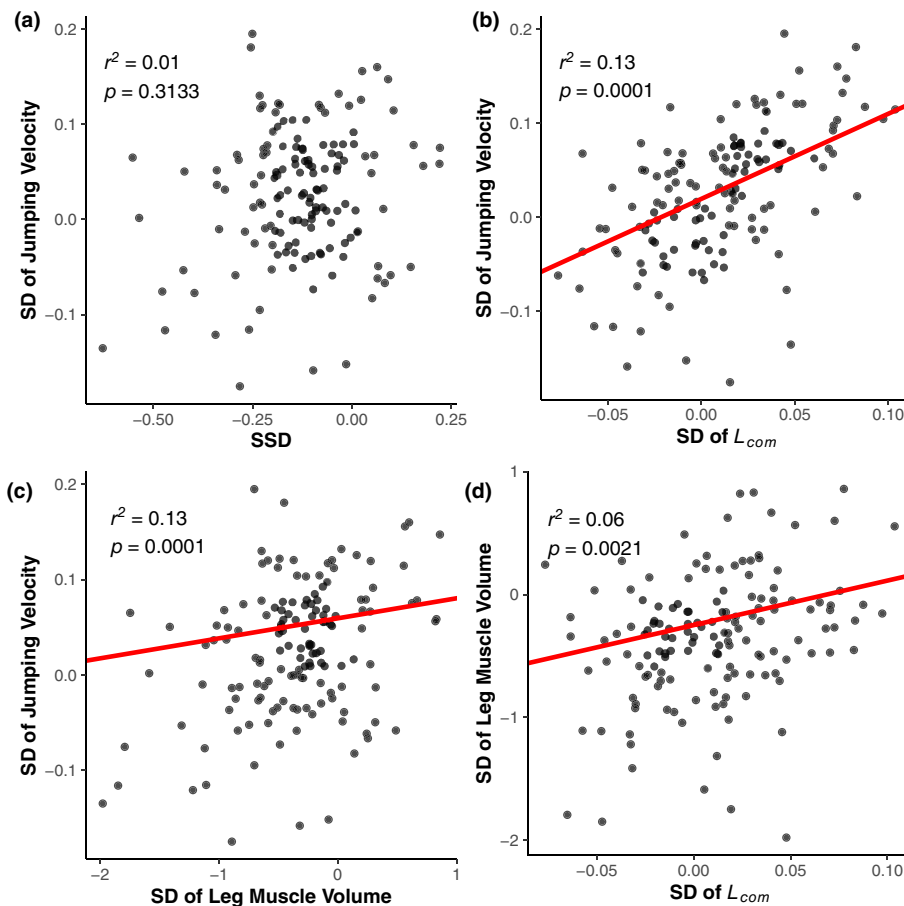


FIGURE 4 Relationships between various aspects of sexual dimorphism in anurans. Red lines indicate statistically significant regression lines. SD is sexual dimorphism, r^2 is the coefficient of determination and p is the p -value. All variables are natural log-transformed. (a) Insignificant relationship between sexual dimorphism of both estimated jumping velocity and body length (snout-vent length). (b) Significant relationship between sexual dimorphism of both estimated jumping velocity and relative L_{com} . Regression line is $y = 0.020 + 0.904x$. (c) Significant relationship between sexual dimorphism of both estimated jumping velocity and relative leg muscle volume. Regression line is $y = 0.059 + 0.021x$. (d) Significant relationship between sexual dimorphism of both relative leg muscle volume and relative L_{com} . Regression line is $y = -0.249 + 3.622x$.

many species, anurans as a whole did not exhibit SJD in velocity (phylogenetic paired t -test: $t = 0.93$, $df = 144$, $p = 0.35$) or energy ($t = -0.32$, $df = 144$, $p = 0.75$). In other words, the average

male-female difference in jumping velocity and energy after accounting for evolutionary relatedness was statistically indistinguishable from zero.

Furthermore, we found females were, on average, 1.14 times as long (median = 1.13, range = 0.80–1.87; [Figure 3c](#)) and 1.51 times as heavy as males (median = 1.44, range = 0.5–6.03; [Figure 3d](#)). As an extreme example, *Odorrana hosii* females measured an average of 77.67 mm in body length and weighed an average of 32.65 g, while males measured 44.72 mm in length and weighed 5.41 g. Although SSD was highly prevalent in anurans, differences in SSD seem to be explained mostly by evolutionary history. In other words, after accounting for evolutionary relatedness, we found the average anuran does not display sexual size dimorphism when considering mass ($t = -0.57$, $df = 144$, $p = 0.57$) or body length ($t = -0.79$, $df = 144$, $p = 0.43$). We did not find an average sexual difference in relative L_{com} (mean = 1.01, median = 1.01, range = 0.93–1.11; $t = 1.22$, $df = 144$, $p = 0.22$; [Figure 3e](#)). Finally, females possessed relative leg muscle volumes that were on average 1.42 times larger (median = 1.37, range = 0.42–7.23) than in males ([Figure 3f](#)). For example, *Strabomantis sulcatus* females exhibited 7.23 times more leg muscle volume than males, after accounting for body-size differences. Although the average sexual difference in relative leg muscle volume was 42%, we found no evidence for a consistent difference across species after accounting for evolutionary relatedness ($t = -0.20$, $df = 144$, $p = 0.84$). Overall, the results of the phylogenetic t-tests suggest a high degree of relatedness among species with substantial SD.

3.2 | Sexual dimorphism of jumping performance is correlated with morphology

We found that evolutionary patterns of SJD in jumping velocity were related to some but not all aspects of SD in morphology. Interactions between microhabitat and SD of morphology overall did not yield significant results after accounting for multiple comparisons (see [Appendix S4](#)). SJD in jumping velocity was not related to SSD ($F = 1.06$, $r^2 = 0.01$, $Z = 0.55$, $p = 0.3133$; [Figure 4a](#)) but was significantly related to SD of L_{com} ($F = 24.30$, $r^2 = 0.13$, $Z = 3.56$, $p = 0.0001$; [Figure 4b](#)). Additionally, we found the relationship between SJD in velocity and SD of leg muscle volume depended on whether the latter was added to the model before the SD of L_{com} . The effect of SD of leg muscle volume was not significant if added to the model last ($F = 1.52$, $r^2 = 0.01$, $Z = 0.83$, $p = 0.2176$), but significant otherwise ($F = 24.63$, $r^2 = 0.13$, $Z = 3.57$, $p = 0.0001$; [Figure 4c](#)). The effect of SD of L_{com} was significant even if added to the model last ($F = 47.41$, $r^2 = 0.25$, $Z = 4.49$, $p = 0.0001$), implying a correlation between SD of L_{com} and leg muscle volume. We confirmed this significant (but weak) relationship separately ($F = 9.96$, $r^2 = 0.06$, $Z = 2.46$, $p = 0.0021$; [Figure 4d](#)).

SJD in jumping energy was significantly related to body size, L_{com} and leg muscle volume. Interactions between microhabitat and SD of morphology were insignificant or accounted for less than 0.5% of the variance in SJD of jumping energy (see [Appendix S4](#)). We found that SJD in jumping energy was significantly related to SD in snout-vent length ($F = 18595.82$, $r^2 = 0.94$, $Z = 21.67$, $p = 0.0001$),

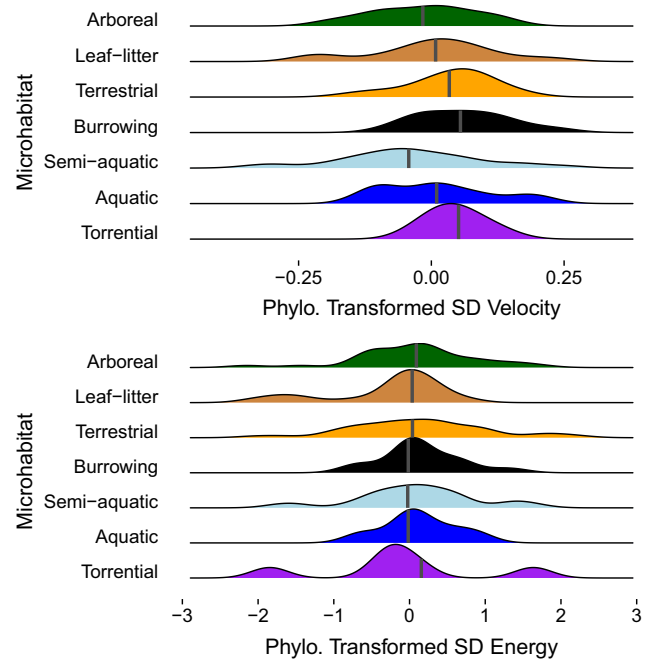


FIGURE 5 Probability density functions of phylogenetically transformed sexual dimorphism (SD) in peak jumping velocity and energy across microhabitats. SD was estimated as natural log(M/F) values. Vertical grey lines are averages for each distribution. Colours follow the schematic used in other figures. Note that velocity and energy are logged ratios and thus do not have units.

L_{com} ($F = 622.00$, $r^2 = 0.03$, $Z = 9.81$, $p = 0.0001$) and leg muscle volume ($F = 343.33$, $r^2 = 0.02$, $Z = 8.04$, $p = 0.0001$). The statistical significance of model terms (SD of snout-vent length, L_{com} and leg muscle volume) did not depend on the order in which they were added to the model. Notably, the effect sizes (e.g., r^2 and Z-scores) of SD of L_{com} and leg muscle volume were minimal compared to SSD, which explained most (94%) of trait variance in SJD in jumping energy. Since energy is proportional to body mass ($E = \frac{1}{2}mv^2$), we may reasonably expect strong correlations between energy, body size (snout-vent length or body mass), or the dimorphism of each.

3.3 | Sexual dimorphism in jumping performance across microhabitats

Aside from predictions based on fecundity selection, we next examined how natural selection through microhabitat-specific evolutionary pressures might have influenced the evolution of jumping performance. Using phylogenetic multiple regression, we found that SD in jumping velocity was unrelated to SSD ($F = 0.95$, $r^2 = 0.01$, $Z = 0.48$, $p = 0.3398$) but varied by microhabitat ($F = 5.60$, $r^2 = 0.19$, $Z = 3.80$, $p = 0.0002$; [Figure 5](#)). We also found that SJD in jumping energy was significantly related to both SD of mass ($F = 2351.46$, $r^2 = 0.93$, $Z = 13.77$, $p = 0.0001$) and microhabitat ($F = 5.65$, $r^2 = 0.01$, $Z = 3.82$, $p = 0.0001$; [Figure 5](#)). Despite a statistically significant overall effect of microhabitat on SJD, pairwise tests did not reveal any significant differences between specific microhabitats, after

accounting for multiple comparisons. All pairwise tables are found in the SI.

3.4 | Sex-specific diversity in jumping performance

When jumping performance was evaluated for each sex individually, we found no relationship between male jumping velocity and body length ($F = 0.02$, $r^2 = 0.00$, $Z = -1.27$, $p = 0.8838$) or microhabitat use ($F = 1.54$, $r^2 = 0.06$, $Z = 0.94$, $p = 0.1698$). In contrast, we found that male jumping energy was related to body mass ($F = 2035.55$, $r^2 = 0.93$, $Z = 13.29$, $p = 0.0001$) but not microhabitat ($F = 1.37$, $r^2 = 0.00$, $Z = 0.74$, $p = 0.2266$).

In females, we found that jumping velocity was not explained by body length ($F = 0.70$, $r^2 = 0.00$, $Z = 0.29$, $p = 0.4062$) but was significantly related to microhabitat ($F = 3.65$, $r^2 = 0.13$, $Z = 2.55$, $p = 0.0058$; Figure 6). Pairwise tests, after accounting for multiple comparisons, revealed that burrowing females tended to jump more slowly than arboreal females ($p_{\text{adj}} = 0.0187$) and leaf-litter females ($p_{\text{adj}} = 0.0218$; for complete results see SI). As in males, female jumping energy was related to body mass ($F = 1973.60$, $r^2 = 0.93$, $Z = 12.77$, $p = 0.0001$), but female jumping energy also differed between microhabitats ($F = 3.55$, $r^2 = 0.01$, $Z = 2.51$, $p = 0.0057$; Figure 6). Pairwise tests showed two notable differences in female jumping energy between microhabitats, after accounting for multiple comparisons. Arboreal females jump with more energy

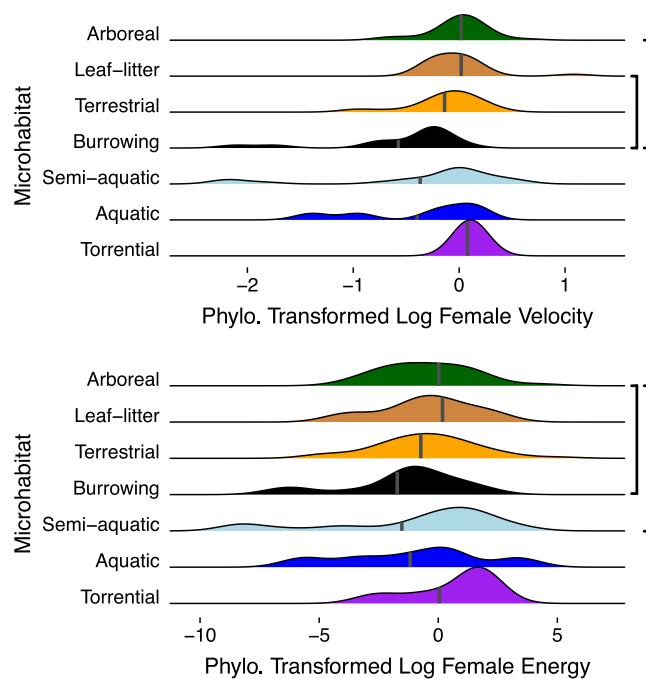


FIGURE 6 Probability density functions of phylogenetically transformed female peak jumping velocity across microhabitats. Vertical grey lines are averages for each distribution. Brackets on the right represent significant pairwise differences (see text). Colours follow the schematic used in other figures. Approximate units for velocity and energy are $\ln(\text{m}^{1/2}\text{kg}^{-1/2})$ and $\ln(\text{m}^3\text{kg}^{-1})$, respectively.

relative to burrowing females ($p_{\text{adj}} = 0.0167$) and semi-aquatic females ($p_{\text{adj}} = 0.0218$). Notably, microhabitat and body mass together accounted for about 93% of trait variance in jumping energy for both males and females.

3.5 | Microhabitat-specific differences in morphology are unrelated to patterns of female jumping evolution

We found that female relative L_{com} was significantly associated with microhabitat use ($F = 3.69$, $r^2 = 0.14$, $Z = 2.34$, $p = 0.0137$). In contrast, neither relative muscle volume ($F = 1.32$, $r^2 = 0.05$, $Z = 0.67$, $p = 0.2541$) nor body mass ($F = 1.26$, $r^2 = 0.05$, $Z = 0.59$, $p = 0.2785$) was associated with microhabitat. Pairwise comparisons did not reveal significant differences in relative L_{com} between any pair of microhabitats. These morphological patterns for L_{com} are distinct from differences in female jumping velocity and energy across microhabitats, suggesting that multiple factors combine idiosyncratically in each species to drive the differences in female jumping across microhabitats.

4 | DISCUSSION

Of longstanding interest in evolutionary biology is understanding how phenotypic diversity evolves and is maintained within the context of the environment. Often this is studied by measuring anatomical traits or quantifying organismal performance and relating diversity to habitat. Considerable effort has been devoted to understanding the macroevolutionary dynamics of a variety of phenotypes and groups. In some groups, most knowledge of macroevolution is drawn from one sex (e.g., males in anurans), which often stems from practicality. However, for groups exhibiting SD, this practice offers further research opportunities for uncovering sex-specific differences in the evolutionary drivers of SD and phenotypic diversity. In this study across 146 species that span the breadth of anuran diversity (43 of 54 families), our results were consistent with evidence of fecundity selection and natural selection (within microhabitats) driving sexually dimorphic and sex-specific patterns of jumping performance and morphology. In addition to discussing the effects of selective pressures on anurans, we also describe major findings of SD in specific traits, newly identified differences in jumping performance between males and females and the roles of microhabitat and morphology in generating phenotypic diversity in frogs and toads.

While many species exhibited dimorphism in the traits we surveyed, we found a lack of statistical support for dimorphism across species. We note this result quantifies the average degree of SD in anurans, rather than falsifying literature evidence of how common SD is across Anura. In fact, our estimate of females being 14% longer than males, on average, falls between two previously reported estimates (16%, Han & Fu, 2013; 11.6%, Portik et al., 2020). Notably,

we found the average magnitude of sexual differences in relative leg muscle volume was greater than previously recognized: females have leg muscles with 42% more volume than those of males after accounting for differences in body length. We also identified a general pattern wherein males tend to jump faster while using less energy compared to females, and this dimorphism seems to have existed in the common ancestor of anurans (Figure 2). Additionally, we found that female jumping velocity and energy differed among microhabitats (unlike in males; Moen, 2019). None of the jumping-related traits (body size, L_{com} , and leg muscle volume) used to estimate jumping performance explained microhabitat-specific differences in female jumping performance, indicating that estimated biomechanical performance depends on the combined influence of each morphological trait. Overall, this study is the first to investigate links between organismal performance, morphology and SD in anurans.

Fecundity selection is an evolutionary factor driving female jumping velocity. Specifically, we found (1) no significant sexual bias in jumping performance and (2) a correlation between SSD and SD of relative L_{com} (and correlated changes in SD of relative leg muscle volume). Each of these results align with the expectations associated with fecundity selection, where females 'account' for reductions in jumping performance related to fecundity-related increases in body mass (i.e., mass increases are due to egg masses) by evolving proportionally longer legs and proportionally more muscle volume. While we did not find a significant (average) size difference between males and females, this result does not indicate that fecundity selection fails to affect female jumping energy. Instead, we interpret this result to signify that fecundity selection and female-biased SSD are common in anurans, but the average degree of SSD is small. This interpretation agrees with previous findings of fecundity selection and female-biased SSD in the literature on anurans (De Lisle & Rowe, 2013; Han & Fu, 2013; Juarez & Adams, 2021; Nali et al., 2014). Our novel finding is that fecundity selection has impacted the evolution of jumping velocity in female anurans.

Natural selection associated with microhabitat-specific differences has influenced jumping energy. For example, arboreal females may jump with more energy compared to semi-aquatic females due to differences in both body size (snout-vent length) and jumping velocity. Aquatic frogs exhibit larger clutch sizes (number of eggs) compared to arboreal frogs (Wells, 2007) and larger clutch sizes are associated with larger body sizes (Furness et al., 2022; Gomez-Mestre et al., 2012). Thus, semi-aquatic frogs with larger bodies and larger clutch sizes may be expected to dedicate a greater proportion of their body mass to reproduction, compared to arboreal females. Arboreal females jumping with greater energy is also consistent with the observation that arboreal females jump faster than semi-aquatic females (though this difference was not statistically significant; Table S6). Additionally, the difference in jumping energy between burrowing frogs and arboreal frogs may best be explained by differences in jumping velocity: burrowing females jump slower than arboreal and leaf-litter females (Table S6), a result likely due to selection for increased burrowing performance. For example, burrowing frogs may exhibit trade-offs between jumping and

burrowing performance (Citadini et al., 2018; Mendoza et al., 2020). Furthermore, our finding that arboreal and leaf-litter females jump faster than burrowing females may also be related to body size. Arboreal and leaf-litter females displayed the smallest average body length of all microhabitats (though body lengths largely overlapped and differences were not significant). Previous work suggests smaller bodies are associated with jumping power amplification due to elastic recoil (Mendoza et al., 2020). Thus, reproductive biology and functional ecology modulate the effects of natural selection on jumping performance, potentially enabling frogs to inhabit specific microhabitats or invade new ones.

Unlike overall female jumping performance, we did not find evidence for microhabitat-specific patterns of SJD. This is related to our finding that males showed similar jumping performance across microhabitats, as identified previously (Moen, 2019; Rebelo & Measey, 2019). SD is an emergent pattern due to differences between the sexes where if males do not differ across microhabitats and females do, we can expect SD to differ across microhabitats due to the female pattern. However, our results do not support this expectation, and this is likely due to very similar distributions of jumping energy between males and females accompanied by small sexual differences in the variance (scale) of jumping energy found across microhabitats (Figures 6 and S1). Overall, we conclude that patterns of male and female jumping performance combine idiosyncratically to result in a lack of an association between SJD and microhabitat. This is possibly due to the large overlap in jumping performance across microhabitats and small sexual differences in the scale of jumping energy.

Lastly, we found that individual female morphological traits (L_{com} and leg muscle volume) are not related to microhabitat in the same way as female jumping performance. This is not surprising, given our findings that anatomical approximations of jumping outperform single anatomical variables in predicting in vivo jumping performance (see SI). Our findings reinforce previous work describing how jumping performance is highly correlated to the combined biomechanical effects of multiple components within the musculoskeletal system (James et al., 2007; Juarez & Adams, 2021; Juarez et al., 2020; Marsh, 1994; Moen, 2019).

Despite our growing knowledge of anuran jumping performance, we still lack extensive interspecific data for potentially important anatomical variables involved in jumping, such as plantaris pinnation angle (Juarez et al., 2020; Mendoza & Azizi, 2021) and most aspects of muscle physiology (Astley, 2016). This might limit our ability to understand the relationship between form and function across the ecomorphological diversity of anurans. Alternatively, in the context of male jumping velocity, the congruence between this study (which uses morphology to approximate jumping performance) and others generates two hypotheses. First, traits such as pinnation angle might not tend to vary across species based on microhabitat. Second, the volume of the leg muscles might account for enough variance in jumping to understand ecomorphological evolution in frogs. This is opposed to the physiological cross-sectional area, which takes both pinnation angle and specific tension into account (see Juarez

et al., 2020). One limitation of our approach (e.g., using muscle volume as a proxy for force) is the inability to directly compare units of approximation and in vivo units of performance. Using the regression equations as in Juarez et al. (2020), more data than are currently available for most species are needed to obtain accurate parameter estimates. Finally, interspecific comparisons of observed (in vivo) jumping performance in both males and females to the approximations herein will be important for confirming our results on sex-based differences in jumping. The lack of data on anuran females relative to males currently precludes such a comparison.

5 | CONCLUSIONS

Our study highlights previously undescribed patterns of how fecundity selection and natural selection may influence phenotypic diversity in jumping performance and jumping-related morphology between the sexes and microhabitats across the anuran tree of life. We have described how sexual differences in jumping performance may arise through natural selection on the various links between jumping performance, ecology and reproduction. Our findings show the culmination of species- and sex-specific selective pressures: species have evolved sexual jumping dimorphism in a great variety of ways, demonstrating the importance of studying interspecific patterns of both organismal performance and morphology in combination to better understand the evolutionary history of diverse taxa. This study serves as a foundation for the study of how patterns of SD evolve in vertebrates, particularly within the context of organismal performance and ecology.

AUTHOR CONTRIBUTIONS

Bryan H. Juarez: Conceptualization (equal); data curation (lead); formal analysis (lead); funding acquisition (equal); investigation (lead); methodology (equal); project administration (supporting); resources (equal); software (equal); supervision (supporting); validation (equal); visualization (equal); writing – original draft (lead); writing – review and editing (lead). **Daniel S. Moen:** Conceptualization (equal); data curation (supporting); formal analysis (supporting); funding acquisition (supporting); investigation (equal); methodology (equal); project administration (supporting); resources (equal); software (equal); supervision (lead); validation (equal); visualization (equal); writing – original draft (supporting); writing – review and editing (equal). **Dean Adams:** Conceptualization (equal); data curation (equal); formal analysis (equal); funding acquisition (equal); investigation (equal); methodology (equal); project administration (lead); resources (lead); software (equal); supervision (lead); validation (equal); visualization (equal); writing – original draft (supporting); writing – review and editing (supporting).

ACKNOWLEDGEMENTS

This work was supported by a National Science Foundation Graduate Research Fellowship, Postdoctoral Research Fellowship in Biology (Program Grant No. 2109850) and a California Academy

of Natural Sciences Michele L. Aldrich Collections Research Grant (to BHJ), and National Science Foundation Grants DBI-1902511 (to DCA) and DEB-1655812 and IOS-1942893 (to DSM). We thank Andrés Vargas for help with data collection and Antigoni Kaliontzopoulou for detailed feedback on prior versions of this manuscript. Finally, we are indebted to the many museum curators and collection managers that made this work possible, including those at the American Museum of Natural History (AMNH); the Academy of Natural Sciences of Drexel University, Vertebrate Zoology Dept (ANSP); the Monte L. Bean Life Science Museum (MLBM) Herpetology Collection at Brigham Young University (BYU); the Department of Herpetology, California Academy of Sciences (CAS); Amphibians and Reptiles (Herpetology) at Carnegie Museum of Natural History (CM); the Dorr Museum of Natural History (COA); Amphibians and Reptiles at the Field Museum of Natural History (FMNH); the Georgia Southern University – Savannah Science Museum Herpetology Collection (GSU); the Biodiversity Institute and Natural History Museum of the University of Kansas (KU); the Natural History Museum of Los Angeles County (LACM); the Museum of Comparative Zoology (MCZ); the Museum of Southwestern Biology (MSB); the Museum of Vertebrate Zoology, University of California, Berkeley (MVZ); the North Carolina Museum of Natural Sciences (NCSM); the Sam Noble Oklahoma Museum of Natural History, University of Oklahoma (OMNH); the Slater Museum of Natural History at the University of Puget Sound (PSM); the San Diego Museum of Natural History (SDNHM); the Biodiversity Research and Teaching Collections, Texas A&M University (TCWC); the Texas Memorial Museum (TMM) and Texas Natural History Collections (TNHC); the University of Michigan Museum of Zoology (UMMZ); the Division of Amphibians and Reptiles, Smithsonian National Museum of Natural History (USNM); the Amphibian and Reptile Diversity Research Center at the University of Texas at Arlington (UTA); the University of Texas at El Paso (UTEP); the University of Washington Burke Museum (UWBM); and the Yale Peabody Museum (YPM). Open access funding provided by the Iowa State University Library.

CONFLICT OF INTEREST STATEMENT

The authors have no conflict of interest to declare.

DATA AVAILABILITY STATEMENT

All data and code associated with this manuscript may be found on DRYAD (<https://doi.org/10.5061/dryad.z612jm6gb>).

ORCID

Bryan H. Juarez  <https://orcid.org/0000-0002-5474-596X>

Daniel S. Moen  <https://orcid.org/0000-0003-1120-0043>

REFERENCES

Adams, D. C. (2014a). A generalized K statistic for estimating phylogenetic signal from shape and other high-dimensional multivariate data. *Systematic Biology*, 63, 685–697.

- Adams, D. C. (2014b). A method for assessing phylogenetic least squares models for shape and other high-dimensional multivariate data. *Evolution*, *68*, 2675–2688.
- Adams, D. C., & Collyer, M. L. (2018a). Multivariate phylogenetic comparative methods: Evaluations, comparisons, and recommendations. *Systematic Biology*, *67*, 14–31.
- Adams, D. C., & Collyer, M. L. (2018b). Phylogenetic ANOVA: Group-clade aggregation, biological challenges, and a refined permutation procedure. *Evolution*, *72*, 1204–1215.
- Adams, D. C., Collyer, M. L., Kaliontzopoulou, A., & Baken, E. K. (2021). Geomorph: Software for geometric morphometric analyses. R package version 4.0. <https://cran.r-project.org/package=geomorph>
- Adams, D. C., Glynn, E., & Kaliontzopoulou, A. (2020). Interspecific allometry for sexual shape dimorphism: Macroevolution of multivariate sexual phenotypes with application to Rensch's rule. *Evolution*, *74*, 1908–1922.
- Amphibia Web. (2022). University of California, Berkeley, CA, USA. Retrieved May 24, 2022 from <https://amphibiaweb.org>
- Arnold, S. J. (1983). Morphology, performance and fitness. *American Zoologist*, *23*, 347–361.
- Astley, H. C. (2016). The diversity and evolution of locomotor muscle properties in anurans. *Journal of Experimental Biology*, *219*, 3163–3173.
- Blackburn, D. C., Siler, C. D., Diesmos, A. C., McGuire, J. A., Cannatella, D. C., & Brown, R. M. (2013). An adaptive radiation of frogs in a south-east Asian island archipelago. *Evolution*, *67*, 2631–2646.
- Blomberg, S. P., Garland, T., & Ives, A. R. (2003). Testing for phylogenetic signal in comparative data: Behavioral traits are more labile. *Evolution*, *57*, 717–745.
- Bonnet, X., Lagarde, F., Henen, B. T., Corbin, J., Nagy, K. A., Naulleau, G., Balhoul, K., Chastel, O., Legrand, A., & Cambag, R. (2001). Sexual dimorphism in steppe tortoises (*Testudo horsfieldii*): Influence of the environment and sexual selection on body shape and mobility. *Biological Journal of the Linnean Society*, *72*, 357–372.
- Butler, M. A., & Losos, J. B. (2002). Multivariate sexual dimorphism, sexual selection, and adaptation in Greater Antillean *Anolis* lizards. *Ecological Monographs*, *72*, 541–559.
- Butler, M. A., Sawyer, S. A., & Losos, J. B. (2007). Sexual dimorphism and adaptive radiation in *Anolis* lizards. *Nature*, *447*, 202–205.
- Butler, M. A., Schoener, T. W., & Losos, J. B. (2000). The relationship between sexual size dimorphism and habitat use in Greater Antillean *Anolis* lizards. *Evolution*, *54*, 259–272.
- Citadini, J. M., Brandt, R., Williams, C. R., & Gomes, F. R. (2018). Evolution of morphology and locomotor performance in anurans: Relationships with microhabitat diversification. *Journal of Evolutionary Biology*, *31*, 371–381.
- Collar, D. C., Schulte, J. A., II, O'Meara, B. C., & Losos, J. B. (2010). Habitat use affects morphological diversification in dragon lizards. *Journal of Evolutionary Biology*, *23*, 1033–1049.
- Collyer, M. L., & Adams, D. C. (2018). RRPP: An R package for fitting linear models to high-dimensional data using residual randomization. *Methods in Ecology and Evolution*, *9*, 1772–1779.
- Collyer, M. L., Sekora, D. J., & Adams, D. C. (2015). A method for analysis of phenotypic change for phenotypes described by high-dimensional data. *Heredity*, *115*, 357–365.
- Connallon, T., & Hall, M. D. (2018). Environmental changes and sexually antagonistic selection. In *Encyclopedia of Life Sciences*. John Wiley and Sons.
- Cox, R. M., Butler, M. A., & John-Alder, H. B. (2007). The evolution of sexual size dimorphism in reptiles. In D. J. Fairbairn, T. Székely, & W. U. Blanckenhorn (Eds.), *Sex, size and gender roles: Evolutionary studies of sexual size dimorphism* (pp. 38–49). Oxford University Press.
- da Silva, J. M., Herrel, A., Measey, G. J., & Tolley, K. A. (2014). Sexual dimorphism in bite performance drives morphological variation in chameleons. *PLoS One*, *9*, e86846.
- De Lisle, S. P. (2019). Understanding the evolution of ecological sex differences: Integrating character displacement and the Darwin-Bateman paradigm. *Evolution Letters*, *3*, 434–447.
- De Lisle, S. P., & Rowe, L. (2013). Correlated evolution of allometry and sexual dimorphism across higher taxa. *American Naturalist*, *182*, 630–639.
- De Lisle, S. P., & Rowe, L. (2017). Disruptive natural selection predicts divergence between the sexes during adaptive radiation. *Ecology and Evolution*, *7*, 3590–3601.
- De Villiers, F. A., & Measey, J. (2017). Overland movement in African clawed frogs (*Xenopus laevis*): Empirical dispersal data from within their native range. *PeerJ*, *5*, e4039.
- Dugo-Cota, Á., Vilà, C., Rodríguez, A., & Gonzalez-Voyer, A. (2019). Ecomorphological convergence in *Eleutherodactylus* frogs: A case of replicate radiations in the Caribbean. *Ecology Letters*, *22*, 884–893.
- Emerson, S. B. (1978). Allometry and jumping in frogs: Helping the twain to meet. *Evolution*, *32*, 551–564.
- Ender, J. A. (1984). Natural and sexual selection on color patterns in poeciliid fishes. In T. M. Zaret (Ed.), *Evolutionary ecology of neotropical freshwater fishes: Proceedings of the 1st international symposium on systematic and evolutionary ecology of neotropical freshwater fishes, held at DeKalb, Illinois, U.S.A* (pp. 95–111). Springer Netherlands.
- Feng, Y. J., Blackburn, D. C., Liang, D., Hillis, D. M., Wake, D. B., Cannatella, D. C., & Zhang, P. (2017). Phylogenomics reveals rapid, simultaneous diversification of three major clades of Gondwanan frogs at the Cretaceous–Paleogene boundary. *Proceedings of the National Academy of Sciences of the United States of America*, *114*, E5864–E5870.
- Frenkel, C., & Guayasamin, J. M. (2022). *Strabomantis sulcatus*. In S. R. Ron, A. Merino-Viteri, & D. A. Ortiz (Eds.), *Anfibios del Ecuador. Versión 2021.0*. Museo de Zoología, Pontificia Universidad Católica del Ecuador. Retrieved June 30, 2022, from <https://bioweb.bio/faunaweb/amphibiaweb/FichaEspecie/Strabomantis%20sulcatus>
- Furness, A. I., Venditti, C., & Capellini, I. (2022). Terrestrial reproduction and parental care drive rapid evolution in the trade-off between offspring size and number across amphibians. *PLoS Biology*, *20*, e3001495.
- Gans, C., & Parsons, T. S. (1966). On the origin of the jumping mechanism in frogs. *Evolution*, *20*, 92–99.
- García-Navas, V., Bonnet, T., Bonal, R., & Postma, E. (2016). The role of fecundity and sexual selection in the evolution of size and sexual size dimorphism in New World and Old World voles (Rodentia: Arvicolinae). *Oikos*, *125*, 1250–1260.
- Garland, T., Jr., & Ives, A. R. (2000). Using the past to predict the present: Confidence intervals for regression equations in phylogenetic comparative methods. *American Naturalist*, *155*, 346–364.
- Gomes, F. R., Bevier, C. R., Navas, C. A., & Gatten, R. E., Jr. (2002). Environmental and physiological factors influence antipredator behavior in *Scinax hiemalis* (Anura: Hylidae). *Copeia*, *2002*, 994–1005.
- Gomes, F. R., Rezende, E. L., Grizante, M. B., & Navas, C. A. (2009). The evolution of jumping performance in anurans: Morphological correlates and ecological implications. *Journal of Evolutionary Biology*, *22*, 1088–1097.
- Gomez-Mestre, I., Pyron, R. A., & Wiens, J. J. (2012). Phylogenetic analyses reveal unexpected patterns in the evolution of reproductive modes in frogs. *Evolution*, *66*, 3687–3700.
- Goodman, B. A., Miles, D. B., & Schwarzkopf, L. (2008). Life on the rocks: Habitat use drives morphological and performance evolution in lizards. *Ecology*, *89*, 3462–3471.
- Han, X., & Fu, J. (2013). Does life history shape sexual size dimorphism in anurans? A comparative analysis. *BMC Evolutionary Biology*, *13*, 1–11.
- Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E., & Challenger, W. (2008). GEIGER: Investigating evolutionary radiations. *Bioinformatics*, *24*, 129–131.
- Herler, J., Kerschbaumer, M., Mitteroecker, P., Postl, L., & Sturmbauer, C. (2010). Sexual dimorphism and population divergence in the Lake Tanganyika cichlid fish genus *Tropheus*. *Frontiers in Zoology*, *7*, 1–10.

- Huey, R. B., & Hertz, P. E. (1982). Effects of body size and slope on sprint speed of a lizard (*Stellio (Agama) stellio*). *Journal of Experimental Biology*, 97, 401–409.
- Jagnandan, K., & Higham, T. E. (2018). How rapid changes in body mass affect the locomotion of terrestrial vertebrates: Ecology, evolution and biomechanics of a natural perturbation. *Biological Journal of the Linnean Society*, 124, 279–293.
- James, R. S., Navas, C. A., & Herrel, A. (2007). How important are skeletal muscle mechanics in setting limits on jumping performance? *Journal of Experimental Biology*, 210, 923–933.
- Jenkins, F. A., Jr., & Shubin, N. H. (1998). *Prosalirus bitis* and the anuran caudopelvic mechanism. *Journal of Vertebrate Paleontology*, 18, 495–510.
- Jongsma, G. F. M., Tobi, E., Dixon-MacCallum, G. P., Bamba-Kaya, A., Yoga, J. A., & Mbega, J. D. (2017). Amphibians of Haut-Ogooué Province, southeastern Gabon. *Amphibian & Reptile Conservation*, 11, 1–23.
- Juarez, B. H., & Adams, D. C. (2021). Evolutionary allometry of sexual dimorphism of jumping performance in anurans. *Evolutionary Ecology*, 36, 717–733.
- Juarez, B. H., Moen, D. S., & Adams, D. C. (2020). A morphological method to approximate jumping performance in anurans for macroevolutionary studies. *Evolutionary Biology*, 47, 260–271.
- Kalioztopoulou, A., Carretero, M. A., & Adams, D. C. (2015). Ecomorphological variation in male and female wall lizards and the macroevolution of sexual dimorphism in relation to habitat use. *Journal of Evolutionary Biology*, 28, 1–15.
- Kalioztopoulou, A., Carretero, M. A., & Llorente, G. A. (2010). Intraspecific ecomorphological variation: Linear and geometric morphometrics reveal habitat-related patterns within *Podarcis bocagei* wall lizards. *Journal of Evolutionary Biology*, 23, 1234–1244.
- Kuo, C.-Y., Gillis, G. B., & Irschick, D. J. (2011). Loading effects on jump performance in green anole lizards, *Anolis carolinensis*. *Journal of Experimental Biology*, 214, 2073–2079.
- Lailvaux, S. P., & Irschick, D. J. (2006). A functional perspective on sexual selection: Insights and future prospects. *Animal Behaviour*, 72, 263–273.
- Lande, R. (1980). Sexual dimorphism, sexual selection, and adaptation in polygenic characters. *Evolution*, 34, 292–305.
- Lindensfors, P., Revell, L. J., & Nunn, C. L. (2010). Sexual dimorphism in primate aerobic capacity: A phylogenetic test. *Journal of Evolutionary Biology*, 23, 1183–1194.
- Losos, J. B. (1990). The evolution of form and function: Morphology and locomotor performance in West Indian *Anolis* lizards. *Evolution*, 44, 1189–1203.
- Marsh, R. L. (1994). Jumping ability of anuran amphibians. *Advances in Veterinary Science and Comparative Medicine*, 38B, 51–111.
- Mendoza, E., & Azizi, E. (2021). Tuned muscle and spring properties increase elastic energy storage. *Journal of Experimental Biology*, 224, jeb243180.
- Mendoza, E., Azizi, E., & Moen, D. S. (2020). What explains vast differences in jumping power within a clade? Diversity, ecology and evolution of anuran jumping power. *Functional Ecology*, 34, 1053–1063.
- Moen, D. S. (2019). What determines the distinct morphology of species with a particular ecology? The roles of many-to-one mapping and trade-offs in the evolution of frog ecomorphology and performance. *American Naturalist*, 194, E81–E95.
- Moen, D. S., Irschick, D. J., & Wiens, J. J. (2013). Evolutionary conservatism and convergence both lead to striking similarity in ecology, morphology and performance across continents in frogs. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20132156.
- Moen, D. S., Morlon, H., & Wiens, J. J. (2016). Testing convergence versus history: Convergence dominates phenotypic evolution over 150 million years in frogs. *Systematic Biology*, 65, 146–160.
- Moen, D. S., Ravelojaona, R. N., Hutter, C. R., & Wiens, J. J. (2021). Testing for adaptive radiation: A new approach applied to Madagascar frogs. *Evolution*, 75, 3008–3025.
- Moen, D. S., & Wiens, J. J. (2017). Microhabitat and climatic niche change explain patterns of diversification among frog families. *American Naturalist*, 190, 29–44.
- MuToss Coding Team, Blanchard, G., Dickhaus, T., Hack, N., Konietzschke, F., Rohmeyer, K., Rosenblatt, J., Scheer, M., & Werft, W. (2017). mutoss: Unified Multiple Testing Procedures. R package version 0.1-12. <https://CRAN.R-project.org/package=muttos>
- Nali, R. C., Zamudio, K. R., Haddad, C. F. B., & Prado, C. P. A. (2014). Size-dependent selective mechanisms on males and females and the evolution of sexual size dimorphism in frogs. *American Naturalist*, 184, 727–740.
- O'Higgins, P., & Collard, M. (2002). Sexual dimorphism and facial growth in papionin monkeys. *Journal of Zoology*, 257, 255–272.
- Olsson, M., Shine, R., Wapstra, E., Ujvari, B., & Madsen, T. (2007). Sexual dimorphism in lizard body shape: The roles of sexual selection and fecundity selection. *Evolution*, 56, 1538–1542.
- Peplowski, M. M., & Marsh, R. L. (1997). Work and power output in the hindlimb muscles of Cuban tree frogs *Osteopilus septentrionalis* during jumping. *Journal of Experimental Biology*, 200, 2861–2870.
- Portik, D. M., Blackburn, D. C., & McGuire, J. A. (2020). Macroevolutionary patterns of sexual size dimorphism among African tree frogs (Family: Hyperoliidae). *Journal of Heredity*, 111, 379–391.
- R Core Team. (2022). *R: A language and environment for statistical computing*. R Foundation for Statistical Computing. <https://www.R-project.org/>
- Rebelo, A. D., & Measey, J. (2019). Locomotor performance constrained by morphology and habitat in a diverse clade of African frogs (Anura: Pyxicephalidae). *Biological Journal of the Linnean Society*, 127, 310–323.
- Revell, L. J. (2012). *phytools*: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3, 217–223.
- Samejima, Y., & Tsubaki, Y. (2010). Body temperature and body size affect flight performance in a damselfly. *Behavioral Ecology and Sociobiology*, 64, 685–692.
- Shine, R. (1989). Ecological causes for the evolution of sexual dimorphism: A review of the evidence. *Quarterly Review of Biology*, 64, 419–461.
- Shine, R. (2005). Life-history evolution in reptiles. *Annual Review of Ecology, Evolution, and Systematics*, 36, 23–46.
- Silva, N. R., Berneck, B. V. M., da Silva, H. R., Haddad, C. F. B., Zamudio, K. R., Mott, T., Nali, R. C., & Prado, C. P. A. (2020). Egg-laying site, fecundity and degree of sexual size dimorphism in frogs. *Biological Journal of the Linnean Society*, 131, 600–610.
- Simon, M. N., Cespedes, A. M., & Lailvaux, S. P. (2022). Sex-specific multivariate morphology/performance relationships in *Anolis carolinensis*. *Journal of Experimental Biology*, 225, jeb.243471.
- Slatkin, M. (1984). Ecological causes of sexual dimorphism. *Evolution*, 38, 622–630.
- Smith, R. J. (1998). Statistics of sexual size dimorphism. *Journal of Human Evolution*, 36, 423–459.
- Temeles, E. J., Miller, J. S., & Rifkin, J. L. (2010). Evolution of sexual dimorphism in bill size and shape of hermit hummingbirds (Phaethornithinae): A role for ecological causation. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 365, 1053–1063.
- Vidal-García, M., & Keogh, J. S. (2015). Convergent evolution across the Australian continent: Ecotype diversification drives morphological convergence in two distantly related clades of Australian frogs. *Journal of Evolutionary Biology*, 28, 2136–2151.

- Wainwright, P. C., & Reilly, S. M. (Eds.). (1994). *Ecological morphology: Integrative organismal biology*. University of Chicago Press.
- Wells, K. D. (2007). *The ecology and behavior of amphibians*. University of Chicago Press.
- Whiting, M. J., Noble, D. W. A., & Somaweera, R. (2015). Sexual dimorphism in conspicuousness and ornamentation in the enigmatic leaf-nosed lizard *Ceratophora tennentii* from Sri Lanka. *Biological Journal of the Linnean Society*, 116, 614–625.
- Wilke, C. O. (2021). ggridges: Ridgeline Plots in 'ggplot2'. R package version 0.5.3. <https://CRAN.R-project.org/package=ggridges>
- Zug, G. R. (1972). Anuran locomotion: Structure and function. I. Preliminary observations on relation between jumping and osteometrics of appendicular and postaxial skeleton. *Copeia*, 1972, 613–624.

SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

How to cite this article: Juarez, B. H., Moen, D. S., & Adams, D. C. (2023). Ecology, sexual dimorphism, and jumping evolution in anurans. *Journal of Evolutionary Biology*, 36, 829–841. <https://doi.org/10.1111/jeb.14171>