

What explains vast differences in jumping power within a clade? Diversity, ecology and evolution of anuran jumping power

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Abstract

1. Anuran (frog and toad) jumping power varies greatly across species, yet muscle power does not. Given that the jumping power of some species is up to five times higher than typical muscle power, power amplification by elastic elements is suggested to explain this discrepancy. However, the ecological reasons for this variation in jumping power remain unclear. One hypothesis is that small jumpers are limited by the time available to accelerate their body during take-off, leading to small species needing greater power production than larger species to achieve similar jumping performance. Another (non-mutually exclusive) hypothesis is that the microhabitat species inhabit may drive variation through trade-offs with performance in microhabitat-specific, non-jumping behaviours.
2. We compared jumping power across 68 anuran species that were diverse in evolutionary relationships, microhabitat use and body mass. We used phylogenetic comparative methods to compare the role of microhabitat and body mass in explaining variation in jumping power across species.
3. We found the strongest support for a model that included two factors and their interaction. First, as body mass increased, jumping power decreased. Second, species that burrowed showed lower jumping power than species that did not burrow. Third, the interaction between body mass and burrowing behaviour showed that jumping power declines more rapidly with body mass in burrowing species than non-burrowing species.
4. The effect of body mass suggests that interspecific variation in jumping power might be partly explained by scaling relationships. Anurans with small body mass may be able to achieve similar locomotor performance (e.g. takeoff velocity) as those with larger body mass, by more effectively amplifying muscle power. Additionally, the effect of burrowing behaviour suggests that species that use hindlimbs to burrow may experience a reduction in their ability to generate jumping power. This may indicate a functional trade-off between jumping and burrowing performance.

KEYWORDS

body mass, burrowing, comparative biology, frogs, microhabitat, power amplification, trade-offs

1 | INTRODUCTION

In animals, movements that require power outputs that are beyond the capacity of muscles must use mechanisms that amplify power. This mechanism relies on the temporary storage of muscle work into elastic structures (e.g. tendon; Alexander, 1988) prior to any significant joint movement and the subsequent release of this work at faster rates. Such amplification occurs in several behaviours, including jumping (Anderson & Deban, 2010; Higham & Irschick, 2013; Patek, Dudek, & Rosario, 2011; Roberts & Azizi, 2011). Although a broad literature exists on the use of elastic mechanisms to amplify power in jumping animals (reviewed in Higham & Irschick, 2013; Ilton et al., 2018; Patek et al., 2011; Roberts & Azizi, 2011), it remains unclear why some animals need more power than their muscles can supply and whether trade-offs with other behaviours shapes the distribution of power amplification.

Given the importance of allometric growth on mechanics (e.g. Biewener, 2005), overall body size may influence the muscle force and power required for a given movement. In a broad analysis, Ilton et al. (2018) modelled how energy storage and release in a power-amplified system were affected by modifying the system's components, including mass. In systems that aim to maximize takeoff velocity, they found that energy storage resulted in high power outputs and a broader range of takeoff velocities for projectiles of small mass, whereas those with larger masses performed better with direct motor (e.g. muscle) actuation. These results suggest that the benefits of mechanisms used to amplify power may be size-dependent in biological systems. In jumping organisms (where the 'projectile' is the organism's body), this size-dependence could relate to the scaling of limb dimensions. If the time available for take-off is proportional to hindlimb length, then larger jumpers will have more time than smaller jumpers to generate force to accelerate their body (Biewener & Patek, 2018). This increased force should result in higher acceleration and thus higher takeoff velocity and jumping distance (Marsh, 1994). Moreover, small organisms need to move their limbs faster than large organisms to achieve a given centre-of-mass velocity, but the higher muscle contraction velocity necessary for faster movement will reduce muscle force (Bobbert, 2013). Thus, if small jumpers need to jump as far as larger species (e.g. to escape predators; Emerson, 1978; James, Navas, & Herrel, 2007), small jumpers may need to compensate for their size using mechanisms that increase power output (Aerts, 1998; Ilton et al., 2018; James et al., 2007).

Ecology and associated trade-offs among different behaviours may also drive variation in jumping power. For example some species of anurans (frogs and toads) dig burrows with their hindlimbs (Emerson, 1976), which are also used for jumping. In such species the use of elastic mechanisms could result in some loss of appendage control and less force transferred to the feet during digging (Higham & Irschick, 2013; Richards & Sawicki, 2012). In contrast, living in some microhabitats may favour increased jumping power. For instance arboreal organisms (e.g. lizards, frogs, bush babies) often jump from one branch to another, and such jumps may require substantial power. Additionally, jumping from compliant perches (i.e. leaves or twigs) may require that animals generate more power to compensate for losing propulsive energy to a

deforming substrate (Astley, Haruta, & Roberts, 2015; Reynaga, Eaton, Strong, & Azizi, 2019).

Despite these two explanations (body size and microhabitat) for variation in jumping power, few studies have investigated potential causes of this variation across a taxonomic group (Astley, 2016). Here, we study variation in jumping power and the correlates of such variation across anurans. We study anurans because their jumps are characterized as fast accelerative movements that require substantial muscle power (Lutz & Rome, 1994; Olson & Marsh, 1998). Large variation in muscle-mass-specific jumping power occurs across anuran species despite similar in-vitro muscle power in the plantaris longus and the semi-membranosus (Astley, 2016; Roberts, Abbott, & Azizi, 2011). These results suggest that variation in jumping power reflects variation in power amplification, not just muscle power (Astley, 2016; Astley & Roberts, 2012, 2014; Marsh, 1994; Roberts et al., 2011). Additionally, anurans are diverse in size (e.g. from 8 to 394 mm body length in males; de Lisle & Rowe, 2013) and inhabit diverse microhabitats (Moen, Irschick, & Wiens, 2013; Moen, Morlon, & Wiens, 2016; Moen & Wiens, 2017), and such microhabitats demand different behaviours. Despite this diversity, anurans have a conserved body form of unique features important for jumping (Jenkins & Shubin, 1998; Zug, 1978). With few exceptions, nearly all frogs use jumping as a primary mode of locomotion after metamorphosis, demonstrating the importance of this trait for survival (e.g. prey capture and predator avoidance; Emerson, 1978; James et al., 2007; Marsh, 1994).

In this study, we aimed to understand the factors that influence variation in anuran jumping power. We measured jumping power across 68 anuran species that show diversity in microhabitat use, body mass and phylogenetic history. Then, we used ancestral-state estimation to map the evolution of anuran jumping power in our 68-species dataset. Finally, we used phylogenetic comparative methods to test the role of microhabitat use and body mass in explaining variation in jumping power across species.

2 | MATERIALS AND METHODS

2.1 | Sampling

We pooled data for this study from four sources: (a) wild-caught animals, (b) pet-trade animals, (c) data from a previous study (Moen et al., 2013) and (d) (D.S. Moen) unpublished data from *Rhinella marina*. First, we collected data from 20 ecologically diverse species of frogs from five families (Bufonidae, Hylidae, Microhylidae, Ranidae and Scaphiropodidae) in Oklahoma and Arkansas in the United States. We collected adult, mostly male frogs (78% of all individuals were male) during the breeding season. Second, we purchased individuals of three species from the pet trade. In total we collected novel data from 23 species (wild-caught and store-bought). Sample size across species averaged 5.09 individuals (range 2–10; Table 1). We maintained frogs on a 12 hr L:D cycle at ambient temperatures (~20°C) and at approximately 40% humidity. The frogs were fed crickets or flightless fruit flies *ad libitum* three times weekly. All animal care

TABLE 1 Summary of morphological and performance data for the 23 species for which novel jumping data were collected in this study

Species	n	Body mass (g)	Takeoff velocity (m/s)	Muscle-mass-specific-power (W/kg _{muscle-mass})	Microhabitat
<i>Acris blanchardi</i>	7	1.21 ± 0.21	2.35 ± 0.33	657.89 ± 150.60	Terrestrial
<i>Anaxyrus americanus</i>	6	26.18 ± 8.04	1.08 ± 0.24	122.75 ± 59.99	Semi-burrowing
<i>Anaxyrus cognatus</i>	5	70.17 ± 20.36	1.18 ± 0.15	104.52 ± 33.41	Semi-burrowing
<i>Anaxyrus woodhousii</i>	3	37.22 ± 15.17	1.16 ± 0.11	102.40 ± 23.21	Semi-burrowing
<i>Bombina orientalis</i> ^a	3	9.30 ± 1.28	1.39 ± 0.06	259.67 ± 10.59	Semi-aquatic
<i>Gastrophryne carolinensis</i>	4	2.19 ± 0.24	1.34 ± 0.14	530.33 ± 178.98	Terrestrial
<i>Gastrophryne olivacea</i>	4	1.89 ± 0.74	1.18 ± 0.15	395.00 ± 101.33	Terrestrial
<i>Hyla avivoca</i>	9	2.61 ± 0.41	2.15 ± 0.14	723.86 ± 183.14	Arboreal
<i>Hyla chrysoscelis</i>	5	8.07 ± 1.10	2.26 ± 0.21	608.76 ± 116.17	Arboreal
<i>Hyla cinerea</i>	9	8.05 ± 1.59	2.53 ± 0.23	581.30 ± 159.95	Arboreal
<i>Kaloula pulchra</i> ^a	2	20.29 ± 2.86	0.99 ± 0.19	208.60 ± 35.50	Arboreal
<i>Phlyctimantis maculatus</i> ^a	3	12.61 ± 3.59	1.94 ± 0.17	406.37 ± 59.69	Arboreal
<i>Pseudacris clarkii</i>	10	0.94 ± 0.18	1.71 ± 0.12	418.84 ± 95.10	Terrestrial
<i>Pseudacris crucifer</i>	7	0.99 ± 0.34	2.77 ± 0.35	1551.66 ± 316.35	Terrestrial
<i>Pseudacris fouquettei</i>	6	1.27 ± 0.25	2.03 ± 0.20	670.40 ± 134.08	Terrestrial
<i>Pseudacris streckeri</i>	4	5.44 ± 0.58	1.60 ± 0.04	288.80 ± 36.48	Terrestrial
<i>Rana blairi</i>	5	43.25 ± 7.96	2.16 ± 0.48	180.02 ± 110.83	Semi-aquatic
<i>Rana catesbeiana</i>	4	244.44 ± 146.41	2.81 ± 0.07	308.58 ± 61.91	Semi-aquatic
<i>Rana clamitans</i>	6	20.96 ± 3.06	2.39 ± 0.30	346.53 ± 92.68	Semi-aquatic
<i>Rana palustris</i>	2	5.69 ± 1.27	2.05 ± 0.04	298.50 ± 25.31	Semi-aquatic
<i>Rana sphenoccephala</i>	5	25.63 ± 6.05	2.73 ± 0.20	374.54 ± 88.55	Semi-aquatic
<i>Scaphiopus huerterii</i>	4	16.31 ± 3.32	1.47 ± 0.06	256.80 ± 42.75	Burrowing
<i>Spea bombifrons</i>	4	9.22 ± 1.39	1.24 ± 0.11	199.13 ± 38.84	Burrowing

^aSpecies that were purchased in the pet trade. All continuous data are reported as species' $M \pm 1$ SD.

procedures followed Oklahoma State University IACUC protocol AS-15-17.

Third, we included jumping and preserved specimen morphological data from Moen et al. (2013) in this study to add more phylogenetic and microhabitat diversity. Briefly, Moen et al. (2013) examined diversity in jumping performance across 44 species from Australia, China and Colombia. They calculated body-mass-specific power and showed that it was variable across species, but they did not focus on understanding the variation in and the evolution of power per se, nor did they calculate muscle-mass-specific power. The latter standardization by muscle mass is the most relevant measurement for comparing power production across species (Astley, 2016; Longo et al., 2019; Roberts et al., 2011). Fourth, we added data for *R. marina* ($n = 5$), previously collected (as in Moen et al., 2013) but (D.S. Moen) unpublished data.

2.2 | Microhabitat and behaviour

We categorized the 23 species with novel data for this study and *R. marina* into one of eight microhabitat categories following

Moen and Wiens (2017; see Figure 1), who explicitly categorized thousands of frog species according to behaviours and time spent in microhabitats outside of the breeding season (i.e. many species lay eggs in water, but are not aquatic). We only assigned microhabitats to these 24 species because Moen et al. (2013) assigned states to the 44 species of that study and such states were consistent with Moen and Wiens (2017). We refer readers to Moen and Wiens (2017) for detailed discussion and justification of microhabitat categories, but we briefly describe them here: aquatic (living almost entirely in water), arboreal (climbing trees or other vegetation), semi-aquatic (sharing time between water and land), semi-arboreal (climbing, but spending appreciable time on the ground), terrestrial (living on the ground) and torrential (climbing vegetation and wet rocks along fast-flowing streams). For burrowing, we distinguish between species that burrow backwards with their hind legs and species that burrow with their head or forelimbs (Emerson, 1976), and only species that burrow with their hindlimbs are categorized here as burrowing (Emerson, 1976; Moen et al., 2013; Moen & Wiens, 2017). Semi-burrowing species were those that are mostly terrestrial, but also burrow. We modified the microhabitat state of three taxa to facilitate statistical analysis (e.g. some analyses did

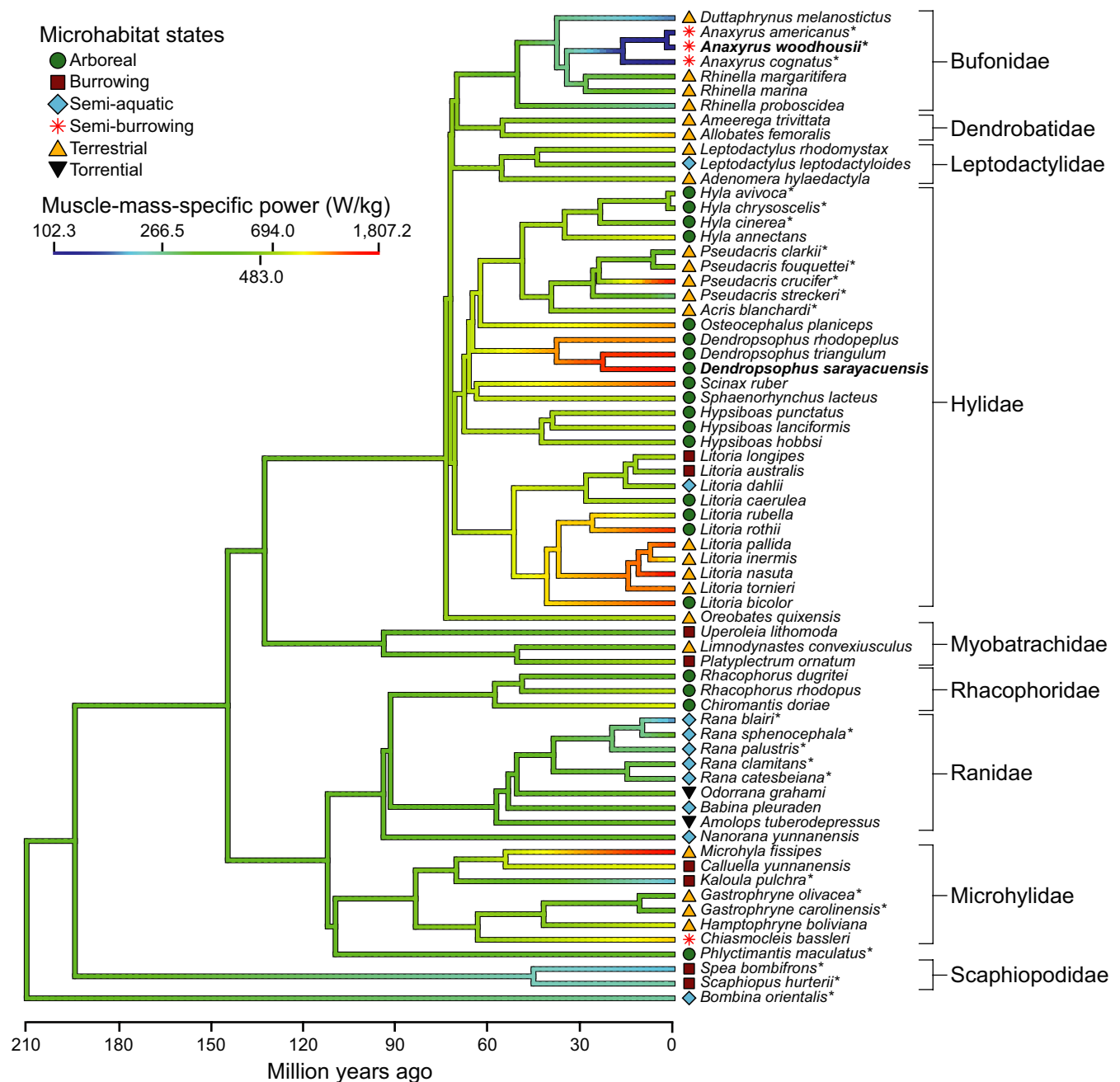


FIGURE 1 Phylogeny illustrating the evolution of jumping power in 68 species of anurans, the families to which they belong, and microhabitat assignment. Asterisks indicate the species from which we collected novel data for this study. The topology and branch lengths are from Pyron (2014), and branch lengths are in millions of years. Node colours refer to muscle-mass-specific power ($\text{W/kg}_{\text{muscle mass}}$) estimated by maximum-likelihood methods (Schluter et al., 1997) in R with the package APE. Plotting of branch colours was done with PHYTOOLS in R (Revell, 2012, 2013), which smoothly interpolates changes between nodes. Colours of muscle-mass-specific jumping power were assigned on a log scale. Moreover, species with the two extremes of jumping power described in the text are indicated in bold. Family membership reflects current taxonomy on AmphibiaWeb (2019). Families with single species are not represented by brackets: Bombinatoridae *Bombina orientalis*, Dicroglossidae *Nanorana yunnanensis*, Hyperoliidae *Phlyctimantis maculatus* and Strabomantidae *Oreobates quixensis*. Jumping power greater than what is physiologically possible for anuran muscle (approximately $483 \text{ W/kg}_{\text{muscle mass}}$; Astley, 2016) likely evolved at the base of the anuran phylogeny. The threshold colour of this muscular limit is indicated in the scale bar to better visualize changes to power amplification

not allow microhabitats with only one species to be included) and to increase statistical power to distinguish models. All changes were to similar states, and we detail these modifications and our justifications for them in the Supporting Information. Overall, since

our results most strongly favour a contrast between burrowing and non-burrowing species (see below) and those states were unaffected by our changes, we expect our results to be robust to most decisions about microhabitat classification.

2.3 | Phylogeny

We used Pyron's (2014) ultrametric phylogenetic tree, which is based on extensive taxon sampling (2,875 species) and multiple genes (~4 genes/species), to obtain phylogenies and their branch lengths for the analyses in this study. First, we pruned Pyron's phylogenetic tree to contain only the 23 species used to estimate the relationship between preserved and unpreserved muscle-mass to body-mass ratios (see below). Second, we pruned the complete tree to contain the 68 species used for all other analyses of this study. While other recent anuran phylogenies (e.g. Feng et al., 2017) show some incongruence with that of Pyron (2014), we used the latter because it was the most comprehensive anuran tree at the time of our analyses, allowing us to avoid making taxon substitutions.

2.4 | Jumping performance

To measure variation in jumping power across species, we constructed a 635 × 914.4 mm jump performance arena made of aluminium rods and plexiglass. We used a FASTEC TS5 high-speed video camera to record jumps at 500 frames per second and an exposure time of 1 ms per frame. We stimulated the frogs to jump by quickly lunging towards the frogs or by tapping them on the back with a paintbrush. For each animal we conducted three jumping sessions. In a given session, we ran jumping trials until animals refused to jump or until we recorded at least three strong efforts (defined as long distance for that species), whichever came first. Between each jump, we gave the frog approximately 5 min to rest. Jumps were collected at ambient temperatures (~20°C) and after each jump we measured body mass. In the Supporting Information, we discuss potential effects of variation in temperature and in timing of jumping performance (e.g. morning vs. night).

We analysed the motion in videos to ultimately calculate the power of jumps. We only recorded the take-off of each jump because, as a ballistic motion, all key aspects of jump performance (e.g. velocity, distance) are set during the take-off (Marsh, 1994). We digitized videos from first motion until three frames after take-off, using ImageJ (ver. 1.50i, Wayne Rasband, National Institutes of Health) to digitize the tip of the snout in each video. We imported these profiles into Igor Pro (ver. 6.37 Wavemetrics) and fit a quintic spline to the displacement profile (Walker, 1998) to reduce error associated with digitization. Then we calculated velocity and acceleration profiles from the smoothed displacement profiles using derivatives (McElroy & McBrayer, 2010). We calculated the body-mass-specific power profile by multiplying the velocity and acceleration profiles. We kept only peak muscle-mass-specific power values per individual across all digitized jumping trials. We calculated peak muscle-mass-specific power by dividing peak body-mass-specific power in watts per kilogram body mass by the muscle-mass to body-mass ratio (Roberts et al., 2011; see below for calculation of muscle-mass

to body-mass ratio). We then calculated species means for statistical analysis.

2.5 | Muscle-mass data

Upon completion of jumping trials, we euthanized frogs with MS-222, followed by double pithing. We recorded wet mass and dissected the hindlimb muscles from the right leg. Then we gently blotted the muscles dry on a paper towel, measured mass of the lower and upper hindlimb muscles, and summed the wet mass of those muscles to calculate total hindlimb muscle mass for one leg. We assumed leg symmetry and multiplied the muscle mass for one leg by two to calculate total hindlimb muscle mass. We then divided this mass by wet body mass to obtain the wet muscle-mass to body-mass ratio.

Additionally, to make the data comparable between Moen et al. (2013) and this study, we converted Moen et al.'s (2013) body-mass-specific power (W/kg) data into muscle-mass-specific power (W/kg) by dividing the body-mass-specific power by the muscle-mass to body-mass ratio. Because Moen et al.'s (2013) muscle masses were calculated from muscles preserved in formalin, this ratio was for preserved muscle mass to preserved body mass. Thus, we estimated the equivalent wet ratio by regressing wet ratio on preserved ratio in the 23 species unique to this study and using the results to estimate the wet ratios for the taxa from Moen et al. (2013) and for *R. marina*. We provide a detailed explanation of this procedure in the Supporting Information.

2.6 | Ancestral-state estimation

Previous studies have suggested that some anuran species amplify mechanical power during jumping, whereas others do not (Astley, 2016; Marsh & John-Alder, 1994; Peplowski & Marsh, 1997; Roberts et al., 2011). However, it remains unknown whether power amplification has arisen multiple times in the evolutionary history of anurans. To address this possibility, we used maximum-likelihood methods (Schluter, Price, Mooers, & Ludwig, 1997) to estimate ancestral muscle-mass-specific power outputs in the anuran phylogeny. For this analysis we used the function *ace* in the R package *APE* (version 5.0; Paradis & Schliep, 2019). We used log-transformed data to model proportional, rather than absolute, change (i.e. the likelihood of doubling power does not depend on the initial value; O'Meara, Ané, Sanderson, & Wainwright, 2006). This reconstruction does not directly indicate the presence of power amplification, because muscle power remains unknown for most of these taxa. However, Astley's (2016) *in vitro* data show that the highest muscle power recorded for anurans is 483 W/kg_{muscle}; thus species with jumping power outputs above 483 W/kg_{muscle} are candidates for power amplification. Finally, given the high species diversity of Anura (>7,000 species; AmphibiaWeb, 2019), we emphasize that this analysis of 68 species is preliminary, though we do not expect our results to substantially

change with additional sampling (see Supporting Information for additional justification).

2.7 | The ecological drivers of variation in jumping power

We tested two key factors that may explain the variation in muscle-mass-specific jumping power across anurans. First, we investigated the relationship between jumping muscle-mass-specific power and body mass. Second, we examined how inhabiting different microhabitats may affect jumping muscle-mass-specific power. We tested microhabitat in three ways. First, we tested the effect of microhabitat in general (i.e. all microhabitat specialists have different jumping power). Second, we tested whether species that showed back-burrowing behaviours exert lower muscle-mass-specific power outputs than all other species. Specifically, because elastic elements deform to store energy from muscle work, there could be a trade-off between storing potential energy in elastic elements versus transmitting force and limb control during behaviours such as burrowing (Higham & Irschick, 2013; Richards & Sawicki, 2012). Thus, we created a second categorization where we placed all burrowing and semi-burrowing species under the class 'burrowing' and all other microhabitat specialists were classified as 'other'. We refer to this model as 'burrowing versus non-burrowing'. Third, we tested whether species that inhabit arboreal environments show higher

muscle-mass-specific power (and amplify more power) than all other species. We considered this a possibility because some of the best anuran jumpers described to date are arboreal (Astley, 2016; Marsh & John-Alder, 1994; Peplowski & Marsh, 1997; Roberts et al., 2011). In this third categorization we placed all arboreal species under the class 'arboreal' and all other microhabitat specialists were classified as 'other'. We refer to this model as 'arboreal versus non-arboreal'.

We tested these hypotheses with phylogenetic generalized least-squares regression (PGLS; Martins & Hansen, 1997), using the *pgls* function in the package *CAPER* (version 0.2) in R (Orme et al., 2013). For these analyses we allowed lambda to take its maximum-likelihood value (Revell, 2010). All models had log-transformed species mean muscle-mass-specific jumping power as the response variable. We compared 11 models, which we describe here but also list in Table 2. The first model was a null model. Models two through five investigated the importance of (logged) body mass, microhabitat, back-burrowing and arboreality individually. Models six through eight combined body mass with one of the three habitat categories, and the final three models were similar to models six through eight but included an interaction term between the two predictor variables. We compared these 11 models using AICc scores, which allow one to simultaneously compare a set of related models (Burnham & Anderson, 2002). We also calculated AICc weights (w_{AICc}), which can be interpreted as the proportional support of each model out of all those considered. Moreover, by summing the AICc weights of all models in which each individual variable occurred, we were able

Model	R^2	AICc	$\Delta AICc$	Weight
Null	—	−0.62	12.79	0.00
Body mass	.15	−11.00	2.40	0.13
Microhabitat	.02	3.40	16.81	0.00
Burrowing versus non-burrowing	.02	−2.64	10.76	0.00
Arboreal versus non-arboreal	.00	−0.93	12.47	0.00
Body mass + Microhabitat	.24	−6.97	6.44	0.02
Body mass + Burrowing versus non-burrowing	.21	−12.60	0.80	0.30
Body mass + Arboreal versus non-arboreal	.16	−9.92	3.48	0.08
Body mass * Microhabitat	.38	−3.28	10.13	0.00
Body mass * Burrowing versus non-burrowing	.26	−13.40	0.00	0.45
Body mass * Arboreal versus non-arboreal	.15	−7.65	5.76	0.02

TABLE 2 Relationship between mean muscle-mass-specific jumping power (response variable) and different predictor variables

Note: The results include 11 regression models (from top to bottom): (1) a null model, (2) body mass only, (3) microhabitat only, and (4) burrowing versus non-burrowing only, (5) arboreal versus non-arboreal, (6) body mass and microhabitat (no interaction), (7) body mass and burrowing versus non-burrowing (no interaction), (8) body mass and arboreal versus non-arboreal (no interaction), (9) body mass and microhabitat and their interaction, and (10) body mass and burrow versus non-burrowing and their interaction and (11) body mass and arboreal versus non-arboreal and their interaction. Bold lines indicate the two models with the strongest statistical support, both of which include body mass and the burrowing factor.

Abbreviations: $\Delta AICc$, change in AICc; AICc, corrected Akaike information criterion; R^2 , adjusted R-squared; weights, AICc weight of each model.

to estimate each variable's importance across models (Johnson & Omland, 2004; Posada & Buckley, 2004).

3 | RESULTS

3.1 | Variation and evolution of jumping power in Anura

Jumping muscle-mass-specific power varied greatly among species. Mean muscle-mass-specific power across all species was $705.16 \text{ W/kg}_{\text{muscle-mass}}$, and it ranged from a species mean of $102.73 \text{ W/kg}_{\text{muscle-mass}}$ in *Anaxyrus woodhousii* (a large, semi-burrowing species) to $1806.16 \text{ W/kg}_{\text{muscle-mass}}$ in *Dendropsophus sarayacuensis* (a small, arboreal species). Jumping power outputs beyond the physiological limit of anuran muscle (max measured $483 \text{ W/kg}_{\text{muscle-mass}}$; Astley, 2016) appear to have evolved once at the base of the anuran tree, which has a reconstructed state value of $380.12 \text{ W/kg}_{\text{muscle-mass}}$ but whose 95% confidence interval goes beyond 483 (95% CI = $[227.54, 635.00] \text{ W/kg}_{\text{muscle-mass}}$; Figure 1). Additionally, this analysis suggested that the ability to exert high jumping power outputs might have been lost at least once in frogs. Reduced muscle-mass-specific power outputs occurred within Bufonidae, and *Anaxyrus* in particular showed a reconstructed value of $143.63 \text{ W/kg}_{\text{muscle-mass}}$ and a confidence interval that excluded typical muscle power for anurans (95% CI = $[120.23, 171.58] \text{ W/kg}_{\text{muscle-mass}}$; Figure 1). This interval also excludes the lowest measured muscle power for bufonids ($183 \text{ W/kg}_{\text{muscle-mass}}$; Astley, 2016), further reducing the likelihood of amplification in this taxon. On the other hand, muscle-mass-specific jumping power outputs far greater than measured for anuran muscle appears at the base of Hylidae with a reconstructed state of $717.45 \text{ W/kg}_{\text{muscle-mass}}$ (95% CI = $[609.91, 843.94] \text{ W/kg}_{\text{muscle-mass}}$; Figure 1).

3.2 | The ecological drivers of variation in jumping power

Of the 11 models we considered, the most strongly supported model included body mass, burrowing versus non-burrowing, and their interaction (Table 2), with an w_{AIC} of 0.45. This model explained 26% of the interspecific variation in muscle-mass-specific jumping power. The second most-supported model included body mass and burrowing versus non-burrowing with no interaction term ($w_{\text{AIC}} = 0.30$). The remaining models had a combined weight of 0.25 (Table 2). The summed AICc weight of the seven models with body mass as a factor was 1.00. The summed weight of models that included burrowing versus non-burrowing was 0.75, whereas the summed weight of models that included all microhabitats was 0.02 and 0.10 for those that included arboreal versus non-arboreal. Thus, across all models, both body mass and burrowing are important in explaining variation in muscle-mass-specific jumping power (Figure 2), while general microhabitat differences and being arboreal are not.

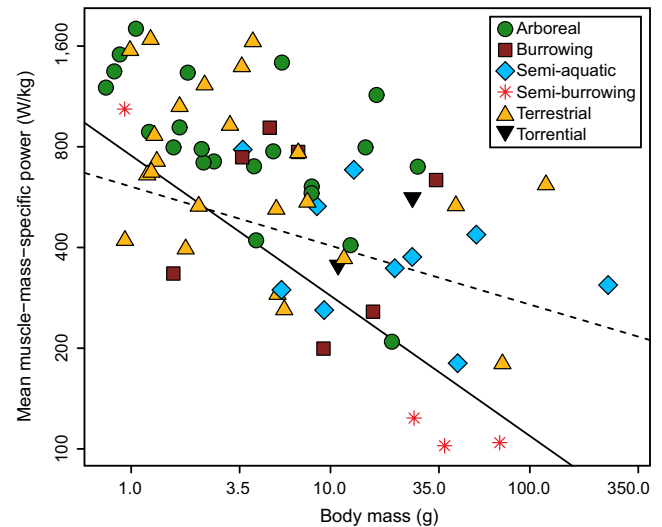


FIGURE 2 Scatterplot illustrating the relationships between microhabitat, body mass and jumping power for 68 species of anurans. Variables are shown on a log scale in original units. The lines represent phylogenetic generalized least-squares regression lines. The dashed line corresponds to the effect of body mass on non-burrowing species and the solid line corresponds to the effect of body mass on burrowing species. Jumping power decreases with an increase in body mass, and it declines at a faster rate with body mass in burrowing than non-burrowing species

4 | DISCUSSION

In this study, we investigated factors that influence variation in jumping power (and power amplification) across 68 anuran species that are diverse in microhabitat use, that vary substantially in body mass, and that represent distantly related clades. We found that some anurans generate muscle-mass-specific power outputs that are over three times higher than muscle power alone, while others jump with almost 20 times less power (than those peak species values). In explaining this variation, our results showed support for effects of body mass, burrowing versus non-burrowing, and their interaction. Additionally, we found that in anurans, high muscle-mass-specific jumping power may have arisen once at the base of the anuran phylogeny and the ability to exert high muscle-mass-specific power may have been secondarily lost or reduced at least once.

The use of elastic mechanisms to generate movements where the maximum power output exceeds the power capacity of muscles has been documented in a number of systems (Higham & Irschick, 2013; Ilton et al., 2018; Longo et al., 2019; Patek et al., 2011; Roberts & Azizi, 2011). Given that muscle power varies little across anurans (Astley, 2016; Roberts et al., 2011), much of the variation we observed in jumping power is likely attributed to variation in the effectiveness of using elastic mechanisms. However, this interpretation assumes that either muscle power is invariant across microhabitat states and body masses (the explanatory variables we investigated), or more generally that the body masses and microhabitat states that we found to have high jumping power do not have high muscle power. We tested these possibilities using

Astley's (2016) muscle-power dataset, using the same methods as above to analyse variation in muscle power of the plantaris longus and semi-membranosus across body masses and microhabitats (see Supporting Information for full details). We found that mass-specific power for both muscles increased with an increase in body mass, in contrast to our pattern of decreased jumping power with increased body mass (Figure 2; Tables S3 and S4; Figure S1). Moreover, power in neither muscle showed a consistent relationship with microhabitat state. These analyses suggest the high jumping power we see here is due to elastic mechanisms used to amplify muscle power. Moreover, the finding that large species seem to have higher muscle power (Astley, 2016; Figure S1) yet lower jumping power (Figure 2) may be indicative of the fact that direct muscle actuation relies on high muscle power outputs whereas the use of elastic elements may relax selection on muscle power since muscles can operate at very slow velocities when loading (Longo et al., 2019).

4.1 | Microhabitat

Anurans are diverse in microhabitat use and ecology (Duellman & Trueb, 1986; Wells, 2007) and show distinctive ecomorphology (Moen et al., 2013, 2016). This morphological distinctiveness could result in potential trade-offs between jumping and microhabitat-specific behaviours (e.g. burrowing; Gomes, Rezende, Grizante, & Navas, 2009; Moen, 2019; Zug, 1978), lowering jumping performance. Alternatively, some environments may demand exceptional jumping ability, perhaps beyond what muscles can power alone. In this study, we found that burrowing was associated with overall lower jumping power and a faster decline in power as body mass increased (Table 2; Figure 2), highlighting the imprint of ecology on performance. As muscle power does not seem to change with microhabitat state (see above), the lower jumping performance of burrowing species suggests lower power amplification in this group. This pattern could result from a reduction in the amount of elastic structures or an increase in their stiffness. Since burrowing demands the generation and transmission of high forces (Emerson, 1976), a reduction in compliance of elastic structures may be beneficial. In terms of force production, the stretch of a compliant tendon can shift the operating length of a muscle to a lower-force region of the force-length curve (Holt & Williams, 2018). Similarly, a muscle shortening against the stretch of an elastic element might contract faster and thus generate less force following the force-velocity relationship (Griffiths, 1991). Future work on elastic structures in anurans will allow for direct mechanistic testing of these hypotheses. Moreover, additional studies should compare the demands of combining high-force behaviours like burrowing with high-power behaviours like jumping, given that optimal power does not generally optimize force (Griffiths, 1991; Marsh, 1994).

Reduced amplification may not be the only reason why burrowing species show lower jumping power for their body size. Some anuran species that burrow with their hindlimbs move by bounding more than long jumping (Reilly et al., 2015). Bounding is characterized as bouts of short hops that rely more on endurance than a single,

powerful movement (Reilly et al., 2015; Wilson, James, Kohlsdorf, & Cox, 2004), reducing the need for high jumping power. Moreover, muscle fibre composition in such cases may favour endurance over power output (Bonine, Gleeson, & Garland, 2001), though thus far there is little support for differing fibre-type composition in anurans (Wilson et al., 2004). It is also unclear that all burrowing species use bounding as a form of locomotion. Regardless, use of a different mode of jumping may be a solution to the potential trade-off conferred by burrowing backwards.

Beyond burrowing, we found no significant effects of other microhabitat states on jumping power. We predicted that arboreal species would be more adept at amplifying power, but we found that the microhabitat model (with body mass) had only an AICc weight of 0.02, and that the arboreality model (with mass) had no weight (Table 2). This finding is surprising, given that arboreal species often show higher power outputs than species from other microhabitats (Astley, 2016; Roberts et al., 2011). However, arboreal species tended to be smaller than other ecomorphs (Figure 2), which may sufficiently account for their high power. Additionally, jumping power in arboreal species may be similar to frogs in other microhabitats because jumping may not show trade-offs with other microhabitat-specific behaviours. For example elastic elements may not compromise swimming performance (e.g. through loss of control of movement during stretching), because the fluid properties of water reduce spring loading during swimming (Richards & Sawicki, 2012). Overall, however, we emphasize that despite the poor performance of general microhabitat models (Table 2), further sampling of species may support additional differences between ecomorphs in power at a given mass (i.e. different intercepts) or effect of mass on power (i.e. different slopes). More generally, future studies on other organisms that both show high variation in power and diverse ecology will help explore the relationships among ecology, trade-offs and locomotor performance.

4.2 | Body size

Ecological opportunities may favour smaller body masses to exploit certain habitats or resources. However, to effectively escape predators, smaller species may need comparable jumping performance to bigger species (Emerson, 1978; James et al., 2007; Marsh, 1994). We assessed this possibility by testing how takeoff velocity (which is strongly correlated with jump distance; Marsh, 1994; Marsh & John-Alder, 1994) related to body mass in our dataset. PGLS regression showed a significant positive relationship between takeoff velocity and log-transformed body mass ($R^2_{\text{adj.}} = .057$, $F_{1,60} = 4.697$, $p = .034$). However, the small $R^2_{\text{adj.}}$ means that the line explains very little of the data, and small species effectively jump at similar velocities as large species. If smaller species are using elastic mechanisms to circumvent the power limits of their muscles to achieve these similar velocities, they may be using slow, forceful contractions to load elastic elements. This interpretation is consistent with available interspecific data showing that muscle power increases with body

mass (Astley, 2016; James, Vanhooydonck, Tallis, & Herrel, 2015; Figure S1).

More generally, Ilton et al. (2018) investigated the conditions under which power-amplifying mechanisms could outperform muscle-powered movements (and vice versa) across a diversity of biological and engineered systems. They found that during fast accelerative movements like jumping, a larger body mass may not gain the same benefits from the use of elastic elements as a smaller mass, since performance may be limited by the inertia of the body, regardless of how quickly elastic elements recoil. As mass increased, the performance of elastically powered systems decreased, such that movements powered by direct transfer of muscle power performed better. This higher reliance on elastic mechanisms at low versus high mass is generally consistent with our results. A subsequent study (Sutton et al., 2019) showed that in terms of maximizing jump height, the range of body mass in anurans spans the transition point where one mechanism becomes favoured over another. However, the mass at this transition point (2.5g) is almost an order of magnitude lower than the mass at which we see a majority of species whose jumping power is equivalent to muscle power (i.e. where species are less likely to amplify power; Figure 2). Future studies could parameterize these models (Ilton et al., 2018; Sutton et al., 2019) with data on anuran muscle physiology to better understand the shift from elastic-powered to muscle-powered jumping with increased body mass.

4.3 | Remaining variation in jumping power

We found that body mass and burrowing behaviour were both important in explaining the variation in jumping muscle-mass-specific power across anuran species. However, the model with the highest statistical support only explained 26% of the total variation in jumping power. What explains the residual variation in power? One possibility is that the elastic elements (i.e. tendon or aponeurosis; Alexander, 1988) may differ in elastic storage capacity across species. Matson, Konow, Miller, Konow, and Roberts (2012) measured the material properties of tendons from different muscle groups in the turkey hindlimb and found that they varied in their elastic modulus (or normalized stiffness), suggesting that their elastic storage capacity may vary. Moreover, beyond material properties, the morphology (e.g. thickness, length) of elastic elements may differ among species, leading to variation in ability to amplify muscle power.

Alternatively, given the large number of upper hindlimb muscles that contribute to locomotion in anurans (Prikryl, Aerts, Havelkova, Herrel, & Rocek, 2009), muscle power still might vary greatly among species and contribute to variation in jumping power. While possible, we consider this improbable for three reasons. First, Olson and Marsh (1998) showed in *Rana catesbeiana* that the semi-membranosus was the most important upper hindlimb muscle for generating jumping power, yet Astley (2016) found that the semi-membranosus did not generate significantly more power than

the plantaris longus, the key lower hindlimb muscle for jumping. Second, some species in our study generated power almost two times higher than the highest muscle power ever recorded in vertebrates (Askew, Marsh, & Ellington, 2001). Third, as in previously published studies (Astley, 2016; Roberts et al., 2011), we used total hindlimb muscle mass to calculate muscle-mass-specific power. This assumes all muscles generate work and power in jumping, a conservative assumption that will underestimate jumping power (Olson & Marsh, 1998; Reynaga et al., 2019), meaning the discrepancy between muscle and jumping power may be even larger than we infer here. However, to directly address this possibility, future studies should measure the power-generating capacity of all muscles involved in jumping.

5 | CONCLUSIONS

We tested whether microhabitat, body mass, both, or neither explained the variation in muscle-mass-specific jumping power across a diversity of anurans. We found that body mass and burrowing are both important in explaining variation in jumping power in anurans, and our results illustrate the effects that behaviours associated with specific microhabitats can have on locomotion. In order to further understand what drives variation in muscle-mass-specific jumping power, future studies should consider testing the material properties of potential elastic elements to examine whether the capacity to utilize elastic energy varies among species of varying body sizes and ecologies. Additionally, future studies should examine how temperature affects energy storage capabilities of elastic elements and if using this mechanism results in jumping performance that is robust to changes in temperature (see Supporting Information).

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AUTHORS' CONTRIBUTIONS

D.S.M. and E.M. conceived the idea and designed the methodology; E.M. and D.S.M. collected the data; E.M. and D.S.M. analysed the data; E.M., E.A. and D.S.M. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

DATA AVAILABILITY STATEMENT

Data available from the Dryad Digital Repository <https://doi.org/10.7280/D1295X> (Mendoza, Azizi, & Moen, 2020).

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REFERENCES

- Aerts, P. (1998). Vertical jumping in *Galago senegalensis*: The quest for an obligate mechanical power amplifier. *Philosophical Transactions of the Royal Society of London B: Biological Sciences*, 353, 1607–1620. <https://doi.org/10.1098/rstb.1998.0313>
- Alexander, R. M. (1988). *Elastic mechanisms in animal movement*. Cambridge, UK: Cambridge University Press.
- AmphibiaWeb. (2019). Berkeley, CA: University of California. Retrieved from <https://amphibiaweb.org>
- Anderson, C. V., & Deban, S. M. (2010). Ballistic tongue projection in chameleons maintains high performance at low temperature. *Proceedings of the National Academy Sciences of the United States of America*, 107, 5495–5499. <https://doi.org/10.1073/pnas.0910778107>
- Askew, G. N., Marsh, R. L., & Ellington, C. P. (2001). The mechanical power output of the flight muscles of blue-breasted quail (*Coturnix chinensis*) during take-off. *Journal of Experimental Biology*, 204, 3601–3619.
- Astley, H. C. (2016). The diversity and evolution of locomotor muscle properties in anurans. *Journal of Experimental Biology*, 219, 3163–3173. <https://doi.org/10.1242/jeb.142315>
- Astley, H. C., Haruta, A., & Roberts, T. J. (2015). Robust jumping performance and elastic energy recovery from compliant perches in tree frogs. *Journal of Experimental Biology*, 218, 3360–3363. <https://doi.org/10.1242/jeb.121715>
- Astley, H. C., & Roberts, T. J. (2012). Evidence for a vertebrate catapult: Elastic energy storage in the plantaris tendon during frog jumping. *Biology Letters*, 8, 386–389. <https://doi.org/10.1098/rsbl.2011.0982>
- Astley, H. C., & Roberts, T. J. (2014). The mechanics of elastic loading and recoil in anuran jumping. *Journal of Experimental Biology*, 217, 4372–4378. <https://doi.org/10.1242/jeb.110296>
- Biewener, A. A. (2005). Biomechanical consequences of scaling. *Journal of Experimental Biology*, 208, 1665–1676. <https://doi.org/10.1242/jeb.01520>
- Biewener, A., & Patek, S. (2018). *Animal locomotion*. Oxford, UK: Oxford University Press.
- Bobbert, M. F. (2013). Effects of isometric scaling on vertical jumping performance. *PLoS ONE*, 8, e71209. <https://doi.org/10.1371/journal.pone.0071209>
- Bonine, K. E., Gleeson, T. T., & Garland, T. Jr. (2001). Comparative analysis of fiber-type composition in the iliofibularis muscle of phrynosomatid lizards (Squamata). *Journal of Morphology*, 250, 265–280. <https://doi.org/10.1002/jmor.1069>
- Burnham, K. P., & Anderson, D. R. (2002). *Model selection and multimodel inference: A practical information-theoretic approach*. New York, NY: Springer.
- de Lisle, S. P., & Rowe, L. (2013). Correlated evolution of allometry and sexual dimorphism across higher taxa. *American Naturalist*, 182, 630–639. <https://doi.org/10.1086/673282>
- Duellman, W. E., & Trueb, L. (1986). *Biology of amphibians*. Baltimore, MD: Johns Hopkins University Press.
- Emerson, S. B. (1976). Burrowing in frogs. *Journal of Morphology*, 149, 437–458. <https://doi.org/10.1002/jmor.1051490402>
- Emerson, S. B. (1978). Allometry and jumping in frogs: Helping the twain to meet. *Evolution*, 32, 551–564. <https://doi.org/10.1111/j.1558-5646.1978.tb04598.x>
- 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. <https://doi.org/10.1073/pnas.1704632114>
- 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. <https://doi.org/10.1111/j.1420-9101.2009.01718.x>
- Griffiths, R. I. (1991). Shortening of muscle fibres during stretch of the active cat medial gastrocnemius muscle: The role of tendon compliance. *Journal of Physiology*, 436, 219–236. <https://doi.org/10.1113/jphysiol.1991.sp018547>
- Higham, T. E., & Irschick, D. J. (2013). Springs, steroids, and slingshots: The roles of enhancers and constraints in animal movement. *Journal of Comparative Physiology B*, 183, 583–595. <https://doi.org/10.1007/s00360-012-0734-z>
- Holt, N. C., & Williams, C. D. (2018). Can strain-dependent inhibition of cross-bridge binding explain shifts in optimum muscle length? *Integrative and Comparative Biology*, 58, 174–185. <https://doi.org/10.1093/ic/icy050>
- Ilton, M., Bhamla, M. S., Ma, X., Cox, S. M., Fitchett, L. L., Kim, Y., ... Patek, S. N. (2018). The principles of cascading power limits in small, fast biological and engineered systems. *Science*, 360, eaao1082. <https://doi.org/10.1126/science.aa01082>
- 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. <https://doi.org/10.1242/jeb.02731>
- James, R. S., Vanhooydonck, B., Tallis, J. A., & Herrel, A. (2015). Larger lacertid lizard species produce higher than expected iliotibialis muscle power output: The evolution of muscle contractile mechanics with body size. *Journal of Experimental Biology*, 218, 3589–3595. <https://doi.org/10.1242/jeb.124974>
- Jenkins, F. A. Jr, & Shubin, N. H. (1998). *Prosalirus bitis* and the anuran caudopelvic mechanism. *Journal of Vertebrate Paleontology*, 18, 495–510. <https://doi.org/10.1080/02724634.1998.10011077>
- Johnson, J. B., & Omland, K. S. (2004). Model selection in ecology and evolution. *Trends in Ecology and Evolution*, 19, 101–108. <https://doi.org/10.1016/j.tree.2003.10.013>
- Longo, S. J., Cox, S. M., Azizi, E., Ilton, M., Olberding, J. P., St Pierre, R., & Patek, S. N. (2019). Beyond power amplification: Latch-mediated spring actuation is an emerging framework for the study of diverse elastic systems. *Journal of Experimental Biology*, 222, jeb197889. <https://doi.org/10.1242/jeb.197889>
- Lutz, G. J., & Rome, L. C. (1994). Built for jumping: The design of the frog muscular system. *Science*, 263, 370–372. <https://doi.org/10.1126/science.8278808>
- Marsh, R. L. (1994). Jumping ability of anuran amphibians. In J. H. Jones (Ed.), *Comparative vertebrate exercise physiology* (pp. 51–111). San Diego: Academic Press Inc.
- Marsh, R. L., & John-Alder, H. B. (1994). Jumping performance of hylid frogs measured with high-speed cine film. *Journal of Experimental Biology*, 188, 131–141.
- Martins, E. P., & Hansen, T. F. (1997). Phylogenies and the comparative method: A general approach to incorporating phylogenetic information into the analysis of interspecific data. *The American Naturalist*, 149, 646–667. <https://doi.org/10.1086/286013>
- Matson, A., Konow, N., Miller, S., Konow, P. P., & Roberts, T. J. (2012). Tendon material properties vary and are interdependent among turkey hindlimb muscles. *Journal of Experimental Biology*, 215, 3552–3558. <https://doi.org/10.1242/jeb.072728>
- McElroy, E. J., & McBrayer, L. D. (2010). Getting up to speed: Acceleration strategies in the Florida scrub lizard, *Sceloporus woodi*.

- Physiological and Biochemical Zoology*, 83, 643–653. <https://doi.org/10.1086/653476>
- Mendoza, E., Azizi, E., & Moen, D. S. (2020). Data from: What explains vast differences in jumping power within a clade? Diversity, ecology, and evolution of anuran jumping power. *Dryad Digital Repository*, <https://doi.org/10.7280/D1295X>
- 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. <https://doi.org/10.1086/704736>
- 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, 2013–2156. <https://doi.org/10.1098/rspb.2013.2156>
- Moen, D. S., Morlon, H., & Wiens, J. J. (2016). Testing convergence versus history: Convergence dominates phenotypic evolution for over 150 million years in frogs. *Systematic Biology*, 65, 146–160. <https://doi.org/10.1093/sysbio/syv073>
- Moen, D. S., & Wiens, J. J. (2017). Microhabitat and climatic niche change explain patterns of diversification among frog families. *The American Naturalist*, 190, 29–44. <https://doi.org/10.1086/692065>
- Olson, J. M., & Marsh, R. L. (1998). Activation patterns and length changes in hindlimb muscles of the bullfrog *Rana catesbeiana* during jumping. *Journal of Experimental Biology*, 201, 2763–2777.
- O'Meara, B. C., Ané, C., Sanderson, M. J., & Wainwright, P. C. (2006). Testing for different rates of continuous trait evolution using likelihood. *Evolution*, 60, 922–933. <https://doi.org/10.1111/j.0014-3820.2006.tb01171.x>
- Orme, C. D. L., Freckleton, R. P., Thomas, G. H., Petzoldt, T., Fritz, S. A., Isaac, N., & Pearce, W. (2013). Caper: comparative analyses of phylogenetics and evolution using R, version 0.5.2. Retrieved from <http://cran.r-project.org/package=caper>
- Paradis, E., & Schliep, K. (2019). ape 5.0: An environment for modern phylogenetics and evolutionary analyses in R. *Bioinformatics*, 35, 526–528. <https://doi.org/10.1093/bioinformatics/bty633>
- Patek, S. N., Dudek, D. M., & Rosario, M. V. (2011). From bouncy legs to poisoned arrows: Elastic movements in invertebrates. *Journal of Experimental Biology*, 214, 1973–1980. <https://doi.org/10.1242/jeb.038596>
- 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.
- Posada, D., & Buckley, T. R. (2004). Model selection and model averaging in phylogenetics: Advantages of Akaike information criterion and Bayesian approaches over likelihood ratio tests. *Systematic Biology*, 53, 793–808. <https://doi.org/10.1080/10635150490522304>
- Prikryl, T., Aerts, P., Havelkova, P., Herrel, A., & Rocek, Z. (2009). Pelvic and thigh musculature in frogs (*Anura*) and origin of anuran jumping locomotion. *Journal of Anatomy*, 214, 100–139. <https://doi.org/10.1111/j.1469-7580.2008.01006.x>
- Pyron, R. A. (2014). Biogeographic analysis reveals ancient continental vicariance and recent oceanic dispersal in amphibians. *Systematic Biology*, 63, 779–797. <https://doi.org/10.1093/sysbio/syu042>
- Reilly, S. M., Montuelle, S. J., Schmidt, A., Naylor, E., Jorgensen, M. E., Halsey, L. G., & Essner, R. L. (2015). Conquering the world in leaps and bounds: Hopping locomotion in toads is actually bounding. *Functional Ecology*, 29, 1308–1316. <https://doi.org/10.1111/1365-2435.12414>
- Revell, L. J. (2010). Phylogenetic signal and linear regression on species data. *Methods in Ecology and Evolution*, 1, 319–329. <https://doi.org/10.1111/j.2041-210X.2010.00044.x>
- Revell, L. J. (2012). phytools: An R package for phylogenetic comparative biology (and other things). *Methods in Ecology and Evolution*, 3, 217–223. <https://doi.org/10.1111/j.2041-210X.2011.00169.x>
- Revell, L. J. (2013). Two new graphical methods for mapping trait evolution on phylogenies. *Methods in Ecology and Evolution*, 4, 754–759. <https://doi.org/10.1111/2041-210X.12066>
- Reynaga, C. M., Eaton, C. E., Strong, G. A., & Azizi, E. (2019). Compliant substrates disrupt elastic energy storage in jumping tree frogs. *Integrative and Comparative Biology*, 59(6), 1535–1545. <https://doi.org/10.1093/icb/icz069>
- Richards, C. T., & Sawicki, G. S. (2012). Elastic recoil can either amplify or attenuate muscle-tendon power, depending on inertial vs. fluid dynamic loading. *Journal of Theoretical Biology*, 313, 68–78. <https://doi.org/10.1016/j.jtbi.2012.07.033>
- Roberts, T. J., Abbott, E. M., & Azizi, E. (2011). The weak link: Do muscle properties determine locomotor performance in frogs? *Philosophical Transactions of the Royal Society B: Biological Sciences*, 366, 1488–1495. <https://doi.org/10.1098/rstb.2010.0326>
- Roberts, T. J., & Azizi, E. (2011). Flexible mechanisms: The diverse roles of biological springs in vertebrate movement. *Journal of Experimental Biology*, 214, 353–361. <https://doi.org/10.1242/jeb.038588>
- Schluter, D., Price, T., Mooers, A. Ø., & Ludwig, D. (1997). Likelihood of ancestor states in adaptive radiation. *Evolution*, 51, 1699–1711. <https://doi.org/10.1111/j.1558-5646.1997.tb05095.x>
- Sutton, G. P., Mendoza, E., Azizi, E., Longo, S. J., Olberding, J. P., Ilton, M., & Patek, S. N. (2019). Why do large animals never actuate their jumps with latch-mediated springs? Because they can jump higher without them. *Integrative and Comparative Biology*, 59(6), 1609–1618. <https://doi.org/10.1093/icb/icz145>
- Walker, J. A. (1998). Estimating velocities and accelerations of animal locomotion: A simulation experiment comparing numerical differentiation algorithms. *Journal of Experimental Biology*, 201, 981–995.
- Wells, K. D. (2007). *The ecology and behavior of amphibians*. Chicago, IL: University of Chicago Press.
- Wilson, R. S., James, R. S., Kohlsdorf, T., & Cox, V. M. (2004). Interindividual variation of isolated muscle performance and fibre-type composition in the toad *Bufo viridis*. *Journal of Comparative Physiology B*, 174, 453–459. <https://doi.org/10.1007/s00360-004-0431-7>
- Zug, G. R. (1978). Anuran locomotion—structure and function, 2: Jumping performance of semiaquatic, terrestrial, and arboreal frogs. *Smithsonian Contributions to Zoology*, 276, 1–32.

SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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