1   **Title: A morphological method to approximate jumping performance in anurans for**

2   **macroevolutionary studies**

3   **Running Title: Approximating jumping performance for macroevolution**

4

5   Authors: Juarez, Bryan H.[1, *], Daniel S. Moen[2], and Dean C. Adams[1]

6

7   Affiliations: 1. Department of Ecology, Evolution, and Organismal Biology; Iowa State

8   University; Ames, Iowa 50010, USA. 2. Department of Integrative Biology; Oklahoma State

9   University; Stillwater, Oklahoma 74078, USA.

10   *Corresponding Author Email: bryanhjuarez@gmail.com.

11

12   ORCIDs: Juarez, https://orcid.org/0000-0002-5474-596X; Moen, https://orcid.org/0000-0003-

13   1120-0043.

14

15   Key Words: anatomy, frogs, regression, phylogenetic signal, phylomorphospace

16

20

21   **Abstract**

22   Organismal performance is often key in understanding macroevolutionary patterns but

23   characterizing performance across many species is challenging, as the disparate geographic

24   locations of taxa often prohibit *in vivo* measures. In theory, however, inferences on the evolution

25   of performance could be investigated using anatomical approximations of performance

26   parameters, allowing for a wider range of species to be sampled. In this study, we use biological

27   and physical principles to mathematically derive three size-standardized anatomical

28   approximations for three different aspects of jumping performance at take-off in anurans: peak

29   jumping velocity, energy, and power. We also describe several ways to parameterize these

30   approximations using, for example, measurements of leg length, leg muscle mass, and body

31   mass. We evaluate the efficacy of these approaches via comparison with direct size-standardized

32   measures of jumping performance across 256 individuals from 51 anuran species. Using both

33   phylogenetic and non-phylogenetic approaches, we find that two of the three anatomical

34   approximations (velocity and energy) are highly correlated with *in vivo* measures, while a third

35   (power) is not. This reveals that the former may serve as reliable estimates of those aspects of

36   jumping performance, while the latter approximation does not capture all aspects of jumping

37   power in anurans. We also report significant phylogenetic signal for the approximations, as

38   found in *in vivo* measures. These analyses demonstrate the utility of anatomical approximations

39   for use in macroevolutionary studies. Relative to *in vivo* laboratory methods, this new method

40   allows for broad museum-based taxonomic surveys of jumping performance in anurans and

41   possibly other jumping animals.

42

43

Introduction

Understanding the relationship between form and function is paramount in explaining how organisms perform tasks. Arnold (1983) expanded the theoretical context of research on form and function to include individual fitness by proposing the ecomorphological paradigm. This paradigm states that the association between morphology (form) and fitness is mediated by organismal performance (function). Arnold's pioneering work provided a framework for linking morphological variation with ecology and organismal performance (e.g. Pounds 1988; Losos 1990a; Patek et al. 2007; Kaliontzopoulou et al. 2012). Studies based on it have led to diverse insights into the evolutionary processes that have shaped patterns of phenotypic diversity (e.g. Losos 1990b; Kaliontzopoulou et al. 2015; Muñoz et al. 2017).

Anuran amphibians have long been a focus of understanding the relationship between anatomical form and organismal performance. These studies have largely focused on jumping and the degree to which anatomical traits relate to measures of jumping performance. Early work identified statistical associations between morphological measures such as leg length or body size, with performance measures such as jumping distance or acceleration (e.g. Rand and Rand 1966; Zug 1972, 1978; Emerson 1978). Notably, integrating biomechanical theory with functional morphology resulted in a series of analytical equations that relate different aspects of jumping performance, such as velocity and angle at take-off to peak jumping distance (Alexander 1968; Bennet-Clark 1977; Marsh 1994; Peplowski and Marsh 1997). Such measures have proven useful in characterizing variation in jumping performance within species (Marsh and John-Alder 1994; Wilson et al. 2000; James et al. 2007; for non-anuran examples see: Toro et al. 2003; Toro et al. 2004).

66   In recent years, researchers have used a cross-species approach to examine the

67   evolutionary associations between anuran morphology, performance, and ecology from a

68   phylogenetic perspective (e.g., Gomes et al. 2009; Moen et al. 2013; Citadini et al. 2018; Astley

69   2016; Moen 2019). For example, Gomes et al. (2009) showed that jumping distance in anurans

70   depends on both microhabitat use and body size. Likewise, Moen et al. (2013) revealed that

71   across continents, locomotor performance and morphology were associated with microhabitat

72   use, a pattern implying evolutionary convergence of functional traits. Such studies have revealed

73   much about the extent to which ecomorphological patterns are shaped by ecological and

74   evolutionary factors. Nevertheless, the degree to which such trends are displayed across the

75   broader diversity of anurans remains underexamined. One reason for this is that, as a clade,

76   anurans are circumglobal and species are found in diverse ecological communities across six

77   continents (Pyron and Wiens 2013; Moen et al. 2016). As such, obtaining comprehensive

78   datasets of live-animal jumping performance across many species is logistically challenging.

79   An alternative approach to collecting *in vivo* measurements of performance is to develop

80   anatomical estimates that may serve as approximations for jumping performance. For instance,

81   Carroll et al. (2004) developed a biomechanical model for predicting suction feeding

82   performance in centrarchid fishes, based on a series of anatomical parameters. They found a

83   strong relationship ($r^2 = 0.71$) between *in vivo* suction feeding performance and that predicted by

84   morphology across five species, implying that their model may serve as an approximation for

85   suction performance in this group. The approach of Carroll et al. (2004) serves as a conceptual

86   template for how anatomical approximations may be developed for other aspects of organismal

87   performance.

88   Motivated by their example, we develop three size-standardized anatomical

89   approximations for jumping performance to serve as estimates of three key aspects of jumping

90   performance at take-off in anurans: peak velocity, energy, and power. Since these three

91   performance measures commonly scale with body size (see e.g., Marsh and John-Alder 1994;

92   Astley 2016), we account for this pattern by size-standardizing the approximations. Specifically,

93   our concern is whether these may serve as reasonable approximations of the relative differences

94   in jumping performance between species, and thus may serve as approximate measures of

95   performance in macroevolutionary studies. Thus, we evaluate the efficacy of the size-

96   standardized approximations by comparing them with direct size-standardized measures of

97   performance using a dataset containing 256 individuals and 51 species of anurans that span a

98   broad range of morphological, ecological, and geographic diversity. We also describe several

99   ways to parameterize these anatomical approximations to obtain precise estimates of jumping

100   performance. In developing these approximations, we provide a new avenue for obtaining

101   estimates of jumping performance, and we set the stage for future broad-scale macroevolutionary

102   studies of jumping performance in anurans and potentially other jumping animals.

103

104   **Methods**

105   *Anatomical approximations for jumping performance*:

106   Here we derive approximations for several aspects of jumping performance during take-

107   off, including peak velocity (Eq. 1), peak energy (Eq. 3), and peak power (Eq. 5). These

108   approximations are derived through mathematical equivalencies between equations from physics

109   and their analogous equations obtained from functional morphology (e.g. Peplowski and Marsh

110   1997). We then describe size-standardization using conventional methods. Specific

111   morphological measures used as input variables to estimate our model parameters are discussed

112   below. Presently, we do not consider the effects of limb positioning or power amplification on

113   jumping, since these phenomena have not been yet been characterized across a sufficiently wide

114   set of taxa to facilitate parameterization (see Discussion).

115

116   *Peak jumping velocity*:

117   We first note that many of our kinematic equations assume constant acceleration, which

118   does not occur in frog jumping (Marsh and John-Alder 1994). Although variable acceleration

119   influences the relationship between velocity and time, previous work has shown that acceleration

120   profiles have similar shapes across individuals and species (e.g. Marsh and John-Alder 1994;

121   James and Wilson 2008; Moen et al. 2013). Thus, for example, the relationship between any

122   estimate of average jumping velocity (v_{avg}) and peak velocity (v_f) at take-off should be constant

123   across individuals and species. We can leverage the comparative nature of our study to find an

124   estimator of peak jumping velocity, because differences between mean velocity estimates under

125   constant acceleration and under variable acceleration will be similar across species.

126   Under constant acceleration, the movement of an organism during a jump is described by

127   the kinematic equation $v_f^2 = v_i^2 + 2da$, where v_i is the initial velocity, *d* is the distance traveled

128   by a body, and *a* is acceleration in the direction of motion during takeoff. $v_i = 0$ for organisms at

129   rest, before the start of a jump. One can substitute *d* with a morphology-based estimate, L_{com}, the

130   distance from the tip of the toes to the center of mass of the organism (Peplowski and Marsh

131   1997). By solving for v_f and applying Newton's second law (*F* = *ma*, where *m* is body mass and

132   *F* is muscle force), we arrive at an approximation for peak jumping velocity whose parameters

133   can be estimated entirely from anatomical measurements:

134

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

136

137 Here, F_{PCSA} is an estimate of muscle force obtained from muscle physiological cross-sectional

138 area (PCSA; see section on morphological measures below). Dimensional analysis of this

139 anatomical approximation for velocity yields dimensions of length per time, as in actual velocity.

140 Possible morphological measures that may be used as input variables for m, L_{com}, and F_{PCSA} are

141 discussed below. Note that for interspecific datasets used in phylogenetic comparative studies,

142 size is a confounding factor. Thus, as is implemented in some comparative biomechanical studies

143 (e.g. Marsh and John-Alder 1994; Astley 2016), snout-vent length (*SVL*) may be used to size-

144 standardize $v_{Appx.}$, yielding units of body lengths per time (if L_{com} and *SVL* share the same units).

145

146 *Peak jumping energy*:

147   From classical physics, we know that kinetic energy (*E*) at take-off is:

148

$$E = \frac{1}{2}mv_f^2.$$ (2)

150

151 By using Eq. 1 to estimate v_f in Eq. 2, we arrive at an anatomical approximation for peak

152 jumping energy as (Eq. 3):

153

$$E_{Appx.} = L_{com}F_{PCSA}.$$ (3)

155

156   Dimensional analysis of $E_{Appx.}$ yields dimensions of mass times length squared per time squared

157   (i.e. the same dimensions as kinetic energy), and units of Joules (J) if estimated using SI units.

158   We note that change in energy, or the product of force and distance, is the work done in

159   performing a jump. Work and peak jumping energy are equivalent when initial energy is 0, as in

160   an organism at rest prior to initiating a jump. As above, interspecific datasets used in

161   phylogenetic comparative studies must account for differing body sizes among species. In this

162   case, we use body mass (m) to size-standardize $E_{Appx.}$ (see Marsh and John-Alder 1994). We

163   note that other standardizations are possible. For example, Astley (2016) standardized peak

164   energy by muscle mass instead of body mass.

165

166   *Peak jumping power*:

167   Jumping power, like acceleration, is also known to vary throughout the take-off phase

168   (Marsh and John-Alder 1994). Similar to how average jumping velocity (v_{avg}) is a summary

169   statistic of change in position, average power (P_{avg}) describes the average amount of mechanical

170   work done per unit time during take-off. Average power (P_{avg}) from rest to take-off (see Eq. 15

171   in Marsh, 1994) is peak kinetic energy (at take-off) divided by contact time:

172

173     $$P_{avg.} = \frac{mv_f^2}{2t}.$$ (4)

174

175   To estimate peak power (P) at take-off, we may substitute Eq. 1 to estimate v_f and the

176   relationship $t = \frac{2L_{com}}{v_f}$ (Marsh and John-Alder 1994) into Eq. 4, and double it ($P = 2P_{avg}$;

177   Peplowski and Marsh 1997) to arrive at an anatomical approximation for peak jumping power

178   (Eq. 5):

179

180   $$P_{Appx.} = \sqrt{\frac{2L_{com}F_{PCSA}^3}{m}}.$$ (5)

181

182   Dimensional analysis of $P_{Appx.}$ yields dimensions of mass times length squared per time cubed

183   (as in actual power), and units of Watts (W) if estimated using SI units. As we did for peak

184   jumping energy, we standardized $P_{Appx.}$ to size with body mass (m; see Marsh and John-Alder

185   1994). As above, an alternative standardization is given by Astley (2016), who standardized peak

186   power by muscle mass.

187

188   *Morphological measures used in approximations:*

189   Eqs. 1-5 provide mathematical derivations of approximations for peak jumping velocity,

190   energy, and power based on anatomical measurements. Estimating jumping performance for an

191   individual using the anatomical approximations above requires that specific morphological

192   measures be used as input variables for m, L_{com}, and F_{PCSA}. Overall, we emphasize that the

193   specific measurements chosen for study will affect the values and scaling of the approximations

194   and hence their correspondence to *in vivo* measurements of performance. In most cases the exact

195   values of the approximations will not be equivalent to those from observed performance

196   estimates (see below for further discussion).

197   While a number of different measurement schemes can be envisioned (see Online

198   Resources 1A and 1B), the following approach based on data available in Moen et al. (2013) and

199   Astley (2016) was used in this study. 1: Mass (m): the body mass of the individual during the

200   trial in which it produced its peak jumping velocity (i.e. the trial whose performance data were

201   published by Moen et al. 2013) or at the time of dissection (Astley 2016). See Online Resource

202   1A for discussion of using wet and preserved body masses as estimates of body mass. 2: L_{com}:

203   Previous authors (Peplowski and Marsh 1997) have defined L_{com} as the distance from the tip of

204   the toes to the center of mass of the organism. For the present study, we used total hind limb

205   length (L_{hl}) as our measure, which will be shorter. 3: muscle force (*F):* For a single muscle, force

206   is equivalent to its physiological cross-sectional area (*PCSA*) times the specific tension of the

207   muscle: $F = PCSA * specific\ tension$ (Sacks and Roy 1982). See Online Resource 1B for

208   additional alternative estimates of *F*. For a given value of *specific tension*, which has been shown

209   to be relatively invariant among different types of muscle fibers, muscles, and vertebrates (see

210   Online Resource 1C), *F* is thus proportional to *PCSA*: $F \propto PCSA$. Notably, Fukunaga et al.

211   (1996) reported a strong correlation between muscle force exerted on the Achilles tendon in

212   humans and both the *PCSA* and anatomical cross-sectional area (*ACSA*) of the ankle flexors.

213   Furthermore, Hellam and Podolsky (1969) found that *F* is highly correlated to anatomical cross-

214   sectional area (*ACSA*) in the semitendinosus muscle of the upper leg in *Rana pipiens*. ACSA may

215   be used to approximate *PCSA*, but this does not account for muscle pinnation. Thus, this

216   approximation will be most problematic for heavily pinnate muscles, such as the plantaris longus

217   (Calow and Alexander 1973). However, all upper-leg muscles that contribute to the jump are

218   parallel-fibered (Calow and Alexander 1973; Olson and Marsh 1998). Moreover, most gross

219   architecture of anuran muscles (e.g. identities of muscles; whether a given muscle is parallel-

220   fibered or pinnate) is congruent across highly divergent species (Duellman and Trueb 1986;

221   Prikryl et al. 2009), and data on fine-scale architecture (e.g. angle of pinnation in the plantaris) is

222   not available for most species. Therefore, following Marsh (1994), and assuming geometric

223   isometry of muscles across species, we used the 2/3 root of muscle mass to estimate muscle force

224   (F):

225

$$F \propto ACSA \propto m_{muscle}^{2/3}. \qquad (6)$$

227

228   As we suggested before, all muscle fibers (i.e. the total cross-sectional area) from some

229   extensor muscles in the upper and lower leg generate force during a jump (Hirano and Rome

230   1984; Lutz and Rome 1994). Therefore, following Eq. 6, we used the combined bilateral sum of

231   muscle masses from the upper and lower portions of the hind limb to represent F. Although we

232   use muscle mass to approximate muscle force (F), we recognize that alternative morphological

233   measurements may provide improved representations of muscle force. For example, the muscles

234   of the back and pelvis function in powering and controlling jumps (Richards et al. 2018).

235   However, since back muscles make up <0.5% of body mass (Emerson and DeJongh 1980), their

236   contribution to jumping is small compared to leg muscle mass, which makes up 5–30% of body

237   mass in anurans (Mendoza et al. 2020). Furthermore, Clemente and Richards (2013) found that

238   plantaris muscle force scaled with body mass to the 0.94 power in *Xenopus laevis*, and not 2/3 as

239   predicted above by geometric isometry. Thus, an improved estimate of the m_{muscle} exponent in

240   Eq. 6 is possible for some species. However, across a broader set of body sizes and habitat

241   utilization, the scaling of Marsh (1994) may be preferable (see additional discussion in Online

242   Resources 1B and 1C). Future improvements of our approach should include more precise

243   species-specific estimates of plantaris pinnation, specific tension of various muscles, and thus

244   force.

245

246   *Data Collection:*

247   To determine the relationship between each anatomical approximation and *in vivo*

248   measurements of jumping performance, we used the subset of data from Moen et al. (2013) and

249   Astley (2016) that included necessary trait measurements (i.e. leg muscle mass) and species with

250   more than one individual. Additionally, we did not include Astley's (2016) data on *Heterixalus*

251   *alboguttatus* because these values showed unusually low performance for this genus; power

252   values were more than an order of magnitude lower than our (DSM's) unpublished data on two

253   other congeners and are inconsistent with all other published data on arboreal frogs of the same

254   body size (Mendoza et al. 2020). Overall, our dataset comprised morphological measures and

255   jumping performance from a total of 256 adult anurans from 51 species, which spanned a wide

256   body-size range and were found in a variety of microhabitats.

257   The morphological measurements of Astley (2016) were collected from freshly dissected

258   individuals. Morphological measurements from Moen et al. (2013) were collected on preserved

259   specimens, with the exception of live body mass, which was the body-mass measurement made

260   just prior to that individuals' highest velocity jump. The preserved length measurements included

261   length of the femur, tibiofibula, tarsus, and foot. We obtained estimates of wet muscle mass for

262   these individuals from Mendoza et al. (2020), who estimated wet muscle mass for the Moen et

263   al. (2013) taxa as the product of live body mass and the live muscle-mass-to-body-mass ratio

264   from a subset of taxa for which both types of data were available. These wet muscle mass

265   estimates from Mendoza et al. (2020) came from the same individuals for which linear

266   measurements were obtained (Moen et al. 2013). Although preservation is known to change the

267   magnitude of original trait values through dehydration (Vervust et al. 2009; Shu et al. 2017;

268   Sotola et al. 2019), the correlation between live and preserved body mass in anurans can be quite

269   high ($r > 0.98$; Shu et al. 2017). Similarly, in our study we found a correlation of $r > 0.99$ (see

270   Online Resource 1A). Thus, we expect that future comparative studies that use only museum

271   specimens (and thus preserved body and muscle mass) will give largely consistent results as with

272   live or otherwise unpreserved measures (as we consider here).

273   Moen et al. (2013) and Astley (2016) obtained jumping performance from individual live

274   frogs, including data used to calculate size-standardized peak velocity, energy, and power at

275   takeoff for this study. Both studies reported peak performance as the estimates collected from

276   each individual's single fastest jump. Moen et al. (2013) took high-speed videos of jumping take-

277   off for each frog, digitized and smoothed the distance-time plots, and calculated derivatives of

278   these plots to estimate peak velocity and acceleration. Frogs were jumped over 3-5 sessions

279   during the course of a week until performance was visually reduced (usually after 4–5 jumps) in

280   each session (for additional details, see Moen et al. 2013). Astley (2016) collected performance

281   data using either a force plate or high-speed videos, using methods similar to those found in

282   Moen et al. (2013) to analyze data from high-speed videos. Frogs were jumped over a minimum

283   of 5 sessions and with a period of 5 minutes rest between trials (for additional details, see Astley

284   2016). Finally, we calculated species means for each approximation and jumping performance

285   measure and followed the size-standardization procedures described above to account for

286   differences in mean body size across species.

287

288   *Statistical Analysis:*

289   We evaluated the efficacy of each anatomical approximation using several procedures.

290   First, since species means are not independent due to shared ancestry (Felsenstein 1985), we

291   used phylogenetic generalized least squares (PGLS) regression (Martins and Hansen 1997;

292   Blomberg et al. 2012; Adams 2014) to test for an association between each size-standardized

293   approximation and its corresponding size-standardized measure of jumping performance. To

294   obtain a time-scaled phylogeny, we drew 1000 replicate trees from a pseudo-posterior

295   distribution of time-calibrated molecular phylogenies (Jetz and Pyron 2018) which included

296   every species in the datasets of Moen et al. (2013) and Astley (2016). We calculated mean

297   branch lengths for a consensus topology of these 1000 replicate trees. We then pruned this

298   phylogeny for correspondence with the dataset using *geiger* version 2.0.7 (Harmon et al. 2008).

299   See Online Resource 1D and 2 for further details on phylogeny generation for our analyses and

300   access to the phylogeny. Additionally, we evaluated the relationship between the size-

301   standardized approximations and measures of jumping performance using ordinary least squares

302   (OLS) regression. See Online Resource 1E for details on OLS regressions. Finally, we used the

303   Akaike Information Criterion (AIC) to evaluate the efficacy to predict *in vivo* jumping

304   performance from the size-standardized approximations versus several linear anatomical

305   measurements treated individually. These individual anatomical measurements included the

306   input variables for each approximation. We standardized each individual variable using SVL or

307   body mass, where appropriate, following previous studies linking morphology with jumping

308   performance in anurans (e.g. Gomes et al. 2009; Astley 2016; Moen 2019). For example, we

309   compared $v_{Appx.}$ with each one of its input variables including L_{com}, leg muscle mass, and body

310   mass, after standardizing each by SVL.

311   For both the OLS and PGLS regressions, we report traditional regression statistics

312   alongside standardized effect sizes (z-scores) obtained from empirical sampling distributions

313   (sensu Collyer et al. 2015). We also calculated 95% confidence intervals and obtained the

314   coefficient of determination (r^2) for these models, which is interpreted as a measure of the utility

315   of the anatomical approximations. While we derived the approximations to have the same units

316   as *in vivo* measurements of performance, our use of muscle mass to represent force changes the

317   units and relative scale of the approximations (see Figs. 1-3), rendering the slope and intercept

318   less useful as measures of utility than overall correspondence between approximated and

319   observed performance. We implemented regressions and obtained confidence intervals and effect

320   sizes (z-scores) using RRPP, a procedure where residuals are randomized (i.e., permuted) to

321   obtain model effects and evaluate model significance (for details see: Collyer et al. 2015; Adams

322   and Collyer 2018a,b). We used the R-package *RRPP* version 0.6.0.9000 (Collyer and Adams

323   2018) to implement our regressions, using 10,000 permutations for tests of statistical

324   significance. Further investigation comparing models based on individuals rather than mean

325   values, and the effect of sex on our approximations, may be found in Online Resources 1F and

326   1G.

327   Finally, to illustrate the utility of these anatomical approximations for evaluating

328   evolutionary trends, we performed a series of phylogenetic signal analyses to determine if

329   covariation in jumping performance (as estimated by size-standardized anatomical

330   approximations) matches the evolutionary relationships among taxa, and the degree to which

331   they might. To do this we estimated both multivariate phylogenetic signal K_{mult} (Adams 2014),

332   for the dataset encompassing all three approximations, and the univariate estimate of

333   phylogenetic signal K (Blomberg et al. 2003) for each of the three traits treated separately. We

334   also estimated phylogenetic signal in the same manner for the *in vivo* measurements of peak

335   jumping performance, for comparison. For each, we used 10,000 permutations to obtain model

336   effects and evaluate significance. We then used principal components analysis and a

337   phylomorphospace approach (by scaling each variable to unit variance) to investigate

15

338   macroevolutionary trends and structure in our data (Sidlauskas 2008). Since the signs of all

339   variable loadings and scores are arbitrary and only their relative sign patterns (contrasts) and

340   relative magnitudes are meaningful (Jolliffe and Cadima 2016), we multiplied PC1 loadings and

341   scores by -1 to enhance interpretability. Additionally, we labeled species by microhabitat using

342   the data of Moen et al. (2013) and data found on AmphibiaWeb (2020). We analyzed

343   phylogenetic signal and made phylomorphospace plots using *geomorph* version 3.3.1 (Adams et

344   al. 2020).

345

346   **Results**

347   We found that size-standardized anatomical approximations for peak jumping velocity

348   and energy, but not the approximation for jumping power, were highly and significantly

349   correlated with jumping performance, regardless of whether we used ordinary least squares

350   (OLS) or phylogenetic generalized least squares (PGLS) regression. PGLS regression yielded

351   both high r^2 values and effect sizes (empirically-derived z-scores) for peak jumping velocity

352   (Fig. 1; $F = 141.35$, $r^2 = 0.74$, $P < 0.0001$, $z = 2.78$) and peak jumping energy (Fig. 2; $F =$

353   118.18, $r^2 = 0.71$, $P < 0.0001$, $z = 2.68$). We found a relatively lower r^2 for the approximation of

354   peak jumping power (Fig. 3; $F = 25.83$, $r^2 = 0.35$, $P < 0.0001$, $z = 2.03$). We present results for

355   OLS regressions in Online Resource 1E. Model comparisons revealed that in the case of jumping

356   velocity, the approximation outperformed other size-standardized variables including leg length

357   (ΔAIC $= 63$, $r^2 = 0.10$), leg muscle mass (ΔAIC $= 63$, $r^2 = 0.10$), and body mass (ΔAIC $= 56$, $r^2 =$

358   0.23). These relationships between velocity, leg length, and leg muscle mass are weaker than

359   those found previously (Moen 2019), but the differences between studies disappear when we do

360   not standardize velocity by body length (as in Moen 2019, results not shown). The

361 approximation for jumping energy outperformed leg length (ΔAIC = 56, r^2 = 0.12) and leg

362 muscle mass (ΔAIC = 6, r^2 = 0.67). Finally, we found that the jumping power approximation did

363 not outperform all other variables, with the preferred variable being leg muscle mass (ΔAIC = 0,

364 r^2 = 0.48), followed by the approximation (ΔAIC = 12, r^2 = 0.35), and leg length (ΔAIC = 33, r^2

365 = 0.00). These latter results indicate that some aspects of jumping power are not captured well

366 with this approximation.

367   Additionally, we found significant phylogenetic signal (though with traits showing less

368 signal than expected under Brownian Motion) and strong effect sizes in our data for both the

369 anatomical approximations and *in vivo* measures of jumping performance. In a multivariate

370 context, the phylogenetic signal for the approximations of jumping performance was K_{mult} =

371 0.71 ($P < 0.0001$, $z = 5.36$). Likewise, univariate phylogenetic signal for the approximations

372 showed significant phylogenetic signal and strong effect sizes (peak jumping velocity: $K = 0.58$,

373 $P < 0.0049$, $z = 3.03$; energy: $K = 0.77$, $P < 0.0002$, $z = 4.45$; power: $K = 0.78$, $P < 0.0006$, $z =$

374 4.38). Analyses of phylogenetic signal for *in vivo* measurements of jumping performance yielded

375 similar estimates ($K < 1$) for the multivariate set of traits ($K_{mult} = 0.72$, $P < 0.0012$, $z = 4.36$) and

376 each trait individually: peak jumping velocity ($K = 0.82$, $P < 0.0003$, $z = 4.77$), energy ($K = 0.63$,

377 $P < 0.0053$, $z = 3.09$), and power ($K = 0.76$, $P < 0.0048$, $z = 3.41$). These results emphasize the

378 correspondence of macroevolutionary results between anatomical approximations and *in vivo*

379 measurements of peak jumping performance. Investigation of these size-standardized variables

380 using principal components demonstrated that most of the variation in the dataset (70.53%; Table

381 1) is encompassed by an axis which contrasts species with high values for all three aspects of

382 peak jumping performance and species with low values for all three variables. Thus, PC1 of the

383 resulting phylomorphospace (Fig. 4) represents an evolutionary contrast between strong and

384   weak jumpers. For example, we found the best jumper in the dataset (the striped rocket frog

385   *Litoria nasuta*) and the worst jumper (*Duttaphrynus melanostictus*) on opposite ends of PC1.

386   Likewise, variation along PC2 was defined by 'inefficient' and 'efficient' jumpers who display

387   contrasting levels of mass-specific energy, relative to their peak jumping velocity. For example,

388   we found *Odorrana grahami* (a high mass-specific energy, low velocity jumper) and *Syncope*

389   *bassleri* (a low mass-specific energy, high velocity jumper) on opposite ends of PC2.

390

391   **Discussion**

392   In this study, we developed a series of size-standardized anatomical approximations for

393   three estimates of jumping performance (peak velocity, energy, and power at take-off). We found

394   strong, statistically significant relationships relating *in vivo* jumping performance of 51 species

395   and the velocity and energy approximations based on their morphology. These approximations

396   outperformed individual anatomical variables. Such results imply that our approach – based

397   solely on anatomy – may serve as useful approximations of relative jumping performance in

398   anurans. By contrast, we found the approximation for jumping power to be a poor predictor of *in*

399   *vivo* jumping performance, implying that some aspects of anuran jumping power are not captured

400   with this approximation (see below). We also characterized the phylogenetic signal of these size-

401   standardized approximations of peak jumping performance and determined the principal

402   evolutionary axes of variation in these traits, confirming the utility of these approximations in a

403   phylogenetic comparative context. These findings demonstrate that anatomical approximations

404   of anuran jumping performance can potentially further our understanding of macroevolution and

405   the evolutionary shifts in these traits throughout the diversification of a lineage. In addition,

406   given that our dataset encompassed a broad degree of taxonomic, morphological, and ecological

407   diversity, the approximations presented here represent a new tool useful in comparative studies

408   that can be used to obtain relative estimates of jumping performance. They can also be used to

409   leverage data from museum specimens in studies of functional evolution. As such we argue that

410   the results of this work can be used to learn about relative jumping performance, in a

411   comparative context, by facilitating the incorporation of additional taxa where direct estimates of

412   performance are not possible.

413   One key benefit of the approach used here is that the approximations are flexible; they

414   may be estimated using a variety of different morphological measures and do not require

415   procedures that may damage museum specimens. For example, non-invasive measurements of

416   the external dimensions of leg muscles may be used to estimate the cross-sectional area of those

417   muscles to be used as approximations of muscle force, given the allometric principles described

418   in Eq. 6. This is especially important in cases where leg muscle mass cannot be obtained (e.g.

419   endangered species, rare museum specimens). It should be emphasized that the anatomical

420   approximations are only in the same absolute units as the traditional measures of jumping

421   performance when actual estimates of muscle force are used, rather than the allometric scaling

422   approximations based on mass that we used here. For this reason, direct comparisons of the

423   values of the approximations to estimates obtained using *in vivo* laboratory methods are not

424   advised, given that they do not scale equally (e.g. compare axes of Figs. 1–3).

425   Our results demonstrate the efficacy of anatomical approximations of jumping

426   performance. However, we recognize that our approach does not capture some aspects of the

427   biomechanics of jumping. For instance, power amplification (Marsh and John-Alder 1994;

428   Astley and Roberts 2012) and limb positioning (Kargo and Rome 2002; Nauwelaerts and Aerts

429   2006) may contribute to jumping ability in certain anuran species. Moreover, smaller species

430   may use power amplification to a greater extent than do larger species (Sutton et al. 2019;

431   Mendoza et al. 2020). Thus, power amplification and/or limb positioning across taxa of differing

432   body sizes could affect variation in jumping performance at the macroevolutionary scale (such as

433   in burrowing species; Mendoza et al. 2020). As others have discussed, percent muscle mass has

434   been shown to play a large role in powering a jump (James and Wilson 2008; Astley 2016; Moen

435   2019). Specifically, muscle mass of the hamstring (semimembranosus) and calf (plantaris)

436   muscles in anurans has been shown to correlate with power amplification (Roberts and Marsh

437   2003; Astley and Roberts 2012; Astley 2016). Thus, our result that the proportion of muscle

438   mass relative to body mass outperformed the power approximation may imply that our

439   approximation does not capture relevant variables involved in power amplification, offering little

440   advantage over prior approaches based on relative muscle mass alone. Further research should

441   seek improvements to the power approximation, perhaps including aspects of power

442   amplification that may partially decouple power from F_{PCSA} (e.g. material properties of elastic

443   elements, muscle power). However, at present we cannot incorporate these effects into the

444   anatomical approximations presented here, as one must first develop reliable biomechanical

445   models used to predict the degree of power amplification found across a wide range of anuran

446   species. Nonetheless, as we elucidate the extent to which different species use power

447   amplification (Mendoza et al. 2020), refinements to the approximations that accommodate such

448   effects could be developed.

449   An additional caveat with the approximations presented here is that they are not

450   guaranteed to yield reliable values in situations when morphology does not match behavioral

451   performance. For example, some walking or swimming species may jump poorly due to

452   behavioral differences but retain ancestral hindlimb proportions characteristic of primarily

453 jumping close relatives. This may lead to imprecise estimates of jumping performance in those

454 taxa because the anatomical approximations do not reflect behavior. Thus, a strong knowledge of

455 the natural history of the species under investigation remains useful for interpreting patterns

456 obtained from these estimates. We also note that while primary locomotor mode might change,

457 some of these species retain the ability to jump well (e.g. the "running" frog *Kassina*; Porro et al.

458 2017; Richards et al. 2017). That said, we generally advise that anatomical approximations of

459 jumping performance be applied only to species whose primary mode of locomotion is jumping.

460   We did not address here whether the approximations are capable of predicting jumping

461 performance within species. Given our results using interspecific data, we anticipate that the

462 relationship between form and function captured by the approximations is also reflected at the

463 intraspecific level. However, the influence of scale (range of values) on the relationship between

464 the approximations and jumping performance found in an intraspecific dataset may yield novel

465 results, especially given that some studies have shown a reduced fit between morphology and

466 performance within species (Emerson 1978; Wilson et al. 2000) as compared to across them

467 (Emerson 1978; Gomes et al. 2009; Astley 2016; Moen 2019).

468   Additionally, sexual size dimorphism is prevalent in anurans (> 90% of species; DeLisle

469 and Rowe 2013; Han and Fu 2013; Nali et al. 2014). Yet little is known about patterns of sexual

470 shape dimorphism in anurans and its relationship to jumping. While there is some evidence that

471 jumping performance (Moen et al. 2013) and hindlimb morphology (Petrović et al. 2017) may be

472 similar between sexes across some taxa, this has yet to be examined thoroughly in an allometric

473 context. This, then, raises the question as to whether morphology and jumping performance have

474 evolved differently in male and female anurans. For example, in anurans, sexual dimorphism

475 related to locomotor traits has been described within and between species (Hudson et al. 2016;

476   Petrović et al. 2017). Furthermore, in lizards, it has been shown that morphological patterns

477   evolve as a function of distinctive selective pressures associated with sex-specific habitat use

478   (Kaliontzopoulou et al. 2015). If such trends are also present in anurans, selection for jumping

479   performance and its associated traits (e.g. body mass, leg length) may also differ relative to

480   allometry. As such, the evolution of sexual size and shape dimorphism, and how jumping

481   performance relates to shape in an allometric context, is an important area of future research.

482   One trait of particular relevance in anurans is mass, which in females may be greatly influenced

483   by the amount of eggs being carried. Studies in lizards have found a negative relationship

484   between increased loads and jumping take-off speeds (Kuo et al. 2011) or sprinting speed

485   (Sinervo et al. 1991; Shine 2003). Since mass is explicitly incorporated in our approximations, at

486   least some of the effect of an increased load exhibited by egg-carrying females should be

487   reflected in the approximation values. Yet, this represents an area of further development in these

488   anatomical approximations.

489   Finally, a particularly exciting avenue of future research concerns whether the

490   approximations developed here can predict jumping performance in other jumping organisms,

491   including mammals, lizards, arachnids, and insects. The same equations from functional

492   morphology have been used independently to estimate jumping performance in both anurans

493   (Marsh 1994; Marsh and John-Alder 1994; James et al. 2007) and *Anolis* lizards (Pounds 1988;

494   Losos 1990a,b; Toro et al. 2003; Toro et al. 2004). All of these studies are ultimately based on

495   the work of Alexander (1968), which provided the foundation of the ballistics equations used in

496   these other studies, implying that the approximations derived here may be applicable across a

497   wide variety of jumping organisms. We hypothesize that our approximations should be useful in

498   estimating relative differences in jumping performance in all jumping vertebrates, given that

499   most vertebrates are large enough that air resistance will not greatly affect jumping performance

500   (Vogel 2005). One area of future research concerns whether the anatomical approximations

501   presented here are useful in arthropods, which use a combination of muscle extensors and

502   hydraulic pressure to produce force during a jump (Ellis 1944; Dillon 1952).

503

504   **Conclusion**

505   Estimating jumping performance using traditional *in vivo* techniques for frogs that live all

506   around the world is logistically challenging. To bypass some of these challenges, we provide an

507   alternative way of estimating relative jumping performance via anatomical approximation. By

508   combining equations from physics and functional morphology, we derive size-standardized

509   anatomical approximations that are able to predict jumping performance with high precision

510   using only morphological data. These approximations are designed to be flexible through the use

511   of input data such as muscle mass or diameter, which would minimize destructive sampling of

512   museum specimens. Using this new approach, on one hand our results echo previous studies:

513   there is a strong relationship between percent muscle mass and peak jumping power, highlighting

514   the role of power amplification at macroevolutionary scales. On the other hand, we demonstrate

515   the efficacy of estimates for peak jumping velocity and energy, which implies that they may be

516   useful in further elucidating the associations between morphology, performance, and ecology in

517   anurans.

518

519   **Declarations**

520   *Funding:*

523

524   *Conflicts of Interest/Competing interests:*

525   The authors declare no conflicts or competing interests.

526

527   *Ethics approval:*

528   Not applicable.

529

530   *Consent to participate:*

531   Not applicable.

532

533   *Consent for publication:*

534   The authors all consent to publication.

535

536   *Availability of data and material:*

537   Time-scaled phylogenetic tree used in analyses may be found in the Online Resource.

538

539   *Code availability:*

540   Scripts for all analyses in this study can be found at github.com/bhjuarez/approximations-for-

541   jumping.

542   **References**

543   Adams, D. C. (2004). A generalized *K* statistic for estimating phylogenetic signal from shape and

544   other high-dimensional multivariate data. *Syst. Biol.,* 63(5), 685–697.

545   Adams, D. C. (2014). A method for assessing phylogenetic least squares models for shape and

546   other high-dimensional multivariate data. *Evolution,* 68(9), 2675–2688.

547   Adams, D. C., & Collyer, M. L. (2018a). Multivariate phylogenetic comparative methods:

548   evaluations, comparisons, and recommendations. *Syst. Biol.,* 67(1), 14–31.

549   Adams, D. C., & Collyer, M. L. (2018b). Phylogenetic ANOVA: Group-clade aggregation,

550   biological challenges, and a refined permutation procedure. *Evolution,* 72(6), 1204–1215.

551   Adams, D. C., Collyer, M. L., & Kaliontzopoulou, A. (2020). Geomorph: Software for geometric

552   morphometric analyses. R package version 3.2.1.0900. https://cran.r-

553   project.org/package=geomorph.

554   Alexander, R. McN. (1968). *Animal Mechanics*. Seattle, Washington, USA: University of

555   Washington Press.

556   AmphibiaWeb. (2020). <https://amphibiaweb.org> University of California, Berkeley, CA,

557   USA. Accessed 20 Mar 2020.

558   Arnold, S. J. (1983). Morphology, performance, fitness. *Am. Zool.,* 23(2), 347–361.

559   Astley, H. C. (2016). The diversity ad evolution of locomotor muscle properties in anurans. *J.*

560   *Exp. Biol.,* 219, 3163–3173.

561   Astley, H. C., & Roberts, T. J. (2012). Evidence for a vertebrate catapult: elastic energy storage

562   in the plantaris tendon during frog jumping. *Biol. Lett.,* 8(3), 386–389.

563   Bennet-Clark, H. C. (1977). Scale effects in jumping animals. In *Scale effects in animal*

564   *locomotion* (ed. T.J. Pedley), pp. 195–201. New York: Academic Press.

565   Blomberg, S. P., Garland, T., & Ives, A. R. (2003). Testing for phylogenetic signal in

566   comparative data: behavioral traits are more labile. *Evolution,* 57(4), 717–745.

567   Blomberg, S. P., Lefevre, J. G., Wells, J. A., & Waterhouse, M. (2012). Independent contrasts

568   and PGLS regression estimators are equivalent. *Syst. Biol.,* 61(3), 382–391.

569   Calow, L. J., & Alexander, R. McN. (1973). A mechanical analysis of a hind leg of a frog (*Rana*

570   *temporaria*). *J. Zool.*, 171(3), 293–321.

571   Carroll, A. M., Wainwright, P. C., Huskey, S. H., Collar, D. C., & Turingan, R. G. (2004).

572   Morphology predicts suction feeding performance in centrarchid fishes. *J. Exp. Biol.,*

573   207(22), 3873–3881.

574   Citadini, J. M., Brandt, R., Williams, C. R., & Gomes, F. R. (2018). Evolution of morphology

575   and locomotor performance in anurans: relationships with microhabitat diversification. *J.*

576   *Evol. Biol.,* 31(3), 371–381.

577   Clemente, C. J., & Richards, C. (2013). Muscle function and hydrodynamics limit power and

578   speed in swimming frogs. *Nat. Commun.,* 4, 1–8.

579   Close, R. I. (1972). Dynamic properties of mammalian skeletal muscles. *Physiol. Rev.,* 52(1),

580   129–197.

581   Collyer, M. L., & Adams, D. C. (2018). RRPP: An R package for fitting linear models to high-

582   dimensional data using residual randomization. *Methods Ecol. Evol.,* 9(7), 1772–1779.

583   Collyer, M. L., Sekora, D. J., & Adams, D. C. (2015). A method for analysis of phenotypic

584   change for phenotypes described by high-dimensional data. *Heredity,* 115, 357–365.

585   De Lisle, S. P., & Rowe, L. (2013). Correlated evolution of allometry and sexual dimorphism

586   across higher taxa. *Am. Nat.,* 182(5), 630–639.

587   Dillon, L. S. (1952). The myology of the araneid leg. *J. Morphol.,* 90(3), 467–480.

588 Duellman, W. E., & Trueb, L. (1986). *Biology of Amphibians*. Baltimore, MD: Johns Hopkins

589   University Press.

590 Ellis, C. H. (1944). The mechanism of extension in the legs of spiders. *Biol. Bull.,* 86(1), 41-50.

591 Emerson, S. B. (1978). Allometry and jumping in frogs: Helping the twain to meet. *Evolution,*

592   32(3), 551–564.

593 Emerson, S. B., & De Jongh, H. J. (1980). Muscle activity at the ilio-sacral articulation of frogs.

594   *J. Morphol.*, 166(2), 129–144.

595 Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.,* 125(1), 1–15.

596 Fukunaga, T., Roy, R. R., Shellock, F. G., Hodgson, J. A., & Edgerton, V. R. (1996). Specific

597   tension of human plantar flexors and dorsiflexors. *J. Appl. Physiol.,* 80(1), 158–165.

598 Gillis, G. B., & Biewener, A. A. (2000). Hindlimb extensor muscle function during jumping and

599   swimming in the toad (*Bufo marinus*). *J. Exp. Biol.,* 203(23), 3547–3563.

600 Gomes, F. R., Rezende, E. L., Grizante, M. B., & Navas, C. A. (2009). The evolution of jumping

601   performance in anurans: morphological correlates and ecological implications. *J.*

602   *Evolution. Biol.,* 22(5), 1088–1097.

603 Han, X., & Fu, J. (2013). Does life history shape sexual size dimorphism in anurans? A

604   comparative analysis. *BMC Evol. Biol.*, 13(27), 1-11.

605 Harmon, L. J., Weir, J. T., Brock, C. D., Glor, R. E., & Challenger, W. (2008). GEIGER:

606   investigating evolutionary radiations. *Bioinformatics,* 24(1), 129–131.

607 Hirano, M., & Rome, L. C. (1984). Jumping performance of frogs (*Rana pipiens*) as a function

608   of muscle temperature. *J. Exp. Biol.,* 108(2), 429–439.

609 Hellam, D. C., & Podolsky, R. J. (1969). Force measurements in skinned muscle fibres. *J.*

610   *Physiol.,* 200(3), 807–819.

611 Huby, A., Lowie, A., Herrel, A., Vigouroux, R., Frédérich, B., Raick, X., Kurchevski, G.,

612 Godinho, A. L., & Parmentier, E. (2019). Functional diversity in biters: the evolutionary

613 morphology of the oral jaw system in pacus, piranhas and relatives (Teleostei:

614 Serrasalmidae). *Biol. J. Linn. Soc.,* 127(4), 722–741.

615 Hudson, C. M., Brown, G. P., & Shine, R. (2016). Athletic anurans: the impact of morphology,

616 ecology and evolution on climbing ability in invasive cane toads. *Biol. J. Linn. Soc.*,

617 119(4), 992–999.

618 James, R. S., Navas, C. A., & Herrel, A. (2007). How important are skeletal muscle mechanics in

619 setting limits on jumping performance? *J. Exp. Biol.,* 210(6), 923–933.

620 James, R. S., & Wilson, R. S. (2008). Explosive jumping: Extreme morphological and

621 physiological specializations of Australian rocket frogs (*Litoria nasuta*). *Physiol.*

622 *Biochecm. Zool.*, 81(2), 176–185.

623 Jetz, W., & Pyron, R. A. (2018). The interplay of past diversification and evolutionary isolation

624 with present imperilment across the amphibian tree of life. *Nat. Ecol. Evol.,* 2(5), 850-

625 858.

626 Jolliffe, I. T., & Cadima, J. (2016). Principal components analysis: a review and recent

627 developments. *Phil. Trans. R. Soc. A*, 374, 20150202.

628 http://dx.doi.org/10.1098/rsta.2015.0202

629 Kaliontzopoulou, A., Adams, D. C., van der Meijden, A., Perera, A., & Carretero, M. A. (2012).

630 Relationships between head morphology, bite performance and ecology in two species of

631 *Podarcis* wall lizards. *Evol. Ecol.,* 26, 825–845.

632 Kaliontzopoulou, A., Carretero, M. A., & Adams, D. C. (2015). Ecomorphological variation in

633   male and female wall lizards and the macroevolution of sexual dimorphism in relation to

634   habitat use. *J. Evol. Biol.,* 28(1), 80–94.

635 Kargo, W. J., & Rome, L. C. (2002). Functional morphology of proximal hindlimb muscles in

636   the frog *Rana pipiens. J. Exp. Biol.,* 205(14), 1987–2004.

637 Kuo, C., Gillis, G. B., & Irschick, D. J. (2011). Loading effects on jump performance in green

638   anole lizards, *Anolis carolinensis. J. Exp. Biol.,* 214(12), 2073–2079.

639 Lieber, R. L., & Boakes, J. L. (1988). Muscle force and moment arm contributions to torque

640   production in frog hindlimb. *Am. J. Physiol.,* 254(6), C769–772.

641 Losos, J. B. (1990a). The evolution of form and function: morphology and locomotor

642   performance in West Indian *Anolis* lizards. *Evolution,* 44(5), 1189–1203.

643 Losos, J. B. (1990b). Ecomorphology, performance capability, and scaling of West Indian *Anolis*

644   lizards: an evolutionary analysis. *Ecol. Monogr.,* 60(3), 369–388.

645 Lutz, G. J., & Rome, L. C. (1994). Built for jumping: The design of the frog muscular system.

646   *Science,* 263, 370–372.

647 Marsh, R. L. (1994). Jumping ability of anuran amphibians. *Adv. Vet. Sci. Comp. Med.,* 38B, 51–

648   111.

649 Marsh, R. L., & John-Alder, H. B. (1994). Jumping performance of hylid frogs measured with

650   high-speed cine film. *J Exp. Biol.,* 188, 131–141.

651 Martins, E. P., & Hansen, T. F. (1997). Phylogenies and the comparative method: a general

652   approach to incorporating phylogenetic information into the analysis of interspecific data.

653   *Am. Nat.,* 149(4), 646–667.

654 Mendoza, E., Azizi, E., & Moen, D. S. (2020). What explains vast differences in jumping power

655   within a clade? Diversity, ecology and evolution of anuran jumping power. *Funct. Ecol.,*

656   00, 1-11.

657 Moen, D. S., Irschick, D. J., & Wiens, J. J. (2013). Evolutionary conservatism and convergence

658   both lead to striking similarity in ecology, morphology and performance across

659   continents in frogs. *P. Roy. Soc. B,* 280(1773), 20132156.

660 Moen, D. S., Morlon, H., & Wiens, J. J. (2016). Testing convergence versus history:

661   Convergence dominates phenotypic evolution for over 150 million years in frogs. *Syst.*

662   *Biol.,* 65(1), 146–160.

663 Moen, D. S. (2019). What determines the distinct morphology of species with a particular

664   ecology? The roles of many-to-one mapping and trade-offs in the evolution of frog

665   ecomorphology and performance. *Am. Nat.,* 194(4), E81–95.

666 Muñoz, M. M., Anderson, P. S. L., & Patek, S. N. (2017). Mechanical sensitivity and the

667   dynamics of evolutionary rate shifts in biomechanical systems. *P. Roy. Soc. B,*

668   284(1847), 20162325.

669 Nali, R. C., Zamudio, K. R., Haddad, C. F., & Prado, C. P. (2014). Size-dependent selective

670   mechanisms on males and females and the evolution of sexual size dimorphism in frogs.

671   *Am. Nat.,* 184(6), 727–740.

672 Nauwelaerts, S., & Aerts, P. (2006). Take-off and landing forces in jumping frogs. *J. Exp. Biol.,*

673   209(1), 67–77.

674 Olson, J. M., & Marsh, R. L. (1998). Activation patterns and length changes in hindlimb muscles

675   of the bullfrog *Rana catesbeiana* during jumping. *J. Exp. Biol.,* 201(19), 2763–2777.

676 Patek, S. N., Nowroozi, B. N., Baio, J. E., Caldwell, R. L., & Summers, A. P. (2007). Linkage

677   mechanics and power amplification of the mantis shrimp's strike. *J. Exp. Biol.,* 210(20),

678   3677–3688. doi:10.1242/jeb.006486

679 Paradis, E., &, Schliep, K. (2018). ape 5.0: an environment for modern phylogenetics and

680   evolutionary analyses in R. *Bioinformatics*, 35, 526–528.

681 Peplowski, M. M., & Marsh, R. L. (1997). Work and power output in the hindlimb muscles of

682   Cuban tree frogs *Osteopilus septentrionalis* during jumping. *J. Exp. Biol.,* 200(22), 2861–

683   2870.

684 Petrović, T. M., Vukov, T. D., & Kolarov, N. T. (2017). Sexual dimorphism in size and shape of

685   traits related to locomotion in nine anuran species from Serbia and Montenegro. *Folia*

686   *Zool.,* 66(1), 11–21.

687 Porro, L. B., Collings, A. J., Ebergard, E. A., Chadwick, K. P., & Richards, C. T. (2017). Inverse

688   dynamic modelling of jumping in the red-legged frog, *Kassina maculata*. *J. Exp. Biol.*,

689   220():1882-1893. Doi: 10.1242/jeb.155416

690 Pounds, J. A. (1988). Ecomorphology, locomotion, and microhabitat structure: patterns in a

691   tropical mainland *Anolis* community. *Ecol. Monogr.,* 58(4), 299–320.

692 Powell, P. L., Roy, R. R., Kanim, P., Bello, M. A., & Edgerton, V. R. (1984). Predictability of

693   skeletal muscle tension from architectural determinations in guinea pig hindlimbs. *J.*

694   *Appl. Physiol.,* 57(6), 1715–1721.

695 Prikryl, T., Aerts, P., Havelkova, P., Herrel, A., & Rocek, Z. (2009). Pelvic and thigh

696   musculature in frogs (Anura) and origin of anuran jumping locomotion. *J. Anat.,* 214,

697   100–139. Doi:10.1111/j.1469-7580.2008.01006.x

698   Pyron, R. A., & Wiens, J. J. (2013). Large-scale phylogenetic analyses reveal the causes of high

699   tropical amphibian diversity. *P Roy. Soc. B,* 280(1770), 20131622.

700   Rand, A. S., & Rand, P. J. (1966). The relation of size and distance jumped in *Bufo marinus*.

701   *Herpetologica,* 22(3), 206–209.

702   Richards, C. T., Porro, L. B. and Collings, A. J. (2017). Kinematic control of extreme jump

703   angles in the red-legged running frog, *Kassina maculata*. J. Exp. Biol. 220, 1894-1904.

704   Richards, C. T., Eberhard, E. A., & Collings, A. J. (2018). The dynamic role of the ilio-sacral

705   joint in jumping frogs. *Biol. Lett.*, 14, 20180367. Doi: 10.1098/rsbl.2018.0367

706   Roberts, T. J., & Marsh, R. L. (2003). Probing the limits to muscle-powered accelerations:

707   lessons from jumping bullfrogs. *J. Exp. Biol.*, 206, 2567–2580.

708   Rospars, Jean-P., & Meyer-Vernet, N. (2016). Force per cross-sectional area from molecules to

709   muscles: a general property of biological motors. *R. Soc. Open Sci.,* 3(7),160313.

710   Sacks, R. D., & Roy, R. R. (1982). Architecture of the hind limb muscles of cats: functional

711   significance. *J. Morphol.,* 173(2), 185–195.

712   Shine, R. (2003). Effects of pregnancy on locomotor performance: an experimental study on

713   lizards. *Oecologia,* 136(3), 450–6.

714   Shu, G., Gong, Y., Xie, F., Wu, N. C., & Li, C. (2017). Effects of long-term preservation on

715   amphibian body conditions: implications for historical morphological research. *PeerJ*, 5,

716   e3805.

717   Sidlauskas, B. (2008). Continuous and arrested morphological diversification in sister clades of

718   characiform fishes: A phylomorphospace approach. *Evolution*, 62(12), 3135–3156.

719   Sinervo, B., Hedges, R., & Adolph, S. C. (1991). Decreased sprint speed as a cost of

720   reproduction in the lizard *Sceloporus occidentalis*: variation among populations. *J. Exp.*

721   *Biol.,* 155, 323–336.

722   Sotola, V. A., Craig, C. A., Pfaff, P. J., Maikoetter, J. D., Martin, N. H., & Bonner, T. H. (2019).

723   Effect of preservation on fish morphology over time: Implications for morphological

724   studies. *PLoS One*, 14(3), e0213915.

725   Suchard, M. A., Lerney, P., Baele, G., Ayres, D. L., Drummond, A. J., & Rambaut, A. (2018)

726   Bayesian phylogenetic and phylodynamic data integration using BEAST 1.10. *Virus*

727   *Evol.,* 4(1), vey016.

728   Sutton, G. P., Mendoza, E., Azizi, E., Longo, S. J., Olberding, J. P., Ilton, M., & Patek, S. N.

729   (2019). Why do large animals never actuate their jumps with latch-mediated springs?

730   Because they can jump higher without them. *Intgr. Comp. Biol.,* 59(6), 1609–1618.

731   Toro, E., Herrel, A., Vanhooydonck, B., & Irschick, D. J. (2003). A biomechanical analysis of

732   intra- and interspecific scaling of jumping and morphology in Carribean *Anolis* lizards. *J.*

733   *Exp. Biol.,* 206(15), 2641–2642.

734   Toro, E., Herrel, A., & Irschick, D. (2004). The evolution of jumping performance in Caribbean

735   *Anolis* lizards: solutions to biomechanical trade-offs. *Am. Nat.,* 163(6), 844–856.

736   Vervust, B., Van Dongen, S., & Van Damme, R. (2009). The effect of preservation on lizard

737   morphometrics – an experimental study. *Amphibia-Reptilia*, 30(3), 321–329.

738   Vogel, S. (2005) Living in a physical world II. The bio-ballistics of small projectiles. *J.*

739   *Biosciences,* 30(2), 167–175.

740   Wilson, R. S., Franklin, C. E., & James, R. S. (2000). Allometric scaling relationships of

741   jumping performance in the Striped Marsh Frog *Limnodynastes peronii*. *J. Exp. Biol.,*

742   203(12), 1937–1946.

743   Zug, G. R. (1972). Anuran locomotion: structure and function. I. Preliminary observations on

744   relation between jumping and osteometrics of appendicular and postaxial skeleton.

745   *Copeia,* 4(4), 613–624.

746   Zug, G. R. (1978). Anuran locomotion–structure and function, 2: Jumping performance of

747   semiaquatic, terrestrial, and arboreal frogs. *Sm. C. Zool.,* 276, 1–31.

Table and Figure Headings

Table 1. Eigenvectors of principal components analysis (variable loadings) based on approximations for peak jumping performance. Parentheses of PC axes indicate percent variance explained.

Figure 1. Approximating peak jumping velocity. Points are species means. Dashed lines indicate upper and lower bounds of a 95% confidence interval for the phylogenetic generalized least squares regression line. In anurans, "body length" refers to snout-to-vent length (SVL). Statistics are as follows: $F = 141.35$, $r^2 = 0.74$, $P < 0.0001$, $z = 2.78$. Regression equation is:

$Approximation = 3.972 + 0.148 \frac{Velocity}{SVL}$, where SVL is snout-vent length.

Figure 2. Approximating peak jumping energy. Points are species means. Dashed lines indicate upper and lower bounds of a 95% confidence interval for the phylogenetic generalized least squares regression line. Statistics are as follows: $F = 118.18$, $r^2 = 0.71$, $P < 0.0001$, $z = 2.68$. Regression equation is: $Approximation = 0.055 + 0.016 \, Mass\text{--}Specific \, Energy$.

Figure 3. Approximating peak jumping power. Points are species means. Dashed lines indicate upper and lower bounds of a 95% confidence interval for the phylogenetic generalized least squares regression line. Statistics are as follows: $F = 25.83$, $r^2 = 0.35$, $P < 0.0001$, $z = 2.03$. Regression equation is: $Approximation = 0.427 + 0.002 \, Mass\text{--}Specific \, Power$.

770 **Figure 4. Phylomorphospace of size-standardized peak jumping performance**

771 **approximations.** Variables in analysis included each approximation for peak jumping velocity,

772 energy, and power. Variables were scaled to unit variance prior to analysis. Large colored

773 squares are species. See Table 1 for variable loadings and variation explained by each axis.

774

775 **Online Resource Captions**

776 *1A: Body Mass*

777 *1B: Muscle Force*

778 *1C: Specific Tension*

779 *1D: Time-scaled Phylogeny Methods*

780 *1E: OLS Regressions*

781 *1F: Individual Regressions*

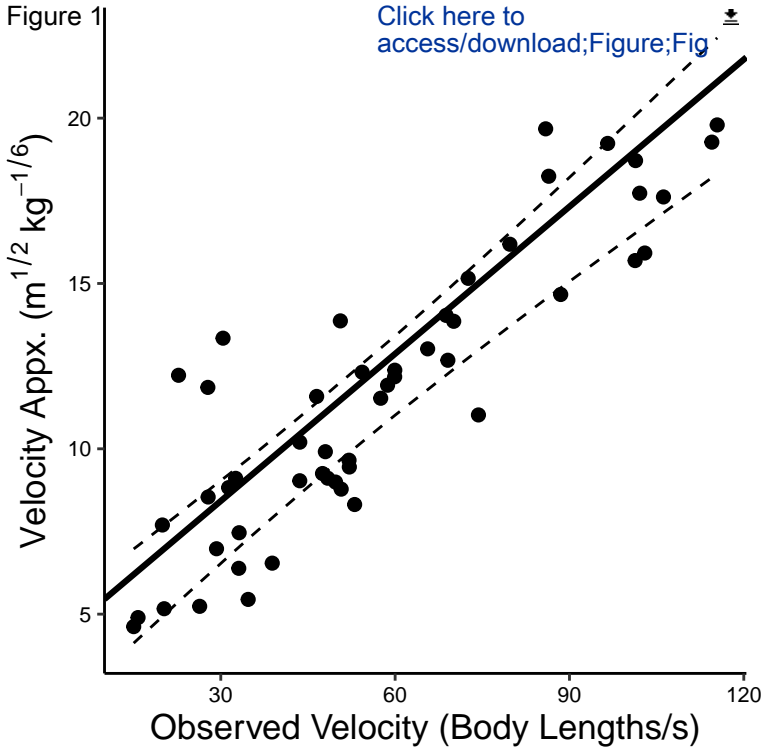782 *1G: Sex-specific Relationships*

783 *2: Time-scaled Phylogeny File*
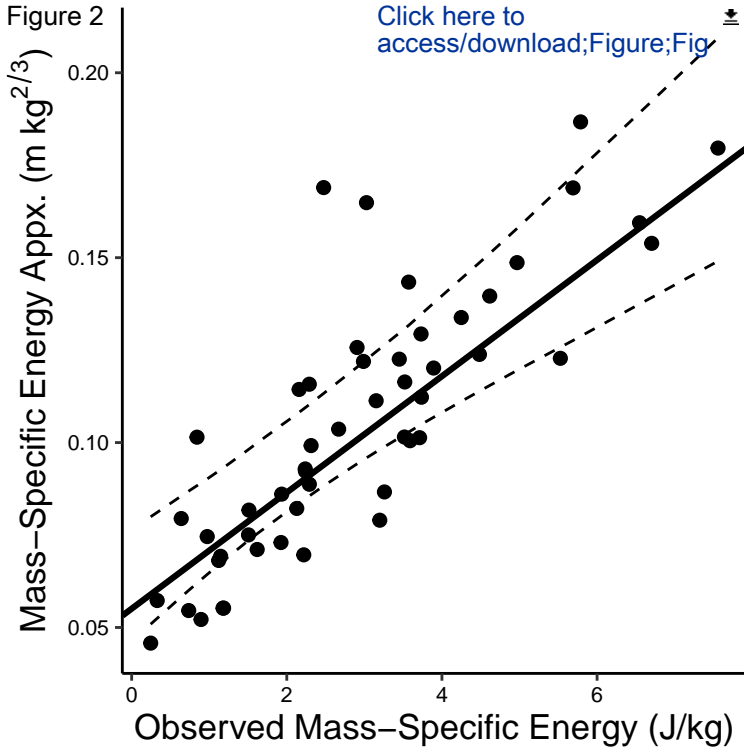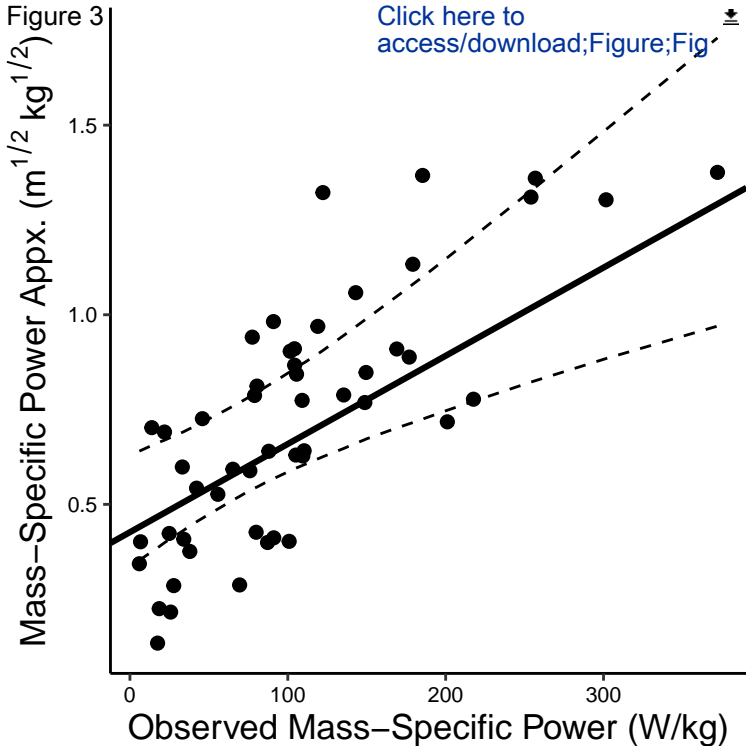
Figure 1

Figure 2

Mass−Specific Energy Appx. (m kg$^{2/3}$)

Observed Mass−Specific Energy (J/kg)
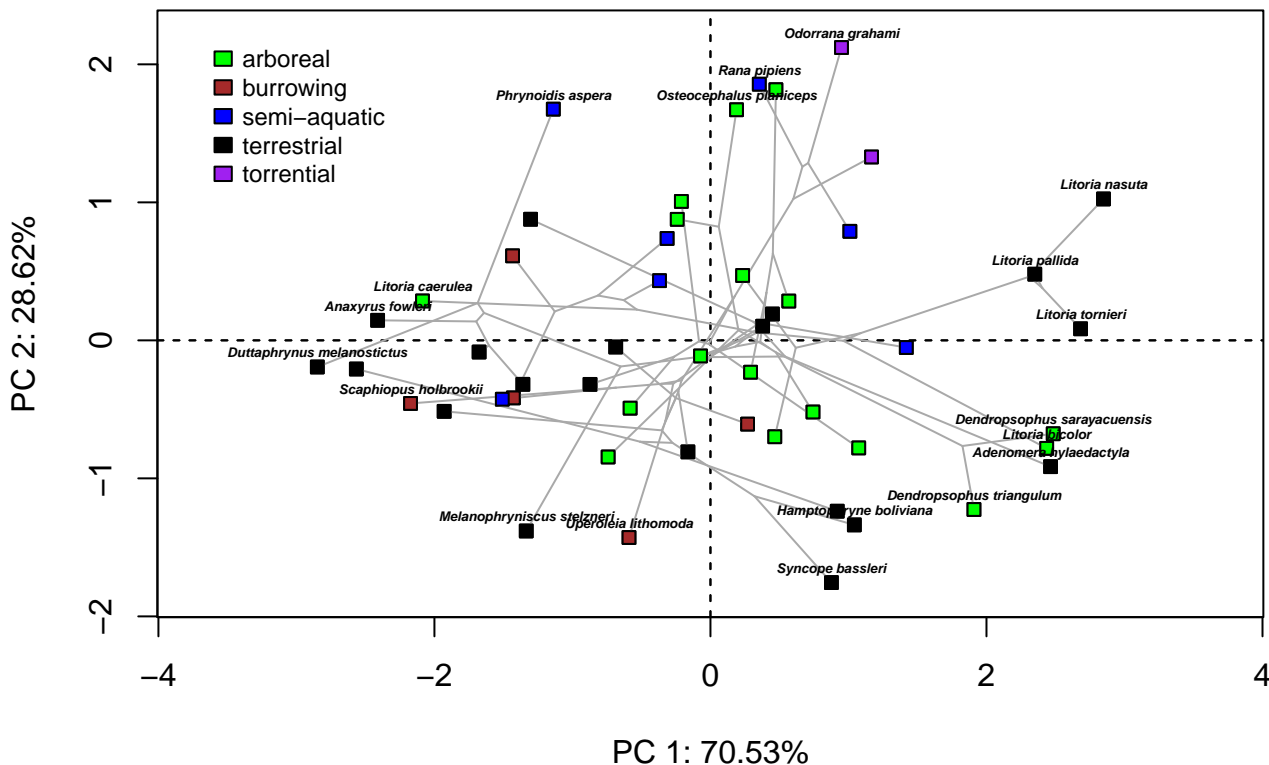
Figure 3

Figure 4

Table 1

Table 1. Eigenvectors of principal components analysis (variable loadings) based on approximations for peak jumping performance. Parentheses of PC axes indicate percent variance explained.

	PC1 (70.53%)	PC2 (28.62%)	PC3 (0.86%)
$v_{Appx.}$	0.582	-0.564	-0.585
$E_{Appx.}$	0.442	0.823	-0.354
$P_{Appx.}$	0.682	-0.052	0.730