1　　　Climate Ecology as a Driver of Global Breeding Periods in Anurans

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19　also found at github.com/bhjuarez/breeding-period in R, Rmarkdown, and HTML formats.

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23 Abstract

24 Climate can have profound effects on reproductive behavior and physiology, especially in

25 ectothermic animals. In amphibians, the evolution of breeding period due to climate has

26 received little attention despite its direct connection to fitness and relevance to conservation. We

27 used phylogenetic comparative methods to analyze a global dataset of frog breeding periods,

28 climate, body size, and microhabitat for 497 species (41 of 54 families). We found support for

29 the hypothesis that breeding periods are longer in the warmer, wetter, aseasonal tropics and

30 shorter in the colder, dryer, seasonal temperate zone. However, this latitudinal reproduction

31 gradient is more complex than expected; the effect of climate depends on body size.

32 Additionally, breeding periods were similar across microhabitats. Overall, our model describes

33 ~20% of variation in breeding periods and these results are robust to phylogenetic uncertainty.

34 Our results set within an eco-physiology framework have broad implications for more targeted

35 priorities in amphibian conservation.

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Introduction

40   Climate change is increasingly threatening global biodiversity with increasing extinctions

41   as environments are altered (Arneth *et al.* 2020; Bellard *et al.* 2012; Thomas *et al.* 2004; Urban

42   2015). While climate change is a growing problem in the present, its past effects have molded

43   the behavior and physiology of species still around today. Thus, by studying coevolution

44   between organisms and the environment, we can better understand how climate change will

45   differentially affect species survival. Importantly, evolutionary biology is taking a key role in

46   conservation biology (Zizka *et al.* 2021), with climate change and anthropogenic impacts at the

47   heart of these studies. As successful reproduction is necessary for survival and fitness, studies

48   of the ecology and evolution of reproductive traits are needed to understand the effects of

49   climate change on species reproductive success. For example, climate change has led to

50   shifting clutch sizes, offspring sizes, and breeding season start times in vertebrates (Bronson

51   2009; Padilla Perez and Angilletta 2022; Pankhurst and Munday 2011; Telemeco *et al.* 2013;

52   Todd *et al.* 2011; Visser *et al.* 2004). However, limited natural history observations across many

53   species and vertebrate groups has stalled research that would help us better understand how

54   climate impacts various reproductive behaviors. Therefore, ideal model systems for learning

55   how climate affects reproductive behaviors and success include groups with abundant natural

56   history observations and whose reproduction is tied to particular environments.

57   Anurans (frogs and toads) are an ecologically and taxonomically diverse ectotherm

58   group (>7,400 species; AmphibiaWeb 2022) whose reproduction and development is generally

59   dependent on water availability during breeding. Their iconic calling behavior used for

60   reproduction has made them a prime target for natural history studies, making their reproductive

61   behaviors reasonably well-known. Anurans inhabit a wide array of habitats around the world

62   including tropical rainforests, arid deserts, temperate forests, freezing tundras, and more. These

63   habitats are used differently by various species which specialize in aquatic, terrestrial, fossorial

64   (underground), or arboreal (above ground) microhabitats (Moen & Wiens 2017). Studies of

65   amphibian reproduction and climate are dominated by advancements in our understanding of

66   reproductive modes (e.g., Gomez-Mestre *et al.* 2012) or reproductive timing (Beattie 1985;

67   Benard 2015; Neveu 2009; Reading 2003; Todd *et al.* 2011; While and Uller 2014).

68   Comparatively little is known about the relationship between climate and breeding period (sensu

69   Wells 1977), the duration of breeding within a population, which is unique from the duration of

70   breeding across populations of a single species. This is despite the stunning contrast of tropical

71   species that breed year-round to explosive-breeding species that limit reproduction to only a few

72   days or weeks of the year (Wells 1977). Common knowledge in herpetology says there exists a

73   latitudinal gradient in breeding periods, where tropical amphibians breed for generally longer

74   periods compared to temperate amphibians (Wells 2007). However, the precise role of climate

75   on breeding periods has yet to be identified across the phylogeny of anurans and further study

76   is necessary given widespread amphibian declines (Campbell Grant *et al.* 2020; Fisher and

77   Garner 2020).

78   If climate has an effect on breeding periods, we can expect physiology to play a central

79   role since frogs are especially sensitive to the environment as ectotherms and are reliant on

80   water for reproduction. Natural selection has likely led to physiological changes such that

81   populations maximize their reproductive investment leading to longer breeding periods in the

82   context of specific climate exposure or microhabitat use (Huey *et al.* 2012; Williams *et al.* 2008).

83   Thus, climate is tied to physiological and reproductive traits to the extent that individuals

84   experience changes in regional climate and atmospheric conditions during the breeding period

85   while in water or on land. These links have been shown previously, where body temperature is

86   correlated with substrate temperature and air temperature in the toad *Bufo canorus*

87   (Cunningham 1963). Both temperature and water are known breeding cues in frogs and warmer

88   temperatures likely lead to longer breeding periods due to greater food supply, reproductive

89   investment, and egg formation in frogs (Girish and Saidapur 2000; Lardner and Loman 2003;

90   Rastogi *et al.* 1983). Additionally, since reproduction in anurans is generally tied to water, we

91   can expect increased water availability to result in longer breeding periods. These abiotic

92   variables can also interact, as higher temperatures in drier environments may lead to increased

93   rates of water loss. From this perspective, larger-bodied species with lower surface area:volume

94   (SA:V) ratios may benefit from lower rates of water loss relative to smaller species. Alternatively,

95   larger-bodied species may be at a disadvantage in sub-optimal environments due to greater

96   resource demand and limited area for water or heat exchange. Species body size likely

97   influences the effect climate has on breeding period due to trade-offs between reproduction and

98   physiological performance over the course of the breeding period. Knowledge of how climate

99   and body size interact to influence anuran breeding periods is unknown but is likely to allow for

100   more targeted conservation efforts.

101   The goal of this study is to identify how ecological factors are related to reproduction

102   (breeding periods) in anurans on a global scale. Specifically, we test (H1) whether longer

103   breeding periods are the result of warmer, wetter climates, (H2) whether differences in body

104   size significantly alter the way climate influences breeding periods, (H3) whether species with

105   different non-breeding microhabitat preferences exhibit differences in breeding period, and (H4)

106   whether climate differs significantly between species microhabitat and geographical (temperate

107   and tropical) zones. Here, we provide the first quantitative assessment of the latitudinal gradient

108   of reproduction in anurans, including climatic and possible physiological drivers.

109   Material and Methods

110   Climate data

111   We obtained coordinate data for 497 species representing 41 of 54 anuran families from

112   GBIF.org (GBIF.org 2021a,b,c,d) accessed 3 October 2021. These queries were for presence

113   coordinate data for non-fossil native observations lacking geospatial issues. We cleaned the

114   data by removing coordinates points with >100km uncertainty or outside land boundaries of a

115   high resolution (1:10m) world countries map using the R v4.2.1 (R Core Team 2021) package

116   *rworldxtra* v1.01 (South 2012). We also removed coordinates incorrectly associated with and

117   within 100m of biodiversity collections outside of the natural range of the species. Additionally,

118   we removed *Corythomantis greeningi* since its coordinates mapped to a continent far outside its

119   natural range. We restricted data for the invasive Cane Toad (*Rhinella marina*) to its naturally

120   occurring range from southern United States to South America (AmphibiaWeb 2021). Next, we

121   removed species with less than 3 unique observations from the dataset and retained only

122   unique coordinates for each species to minimize the effects of spatial autocorrelation. Lastly, we

123   removed data outside the spatial 95% Confidence Interval for each species distribution with a

124   minimum of 30 occurrences using the median absolute deviation (mad) method (Huber 1981).

125   This resulted in a final coordinate dataset of 822,953 observations (mean = 1,656 observations

126   per species) after removing species without behavior or body size (see below) or missing from

127   the phylogeny of Jetz and Pyron (2018). Data cleaning was performed using the

128   *CoordinateCleaner* package v2.0-20 (Zizka *et al.* 2019).

129   We extracted seven variables from each coordinate using the WorldClim 2.1 (Fick &

130   Hijmans 2017) and envirem (Title & Bemmels 2018) databases at 30 seconds (~1km^2)

131   resolution. Our data included variables affecting temperature and water availability and covering

132   all possible breeding period values (0–365 days). The final dataset included annual mean

133   temperature, temperature seasonality, annual precipitation, precipitation seasonality, annual

134   potential evapotranspiration (PET), PET seasonality, and topographic wetness. Topographic

135   wetness is the land's ability to retain water obtained from estimates of upslope incurrent areas

136   and local slope, which is correlated to vascular plant species richness and soil moisture (see

137   Sørensen *et al.* 2005). We calculated species means for each climate variable to analyze the

138   dataset in a phylogenetic comparative framework.

139   Behavior data

140   We collected species means of breeding period (sensu Wells 1977) for each species in

141   this study. To obtain species means, we collected approximate start and end dates for breeding

142   periods from the primary literature or AmphibiaWeb (2022) and averaged all available breeding

143   period data for individual populations. We then calculated the difference in calendar days

144   between the start and end dates, assuming 365 calendar days. Since some dates were reported

145   as qualitative data (e.g., "May", or "early May"), we ascribed values of either the first or last day

146   of the month when breeding periods were reported as starting or ending on a specific month

147   without a specific date given. When breeding periods were reported as the "early" or "late" parts

148   of a month, we matched this to the end of the 1st week and 3rd week, respectively. Rarely,

149   breeding periods were reported as specific seasons (e.g., "Summer" or "wet season") and we

150   defined these as the number of days corresponding to each season and country. Populations

151   from species which are explosive breeders are typically associated with breeding periods lasting

152   only a few days to weeks, but never more than a month (Wells 1977). Since we never observed

153   published data reporting explosive breeding over a period longer than 2 weeks, we

154   conservatively assigned a period of 2 weeks to species whose only description of the breeding

155   period was "explosive breeding".

156   Body size, habitat, and phylogenetic data

157   We collected maximum male body sizes (snout-vent length) and habitat data for every

158   species in this study from the primary literature and other datasets (AmphibiaWeb 2022; IUCN

159   2022; Moen and Wiens 2017; Womack and Bell 2020). Species were assigned to microhabitat

160   categories following Moen and Wiens (2017) and included: (1) aquatic, (2) arboreal, (3)

161   burrowing, (4) terrestrial, and (5) torrential. We also included partial categories such as: (6)

162   semi-arboreal, (7) semi-aquatic, and (8) semi-burrowing. Finally, we calculated phylogenetic

163   covariance matrices from the consensus tree of Jetz and Pyron (2018) to incorporate

164   evolutionary history as weights in phylogenetic regression. Additionally, we used 1,000 samples

165   from the pseudoposterior distribution of trees from Jetz and Pyron (2018) to assess models in

166   terms of phylogenetic uncertainty (see below).

167   Statistical analysis and visualization

168   All analyses were performed in R. We used *ggtree* v3.4.0 (Yu 2020; Yu *et al.* 2018; Yu *et*

169   *al.* 2017) to plot average species breeding periods and temperate-tropical geographical zones.

170   We analyzed the data using phylogenetic generalized least squares (PGLS; Grafen 1989;

171   Martins & Hansen 1997) implemented through *RRPP* v1.3.0 (Collyer and Adams 2018, 2019).

172   Notably, *RRPP* uses a residual randomized permutation procedure to fit models, evaluate

173   significance, and calculate effect sizes for model terms. We used 9,999 iterations for

174   significance testing in all models. We estimated phylogenetic covariance matrices using *ape*

175   v5.6-2 (Paradis & Schliep 2019).

176   We scaled each climate variable and performed a principal component analysis (PCA) to

177   avoid collinearity issues in our models. To test our hypotheses, we used phylogenetic multiple

178   regression to examine the relationship of breeding period, all 7 principal components (PCs), and

179   body size. To account for allometry of body size and since the natural logarithm of surface area-

180   to-volume ratio is expected to scale linearly with the natural logarithm of body size (Castro *et al.*

181   2021; Klein *et al.* 2016; Santini *et al.* 2018), we used the natural logarithm of body size in our

182   models. Additionally, we fit a phylogenetic ANCOVA model which included interactions between

183   each PC and body size. We also used ANOVA to test whether adding these interactions

184   resulted in a significant improvement in model performance. To aid in interpretation of these

185   models, we used phylogenetic regression to determine the relationship between breeding period

186   and each individual climate variable. We determined the effects of phylogenetic uncertainty in

187   our models by rerunning the ANCOVA model once each for 1,000 trees from the

188   pseudoposterior distribution of Jetz and Pyron (2018), following Baken *et al.* (2021). From these

189   analyses we obtained one distribution of 1,000 Z-scores per model term and visualized the

190   proportion of trees under which terms were not significant. We plotted these distributions using

191   ggridges v0.5.3 (Wilke 2021).

192   We used phylogenetic ANOVA to test whether breeding periods differ between

193   microhabitat categories, followed by evaluation of pairwise comparisons. We controlled for Type

194   I error rates due to multiple comparisons using the Sidak-like step-down procedure, which is

195   more powerful than the Sidak and Bonferroni methods (Holland & Copenhaver 1987), using

196   *mutoss* v0.1-12 (MuToss Coding Team *et al.* 2017). We used a phylogenetic factorial

197   MANCOVA to determine how climate (all 7 PC's) differs among microhabitats and

198   temperate/tropical zones. Finally, we visualized these data by plotting conver hulls for groupings

199   of microhabitat and geographical zone using *geomorph* v4.0.4 (Adams *et al.* 2021; Baken *et al.*

200   2021b).

Results

Frog breeding periods follow a latitudinal gradient

We examined phylogenetic patterns of average breeding period (mean = 148 days, range = 1–365 days, std. error = 4.5 days) and geographical zone (temperate/tropical) (Fig. 1) and found species with longer breeding periods tend to live in tropical regions, whereas temperate species breed for shorter periods. However, this pattern has several exceptions, such as temperate species with long breeding periods and tropical species with very short breeding periods. Overall, temperate species breed for an average of 127.8 days (median = 107 days, range = 1–365 days, std. error = 5.87 days) and tropical species breed for an average of 167.3 days (median = 181 days, range = 5–365 days, std. error = 6.52 days). Climate principal components (PCs) 1–3 explained 90% of data variance (Table 1; SI 1). We found variable loadings for PC1 to be similar to known latitudinal climate differences and determined PC1 was highly correlated (r = -0.94) with the absolute value of median latitude for each species (SI 1).

Climate and body size impact breeding periods

As body size can play a large role in thermal physiology and desiccation, we compared model fits between two models with and without interactions between climate and body size (snout-vent length). Indeed, including body size substantially improved model fit (F = 2.40, p = 0.0082; Table 2). Overall, this model explained 18% of variation in breeding periods.

We next describe this model in the context of phylogenetic uncertainty and given the individual effects of each climate variable (see SI 1). We found larger species from the tropics (high scores on PC1) tend to exhibit longer breeding periods relative to smaller species and the magnitude of this effect can be up to 60-90 days. However, this pattern reverses in the temperate zone where relatively smaller species exhibit longer breeding periods (Fig. 2A). For

224　example, *Rana pretiosa* (median latitude = 42.60) can be 14mm larger than *Rana macrocnemis*

225　(median latitude = 45.33) but exhibit a breeding period 48 days shorter (61-13=48 days). This

226　effect was due to latitudinal differences in temperature, temperature seasonality, precipitation,

227　and potential evapotranspiration (PET) seasonality, each showing similar effects when analyzed

228　individually (SI 1 Table 1). Since PET did not have a significant individual effect on breeding

229　periods, it likely does not affect breeding periods although it loads highly onto PC1; we do not

230　interpret PET further for any PC. The effect of PC1 was robust to phylogenetic uncertainty and

231　significant in 89.7% of surveyed trees while its combined effect with body size was supported in

232　64.2% of trees (Fig. 3). Independent of latitude (PC1), we found a significant impact of PC2 and

233　body size on breeding periods (Fig. 2B). Specifically, we found that relatively larger species

234　breed for longer periods in rainy environments with low topographic wetness (high values for

235　PC2) and smaller species breed for longer periods in environments with little rain but high

236　topographic wetness. Although topographic wetness had no individual effect on breeding

237　periods, it did exhibit a significant impact when paired with body size. This trend showed

238　moderate support across surveyed phylogenies with significance of PC2 and the interaction with

239　size supported in 0.714% and 0.704% of trees, respectively (Fig. 3). Additionally, we found

240　support for a size-independent role of PC3, where species living regions with low precipitation

241　seasonality (PC3) exhibit longer breeding periods (Fig. 2C). This pattern was significant in

242　87.9% of surveyed trees compared to only 31.4% of trees when taking size into account (Fig. 3).

243　Finally, we also found a size-independent effect of PC7 associated with warmer temperatures,

244　independent of temperature effects of other PC's, where longer breeding periods are associated

245　with warmer temperatures. This pattern was supported in 66.9% of surveyed phylogenetic

246　histories.

247   Breeding periods are not different between microhabitats

248   The microhabitats species occupy can have different effects on breeding period

249   depending on differences in temperature and moisture within temperate or tropical regions.

250   Therefore, we tested whether anuran species with different microhabitat preferences exhibit

251   differences in breeding periods. We initially found support for this relationship, where species

252   from various microhabitats have different breeding periods ($F = 4.09$, $p = 0.0062$). However,

253   pairwise differences between microhabitats were not significant after accounting for multiple

254   comparisons (see SI 1 Table 2). In contrast to our expectation, we found large overlap in

255   breeding periods across microhabitat categories (Fig. 4A), including a wide breeding period

256   range associated with burrowing and semi-burrowing species. Semi-arboreal species had the

257   greatest proportion of species with a long breeding period. We next used a factorial MANCOVA

258   used examine climatic differences corresponding to combinations of microhabitat and

259   geographical zone (i.e., their interaction; $F = 2.05$, $r^2 = 0.02$, $Z = 2.27$, $p = 0.0124$), but none of

260   these were significant after correcting for multiple comparisons (see SI 1 Table 3). Finally, we

261   found significant climate differences among microhabitats ($F = 7.01$, $r^2 = 0.08$, $Z = 3.77$, $p =$

262   0.0001; Fig. 4B) and between temperate and tropical zones ($F = 87.46$, $r^2 = 0.14$, $Z = 8.93$, $p =$

263   0.0001) but we did not find pairwise differences in the former after accounting for geographical

264   zone (see SI 1 Table 4).

265   Discussion

266   This study documents the evolution of reproductive behavior associated with climate in

267   one of the largest vertebrate groups. Here we present the first quantitative evidence, to our

268   knowledge, of the latitudinal gradient of breeding period in anurans and its relationship to

269   climate. Our overall findings support longer breeding periods where frogs invest more time into

270   reproduction in warmer and wetter habitats with little seasonality. We also discovered that the

271   time invested into reproduction, within the context of particular climates, is influenced by body

272   size. We discuss our results in the context of physiology and reproduction and suggest how this

273   new information can guide conservation management priorities of anurans in different climates.

274   Body size played an important role in determining how climate affects breeding periods.

275   This is likely due to its effect on physiological processes such as regulating body temperature

276   and water loss, where larger frogs are better at maintaining body temperatures and are slower

277   to dessicate (Castro *et al.* 2021; Klein *et al.* 2016; Santini *et al.* 2018; Tracy *et al.* 2010). The

278   size-dependent effect of climate on anuran reproduction is most notable when comparing 1)

279   temperate versus tropical environments, and 2) regions with high rainfall and limited propensity

280   to hold water versus regions with low rainfall and high topographic water retention. These

281   results are consistent with our hypothesis that larger body sizes are associated with greater

282   resource demands and limited area for water and heat exchange, resulting in shorter breeding

283   periods in environments with little rain, cooler temperatures, and low topographic water

284   retention. High temperature seasonality and high potential evapotranspiration seasonality also

285   seem to shorten breeding periods in larger species, possibly due to their combined effect and

286   this may be due to meeting physiological demands in relatively unpredictable environments.

287   Interestingly, environments which shorten breeding periods in larger species seem to be less

288   detrimental to smaller species, possibly due to their lower resource demand and relatively

289   greater area for water and heat exchange. Furthermore, larger-bodied species may be at a

290   disadvantage in cool and dry environments because the amount of energy used for maintaining

291   homeostasis (hydration) may limit the amount of reproductive investment females are able to

292   make, since egg formation is energetically costly for females. This seems likely, given that we

293   know larger frog species exhibit greater reproductive investment in the form of forming larger

294   clutches and larger eggs (Prado & Haddad 2005; Silva *et al.* 2020). Body size is also correlated

295   with reproductive investment in seasonally breeding endotherms like lagomorphs, whose body

296   size is correlated with neonatal mass, gestation time, and maternal reproductive effort (Swihart

297   1984). Temperature and water preferences and limits can evolve in a correlated fashion (Bonetti

298   and Wiens 2014; Guevara-Molina *et al.* 2020; Köhler *et al.* 2011) and likely involve

299   underexplored molecular and morphological traits associated with the skin and body size in

300   amphibians (Finn *et al.* 2014; Shibata *et al.* 2014; Tracy *et al.* 2010). How temperature and

301   water limits have shaped anuran breeding physiology is unclear and is an area that needs more

302   research.

303   Ecology, in addition to physiology, plays an important role in determining breeding

304   periods. Our results suggest seasonal environments present the challenge of overcoming

305   unreliable cues for reproduction, similar to findings at shorter ecological scales (Todd *et al.*

306   2011). Here, we found size-dependent patterns, themselves independent of latitude, where

307   breeding periods in smaller species decline in rainier environments with lower topographic

308   wetness. These qualities are characteristic of high-altitude rainforests, or cloud forests, such as

309   those found in Central and South America, which hold much of the world's anuran diversity

310   (Cortés *et al.* 2008; Duellman 1988; Giaretta *et al.* 1999). One explanation for this pattern is that

311   cloud forests exhibit relatively rapid local drainage of water resources necessary for prolonged

312   amphibian reproduction. Another possible explanation is that areas with low topographic

313   wetness and correspondingly low vascular plant species richness (Sørensen *et al.* 2005)

314   presents a challenge for prolonged breeding periods in smaller species by limiting protection

315   from canopy cover or reproductive opportunities associated with leaf- or phytotelma-breeding

316   species (Donnelly and Guyer 1994; Poelman *et al.* 2013; Schulte *et al.* 2010). Predation risk

317   may also differ between small and large species, where larger species are less reliant on

318   canopy cover due to their large size reducing predation pressure (Nakazawa *et al.* 2013),

319   resulting in longer breeding periods. Future research investigating the role of plant diversity and

320   predator-prey relationships in anurans seems likely to explain this variability in amphibian

321   reproduction.

322   Microhabitat use across and within species undoubtedly plays a critical role in how

323   animals experience broader regional climates and together they define climate exposure (Huey

324   *et al.* 2012; Williams *et al.* 2008). While ambient and body temperatures are connected

325   (Cunningham 1963), water stream and air temperatures are also correlated to atmospheric

326   temperatures in both warmer and colder climatic zones (Erickson and Stefan 1996; Mohseni

327   and Stefan 1999; Pilgrim *et al.* 1995). However, support for our hypothesis of differences in

328   breeding periods between species occupying different microhabitats was lacking. Instead, we

329   found a minority of burrowing species exhibit explosive breeding (extremely short breeding

330   periods) and an overabundance of semi-arboreal species which breed for longer periods. The

331   latter is likely related to radiations of small semi-arboreal frogs in the tropics of Central and

332   South America, one of the most diverse regions of the world. Perhaps unsurprisingly, we did not

333   find discernible climatic differences between microhabitats. This could reflect a low correlation

334   between regional climate and ambient conditions within microhabitats (e.g., a burrow). However,

335   such a strong role of microhabitat buffering seems unlikely if we expect, for example,

336   microhabitats within a temperate desert to resemble each other more closely than microhabitats

337   within a tropical rainforest. Instead, the lack of breeding period differences among microhabitats

338   most likely reflects the ecological breadth of frog communities and global convergent evolution

339   of microhabitat use across anurans (Moen *et al.* 2015). Further study of the relationships

340   between microhabitat, reproductive traits, and climate would likely result in additional model

341   improvements and better predictions of breeding period. For example, previous work found

342   decreased fecundity in anurans was associated with warmer winters within species (Benard

343   2015; Neveu 2009; Reading 2003) and warm, wet climates across terrestrial egg-laying species

344   (Gomez-Mestre *et al.* 2012). Notably, species in seasonal environments may have evolved

345   larger clutches in response to shorter breeding periods (Sheridan 2009). Future research will

346   continue to disentangle the relationships between behaviors, the environment, and further

347   investigate the role of life history in determining the effect of climate on reproductive ecology.

348   Unfortunately, we still know very little about the life histories of many frogs. A sustained push for

349   deeper understanding of life history diversity is necessary for identifying causal mechanisms

350   related to eco-evolutionary patterns.

351   Adaptation to changing climates is a key part of amphibian evolutionary history and

352   should be centered in future amphibian conservation efforts. Previous research has shown

353   conclusive evidence of adaptation to changing climates over ecological timescales (<40 yrs.;

354   Beattie 1985; Benard 2015; Freidenburg and Skelly 2004; Neveu 2009; Reading 2003; Skelly

355   and Freidenburg 2008; Skelly *et al.* 2007; Todd *et al.* 2011). This work, along with previous

356   studies on breeding start date (Beattie 1985; Ulloa *et al.* 2019; While and Uller 2014), identify

357   both water and temperature as important environmental cues for the start of the breeding

358   period. Associated neuroendocrine systems, thermal preferences, and critical thermal limits

359   seem to show flexibility in responding to changing climate, but this might change as the effects

360   of climate change become more severe. Huey *et al.* (2012) provide a model used to assess

361   extinction vulnerability over time, which can be affected by behavioral thermoregulation,

362   acclimation, and adaptation. Unfortunately, most anuran species live in warm, dry environments

363   and these same species exhibit narrow climatic niche breadths (Bonetti & Wiens 2014) which

364   can restrict dispersal (Chejanovski & Wiens 2014). The current study shows how species with

365   restricted breeding periods living in the cold, dry, and seasonal environments may be less

366   tolerant of climate change. Within the temperate zone, larger frogs with greater resource

367   demands may be particularly vulnerable, while smaller frogs are most vulnerable in the tropics.

368   Independent of latitude differences, we also found larger species may be vulnerable in areas

369   receiving little rain. Without physiological adaptation to climate change, frogs might mistime their

370   reproduction and be faced with either extinction, or potentially speciation through temporal

371   isolation of reproduction. This might be one of the possible mechanisms linking diversification

372   rates and rates of climatic niche change in anurans (Moen & Wiens 2017).

373   Amphibians are facing unprecedented threats due to climate change from the lens of

374   eco-physiology. Notably, climate change seems to amplify the current amphibian chytrid fungus

375   epidemic due to size-related osmoregulatory costs (Wu *et al.* 2018). Given the several factors

376   contributing to growing extinction risks faced by frogs and toads, an attempt to maintain

377   reproductive fitness by maximizing breeding duration seems critical. Overall, our research

378   suggests a regional-based approach toward conserving species' flexibility in the timing and

379   period of breeding. There are multiple factors impacting amphibian breeding periods but

380   regional climate has a noticeable average effect on breeding periods worldwide. Extinction risks

381   due to the mistiming of reproduction or shortened breeding periods might be highest in smaller

382   tropical species which are common in tropical lowlands. Species living in tropical lowlands along

383   with those living in cloud forests have both been identified as being under threat of extinction

384   (von May *et al.* 2019; Meza-Parral and Pineda 2015; Murrieta-Galindo *et al.* 2013; Ponce-Reyes

385   *et al.* 2013). Further research is needed to understand the neuroendocrine cues used for timing

386   reproduction in frogs, thermal preferences, and the role of molecular or morphological

387   adaptations related to water and heat stress. Without this research, future temperature

388   instability will increase extinction risk without either dispersal to suitable habitats or the ability to

389   acclimate and adapt to their changing environment (Huey *et al.* 2012). Perhaps the existence of

390   tropical explosive breeders shows capacity for adaptation and persistence in the face of climate

391   change. For example, species faced with limited breeding periods may also adapt to produce

392   more eggs (Sheridan 2009) and habitat shifts associated with thermal preference and choosing

393   egg-laying sites may help mitigate negative thermal climatic effects on tadpoles (Pintanel *et al.*

394   2022; Todd *et al.* 2011). Amphibians have much to benefit from dedicated conservation efforts

395   to protect large and diverse landscapes allowing dispersal, protecting plant diversity, and

396   preserving a thermally-diverse range of habitat options. Similar efforts have been successful in

397   partially restoring amphibian diversity in cloud forests (Díaz-García *et al.* 2020). Future research

398   might seek to combine environmental, behavioral, and physiological data to assess extinction

399   risk and habitat suitability (Greenberg and Palen 2021; Griffis-Kyle 2016; Huey 1991).

400   Acknowledgements

409
410   Tables
411
412   **Table 1. PCA summary and loadings of climate variables.** PCA based on means for 497 species.

413   Cumulative proportion of variance is given in parentheses next to PC heading. Loadings with a magnitude

414   >=0.30 are in bold. Asterisks indicate variables with a significant individual effect on breeding periods and

415   carets indicate variables with a significant interaction with body size (see SI).

416

Variable	PC1 (52)	PC2 (76)	PC3 (90)	PC4 (94)	PC5 (97)	PC6 (99)	PC7 (100)
Annual Mean Temperature*^	**0.47**	-0.28	0.08	-0.02	0.24	0.15	**0.78**
Temperature Seasonality*^	**-0.47**	-0.14	-0.09	**0.44**	0.25	**0.70**	0.04
Annual Precipitation*^	**0.38**	**0.38**	0.13	**0.75**	0.27	-0.21	-0.14
Precipitation Seasonality*^	0.15	-0.26	**-0.90**	0.23	-0.16	-0.15	0.00

Annual Potential Evapotranspiration (PET)	**0.42**	**-0.4**	0.00	-0.23	**0.47**	0.21	**-0.59**
PET Seasonality*^	**-0.45**	-0.28	0.01	0.02	**0.59**	**-0.60**	0.11
Topographic Wetness^	0.01	**-0.67**	**0.40**	**0.37**	**-0.47**	-0.15	-0.10

417
418
419 **Table 2. Model summary of the effects of climate and body size on breeding periods in 497 frog**

420 **species.** Climate shown as PC's. Body size is snout-vent length (SVL) in mm. Breeding periods are

421 species means. *Df* = degrees of freedom, *SS* = sum of squares, *MS* = mean square, *Rsq* = coefficient of

422 determination, *F* = *F*-statistic, *Z* = standardized effect size (*Z*-score), and *P* = *p*-value. Rows with

423 significant terms ($p < 0.05$) are in bold.

424

Term	***Df***	***SS***	***MS***	***Rsq***	***F***	***Z***	***P***
PC1	**1**	**6279.32**	**6279.32**	**0.05**	**26.34**	**3.69**	**1e-04**
PC2	**1**	**2443.75**	**2443.75**	**0.02**	**10.25**	**2.59**	**0.0017**
PC3	**1**	**6756.84**	**6756.84**	**0.05**	**28.34**	**3.83**	**1e-04**
PC4	1	22.69	22.69	0	0.10	-0.71	0.7519
PC5	1	734.96	734.96	0.01	3.08	1.39	0.0810
PC6	1	601.68	601.68	0	2.52	1.22	0.1152
PC7	**1**	**1643.48**	**1643.48**	**0.01**	**6.89**	**2.12**	**0.0096**
SVL	**1**	**1058.17**	**1058.17**	**0.01**	**4.44**	**1.71**	**0.0389**
PC1:SVL	**1**	**1555.92**	**1555.92**	**0.01**	**6.53**	**2.07**	**0.0115**

PC2:SVL	**1**	**2228.56**	**2228.56**	**0.02**	**9.35**	**2.49**	**0.0020**
PC3:SVL	1	831.79	831.79	0.01	3.49	1.51	0.0599
PC4:SVL	1	0.12	0.12	0	0	-2.05	0.9812
PC5:SVL	1	30.6	30.6	0	0.13	-0.62	0.7241
PC6:SVL	1	57.72	57.72	0	0.24	-0.32	0.6277
PC7:SVL	1	103.47	103.47	0	0.43	0.02	0.5090
Residuals	481	114677.84	238.42	0.82	NA	NA	NA
Total	496	139026.91	NA	NA	NA	NA	NA

425
426 Figure Legends
427
428 **Figure 1. Phylogenetic differences in average breeding period and geographic region across 497**

429 **species of frogs. A.** Phylogeny of 497 species with breeding period and region mapped at the tips. Node

430 labels identify the 4 highest-sampled families in our dataset. Inner ring shows tropical versus temperate

431 regions. The tropical zone is shown in red and the temperate zone is shown in blue. Outer ring shows the

432 breeding period. Species with shorter breeding periods are shown in lighter colors while species with

433 longer breeding periods are shown in darker colors. **B.** Boxplot showing differences in breeding period

434 between temperate (N = 237) and tropical (N = 260) species. Temperate species breed for an average of

435 127.8 days (median = 107 days, range = 1–365 days, std. error = 5.87 days) and tropical species breed

436 for an average of 167.3 days (median = 181 days, range = 5–365 days, std. error = 6.52 days).

437 Combined, anurans breed for a mean of 148 days (range = 1–365 days, std. error = 4.5 days).

438
439 **Figure 2. Climate and body size (snout-vent length) influence breeding periods in 497 frog**

440 **species.** All relationships are significant at p < 0.0115. Regression lines for A,B represent effects at 10th

441 and 90th percentiles of body size (snout-vent length; 24 and 80 mm). **A.** High scores on PC1 represent

442 warm, rainy areas with low temperature and annual potential evapotranspiration seasonality and are

443   correlated with latitude. Larger species have longer breeding periods in the tropics; smaller species have

444   longer breeding periods in the temperate zone. Combined effects of PC1 and body size yield *Rsq* = 0.07.

445   **B**. High PC2 scores are regions with relatively higher annual precipitation but low topographic wetness.

446   Larger species have longer breeding periods in rainy climates with low topographic wetness. Smaller

447   species have longer breeding periods in less rainy climates with high topographic wetness. The combined

448   effect of PC2 and body size yields *Rsq* = 0.05 **C**. High PC3 scores are regions with relatively lower

449   precipitation seasonality but higher topographic wetness. Regression line shown in red. Longer breeding

450   periods are common in areas with lower precipitation seasonality and higher topographic wetness. *Rsq* =

451   0.05. **D.** Density plot showing the distribution of raw (untransformed) body sizes of species used in this

452   study.

453
454   **Figure 3. Effect of phylogenetic uncertainty on effect sizes (z-scores) relating climate and body**

455   **size to breeding periods.** Z-scores for each model term calculated from 1,000 trees of the

456   pseudoposterior distribution of Jetz and Pyron (2018). PC's are climate variables; SVL is snout-vent

457   length. Vertical line denotes the Z = 1.645 significance cutoff for empirically generated Z-scores. Values

458   to the right of distributions indicate percent of significant Z-scores per distribution. Red highlights portions

459   of the density within the 10th percentile.

460
461   **Figure 4. Breeding period and climate differences between microhabitats across 497 frog species.**

462   **A.** Average breeding periods do not differ between microhabitats; most ranges overlap. semi-arboreal

463   species stand out in having the greatest proportion of species with longer breeding periods. **B.** Scatterplot

464   of first two PCA axes corresponding to climate variables. Polygon outlines encase species in

465   microhabitats corresponding in color. PC1 is correlated with absolute latitude (r = -0.94). Temperate

466   species denoted by circles and encased in solid lines. Tropical species denoted by triangles and encased

467   in dashed lines.

468
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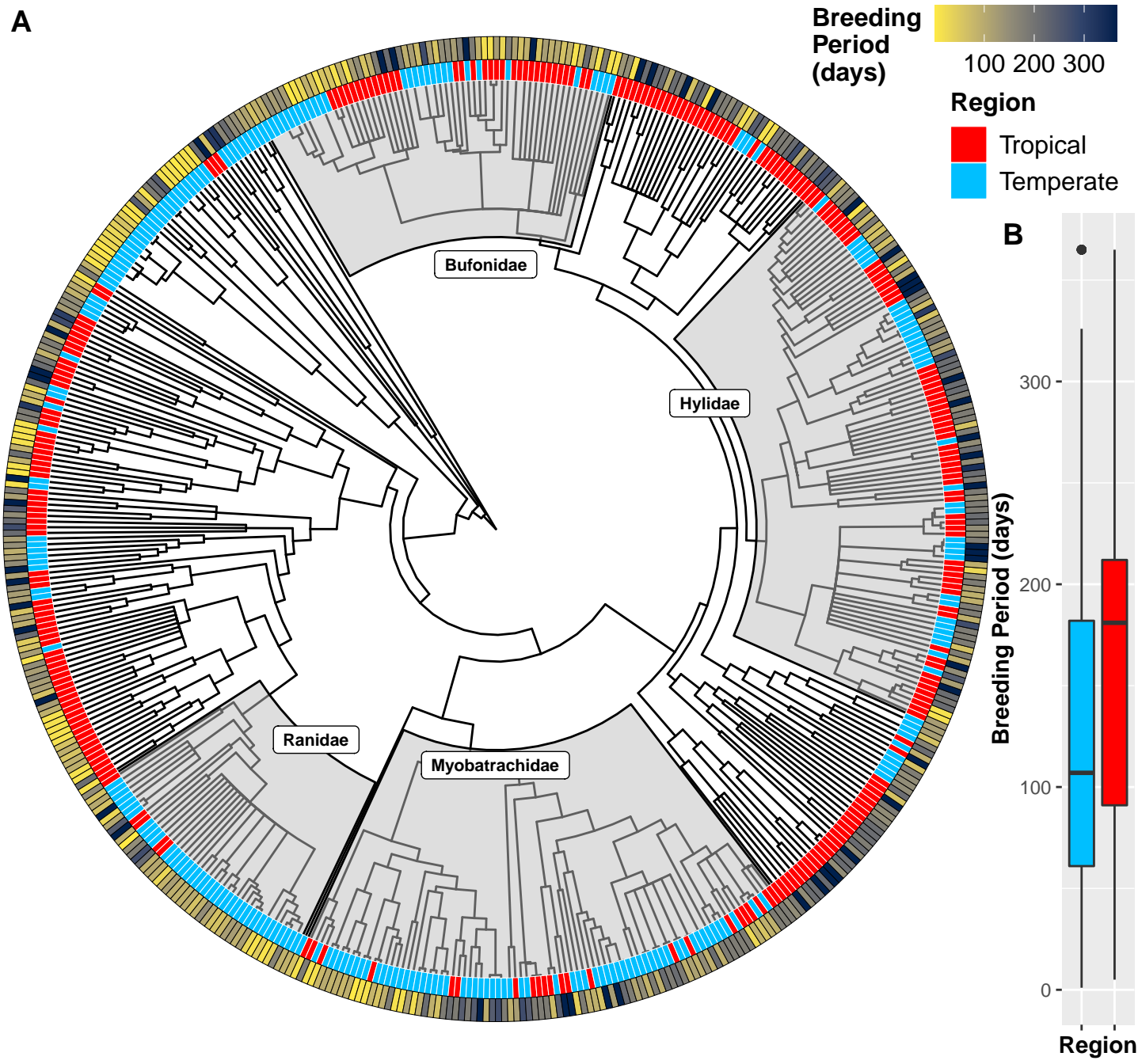
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