

The global macroecology of brood size in amphibians reveals a predisposition of low-fecundity species to extinction

Daniel Pincheira-Donoso^{1,7}, Lilly P. Harvey², Sheena C. Cotter³, Gavin Stark⁴, Shai Meiri^{4,5} & Dave J. Hodgson⁶

¹MacroBiodiversity Lab, School of Biological Sciences, Queen's University Belfast, 19 Chlorine Gardens, Belfast, BT9 5DL, United Kingdom

²School of Science and Technology, Nottingham Trent University, Clifton Campus, Nottingham, NG11 8NS, United Kingdom

³School of Life Sciences, Joseph Banks Laboratories, University of Lincoln, Brayford Campus, Lincoln, LN6 7DL, United Kingdom

⁴School of Zoology, Tel Aviv University, 6997801, Tel Aviv, Israel

⁵The Steinhardt Museum of Natural History, Tel Aviv University, 12 Klausner Street, 6997801, Tel Aviv, Israel

⁶Centre for Ecology and Conservation, College of Life and Environmental Sciences, University of Exeter, Cornwall Campus, Penryn, TR10 9FE, Cornwall, United Kingdom

⁷Corresponding author: D. Pincheira-Donoso (D.Pincheira-Donoso@gub.ac.uk)

Running head: Amphibian fecundity and extinction risk

Abstract

Aim. The diversity of brood size across animal species exceeds the diversity of most other life history traits. In some environments, reproductive success increases with brood size, while in others it increases with smaller broods. The dominant hypothesis explaining such diversity predicts that selection on brood size varies along climatic gradients, creating latitudinal fecundity patterns. Another hypothesis predicts that diversity in fecundity arises among species adapted to different microhabitats within assemblages. A more recent hypothesis concerned with the consequences of these evolutionary processes in the era of anthropogenic environmental change predicts that low-fecundity species may fail to recover from demographic collapses caused by rapid environmental alterations, making them more susceptible to extinctions. These hypotheses have predominantly been addressed in endotherms, and only rarely in other taxa. Here, we address all three hypotheses in amphibians globally.

Location. Global.

Time period. Present.

Major taxa studied. Class Amphibia.

Methods. Using a dataset spanning 2,045 species from all three amphibian orders, we employ multiple phylogenetic approaches to investigate the association between brood size and climatic, ecological, and phenotypic predictors, and against species conservation status.

Results. Brood size increases with latitude. This tendency is much stronger in frogs, where temperature seasonality is the dominant driver, whereas salamander fecundity increases towards regions with more constant rainfall. These relationships vary across continents, but confirm seasonality as the key driver of fecundity. Ecologically, nesting sites predict brood size in frogs, but not in salamanders. Finally, we show that extinction risk consistently increases with decreasing fecundity across amphibians, whereas body size is a 'by-product' correlate of extinction given its relationship with fecundity.

Main conclusions. Climatic seasonality and microhabitats are primary drivers of fecundity evolution. Our findings that low fecundity increases extinction risk reinforces the need to re-focus extinction hypotheses based on a suggested role for body size.

Keywords: Life history, clutch size, climate change, seasonality, microhabitats, extinction, amphibians

Introduction

The diversity of fecundity across animals is one of the most remarkable examples of life history variation in nature (Godfray *et al.*, 1991; Roff, 2002; Pincheira-Donoso & Hunt, 2017). Among vertebrates alone, fecundity ranges from species where broods consist of a single offspring (Roff, 2002; Sales, 2005; Losos, 2009; Meiri *et al.*, 2020) to others such as the ocean sunfish that lay up to 300 million eggs per reproductive episode (Freedman & Noakes, 2002). Even within a single class, variation in brood size can span several orders of magnitude (Roff, 2002; Wells, 2007). Decades of research have revealed a strong geographic signal in the distribution of brood size across species, suggesting a widespread link between climatic gradients and fecundity (Lack, 1947; Jetz *et al.*, 2008; Pincheira-Donoso & Hunt, 2017; Meiri *et al.*, 2020).

Since the foundations of life history theory (Moreau, 1944; Lack, 1954), the study of the geography of fecundity has developed around the widespread positive relationship between latitude and brood size observed across multiple vertebrate lineages (Bennett & Owens, 2002; Jetz *et al.*, 2008; McNamara *et al.*, 2008; Griebeler *et al.*, 2010; Rose & Lyon, 2013; Pincheira-Donoso & Hunt, 2017; Meiri *et al.*, 2020). The dominant macroecological hypothesis posits that geographic gradients in climate create selection for larger brood sizes towards higher latitudes as a result of gradients in seasonality and resource abundance (Moreau, 1944; Ricklefs, 1980; Jetz *et al.*, 2008; Pincheira-Donoso & Hunt, 2017). One suggested mechanism is that bursts of mortality during the non-breeding ('harsh') season reduce population densities, offering survivors higher resource abundance for allocation into the production of higher numbers of offspring during the breeding season (Ashmole, 1963; Martin, 2004; Jetz *et al.*, 2008; Pincheira-Donoso & Hunt, 2017). An alternative mechanism suggests that larger brood sizes evolve by increasingly stronger fecundity selection towards higher latitudes to compensate for either reduced reproductive opportunities as breeding seasons shorten (Cox *et al.*, 2003; Pincheira-Donoso & Tregenza, 2011), or for the reduced likelihood to survive until the next breeding season (Martin, 2004; Jetz *et al.*, 2008). In addition to the stream of studies on specific clades or geographic areas (reviewed in Pincheira-Donoso & Hunt, 2017), global-scale studies on birds (Jetz *et al.*, 2008) and lizards (Meiri *et al.*, 2020) have supported this macroecological hypothesis. Whether the generality of this pattern holds at global scale for other organisms remains unknown.

In addition, a 'microhabitat hypothesis' predicts that intra-clade variation in brood size is partitioned across species adapted to different microhabitat structures within assemblages. In lineages where high species diversities accumulate within narrow geographic extensions (e.g., Kornfield & Smith, 2000; Schluter, 2000; Pincheira-Donoso *et al.*, 2018), partitioning of niche space across species is likely to create divergent natural selection on life history traits. As expected, adaptations to different microhabitats often lead to divergence in body size (Schluter, 2000; Losos, 2009), which is in turn a prevalent predictor of brood size, especially among ectotherms (Roff, 2002; Shine, 2005; Pincheira-Donoso & Hunt, 2017; Meiri *et al.*, 2020). Likewise, functional constraints imposed by different habitat structures can more directly influence clutch size. For example, constraints on nesting space and locomotion are intrinsically greater for arboreal species than for species that occupy 'open' sites, such as the ground, which leads to smaller clutches (Meiri *et al.*, 2020; Silva *et al.*, 2020). However, evidence for this 'microhabitat hypothesis' comes from a handful of studies (Lack, 1947; Jetz *et al.*, 2008; Meiri *et al.*, 2020; Silva *et al.*, 2020). Therefore, comparative studies aimed to establish its wider generality are needed.

The rapid decline of global biodiversity (Dirzo *et al.*, 2014; Ceballos *et al.*, 2017) has more recently led to an 'extinction hypothesis', aimed to elucidate the drivers behind interspecific variation in extinction risk – within the same lineages, some species thrive while others collapse to extinction (Sinervo *et al.*, 2010;

Pimm *et al.*, 2014; Ceballos *et al.*, 2020). Such asymmetries in extinction risk arise as environmental factors interact with species traits (Cardillo *et al.*, 2006; Dirzo *et al.*, 2014), and life history traits in particular have been suggested to play a pivotal role in influencing the predisposition of populations to decline (Pimm *et al.*, 1988; Bennett & Owens, 1997; Purvis *et al.*, 2000; Isaac, 2009; Hutchings *et al.*, 2012; Pincheira-Donoso *et al.*, 2013; Jara *et al.*, 2019). Not surprisingly, the accumulation of evidence has led to the widespread view that body size – a ‘catch-all’ life history trait – is a consistent predictor of extinction risk (Gaston & Blackburn, 1995; Cardillo & Bromham, 2001; Brashares, 2003; Cardillo, 2003; Lips *et al.*, 2003; Cardillo *et al.*, 2005; Olden *et al.*, 2007a; Sodhi *et al.*, 2008; Isaac, 2009; Ripple *et al.*, 2017), especially among endotherms, where larger body size tends to be associated with higher extinction risk (Bennett & Owens, 1997; Purvis *et al.*, 2000; Cardillo *et al.*, 2005, 2006; Ripple *et al.*, 2017). Evidence is conflicting among ectotherms – comparative studies have failed to identify a consistent role for body size as a predictor of extinction risk (Lips *et al.*, 2003; Murray & Hose, 2005; Cooper *et al.*, 2008; Sodhi *et al.*, 2008). Despite this widely recognised role for body size, variation in fecundity lies at the root of the extinction hypothesis. Given that low fecundity is largely associated with slower reproductive rates and lower genetic diversity (Yasui, 1998; Hoglund, 2009), rates of population recovery under rapid environmental changes are expected to be slower for low-fecundity species, predisposing them to demographic collapses that lead to extinction (MacArthur & Wilson, 1967; Pimm *et al.*, 1988; Bennett & Owens, 1997; Purvis *et al.*, 2000; Cardillo *et al.*, 2005, 2006; Isaac, 2009). However, a comprehensive study at global-scale investigating this hypothesis on the effects of fecundity in extinctions among ectotherms remains lacking.

Here, we employ a global-scale dataset on amphibian brood sizes, spanning 2,045 species, to address the above three hypotheses. Amphibians combine ideal features to test these predictions given their extreme variation in fecundity, which ranges from species that lay single-egg clutches to species that can lay up to 80,000 eggs – a per-brood reproductive output that exceeds that of any other living tetrapod by several orders of magnitude (Wells, 2007). In addition, their distribution spans most land environments on Earth (Duellman & Trueb, 1994; Roll *et al.*, 2017), and show greater rates of extinction than any other class of vertebrates (Chanson *et al.*, 2008; Hof *et al.*, 2011; Ceballos *et al.*, 2017; Pincheira-Donoso & Hodgson, 2018).

Materials and methods

Life history data

We created a global dataset on brood size for 2,045 amphibian species spanning all three living orders, Anura (frogs, or anurans), Caudata (salamanders, or urodelans), and Gymnophiona (caecilians). This dataset (Supplementary Material 1) is part of the Global Amphibian Biodiversity Project (GABiP, available at www.amphibianbiodiversity.org) initiative. The data were collected predominantly from the primary literature, including articles and books (Supplementary Material 2), and from direct observation of field/museum specimens. We first addressed the fundamental prediction of fecundity selection theory that brood size increases with (predominantly female) body size because larger females can accommodate more eggs in their body cavity, and can maximise energy storage to be allocated into reproduction (Darwin, 1874; Shine, 1988; Pincheira-Donoso & Hunt, 2017). This test is critical to establish an association between body size and brood size. For anurans and salamanders, we used maximum snout-vent length (SVL) as our measure of body size given that this is the most widely used proxy for body size in these two orders. For caecilians, maximum total body length is the traditional measure of size (Pincheira-Donoso *et al.*, 2019), and thus the

proxy we employed. We then investigated whether brood size is constrained by different parity modes. For these analyses, species were classed as having a larval (tadpole) stage, being viviparous, or laying eggs that undergo direct development (Wells, 2007).

Environmental and ecological predictors of brood size

First, to address the climatic/geographic macroecological hypothesis, we obtained extent of occurrence range maps for all amphibian species available at the International Union for Conservation of Nature (IUCN) archive (www.iucnredlist.org) for which fecundity data exist (Supplementary Material 1). Non-native/introduced species were excluded from these analyses. We then obtained the mean annual temperature (averaged across 12 months of the year, in degrees Celsius), temperature seasonality (calculated as the standard deviation of annual mean temperature x100, in degrees Celsius), mean annual precipitation (the amount of rainfall measured in mm per year), and precipitation seasonality (coefficient of variation of monthly precipitation across the year) across the range of each species. These climatic predictors were obtained from the WorldClim 2 database (Hijmans *et al.*, 2005; Fick & Hijmans, 2017), expressed at a spatial resolution of 2.5 arc-minutes (~5 km at the equator). We assigned each species a single value per predictor, calculated as the average of all values obtained by dividing the geographic range polygon of each variable for each species into 2.5 arc-minute grid cells (see Supplementary Material 1) using ArcGIS 10.2. Finally, we extracted latitude (centroids) for each species from the above IUCN distribution maps.

To test the microhabitat hypothesis, we created a dataset consisting of both microhabitats used by species as 'perching' sites ('microhabitats'), and microhabitat structures for egg deposition ('nesting sites'). Each species was assigned to one of four perching microhabitat structures: aquatic (species which depend on direct contact with water bodies, including strict aquatic species and species whose subsistence depends on permanent contact with water bodies), terrestrial (ground-dwellers that do not depend on permanent contact with water), vegetation (bush-dweller and arboreal species), and fossorial (species that, except for the breeding seasons, have underground lifestyles). For nesting site data, we assigned each species to one of five categories depending on whether parents lay their eggs in water (e.g., streams, lakes and seasonal pools, but not on vegetation, e.g., pitcher plants), the ground (terrestrial sites separated from water), burrows (enclosed nests in the ground, or in caves), on vegetation (bushes and trees, including those that use small accumulations of water within flowers and pitchers, or between leaves), or in the body of the parents in gastric or skin-brooder species (Supplementary Material 1). Species for which different literature sources provided conflicting data on use of habitat structures were removed from the analyses.

Extinction risk data

We created a dataset on species extinction risk using the IUCN Red List (www.iucnredlist.org). We defined extinction risk as a binary response variable, where we treated the IUCN categories Critically Endangered (CR), Endangered (E) and Vulnerable (VU) as "threatened", while the Near Threatened (NT) and Least Concern (LC) categories were treated as "non-threatened" (Böhm *et al.*, 2013; Pincheira-Donoso & Hodgson, 2018). All species currently classed as Data Deficient (DD) given the lack of sufficient data to make a conservation assessment were removed from the analyses, resulting in a dataset containing 1,763 species for which conservation categories are known.

Quantitative analyses and phylogenetic control

We performed phylogenetically-controlled linear models (phylogenetic linearized least squares, PGLS) to investigate the effects of our intrinsic (body size, parity mode) and extrinsic (geographic, climatic, ecological) predictors on interspecific variation in brood size. We performed multiple sets of analyses for the different sets of predictors. All numerical predictor data, as well as fecundity, were log-transformed. We first tested the relationship between body size and brood size. The same phylogenetic analyses were repeated for parity mode, and for each ecological predictor independently (with body size added to each model as a covariate to remove allometric effects). Then, for the macroecological analyses, we performed phylogenetic multiple regressions containing all four environmental predictors (temperature, precipitation, and the seasonality in these two variables). Given that distinctive continent-specific patterns of macroecological variation have been reported for different traits among ectotherms (Meiri *et al.*, 2020; Pincheira-Donoso *et al.*, 2021), we investigated whether the differences in climatic pressures across continental regions drive distinctive macroecological patterns of amphibian brood size evolution that could remain concealed under the global models. To conduct these analyses, we repeated the same multivariate climatic models for anurans and salamanders separately, but separately for the Americas, Eurasia, Africa and Australia. Island species were excluded from these analyses. Although latitude has extensively been used as a key predictor in macroecology, it represents a proxy for most environmental factors that vary geographically. Therefore, latitude should not be incorporated into the same models with the environmental predictors that strongly covary with it. Thus, the relationship between brood size and latitude was examined in a separate model. All analyses included body size as a covariate.

Finally, we constructed composite models containing all significant predictors to quantify their effects on brood size. Given the intrinsic differences in brood size and body plans among amphibian orders, and that anurans strongly dominate global amphibian species diversity (representing >86% of amphibian species in our dataset, and >88% of all known amphibians), we performed all analyses separately for Anura, Caudata and Gymnophiona. Results of models for all amphibians combined were qualitatively identical to results from anurans alone (not shown). All PGLS analyses were performed based on Jetz & Pyron's (2018) amphibian phylogenetic tree which covers ~90% of the world's extant species, using the R packages 'ape' (Paradis *et al.*, 2004), 'caper' (Orme *et al.*, 2012), and 'nlme' (Pinheiro *et al.*, 2018).

We then performed model-averaging analyses using Akaike Information Criterion (AIC) and Akaike model weights to compare all subset regression models that lay within 6 AIC units relative to the model with the lowest AIC (Burnham & Anderson, 2002; Burnham *et al.*, 2011). The importance of each explanatory variable was judged according to AIC-weighted mean effect sizes across the subset of regression models returned by the analyses presented as AIC-weighted slopes and their 95% confidence intervals (Table 1). These analyses were performed by 'dredging' the composite model and then using model-averaging functions implemented in the R package 'MuMIn' (Barton, 2017).

To test the extinction hypothesis, we employed amphibian conservation categories from the IUCN database (see above) to perform logistic regression analyses with phylogenetic control using Monte Carlo Markov Chain Generalised Linear Mixed Models (MCMCglimm), using the R package 'MCMCglimm' (Hadfield, 2010). We used vague Wishart priors on the residuals and on the phylogenetic random effect (scale matrix = 1; degrees of freedom = 1) (Hadfield, 2010). We also included parameter expansion priors to improve convergence (mean = 0; scale = 1000) (Hadfield, 2010). We regressed extinction risk against body size and fecundity, both scaled to zero mean and unit standard deviation, and included their interactions with

taxonomic order. We performed single-predictor regressions, then included both body size and fecundity in a multiple regression to test their relative importance. Models were run with 500K MCMC iterations, removing a burn-in of 50K iterations and thinning outputs to every 100 iterations.

Results

Variation in brood size. Brood size varies greatly across amphibian species, ranging from one (e.g., in multiple *Eleutherodactylus* species) to >34,000 eggs on average (in *Rhaebo blombergi*, which also attains a maximum of ~80,000 eggs per clutch, the largest fecundity record for any amphibian) per reproductive episode (median = 93.5 eggs; Supplementary Material 1). The frequency distribution of brood size is strongly right-skewed (Shapiro-Wilk's test, $W = 0.33$, $df = 2045$, $P < 0.0001$; clades shown separately in Fig. 1a-c), with 51.5% of the species in our database having clutches <100 eggs, while 78.7% of all species clutches contain <500 eggs. In contrast, the broods of only 2.6% of species average >5,000 eggs. Anurans lay considerably larger broods (species-level means from 1 to 34,641 in *Rhaebo blombergi*) than salamanders (means from 1 to 2,738 in *Ambystoma flavipiperatum*, while *Ambystoma tigrinum* attains the largest observed clutch of ~7,000 eggs) and caecilians (means from 3 to 93 in *Ichthyophis bombayensis*, which also attains the order's largest recorded clutch of 144 eggs; Fig. 1g).

Life history drivers of brood size. Brood sizes are positively associated with female body size across anurans (PGLS, Pagel's $\lambda = 0.82$, $R^2 = 0.3$, slope = 1.74, $P < 0.0001$, $n = 1,319$; Fig. 1d), salamanders ($\lambda = 0.78$, $R^2 = 0.1$, slope = 0.85, $P = 0.004$, $n = 149$; Fig. 1e), and caecilians ($\lambda = 0.83$, $R^2 = 0.3$, slope = 0.71, $P = 0.004$, $n = 29$; Fig. 1f). We also found that mean brood size differs significantly across orders (Fig. 1g) and across species with different parity modes. This is mostly due to species with larval (tadpole) development having much larger clutches than species with direct development and viviparity (Fig. 1h; see Supplementary Material 3, Fig. S1, for orders separately).

Environmental drivers of brood size. Geographically, brood size increases with latitude among anurans and salamanders, while no such relationship was observed in caecilians (Table 1, Fig. 2a). Regarding environmental factors (which often correlate with latitude), multiple regression models containing all four climatic predictors (controlling for body size) reveal significant increases in brood size with increasing temperature seasonality (but not precipitation seasonality, and with a borderline effect of mean annual temperature) in anurans (Table 1; Fig. 2b). Brood size in salamanders increases with decreasing seasonality in precipitation, but is independent of temperature seasonality (Table 1; Fig. 2c). Annual precipitation was not associated with brood size in any model. Model-averaging analyses confirmed these findings, except for the borderline effect of mean annual temperature in anurans, which was found to be non-significant (Table 1). Consistent with the global models, climatic models performed separately for amphibian orders across continental regions identified seasonality in temperature and precipitation as the dominant drivers of brood size variation (Supplementary Material 4, Table S1). These relationships between seasonality and brood sizes differ across regions between anurans and salamanders. Anuran brood sizes increase with temperature seasonality in the Americas and in Australia, and in Eurasia among salamanders (Supplementary Material 4, Table S1). Increasing seasonality in precipitation, in contrast, is associated with

smaller salamander brood sizes in the Americas (Supplementary Material 4, Table S1). In Africa, we only observed a borderline negative relationship between mean annual precipitation and brood size in anurans.

Ecologically, nesting site was a consistent predictor of fecundity for anurans and salamanders (Table 1). In all cases, species that lay eggs in water bodies have considerably higher fecundities, while plant-nesters have consistently the smallest brood sizes (Figs. 1j-k). In contrast, differences in use of microhabitat structures for perching only predict variation in brood size among anurans in univariate models (Table 1; Fig. 1i), but not in multi-predictor models, or in any model for salamanders (Table 1). Subsequent results, based on composite models containing all significant predictors (climatic, ecological and life history), are consistent with the above analyses. For anurans, composite models revealed a positive relationship between temperature seasonality and brood size, and identified parity mode, nesting site and annual temperature as further predictors of brood size (Table 1; Figs. 1, 2). In contrast, in salamanders, parity mode was the only significant predictor of brood size in addition to seasonality in precipitation (Table 1; Figs. 1, 2). The same composite models rejected a role for microhabitat occupation in anurans, and for nesting site in salamanders (Table 1).

Fecundity and extinction risk. In single-predictor phylogenetic regressions, extinction risk was found to decrease significantly with increasing body size, and to decrease significantly with increasing fecundity (Table 2). We found no credible interaction with order, and no credible differences among orders in brood size intercepts. When both brood size and body size were included in a multiple regression, brood size dominated the signal. We found a consistent negative association between extinction risk and fecundity across all three clades (Fig. 3). Caecilians showed a significant tendency for extinction risk to increase with increasing body size (although this order was only represented by 29 species), whereas anurans and salamanders showed no association between extinction risk and body size, having controlled for brood size (Table 2). Caecilians showed an even stronger negative association between extinction risk and brood size than the other two orders (Table 2).

Discussion

Our global-scale analyses reveal supporting evidence for all three hypotheses. Our findings support the prediction that fecundity is shaped by geographic gradients in seasonality. However, these climatic effects differ between amphibian orders – while larger broods evolve towards more thermally seasonal climates in anurans (as observed in lizards and birds), brood sizes in salamanders increase towards climates where rainfall is more constant throughout the year. Second, our analyses reveal that nesting site preference is a consistent predictor of brood sizes in anurans, but not in salamanders. Both hypotheses are supported when the effects of body size and parity mode are controlled for. Finally, we provide global-scale evidence supporting the prediction that the predisposition of amphibians to extinction risk – across all three orders – increases significantly in species with lower fecundity. This evidence shows that brood size is in fact more important than body size in predicting amphibian declines. Therefore, our findings reinforce the hypothesis that higher fecundity increases the likelihood of population recovery from demographic collapses caused by rapid environmental alterations, thus offsetting declines that lead to extinction (Pimm *et al.*, 1988; Bennett & Owens, 1997; Cardillo *et al.*, 2005). In contrast, the negative relationship between extinction risk and body size observed across amphibians (Pincheira-Donoso & Hodgson, 2018) is more likely to be an incidental by-product of the positive association between body size and fecundity. More widely, this focus on fecundity is

also compatible with the opposite (positive) relationship between body size and extinction risk observed among endotherms (Gaston & Blackburn, 1995; Cardillo & Bromham, 2001; Cardillo, 2003; Olden *et al.*, 2007b; Ripple *et al.*, 2017).

Evolutionary drivers of fecundity

Our evidence supports the roles of seasonality in temperature (in anurans) and precipitation (in salamanders) as drivers of fecundity evolution. This dominant effect of geographic gradients in seasonality remains valid when amphibians are analysed globally or separately across continental regions, which confirms the generality of these climatic factors as sources of selection on brood size (Jetz *et al.*, 2008; Pincheira-Donoso & Hunt, 2017; Meiri *et al.*, 2020). However, we suggest that these findings may motivate a revision of the rationale behind classical hypotheses that have guided research on clutch size evolution (Moreau, 1944; Lack, 1947, 1954; Jetz *et al.*, 2008; Pincheira-Donoso & Hunt, 2017). On the one hand, our analyses in anurans support the hypothesis that increasing temperature seasonality drives evolution of larger brood sizes, above and beyond the effects of body size and parity mode on fecundity (Moreau, 1944; Lack, 1954; Tinkle *et al.*, 1970; Cox *et al.*, 2007; Pincheira-Donoso & Tregenza, 2011; Pincheira-Donoso & Hunt, 2017). On the other hand, brood size in salamanders tends to increase toward more stable precipitation regimes, where resource availability is thus more stable throughout the year. Therefore, two main conclusions can be drawn: (i) while increases in anuran brood sizes are associated with increasing climatic seasonality (as observed in lizards; Meiri *et al.* 2020), we argue that the mechanisms that drive the evolution of similar macroecological patterns in birds are not necessarily the same. Explanations for larger clutches in birds from seasonal regions have been dominated by Moreau-Lack's (Moreau, 1944; Lack, 1954; Pincheira-Donoso & Hunt, 2017) and Ashmole's hypotheses (Ashmole, 1963). These hypotheses predict larger clutches towards seasonal climates given that high mortality during the cold season reduces the intensity of intraspecific competition, thus increasing resource availability for allocation into reproduction during the breeding season. However, this process is only likely to be important in endotherms, which remain active during the cold seasons (this may exclude mammals that hibernate), while it is unjustified for ectothermic vertebrates, which are mostly inactive during cold seasons (Duellman & Trueb, 1994; Wells, 2007; Pough *et al.*, 2015). Likewise, the proposed mechanism that links larger brood size to higher resource availability not only applies to seasonal regions (where resource peaks fluctuate), but also to tropical environments, where productivity is constantly high throughout the year.

Therefore, we instead propose that a more general explanation may relate to the intensification of fecundity selection as breeding seasons shorten towards higher latitudes (and elevations). As seasonality increases, breeding seasons tend to get shorter and fecundity selection is predicted to enlarge brood size to compensate for the progressively reduced opportunities for reproduction (Cox *et al.*, 2003; Pincheira-Donoso & Tregenza, 2011; Pincheira-Donoso & Hunt, 2017). In contrast, towards the tropics, fitness is expected to be enhanced by reductions in brood size via strategies such as partitioning of eggs across multiple, smaller clutches, or investment into larger offspring of 'higher quality' (Shine, 2005; Griebeler *et al.*, 2010; Pincheira-Donoso & Hunt, 2017). This hypothesis thus applies more generally to both endotherms and ectotherms.

The only ecological factor we tested that remained a significant predictor of brood size in the composite models – beyond the effects of climate, parity mode, and body size – was nesting site in anurans. This predictor was not significant in the salamander composite models (and neither was microhabitat occupation in any amphibian group). Therefore, we suggest that nesting site is a main ecological source of

selection on fecundity in anurans only. This conclusion is consistent with recent studies. For example, in a comparative study with a strong (but not exclusive) focus on hylid frogs (Silva *et al.*, 2020), aquatic nesting sites were shown to relax spatial constraints on fecundity, whereas egg-laying on vegetation was found to impose strong constraints on brood size – these costs are further enhanced by the locomotor costs for females that carry eggs and often amplexant males (Silva *et al.*, 2020). Likewise, a global study on lizards revealed that scansorial species have a tendency to evolve smaller clutches than terrestrial species (Meiri *et al.*, 2020). Thus, three non-mutually exclusive pressures intrinsic to nesting site choice are likely to create selection on fecundity: egg safety (from desiccation and predators), constraints imposed by physical space, and possibly the costs that larger clutches can impose on locomotion in species that climb vegetation. Not surprisingly, water-spawning species have evolved by far the largest broods. Burrow-nesters, which are subject to intermediate degrees of space constraints (Wells, 2007), follow with the second largest brood sizes potentially given that humidity available for enclosed eggs is more stable than in the open soil. Although these pressures are expected to apply to amphibians in general, a plausible explanation for the significant effect of nesting site observed in anurans only may relate to the much wider range of selection pressures encompassed by these amphibians across their much broader latitudinal global distribution (-49.3°S – 57.5°N across all continents, $n=5,582$ species), compared to salamanders (-12.5°S – 60.4°N , mostly in North America and the Palearctic, $n=553$). Towards higher latitudes, the increasing levels of seasonality are expected to intensify fecundity selection for larger brood sizes – a prediction supported by our analyses in anurans. In turn, as fecundity increases, the need for nesting sites in which space constraints are relaxed increases. Only water and terrestrial sites meet this condition. However, we have shown that terrestrial nesting sites are associated with small broods, potentially given their environmental instability (in relation to e.g., hydric and temperature conditions), unlike water bodies.

Fecundity and extinction risk

The evidence that susceptibility of amphibians to extinction increases with low fecundity aligns with classic theories on the adaptive evolution of reproductive strategies in stochastic environments (Pimm *et al.*, 1988; Lande, 1993; Lande *et al.*, 2003; Jetz *et al.*, 2008). Under the ongoing pressures of rapidly changing environments, these theories predict higher chances of rapid demographic recovery in high-fecundity ('fast' life history) species, relative to low-fecundity ('slow' life history) species (Pimm *et al.*, 1988; Bennett & Owens, 1997; Cardillo *et al.*, 2005). This is because per-capita population growth rates are increasingly higher with higher reproductive outputs (Lande, 1993; Mace *et al.*, 2008), and because increases in (genetic) variation resulting from higher fecundity provide broods with a wider range of phenotypic variants, which enhances the likelihood that at least some of the offspring survive under fluctuating and strong episodes of selection (Roff, 2002; Lande *et al.*, 2003; Ferriere *et al.*, 2004; Pincheira-Donoso & Hunt, 2017). These benefits are suggested to be enhanced by polyandry for a number of reasons, including reduced inbreeding depression (Yasui, 1998; Slatyer *et al.*, 2012), and resistance to the spread of sex-ratio distorters (Price *et al.*, 2010).

More widely, however, the negative relationship between extinction risk and fecundity observed in amphibians reinforces the need to reset the focus of the widely debated, and yet empirically conflicting, association between body size and extinction risk across animals (Bennett & Owens, 1997; Cardillo *et al.*, 2005, 2006; Meiri, 2008; Sodhi *et al.*, 2008; Ripple *et al.*, 2017; Pincheira-Donoso & Hodgson, 2018). In fact, this extinction-body size link has mostly been made given the tendency for body size to correlate with

fecundity (Darwin, 1874; Pincheira-Donoso & Hunt, 2017), with a negative tendency among endotherms (Bennett & Owens, 1997, 2002; Cardillo *et al.*, 2005) and a positive tendency in ectotherms (Shine, 2005; Pincheira-Donoso & Tregenza, 2011; Pincheira-Donoso & Hunt, 2017; Meiri *et al.*, 2020). Under certain circumstances, body size does play a more direct role in extinctions – most notably, the overexploitation of large mammals that has caused their drastic declines since ancient times (Ripple *et al.*, 2015, 2019; Smith *et al.*, 2018; Faurby *et al.*, 2020). But even in these cases, slower rates of demographic recovery stemming from low fecundity in large mammals are likely to play an underlying role in species declines. Therefore, placing the causal focus of extinctions on reproductive rates (rather than on body size) offers the advantage to explain the discrepancies between body size and extinction known between endotherms and ectotherms (Bennett & Owens, 1997; Cardillo *et al.*, 2006; Ripple *et al.*, 2017; Pincheira-Donoso & Hodgson, 2018). Collectively, this fecundity hypothesis suggests that, independent of a species body size, extinction risk will be more likely to increase in species with lower reproductive rates given their lower rates of demographic recovery.

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Data availability statement: All the datasets used in this study are available as supplementary material to the main article, and will be made open-access at the GABiP initiative’s repository at <http://www.amphibianbiodiversity.org> upon publication.

Supplementary Material

Supplementary Material 1. Dataset used in this study.

Supplementary Material 2. List of literature references from which data have been collected.

Supplementary Material 3. Figure S1.

Supplementary Material 4. Table S1.

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Table 1. Results from phylogenetic regressions and model-averaging analyses of amphibian fecundity. Significant relationships are in boldface. Geographic (i.e., with latitude as predictor) analyses were performed separately from ecological and environmental analyses. PGLS analyses show results from both the multivariate and the bivariate models (with the listed predictors plus body size as covariate). For each multivariate model we only display the slope and 95% CI of the predictors returned by the process of model-averaging analyses given their threshold Δ -AIC<6 (predictors with Δ -AIC>6 not shown), and only significant predictors are in boldface.

| Models | <i>n</i> | PGLS | | | | Model Averaging Analysis | |
|----------------------------------|----------|-----------|-----------------------|----------|-------------------|--------------------------|-------------------------|
| | | λ | <i>R</i> ² | <i>t</i> | <i>P</i> | Slope | 95% CI |
| 1. Anurans | | | | | | | |
| Latitude (Absolute) | 1709 | 0.82 | 0.3 | 5.34 | <0.0001 | 0.02 | – |
| Climatic Model | 1607 | 0.78 | 0.3 | – | <0.0001 | – | – |
| <i>Annual Temperature</i> | | | – | 2.01 | 0.045 | 0.15 | (-0.003, 0.293) |
| <i>Temperature Seasonality</i> | | | – | 6.31 | <0.0001 | 0.82 | (0.608, 1.039) |
| <i>Annual Precipitation</i> | | | – | -1.49 | 0.134 | -0.09 | (-0.210, 0.035) |
| <i>Precipitation Seasonality</i> | | | – | -0.56 | 0.579 | – | – |
| Parity Mode | 1579 | 0.79 | 0.3 | -8.77 | <0.0001 | – | – |
| Nesting Site | 736 | 0.82 | 0.37 | -8.57 | <0.0001 | – | – |
| Microhabitat | 1458 | 0.81 | 0.26 | -2.43 | 0.02 | – | – |
| Composite Model | 629 | 0.81 | 0.45 | – | <0.0001 | – | – |
| <i>Annual Temperature</i> | | | – | 2.21 | 0.03 | 0.28 | (0.031, 0.532) |
| <i>Temperature Seasonality</i> | | | – | 6.67 | <0.0001 | 0.85 | (0.570, 1.134) |
| <i>Parity Mode</i> | | | – | -6.40 | <0.0001 | -1.27 | (-1.662, -0.871) |
| <i>Nesting Site</i> | | | – | -6.64 | <0.0001 | -0.28 | (-0.358, -0.197) |
| <i>Microhabitat</i> | | | – | -0.25 | 0.806 | – | – |
| 2. Salamanders | | | | | | | |
| Latitude (Absolute) | 236 | 0.77 | 0.10 | 2.01 | 0.046 | 0.02 | – |
| Climatic Model | 194 | 0.60 | 0.12 | – | <0.001 | – | – |
| <i>Annual Temperature</i> | | | – | -0.37 | 0.710 | -0.07 | (-0.385, 0.242) |
| <i>Temperature Seasonality</i> | | | – | 0.70 | 0.485 | 0.41 | (-0.325, 1.149) |
| <i>Annual Precipitation</i> | | | – | -0.29 | 0.775 | -0.12 | (-0.514, 0.282) |
| <i>Precipitation Seasonality</i> | | | – | -2.57 | 0.01 | -0.41 | (-0.684, -0.125) |
| Parity Mode | 192 | 0.33 | 0.2 | -5.08 | <0.0001 | – | – |
| Nesting Site | 126 | 0.51 | 0.14 | -2.94 | <0.01 | – | – |
| Microhabitat | 193 | 0.61 | 0.08 | -0.99 | 0.319 | – | – |
| Composite Model | 121 | 0.42 | 0.26 | – | <0.0001 | – | – |
| <i>Precipitation Seasonality</i> | | | – | -2.58 | 0.01 | -0.39 | (-0.683, -0.101) |
| <i>Parity Mode</i> | | | – | -2.81 | <0.01 | -0.88 | (-1.445, -0.310) |
| <i>Nesting Site</i> | | | – | -1.61 | 0.110 | -0.21 | (-0.458, 0.042) |
| 3. Caecilians | | | | | | | |
| Latitude (Absolute) | 28 | 0.84 | 0.3 | 0.35 | 0.729 | 0.01 | – |
| Climatic Model | 29 | 0.87 | 0.34 | – | 0.134 | – | – |

Table 2. Results of single- and multi-predictor phylogenetic regressions of extinction risk against body size and fecundity. All covariates scaled to zero mean and unit standard deviation, and hence, slopes measure change in log-odds of endangerment for standard deviation increase in predictor. All models include order as a categorical predictor. For each model we provide posterior modes and 95% credible intervals of anuran intercepts, slopes, intercept contrasts against anuran intercept, and slope contrasts against anuran slope. We also provide Markov Chain Monte Carlo (MCMC) p -values, which measure the proportion of posterior estimates lying on the other side of zero from the posterior mode.

| | Posterior Mode | 95% Credible Interval | MCMC p -value |
|--|----------------|-----------------------|------------------|
| 1. Brood Size | | | |
| Anuran intercept | -3.09 | -12.13, 5.33 | 0.473 |
| Scaled Brood Size (slope) | -1.38 | -1.88, -0.91 | <0.001 |
| Salamander intercept contrast | -0.03 | -11.82, 11.81 | 0.993 |
| Caecilian intercept contrast | -9.48 | -33.01, 11.90 | 0.405 |
| Salamander slope contrast | 0.37 | -0.84, 1.57 | 0.546 |
| Caecilian slope contrast | -4.81 | -19.92, 7.72 | 0.505 |
| 2. Body size | | | |
| Anuran intercept | -3.66 | -15.79, 6.93 | 0.516 |
| Scaled body size (slope) | -0.99 | -1.55, -0.42 | <0.001 |
| Salamander intercept contrast | 1.27 | -13.97, 16.68 | 0.868 |
| Caecilian intercept contrast | -19.99 | -72.89, 33.83 | 0.457 |
| Salamander slope contrast | 0.43 | -1.16, 1.90 | 0.570 |
| Caecilian slope contrast | 5.80 | -7.41, 19.49 | 0.385 |
| 3. Multiple regression | | | |
| Anuran intercept | -3.38 | -13.62, 6.24 | 0.492 |
| Scaled Brood Size (slope) | -1.36 | -2.02, -0.78 | <0.001 |
| Scaled body size (slope) | -0.23 | -0.81, 0.35 | 0.432 |
| Salamander intercept contrast | 0.47 | -14.21, 13.40 | 0.955 |
| Caecilian intercept contrast | -163.7 | -340.5, -7.40 | 0.027 |
| Salamander Brood Size slope contrast | 0.35 | -0.99, 1.74 | 0.611 |
| Caecilian Brood Size slope contrast | -41.88 | -87.56, 1.56 | 0.032 |
| Salamander body size slope contrast | -0.003 | -1.53, 1.44 | 0.989 |
| Caecilian body size slope contrast | 2.80 | 0.61, 5.91 | 0.037 |

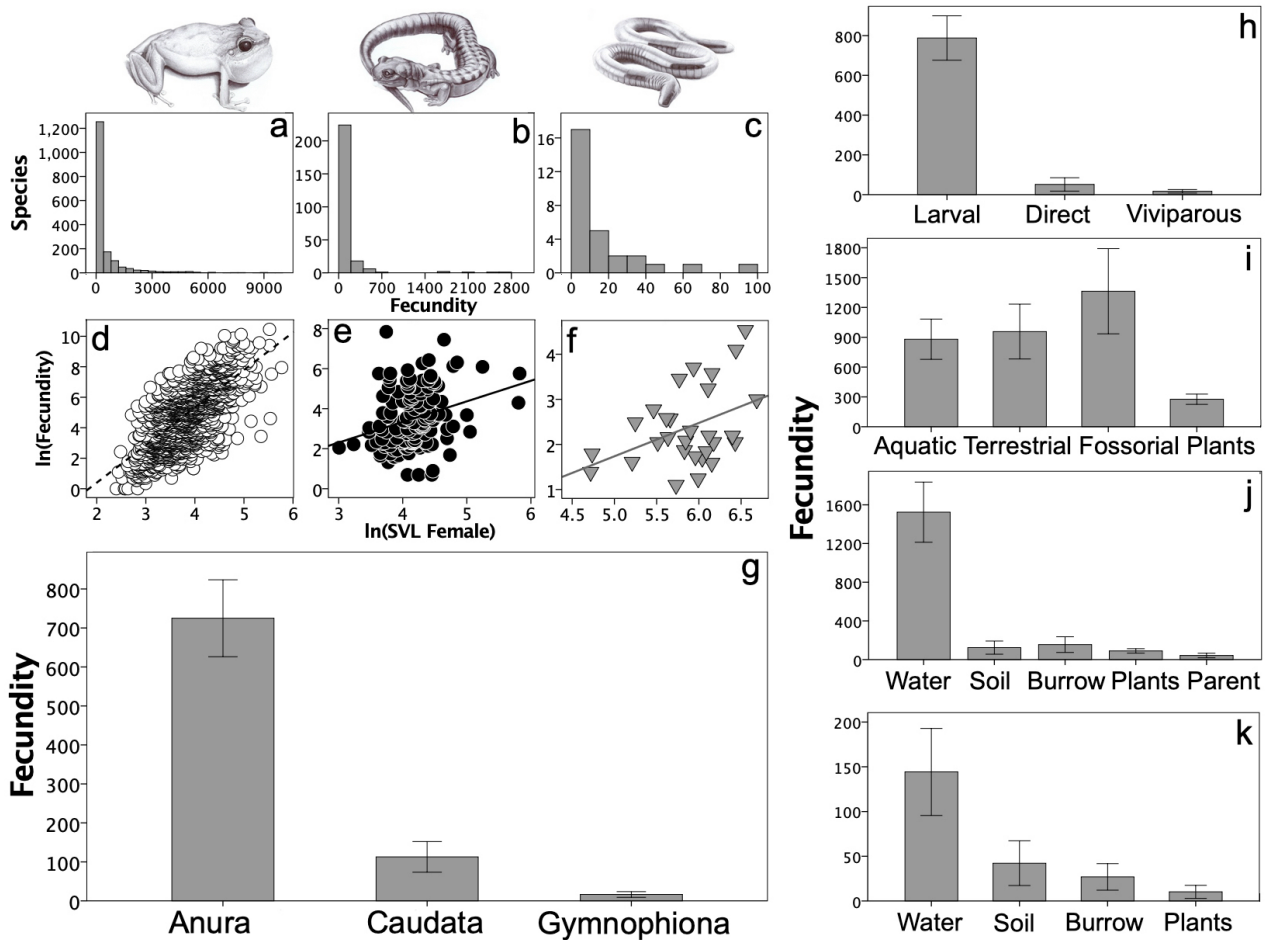


Figure 1. Patterns of variation in amphibian fecundity across phylogenetic, ecological and life history categories. Fecundity is strongly right-skewed in all three orders (a-c), and female body size is a consistent predictor of increasing clutch size (d-f). When comparing orders, levels of fecundity are considerably lower in salamanders (Caudata) and caecilians (Gymnophiona), respectively, relative to anurans (g). Differences in fecundity are strong among parity modes for all amphibians (h), with larval mode yielding the largest clutch sizes. In anurans, clutch size differs among species that occupy different microhabitats, whereby fossorial species have the highest fecundities and vegetation-dwellers the lowest (i). Interestingly, the effects of nesting site on fecundity are fairly consistent among anurans (j) and salamanders (k), with considerably larger clutches in water nesters relative to the other nesting choices. These analyses were not performed on caecilians given the low numbers of species for which data were available.

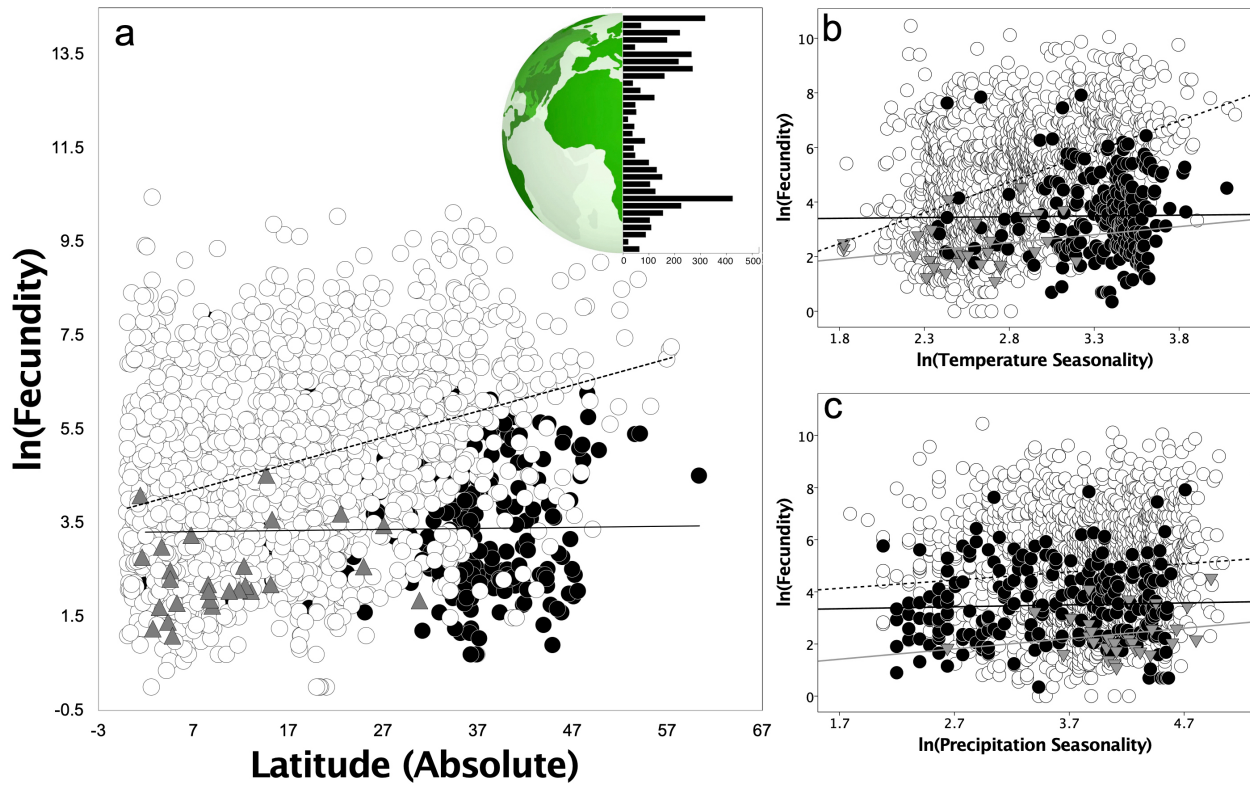


Figure 2. Ecogeographic patterns of fecundity variation in amphibians. Spatial analyses (a) show a strong tendency for fecundity to increase with increasing latitude in anurans (dashed lines), while the tendency is weak in salamanders (black lines) and lacking in caecilians (grey lines). The inset graph (in a) shows the distribution of fecundity along the whole north-south global gradient of latitude for amphibians combined, in which a strongly bimodal pattern is observed. Climatic analyses reveal that fecundity increases predictably with increasing seasonality in temperature among anurans only (b), while decreases in fecundity among salamanders are associated with increasing seasonality in precipitation (c). Slopes and intercepts for the fitted lines were calculated using model-averaging and significance values for all the relationships shown in this figure are provided in Table 1.

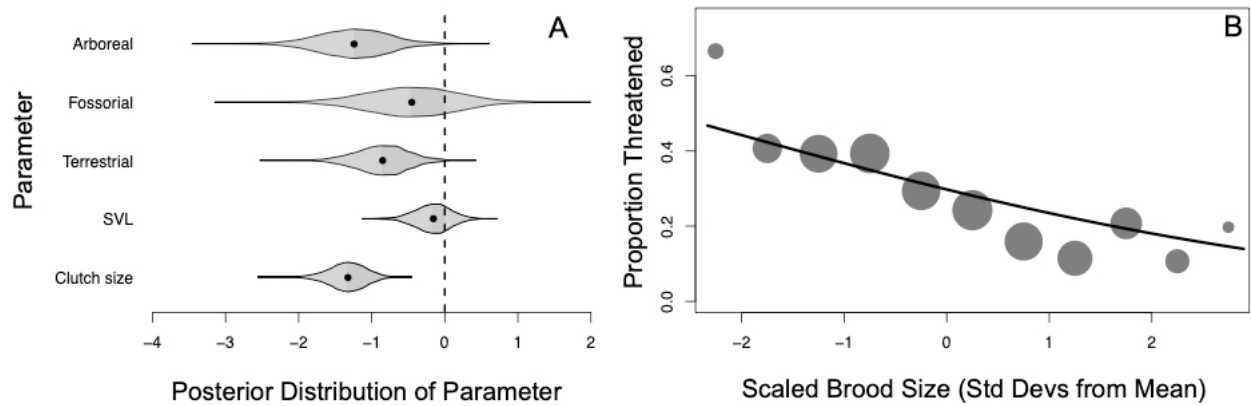


Figure 3. The relationship between brood size and extinction risk. (A) The influence of clutch size and body size (SVL) on extinction risk. For reference, this plot also includes a subset of other factors (microhabitat types) that affect brood size but not extinction risk in amphibians. Posterior distributions of intercepts (for habitat categories) and slopes (for clutch size and SVL, both scaled to zero mean and unit standard deviation), with probability of extinction risk on a logit scale. Posterior distributions inferred using Monte Carlo Markov Chain generalised linear mixed models with phylogenetic control. Points show the mean of each parameter's posterior distribution, and envelopes show the probability density of posterior distributions. Zero line is included to aid judgement of the credibility of slope parameters being non-zero. (B) Proportion of amphibian species that are threatened, in relation to clutch size. Points show proportion of species threatened for species binned according to number of standard deviations away from the mean clutch size. Fitted line derived from Monte Carlo Markov Chain generalised linear model of threat status against clutch size scaled to zero mean and unit standard deviation.