

Cold and dark captivity: Drivers of amphibian longevity

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Abstract

Aim: Longevity is a critical life-history trait of organisms. Multiple abiotic and biotic factors are thought to exert different selection pressures, resulting in a great variation in species longevity. We examined factors that, according to evolutionary theories of senescence, are thought to be related to extrinsic and intrinsic mortality rates, and thus shape the variation in longevity among amphibians.

Location: World-wide.

Time period: Present.

Major taxa studied: Amphibia.

Methods: We collected literature data on the maximum longevity of 527 amphibian species. Correcting for phylogeny and sample size, we modelled the relationship between amphibian longevity and body size. We also examined the effects of chemical protection, activity period, microhabitat preferences and annual temperature on amphibian longevity.

Results: In general, members of larger amphibian species live longer. Body size, however, explained less of the variation in amphibian longevity than it does in mammals and birds. Nocturnal amphibians, species that use poison for defence and those inhabiting cold regions live longer, but microhabitat preferences had little effect.

Main conclusions: Our results supported predictions of evolutionary theories of senescence. Large amphibians living in colder environments probably experience slower growth and metabolic rates, reducing intrinsic drivers of mortality and increasing longevity. Moreover, species that reduce extrinsic mortality pressures via chemical protection and nocturnality have increased longevity. Sampling captive animals and sampling more individuals of a species increases the chances of finding older individuals and should be corrected for when studying maximum longevity.

KEYWORDS

amphibians, annual temperatures, body size, chemical protection, extrinsic mortality, longevity, nocturnality, phylogeny, sample size, senescence

1 | INTRODUCTION

Longevity varies greatly both within and among species and populations (Healy et al., 2014; Holm et al., 2016; Scharf et al., 2015). These differences have been explained with reference to factors related to either 'intrinsic' or 'extrinsic' mortality pressures (Holm et al., 2016). Intrinsic mortality results from processes of physical and functional

degradation originating within the body (e.g., spontaneous chemical reactions, replication errors and metabolic waste products). In contrast, extrinsic mortality is the result of hazards deriving from the environment (such as predation, famine and drought; Koopman, Wensink, Rozing, Bodegom, & Westendorp, 2015).

Individuals that allocate more resources to reproduction, at the expense of somatic maintenance and repair, risk the rapid decline of

physiological process and a rapid accumulation of harmful mutations (Kirkwood, 2001). Such animals are thus expected to experience a faster decline in survival rates as they age (Kirkwood & Austad, 2000; Kirkwood & Rose, 1991; Williams, 1957). Early reproduction is also thought to expose animals to an accumulation of age-specific mutations with pleiotropic effects (Gavrilov & Gavrilova, 2002). This has been associated with the 'antagonistic pleiotropy theory', which suggests that some genes encode phenotypes that offer benefits early on in life, while also encoding other traits that are harmful in advanced age (Hamilton, 1966; Ljubuncic & Reznick, 2009; Medawar, 1952; Stearns, 1992). Such harmful traits, which are expressed late, will be invisible to selection in animals that reproduce young, but will select strongly against animals that reproduce at older ages (Williams, Day, Fletcher, & Rowe, 2006).

Animals suffering low extrinsic mortality rates (i.e., low risk of death from environmental hazards, such as disease, predation, food shortages or accidents) can postpone the onset of reproduction. This can select for a longer life span so that reproductive potential is maximized (Healy et al., 2014; Williams, 1957). As the chances of dying of extrinsic factors decrease, resources can be allocated to maintenance, and this will also lower intrinsic mortality factors, resulting in a longer life (Partridge & Barton, 1993).

Studies of birds, mammals and reptiles have often found longevity to be related strongly to both intrinsic and extrinsic mortality rates (Austad, 1997; Blanco & Sherman, 2005; Healy et al., 2014; Scharf et al., 2015; Valcu, Griesser, Nakagawa, & Kempenaers, 2014; Wilkinson & South, 2002). For example, birds and bats, that can escape predators by flying, presumably suffer lower rates of predation than non-flying species. Accordingly, they live longer than terrestrial mammals of similar sizes and metabolic rates (Austad & Fischer, 1991; Healy et al., 2014). Captive reptiles live longer than individuals in the wild, probably owing to the absence of extrinsic mortality pressures in the form of predators, drought and famine (Scharf et al., 2015).

The factors affecting longevity in amphibians have never been tested formally on a large scale (for comparative studies of small numbers of amphibian species see Blanco & Sherman, 2005; Sinsch & Dehling, 2017; Zhang & Lu, 2012). We sought to determine whether longevity in this large and diverse, ecologically unique, group is affected by similar factors to those found to be important in amniotes. Large-scale comparisons of animal longevity usually use maximum longevity as a measure of the age reached by individuals of different species (Healy et al., 2014; Ridgway, Richardson, & Austad, 2010; Scharf et al., 2015). Moreover, they often combine data from individuals living in the wild with those from captivity (Blanco & Sherman, 2005; Healy et al., 2014; Scharf et al., 2015). We sought to assess and parameterize the effects of sample size and captivity on longevity, through a comparative study. We analysed the relationship between longevity and factors related to mortality rates in light of the theories of senescence. We examined the following five hypotheses:

1. Longevity is positively correlated with body size. Larger animals have a slower metabolism, which translates to slower growth.

This is associated with a reduction in the rate of accumulation of metabolic by-products and oxidative damage (Sohal, 1986). Consequently, large animals are predicted to have longer life span than smaller ones (e.g., Nunn & Barton, 2000).

2. Amphibians possessing serous glands that secrete poison will suffer lower extrinsic mortality rates than those not depending on poison for defence. We therefore hypothesize that poisonous species should exhibit longer life spans. Given that there is typically no predation in captivity, however, we predict that the effects of toxicity will be most pronounced when species are sampled in the wild.
3. Nocturnal amphibians are harder to detect and they avoid predation by most birds, reptiles and fishes and some predatory mammals (e.g., mongooses; Healy et al., 2014; Holmes & Austad, 1994; Pechmann & Semlitsch, 1986; Promislow & Harvey, 1990; Sih, Kats, & Moore, 1992; Taylor, 1983). But they may be exposed to predators such as most mammals, snakes and other amphibians. Night temperatures are lower than those by day, causing a reduction in metabolism in amphibians and, in turn, lower intrinsic mortality resulting from metabolic by-products (Sohal, 1986). Furthermore, ultraviolet (UV) radiation that can cause harmful mutations is of little importance to nocturnal species. We thus hypothesize that nocturnal amphibians will have longer life spans.
4. We hypothesize that amphibian longevity will be negatively correlated with mean annual temperature, because the higher metabolic rates in warm regions will enhance the mortality rate in these ectotherms (Metcalfe & Monaghan, 2003). Ectotherms living in colder environments experience slower rates of living (Meiri et al., 2013; Meiri, Brown, & Sibly, 2012; Valenzano, Terzibasi, Cattaneo, Domenici, & Cellerino, 2006), associated with reduced metabolism, which lowers mutation rates and oxidative damage and, in turn, increases life span (Sohal, 1986).
5. We predict that arboreal, aquatic and, especially, fossorial species will live longer than terrestrial ones, for several reasons. First, fossorial species are less exposed to radiation, high temperatures and predation, lowering intrinsic and extrinsic mortality rates. Second, aquatic species are exposed to lower temperatures, causing lower metabolic rates (lower intrinsic mortality). Third, arboreal species are better able to escape from predators than species that feed on the ground (Buffenstein & Jarvis, 2002; Byrnes & Spence, 2011; Shattuck & Williams, 2010).

2 | METHODS

2.1 | Data collection

We assembled a dataset on the maximum longevity of 527 species of amphibians (367 Anuran species, 155 Urodelan species and five species of Gymnophiona), representing c. 6.7% of their known species diversity (currently 7,843 species of amphibians; AmphibiaWeb, accessed April 2018) belonging to 47 of the 75 families currently

recognized world-wide (AmphibiaWeb, 2017; Frost, 2017). Data on maximum longevity were collected from the primary and secondary literature and from field guides (a list of the data sources is given in Appendix 1). Data on the non-spatial predictor variables were gathered from the same sources used to estimate longevity and, if not reported there, from the primary literature and from field guides.

Longevity data are the maximum life span (in years) reported for each species. There are drawbacks to using maximum values as estimates of longevity. First, the maximum may be unrepresentative of the species as a whole (Carey, 2003). Second, estimates of longevity could be based on unequal numbers of individuals for different species, and maxima are likely to increase with sample size, whereas means are probably unbiased (Scharf et al., 2015). Much more data, however, exist on maximum than on mean or modal longevity (Healy et al., 2014; Scharf et al., 2015). Maxima are therefore the commonest metric of longevity in comparative studies (de Magalhães, Costa, & Church, 2007; Healy et al., 2014; Prothero, 1993; Scharf et al., 2015; Wilkinson & South, 2002). We recorded the sample sizes upon which longevity is estimated for each species to correct for some of the potential biases inherent in the use of maxima. We also introduced a sensitivity analysis, in which we excluded species with low sample sizes ($n < 5$) or for which data on sample sizes could not be obtained (305 species retained) and repeated our analysis of other factors.

Captive animals (kept in zoos, as pets, etc.) generally receive ample nutrition, veterinary care and protection from extrinsic mortality pressures such as predation, intraspecific conflict, hunger and drought (Mason, 2010). Amphibians living in captivity are thus likely to have longer life spans than hetero- and conspecifics living in their natural environments, and we thus treat the origin of the data (captivity or the wild) as an additional predictor in our analyses.

In addition to the analyses of all amphibians, we analysed anurans and Urodela separately to determine whether this major split of the amphibian tree of life influences the traits affecting longevity. A similar analysis for Gymnophiona was impossible owing to low sample size ($n = 5$).

For each species, we collected data on mean body size. When multiple means were available for a species (e.g., from different sources), we calculated the mean of all published means. When only size ranges were available, we used the midpoint of the range (i.e., $[\text{minimum} + \text{maximum}]/2$). To account for differences between the sexes, we averaged the mean body size of females and males.

The standard body size index for anurans is snout-vent length (SVL), whereas for members of the Urodela and Gymnophiona it is total length (TL = SVL + tail length; Slavenko & Meiri, 2015). For such a diverse assemblage, mass is a better size index than length, because it accounts for variation in shape (Feldman & Meiri, 2013). Therefore, to enable a comparison of all amphibian taxa, we converted body length to mass using the most up-to-date order-specific conversion formulas from Santini, Benítez-López, Ficetola, and Huijbregts (2018) for Anura and Urodela. Similar equations were unavailable for the Gymnophiona. We thus generated such an allometric equation anew for this order, by collecting data on the TL

and mass (in grams) of 17 species from the literature. The resulting equation is $\text{mass (in grams)} = 0.000001 \times \text{TL (in millimetres)}^{2.931}$ (see Supporting Information Appendix S1).

Species were defined as either diurnal or nocturnal. We categorized crepuscular species ($n < 10$) as diurnal, because they are exposed to UV radiation and to warm daytime temperatures and thus presumably have high metabolic rates and accelerated accumulation of somatic mutations. Moreover, we classify fossorial and cave species as nocturnal, because they avoid UV radiation and hot temperatures.

We defined species microhabitats as terrestrial, arboreal, fossorial or aquatic. Some species are active in more than one type of microhabitat (e.g., arboreal and terrestrial), and we refer to them as 'variable' (more than one mode of microhabitat).

We classified species as either poisonous or not. Most amphibians have serous (poison) glands (Daly, 1995), and the toxicity of their secretions varies from minimal (e.g., in *Desmognathus quadramaculatus*; Brodie, Dowdey, & Anthony, 1989) to extreme (e.g., in *Phyllobates terribilis*; Daly, 1995). Toxicity is a relative term; exposure to toxins from a specific species might be lethal to some animals but harmless to others (Blanco & Sherman, 2005). Consequently, it was impossible to rank species according to relative toxicity, and we thus treated chemical protection as a dichotomy. This was based on the assumption that species not recorded as using poison are less toxic, on average, than species for which toxicity has been reported.

Mean annual temperatures were collected for each species by intersecting the latitude and longitude of the location where longevity data were collected with a layer of mean annual temperature within 30 arc s (CHELSA; Karger et al., 2017). However, such coordinates were available for only one-fifth of the species in our dataset ($n = 101$). For the other species, we averaged temperature data (also from CHELSA) across all the grid-cells they inhabit, according to maps from the IUCN spatial datasets (IUCN, 2016). To test whether our approximate method is not affecting the reliability of the results, we repeated the analysis using only the 101 species for which we had data on the exact place where they were sampled (and thus to the temperature data from this place).

Finally, we recorded whether longevity data were from captive individuals (in zoos, laboratories, private collections, etc.) or from wild ones. In addition, we directly compared species for which we had longevity data from both captivity and the wild ($n = 140$).

2.2 | Phylogenetic and statistical analyses

We estimated the phylogenetic signal in longevity data using phylogenetic generalized least squares regression (PGLS; Freckleton, Harvey, & Pagel, 2002) on the most recent phylogeny of 7,238 extant amphibian species by Jetz and Pyron (2018). We used the 'caper' package in R (Orme, 2013) to estimate the maximum likelihood value of Pagel's λ , a statistically powerful index for measuring whether data exhibit phylogenetic dependence and how strong it is (Freckleton et al., 2002). The scaling parameter λ represents the magnitude of the phylogenetic signal in the data and model residuals

(Freckleton et al., 2002). A λ of zero indicates that there is no phylogenetic signal (i.e., that the trait has evolved independently of phylogeny and thus close relatives are not more similar on average than distant relatives). A λ of one indicates a strong phylogenetic signal, in agreement with a Brownian motion model of evolution (Münkemüller et al., 2012). In all statistical tests, we accounted for shared ancestry using PGLS (Pagel, 1999).

We \log_{10} -transformed data on body size, maximum longevity and sample size, in order to normalize residuals and reduce heteroscedasticity. We calculated variance inflation factors to determine whether multicollinearity between the predictor variables was present in the data (O'Brien, 2007). No predictors had a variance inflation factor > 1.5, and we thus maintain that our analyses are not biased by multicollinearity (O'Brien, 2007). We obtained literature data on the body size, origin of longevity data (captive or wild), activity period, chemical protection, annual temperature, microhabitat and sample size for most species (ranging from 100% data, for origin of longevity (captive or wild) and for body size, to a minimum of 83.1%, for chemical protection). The uneven number of data points for each predictor precluded the use of Akaike information criterion-based methods for model selection. We thus examined which of these seven variables (and their two-way interactions) related to longevity, using a phylogenetic ANCOVA test starting from a full model and using a backwards stepwise elimination procedure. In many studies, high type 1 error rates associated with the use of $\alpha = .05$ produce results that are difficult to replicate and substantiate (Benjamin et al., 2018). Therefore, we based the model selection on p -values at $\alpha = .005$ according to recent suggestions (Benjamin et al., 2018; Johnson, 2013) in order to reduce this potential source of false-positive results. Sample sizes, however, were treated with $\alpha = .05$, because we wish to make sure it is corrected for (i.e., its effect is a property of the sample rather than a product of evolution). We determined the importance of the selected predictor variables by variance partitioning. All statistical analyses were performed in R 3.3.2 (R Core Team, Vienna, Austria) using the RStudio 1.0.136 (RStudio Inc., Boston, MA) interface.

3 | RESULTS

Data on the longevity of the 527 species in our study, and the values of the predictor variables and the sources for them, are presented in the Supporting Information (Appendix S2). The mean (\pm SE) longevity of the amphibians we analysed is 11.1 ± 0.4 years, with a

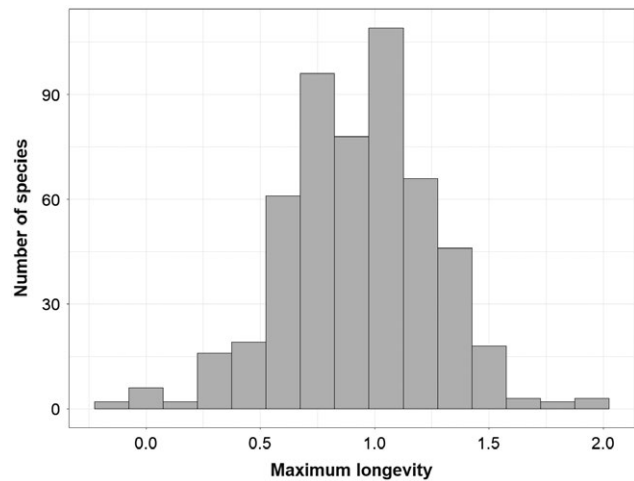


FIGURE 1 Distribution of the (\log_{10}) maximum longevity (in years) of the 527 amphibian species

maximum life span ranging from 6 months (*Phrynobatrachus gutturosus*; Barbault, 1984) to 102 years (*Proteus anguinus*; Voituron, de Fraipont, Issartel, Guillaume, & Clobert, 2011; Figure 1). For anurans, the mean longevity is 8.4 ± 0.3 years (range: 0.6–45, $n = 367$), in urodeles 17.5 ± 1.1 years (range 2–102, $n = 155$) and in the Gymnophiona 11.9 ± 2.6 years (range 5–20, $n = 5$).

Correcting for phylogeny, most of the predictors (except microhabitat) we examined were retained in the minimal adequate model, and some two-way interactions were marginally significant (see Table 1 for effect sizes and other statistics; Supporting Information Appendix S3 Table A1 for the full model). Amphibian longevity increases to the 0.12 power of \log_{10} (mass) (95% CI = 0.060–0.172). Slopes for both Anura (.130 \pm .02, 95% CI = 0.073–0.186) and Urodela (.125 \pm .03, 95% CI = 0.046–0.203; Figure 2) were similar. For Gymnophiona, body size was not correlated with longevity (slope: .27 \pm .39, 95% CI = -1.949 to -2.489). In general, body size explains little of the variance in amphibian longevity (7–14%).

Longevity decreased with increasing mean annual temperatures (Figure 3). Nocturnal species (average life span 35.8% higher than that of diurnal species; Figure 3), amphibians using poison (average life span 26.7% higher than non-chemically protected species) and those for which data originated from captive specimens (average life span 31.2% longer than species recorded in the wild) lived longer. However, we did not find a relationship between microhabitat and longevity ($p = .376$ for aquatic species; $p = .602$

TABLE 1 Longevity as a function of body mass for amphibians, using phylogenetic analysis (PGLS)

Group	R^2	Slope \pm 1 SE	t	Intercept \pm 1 SE	λ	n	p	99.5% CI of the slope
Amphibians	0.07	.123 \pm .02	6.2	0.877 \pm 0.12	.576	527	< .0001	0.060–0.172
Anura	0.08	.130 \pm .02	5.6	0.805 \pm 0.08	.564	367	< .0001	0.073–0.186
Urodela	0.07	.125 \pm .03	3.4	0.947 \pm 0.09	.145	155	.0007	0.046–0.203
Gymnophiona	0.14	.271 \pm .387	0.69	0.556 \pm 0.680	.000	5	.535	-1.949 to -2.489

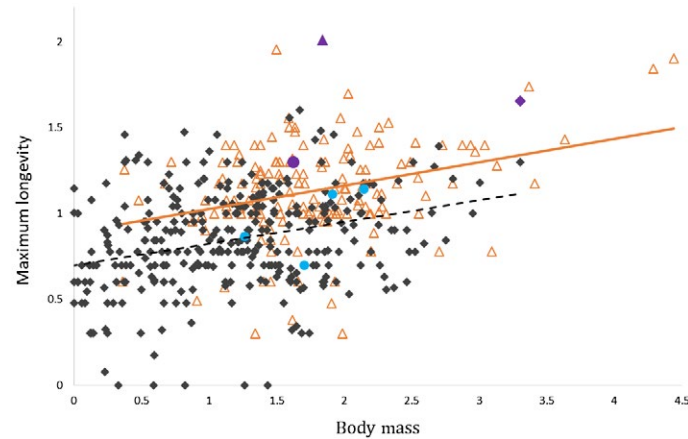


FIGURE 2 The relationship between maximum longevity (in years, \log_{10} transformed) and body mass (in grams, \log_{10} transformed) in the three orders of amphibians: Anura (black filled diamonds and dashed line), Urodela (orange triangles and continuous line) and Gymnophiona (light blue filled circles and no trend line). The longest living species of each order (Anura: *Pyxicephalus adspersus*; Urodela: *Proteus anguinus*; and Gymnophiona: *Geotrypetes seraphini*) in our dataset are indicated in purple

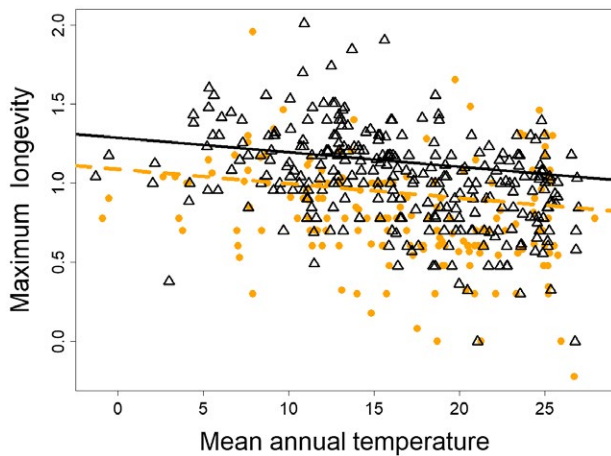


FIGURE 3 The relationship between maximum longevity (in years, \log_{10} transformed), annual temperature (average in degrees Celsius). Diurnal species ($n = 170$) are depicted with orange filled circles (dashed line) and nocturnal species ($n = 303$) with black open triangles (continuous line)

for arboreal species; $p = .129$ for fossorial species; $p = .664$ for species with more than one microhabitat). Surprisingly, for species sampled in the wild ($n = 257$) only, we did not find any effect of toxicity on longevity ($p = .09$). Sample size was positively correlated with longevity (slope = $.041 \pm .013$; $p = .002$). We found marginally significant interactions between captivity and chemical protection ($p = .04$) and annual temperature ($p = .02$). This model explained 28% of the variation in longevity, with body size explaining the largest part of the overall variance in longevity ($\lambda = .46$, 17.0%; Table 2).

Results obtained from the dataset based on species with more than five specimens (285 species) were very similar. The only qualitative difference was that sample size (slope = $-.023 \pm .025$, $p = .37$)

was not correlated with longevity. Moreover, all interactions were non-significant for all predictors ($p > .05$). Body size is the factor explaining most (21.1%) of the variance in longevity in this dataset (see Supporting Information Appendix S3 Table A9).

We found a negative relationship between longevity and temperature (slope: $-.009 \pm .003$, $p = .005$, $n = 101$ species) when analysing only the species for which we had exact coordinates of the location at which longevity was estimated (see Supporting Information Appendix S3 Tables A4 and A5).

Analysed separately, the minimal adequate model for the Anura (367 species) was similar to that of amphibians as a whole. Mean annual temperature was negatively correlated with longevity. Nocturnal anurans, those using poison and those for which data originated from captive specimens had life spans longer, on average, by 30.3, 30.0 and 10.1%, respectively, than diurnal species, non-chemically protected ones and those for which data were from the wild. Microhabitat was not correlated with longevity (all contrasts above $p < .005$). For species studied in the wild, toxic species did not live longer than their non-toxic counterparts ($p = .34$). Sample size was not correlated with longevity according to our analysis (slope = $.029 \pm .017$; $p = .10$). There was one significant two-way interaction between chemical protection and captivity ($p = .002$). This model explains 33% of the variation in anuran longevity (see Table 3; Supporting Information Appendix S3 Table A2 for the full model), with captivity explaining the largest part (11.4%). The best model for the anuran dataset of well-sampled species ($n > 5$ individuals) resembled that for anurans as a whole, but chemical protection ($p = .09$; $n = 63$) and sample size (slope = $-.034 \pm .030$; $p = .26$) were unrelated to longevity. Moreover, there was no interaction between chemical protection and captivity; instead, there was an interaction between activity period and mean annual temperature. Temperature appears to affect nocturnal species more strongly than it does diurnal ones (i.e., the slope is steeper). Captivity explained the largest part of

TABLE 2 The minimal adequate model for the analysis of all amphibian species

Factor	Estimate \pm 1 SE	t	p	Partial R ²
Intercept	0.891 \pm 0.105	8.4	< .0001	NA
Body mass	0.127 \pm 0.021	6.0	< .0001	10.3%
Chemically protected	0.103 \pm 0.029	3.5	.0002	0.1%
Activity period	0.143 \pm 0.027	5.2	< .0001	6.0%
Origin of data	-0.119 \pm 0.026	-4.4	< .0001	0.1%
Annual temperature	-0.009 \pm 0.002	-4.0	.0001	9.6%
Sample size	0.041 \pm 0.013	3.3	.002	1.7%

Note. Estimates for body mass, annual temperature and sample size are slopes; estimates for origin of longevity data (wild or captivity), activity period and chemical protection are intercepts. The first row is the intercept for diurnal non-chemically protected species that were sampled in captivity. For species measured in the wild, those that use poison for protection against predators and those that are active during the daytime, the differences between intercepts are calculated by adding the estimate value in the corresponding row to this value (0.891). The *t* and *p*-values for these categories refer to differences from diurnal species living in captivity and chemically protected, respectively. Partial R² is the contribution of each variable for explaining the variance in longevity. Model parameters $\lambda = 0.458$, $R^2 = 0.28$, $n = 387$, $p < .0001$.

TABLE 3 The minimal adequate model for anuran species

Factor	Estimate \pm 1 SE	t	p	Partial R ²
Intercept	0.921 \pm 0.086	10.6	< .0001	NA
Body mass	0.117 \pm 0.024	4.7	< .0001	9.5%
Chemically protected	0.131 \pm 0.037	3.4	.0005	9.3%
Activity period	0.129 \pm 0.032	4.0	< .0001	6.1%
Origin of data	-0.173 \pm 0.034	-5.1	< .0001	11.4%
Annual temperature	-0.010 \pm 0.002	-3.7	.0003	9.0%
Sample size	0.029 \pm 0.017	1.6	.103	2.9%
Origin of data (wild) * Chemically protected	-0.184 \pm 0.060	-3.0	.0025	5.2%

Note. Estimates for body mass, annual temperature and sample size are slopes. Estimates for origin of longevity data (wild or captivity), activity period and chemical protection are intercepts. The first row is the intercept for diurnal non-chemically protected species that were sampled in captivity. For species measured in the wild, those that use poison for protection against predators and those that are active during the daytime, the differences between intercepts is calculated by adding the estimate value in the corresponding row to this value (0.921). The *t* and *p*-values for these categories refer to differences from diurnal species living in captivity and chemically protected, respectively. Partial R² is the contribution of each variable for explaining the variance in longevity. Model parameters $\lambda = 0.403$, $R^2 = 0.33$, $n = 256$, $p < .0001$.

the variance in longevity (24.5%) in this dataset (see Supporting Information Appendix S3 Table A10).

In the Urodela ($n = 155$), the minimal adequate model contained only body size, activity period and sample size. Body size was positively correlated with longevity. Nocturnal species live longer than diurnal ones by 73.7% on average. Moreover, sample size was positively correlated with longevity (slope = .061 \pm .021, $p = .002$). This model explains 27% of the variation in urodelan longevity. Chemical protection ($p = .229$), annual temperature ($p = .427$), microhabitat ($p = .784$ for aquatic species; $p = .155$ for fossorial species and $p = .231$ for species with more than one microhabitat) and the origin of longevity data ($p = .458$) were not correlated with longevity. Activity period explained more (c. 14.5%) of the variance in longevity than body size and sample size (see Table 4; Supporting Information Appendix S3 Table A3 for the full model). The best model for well-sampled urodelans ($n = 76$) had a phylogenetic signal of zero. Similar to the full Urodela model, nocturnal species lived longer. However, sample size (slope = -.041 \pm .046; $p = .53$) was not

related to longevity, nor was chemical protection ($p = .113$; $n = 70$) or captivity ($p = .20$; $n = 75$). Annual temperature (slope = -.018 \pm .007; $p = .01$) and body size (slope = -.078 \pm .048; $p = .04$) had marginally significant effects. The only (marginally) significant interaction was between annual temperature and activity period (see Supporting Information Appendix S3 Table A8 and A11).

Comparing longevity data from animals held in captivity and those in the wild, of the 140 species for which we had data from both sources, captive species were observed to live longer by 17% (2.4 \pm 0.78 years) than their wild counterparts (paired *t*-test, $t = 3.15$, $p = .002$; see Supporting Information Appendix S4).

4 | DISCUSSION

Our findings indicate that large, captive amphibians, those that live in cold regions, those that use poison as a defence against predators and those that are active at night live longer. This is consistent with

TABLE 4 The minimal adequate model for dataset representing only Urodela species

Factor	Estimate \pm 1 SE	t	p	Partial R^2
Intercept	0.641 \pm 0.081	7.9	< .0001	NA
Body mass	.141 \pm .033	4.2	< .0001	12.5%
Activity period	0.240 \pm 0.053	4.5	< .0001	14.5%
Sample Size	.061 \pm .021	3.3	.002	4.2%

Note. Estimates for body mass and sample size are slopes. The first row is the intercept for diurnal amphibian species. For species active at night, the difference between intercepts is calculated by adding the estimate value in the corresponding row (0.240) to this value (0.641). The t and p-values for these categories refer to differences from diurnal species. Partial R^2 is the contribution of each variable for explaining the variance in longevity. Model parameters $\lambda = 0.060$, $R^2 = 0.27$, $n = 132$, $p < .0001$.

the hypotheses based on classical evolutionary theories of senescence (Kirkwood, 1977; Medawar, 1952; Williams, 1957). However, non-terrestrial amphibians did not live longer than their terrestrial counterparts, and toxic species did not live longer than their non-toxic counterparts in the wild.

Body size is positively, but weakly, related to longevity across amphibians and within the large amphibian orders. Such a positive effect can be observed across all tetrapod groups (e.g., Austad & Fischer, 1991; Healy et al., 2014; Scharf et al., 2015). This general pattern probably derives from the trade-off between growth and reproduction; growing to a large size delays reproduction because development takes longer, and this selects for longer life (Scharf et al., 2015). The allometric slopes for Amphibia (.123), Anura (.130) and Urodela (.125) are below the predicted slope of .25 (Brown, Gillooly, Allen, Savage, & West, 2004; Lindstedt & Calder, 1981; Speakman, 2005). Furthermore, body size explained much less of the variance in amphibian longevity than for endotherms (7% for the full dataset versus > 60% in endotherms; de Magalhães et al., 2007). This is even less than the results obtained for squamates (Scharf et al., 2015: slope = .20, 16% of variance explained). Given that body size explains little of the variation in amphibian longevity, other factors are likely to have a stronger effect on amphibian longevity than on endotherm longevity. We suggest that factors such as ambient temperature can affect metabolic rates and activity periods of ectotherms, such as amphibians and reptiles, to a greater degree than they affect them in endotherms. Thus, temperature (and, potentially, solar radiation) is probably a stronger determinant for the longevity of amphibians and other ectotherms than for mammals and birds. Another potential reason for the lower explanatory power of body size is the relatively narrow range of variation in amphibian sizes (four orders of magnitude in our data: c. 0.2 g to c. 2 kg), compared with five to six orders of magnitude in birds, reptiles and, especially, mammals.

Mean annual temperature showed a negative effect on longevity in amphibians, as has been shown for other ectothermic groups, such as fish, crustaceans and squamates (Munch & Salinas, 2009; Scharf et al., 2015). This may be the result of a faster growth rate in warm regions, leading to a faster accumulation of harmful

metabolic by-products; and it has been linked to the rate-of-living theory and oxidative damage theory of ageing (Bryson, Vanfleteren, & Braeckman, 2007). Additionally, in colder environments amphibians are active for shorter periods during the year (Johnston & Dunn, 1987), thereby reducing their exposure to predation risk and food shortages (Turbill, Bieber, & Ruf, 2011). The slopes for Amphibia (-.009), Anura (-.010) and Urodela (not significantly different from zero) are shallower than the value of -.51 predicted by the metabolic theory of ecology (Brown et al., 2004; McCain & Sanders, 2010).

Amphibians use diverse mechanisms to reduce extrinsic mortality pressures (Blanco & Sherman, 2005; Sinsch & Dehling, 2017; Zhang & Lu, 2012). Most amphibians produce distasteful or toxic substances (Blanco & Sherman, 2005; Daly, 1995; Hossie, Hassall, Knee, & Sherratt, 2013). We have shown that using poison is related to a longer life span and interpret this as a consequence of reduced predation. Species using poison as a defence may reduce extrinsic mortality pressures (in the form of predation) and increase survival rates (Blanco & Sherman, 2005; Hossie et al., 2013). We note that we found an effect of using poison on longevity in the full dataset. However, anurans studied in the wild, and urodeles, did not show this relationship, perhaps because of low statistical power. The efficacy of poison in reducing predation varies both across the amphibians using them and across their potential predators (i.e., not all predators are equally affected by the same poisons). Thus, our dichotomous classification of species as being 'chemically protected' or 'non-chemically protected' is somewhat arbitrary (Blanco & Sherman, 2005). It may also be partly false, because we interpreted absence of evidence of toxicity as evidence of its absence, whereas it is reasonable to expect that some of the species that we classified as non-protected do, in fact, possess potent poisons. This, however, would make our analyses conservative, and thus we posit that the effect we found, despite these limitations, is likely to be real. Chemical protection, however, is only one of several potential anti-predatory mechanisms, which include crypsis, arboreality (Healy et al., 2014) etc., and it may well be that less poisonous species protect themselves from predation using other means. The inconsistent, marginally significant and counter-intuitive interactions between poison and captivity may also have resulted from toxicity not being studied as a quantitative trait.

We found that nocturnal species live longer than diurnal ones. This could result from low exposure of nocturnal species to harmful UV radiation (Sawada & Enesco, 1984), which may be particularly important in amphibians lacking integument protection (e.g., scales or feathers). Furthermore, the low night-time temperatures reduce metabolic rate and, in turn, reduce metabolic by-products and oxidative damage (Sohal, 1986). The main predators of amphibians, such as birds and fish (Wells, 2010), are mostly active by day (Pechmann & Semlitsch, 1986; Taylor, 1983), which may make nocturnality an efficient strategy for reducing predation (Healy et al., 2014; Holmes & Austad, 1994; Promislow & Harvey, 1990; Sih et al., 1992). Whatever the case may be, in all our analyses activity periods were consistently strong predictors of amphibian longevity.

Non-terrestrial species did not live longer than terrestrial ones. This result may suggest that living in different environments may not be a strong predictor of life spans for amphibian species.

Living in captivity seems to increase longevity, because predation is eliminated, climate is controlled and food is plentiful and may be near optimal (Blanco & Sherman, 2005). We found that species living in captivity have a longer life span than their wild conspecifics. A similar result was found across species. We conclude that controlling for the origin of data is extremely important when analysing longevity data across taxa.

Surprisingly, sample size was not correlated with longevity in some analyses (despite our use of less stringent criteria for including an effect of sample size). It appears that increasing sample size does not strongly increase the probability of finding older individuals, although it was significant in the full dataset. Interspecific variation across amphibian species might swamp the effects of sample size. In all cases, the effects of sample size were either non-existent or weak. Nonetheless, we urge controlling for sample size when analysing longevity data, because its effect is not negligible.

Our dataset provides the largest comparative study of amphibian longevity. It is, nonetheless, important to exercise some caution when interpreting the results of such a broad-scale endeavour. Longevity data, whether from captivity or from the wild, relate to individuals that were often still alive when their longevity was reported (or, in the case of skeletochronology, were prematurely killed for the analyses). Furthermore, data for some predictors were missing for some species, and thus models with different predictors were based on different subsections of the dataset. The large sample size, greater spatial scope and the broad taxonomic sampling, however, enabled us to reach generalities that would not have been feasible otherwise. We note, however, that the present study is correlative and thus can only suggest mechanisms but not experimentally support (or refute) them. Such experimental manipulations are, of course, unfeasible (and at times unethical) for such a large dataset and with longevity measured over the course of decades.

In conclusion, our results support the evolutionary senescence hypotheses that were proposed to explain the variation in longevity for different groups of vertebrates (Hamilton, 1966; Kirkwood, 1977; Kirkwood & Austad, 2000; Medawar, 1952). It is important to note that although some studies argue that if extrinsic mortality is not age specific (i.e., if survival probability is reduced equally across all ages) then extrinsic mortality agents will not drive the evolution of increasing life spans (Caswell, 2007; Chen & Maklakov, 2012). We have demonstrated relationships between maximum longevity of amphibians and both body size and annual temperature. Factors related to both extrinsic and intrinsic mortality (e.g., activity periods, captivity and chemical protection) have been shown to contribute to longevity in amphibians. Comparative studies on species-rich taxa have the potential to address and confront conceptually different theoretical approaches to the evolution of senescence and to open up many avenues for further research into the attributes that govern longevity in animals.

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DATA AVAILABILITY STATEMENT

All data used in the analyses and the associated metadata are available in Appendix S1.

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SUPPORTING INFORMATION

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APPENDIX 1. LONGEVITY DATA SOURCES

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