

Cold and isolated ectotherms: drivers of reptilian longevity

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Animal lifespan is determined by extrinsic and intrinsic factors causing mortality. According to the evolutionary theories of senescence, when mortality pressures are low, animals delay reproduction. This enables species to grow more slowly and, consequently, natural selection can act against harmful mutations in adulthood, thereby increasing lifespans. To test predictions of these theories we assembled a dataset on the maximum longevity and relevant ecological variables of 1320 reptilian species. Correcting for phylogeny, we modelled the link between reptile longevity and factors such as body size, microhabitat, activity period, insularity, annual temperature, temperature seasonality, elevation and clutch size that we hypothesized will affect extrinsic mortality rates and hence lifespan. Body mass explained a small proportion of the variance in reptile longevity. Species living on islands, and in colder and more seasonal environments, lived longer. Observed maximum longevity was positively associated with the number of individuals used to estimate it. Our results suggest that species exposed to reduced extrinsic and intrinsic mortality pressures (lower predation, lower metabolic rates and shorter activity periods) live longer. Sampling more individuals increases the chances of finding older specimens and should be corrected for when studying maximum longevity.

ADDITIONAL KEYWORDS: body size – comparative analysis – evolutionary theories of senescence – longevity – phylogeny – seasonal temperature.

INTRODUCTION

Most organisms die as a consequence of exposure to external factors such as diseases, parasitism, social interactions, famine, accidents or predation (Wachter & Finch, 1997). Those that escape such direct factors ultimately face death through intrinsic processes of senescence, such as spontaneous chemical reactions, replication errors and accumulation of metabolic waste products (Koopman *et al.*, 2015). Consequently, mortality has been attributed to either intrinsic or extrinsic causes (Sparkman *et al.*, 2007; Shattuck & Williams, 2010).

Senescence, a decline in fitness with age, can be explained by a decrease in the force of natural selection with age (Medawar, 1952; Williams, 1957; Kirkwood & Rose, 1991). Other theories consider ageing to be a

physiological process that evolved largely independently of ecological factors, pointing to an association between metabolism and progressive intrinsic deterioration of the body (Sohal & Allen, 1986; Finch, 1990).

Those evolutionary theories of senescence predict that members of populations exposed to high levels of extrinsic mortality will evolve short potential lifespans (Healy *et al.*, 2014; Valcu *et al.*, 2014). Because most individuals die from extrinsic causes, natural selection cannot act on reducing intrinsic causes of mortality, which otherwise lead to longer lifespans (Williams, 1957; Hamilton, 1966; Williams & Day, 2003; Williams *et al.*, 2006; Caswell, 2007). High extrinsic mortality rates select for early reproduction, placing organisms under additional stress, which can, in turn, increase intrinsic mortality (Quinlan, 2010). Interspecific and intraspecific comparisons have been used to test whether adaptations that presumably reduce the risk of intrinsic and extrinsic mortality are associated with longer lifespans (Valcu *et al.*, 2014).

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Most studies that focus on the relationship between longevity and the factors related to mortality have been conducted on birds and mammals (e.g. Lindstedt & Calder, 1981; Holmes & Austad, 1994; Wilkinson & South, 2002; Speakman, 2005; Turbill *et al.*, 2011; Healy *et al.*, 2014; Valcu *et al.*, 2014). Stark & Meiri (2018) found that factors such as the use of venom and nocturnality are associated with longer lifespans in amphibians. They ascribed this to reduced predation pressure (low extrinsic mortality rate). Scharf *et al.* (2015) analysed the lifespan records of 1014 squamate species, and consistent with the predictions of the evolutionary theory of senescence, their results suggest that factors such as herbivory, living in regions with low environmental productivity and living at higher latitudes result in longer lifespans, which they ascribed mostly to reduction in intrinsic mortality rates. Scharf *et al.* (2015), however, mostly concentrated on factors co-varying along a fast–slow life-history continuum (i.e. living on the slower side of the continuum results in longer lifespan, because of delayed reproduction), rather than examining the impact of mortality factors. Furthermore, when alluding to mortality factors they mostly examined the effects of intrinsic and not of extrinsic mortality factors (on which we focus here). Moreover, Scharf *et al.* (2015) did not examine either testudines (here signifying all chelonians) or crocodylians, while we include both orders, and use a larger and more comprehensive dataset for squamates as well.

Here we study the effects of factors thought to be related to extrinsic mortality rates on the longevity of reptiles from all orders. In accordance with the evolutionary theories of senescence (Medawar, 1952; Williams, 1957; Kirkwood & Rose, 1991), regarding the effects of environmental and life-history components on longevity, we concentrate on several key traits.

1. Microhabitat: we predict longevity to be highest for fossorial species, then for arboreal species and then for species of all other microhabitat uses (e.g. terrestrial, saxicolous, aquatic). This is because predation pressure (and hence lower extrinsic mortality) will be lower for arboreal, aquatic, especially, fossorial reptiles (Buffenstein & Jarvis, 2002; Shattuck & Williams, 2010; Byrnes & Spence, 2011; Healy *et al.*, 2014).
2. Activity period: nocturnal reptiles are less exposed to solar radiation, and experience lower temperatures than diurnal species, consequently reducing their metabolic rates. This, in turn, leads to lower intrinsic mortality rates (Sohal & Allen, 1986).
3. Ambient temperature: the metabolic rate of ectotherms is often low at low temperature (regions at high latitudes and altitudes: Sohal, 1986; Zhang & Lu, 2012). Thus, intrinsic mortality agents are suspected to operate more slowly in such regions. Moreover,

species living in colder, more seasonal areas experience short activity seasons, and are less exposed to predators during hibernation, reducing extrinsic mortality pressure and perhaps leading to longer lifespans (Turbill *et al.*, 2011; Meiri *et al.*, 2013).

4. Insularity: species living on islands often face few predator, competitor and/or pathogen species. They may thus be less exposed to extrinsic mortality pressures (Austad, 1993; Jordana *et al.*, 2012).
5. Defence mechanisms: venomous snakes and testudines (because of their shell) may experience lower predation pressure than other reptile species (Martín *et al.*, 2005; Fry *et al.*, 2006; Jansa & Voss, 2011; Mori *et al.*, 2012; Hossie *et al.*, 2013). Moreover, venomous snakes usually handle their prey less than non-venomous species (Downes, 2002), lowering the probability of injuries.
6. We predict that short-lived species will have larger clutch size, on average. Species suffering higher mortality pressures may invest more in reproduction, producing more offspring per reproductive event.

METHODS

DATA COLLECTION

We collected literature data on the maximum longevity of 1320 reptile species spanning all reptilian orders (and 67 of 87 families): Squamata (745 lizards including five amphisbaenid species and 353 snake species), Testudines (192 turtle and tortoise species), Crocodylia (all 24 crocodile species) and Sphenodontia (the tuatara, *Sphenodon punctatus*). This represents c. 12.3% of known reptile species diversity (currently 10 793 species: Uetz *et al.*, 2018). Data on the predictor variables were gathered from the same sources used to estimate longevity and, if not reported there, from the literature (see Supporting Information, Appendix S1).

Longevity data are the maximum lifespan (in years) reported for each species. Unfortunately, there are some drawbacks in using maximum values as estimates of longevity. For example, maxima may be unrepresentative of the species as a whole (Carey, 2003), or estimates could be based on unequal numbers of individuals for different species, whereas means are probably unbiased (Scharf *et al.*, 2015). Therefore, we recorded the sample sizes upon which longevity is estimated for each species to correct for these potential biases inherent in the use of maxima (i.e. maxima are expected to increase with sample size; Meiri, 2007). We further introduced a sensitivity analysis for the 531 species for which adequate sample sizes ($N \geq 30$) were reported (for other species, samples were smaller or data on sample sizes were not reported), and repeated

our analysis of the other predictors. We further analysed crocodiles, testudines and squamates separately, to determine whether this basic split of the reptile tree of life influences the traits affecting longevity.

We used data on maximum body masses of reptiles from [Slavenko *et al.* \(2016\)](#). Masses are based on maximum length data that were converted to mass via allometric equations for different reptile clades (mostly family-level equations, taking leg development data into account when this varied within a family; [Feldman & Meiri, 2013](#); [Feldman *et al.*, 2016](#)). Because we focus on maximum longevity, and reptiles usually grow throughout their lives, it is reasonable to expect that the oldest individuals will also be among the largest. Maxima are likewise the most common of size measures available for reptiles (e.g. [Meiri, 2008](#); [Slavenko *et al.*, 2016](#)). Mean sizes, in contrast, are more representative measures than maxima. We collected data on mean body size (length converted to mass as above). When multiple means were available from different sources of literature, we calculated the mean of the highest and lowest published means of males and females. We performed a sensitivity analysis using mean mass to test whether the use of maxima for mass biases our results on the relationship between body size and longevity. We use mass because it is a better size index than length, as it accounts for variation in shape ([Meiri, 2010](#); [Feldman & Meiri, 2014](#); [Feldman *et al.*, 2016](#)). Mass differs greatly between animals of similar length that are as different from each other as colubrid snakes and tortoises.

We classified species as diurnal, nocturnal or cathemeral. We categorized crepuscular species ($N < 15$) as diurnal, because they are exposed to high daytime temperatures and to solar radiation and thus presumably have high metabolic rates ([Buchanan, 1998](#); [Stark & Meiri, 2018](#)). We classified species as terrestrial, arboreal, fossorial (including semi-fossorial) or aquatic. Some species are active in more than one type of habitat (e.g. arboreal and terrestrial or saxicolous and fossorial), and we treat them as ‘variable’. For snakes, we collected data on the possession of venom, and classify snakes as either venomous, rear-fanged or non-venomous ([Blanco & Sherman, 2005](#); [Hossie *et al.*, 2013](#)).

We classified species into insular endemics or continental based on distribution data from [Roll *et al.* \(2017\)](#). We compared the longevity of mainland species to that of insular endemics across all islands, and also to species inhabiting only on islands smaller than 50 000 km², then 5000 km² and finally 1000 km². Mean annual temperatures and temperature seasonality were estimated for each species by intersecting the latitude and longitude of the location where longevity data (from the wild) were collected with a layer of mean annual temperature and temperature

seasonality within 30 arc seconds from [Fick & Hijmans \(2017\)](#) (WorldClim database). Such coordinates, however, were only available for 125 species. For the other species we averaged climatic data (WorldClim) across all the grid-cells they inhabit, according to ranges from [Roll *et al.* \(2017\)](#). We also collected data for the elevation range of 70% of the species in our dataset. We used the mid-point of the elevational range as another predictor (using either the minimum or the maximum elevation reached by a species yielded qualitatively identical results; data not shown).

For clutch or litter size we use species means from [Meiri \(2018\)](#) for lizards, [Itescu \(2012\)](#) for turtles, and [Feldman \(2015\)](#) for snakes. For crocodiles and *Sphenodon* we obtained the data from the same sources listing longevity ([Appendix S1](#)). If means were unavailable we used range midpoints (e.g. the average between the largest and smallest known clutches). Similarly, we use a midpoint of the largest and smallest mean if multiple means were reported.

We tested if longevity is affected by whether data were from captive or wild individuals. While captive specimens are not exposed to extrinsic mortality factors such as predation, we reason that their maximum longevity reflects a life-history strategy that evolved in response to selection pressures in the wild. Nonetheless, captive individuals may have higher longevity because they are not preyed upon, receive ample food, etc. To further examine this we directly compared species for which we had longevity data from both captive and wild individuals ($N = 352$) using a paired *t*-test. We further introduced a sensitivity analysis in which we only use species for which maximum longevity was recorded in the wild, and re-ran our model for all reptiles on this subset (227 species). In all other analyses we used the highest longevity datum for each species.

PHYLOGENETIC ANALYSES

We combined the most up-to-date and complete phylogenetic trees for each order. For squamates we used a 9574-species tree from [Tonini *et al.* \(2016\)](#). For testudines we used a 294-species tree from [Pereira *et al.* \(2017\)](#). We reconstructed a Bayesian inference multilocus tree of Crocodylia using BEAST v.1.8.4 ([Drummond *et al.*, 2012](#)), with sequences from four mitochondrial regions and nine nuclear loci obtained from [Oaks \(2011\)](#). Parameters and priors, as well as the resulting tree, are presented in [Appendix S2](#). We combined the trees, using the methods and R scripts outlined in [Roquet *et al.* \(2014\)](#).

We used the ‘caper’ package in R ([Orme *et al.*, 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](#)). We accounted for shared

ancestry using phylogenetic generalized least square (PGLS) tests, adjusting the strength of phylogenetic non-independence using the maximum likelihood value of the scaling parameter value λ (Pagel, 1999), implemented in the R package ‘caper’ (Orme *et al.*, 2013).

STATISTICAL ANALYSES

We \log_{10} -transformed data on maximum body mass, maximum longevity, clutch size and sample size to normalize residuals and reduce heteroscedasticity. We calculated variance inflation factors (VIFs) to determine whether multicollinearity between the predictor variables was present in the data. No predictor had a VIF higher than 2.5 and we thus maintain that our analyses are not biased by multicollinearity (O’Brien, 2007). We obtained data on the predictor variables for 70% (for elevation) to 100% (body size) of the species in our database. We conducted a phylogenetic ANCOVA test starting from a full model and using a backwards stepwise elimination procedure, sequentially deleting factors with P -values > 0.005 (Johnson, 2013; Benjamin *et al.*, 2018) until arriving at a minimum adequate model where all predictors were significant (at $\alpha < 0.005$).

We compared the allometric PGLS equations (slopes, intercepts) of longevity vs. body size between the three orders (excluding Sphenodontia) using t -tests. Finally, 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 RStudio (1.1.383, RStudio Inc., Boston, MA, USA).

RESULTS

Mean (\pm SE) longevity across all reptile orders we analysed was 17.1 ± 0.5 years, with maximum longevity ranging from 1 year (*Menetia greyii*, Pianka, 2011) to 186 years (*Aldabrachelys gigantea*, living in captivity on St. Helena Island, Castanet, 1994). Modal reptile longevity was 10 years (Fig. 1). For squamates species average maximum longevity was 12.6 ± 0.3 years (range: 1–69, $N = 1103$), for testudines 36.5 ± 2.3 years (range 3.3–186, $N = 192$) and for crocodylians 62.9 ± 4.1 years (range 21.1–100, $N = 24$); the tuatara can live at least 120 years.

Reptile longevity increases to the 0.19 power of mass (99.5% confidence interval = 0.161–0.218). The slope was steepest for lizards, but much shallower for the other taxa (Table 1). Crocodile longevity was not correlated with body size ($P = 0.140$). The interaction between the slopes was significant ($P = 0.001$), but pairwise differences were only significant for the difference between lizards and testudines ($P = 0.005$, Fig. 2). Overall, maximum body size explained just 4% (for testudines) to 23% (for lizards) of the variance in reptilian longevity. We obtained similar results when using mean ($N = 1297$ species) and maximum mass (1320 species) both among and within reptile clades (see Table A1 in Appendix S3.1). Analysis of species with large sample sizes showed similar values (Table A2 in Appendix S3.1).

Longevity decreased in warm regions (slope = -0.006 ± 0.002) and increased in seasonal regions (slope = 0.001 ± 0.001). Insular species ($N = 226$) lived, on average, 12.1% longer than mainland species ($N = 1092$). Insular species lived longer than mainland ones even when we examined only species endemic to islands smaller than 50 000, 5000 and 1000 km² (see Tables A3–A5 in Appendix 3.2). Values of maximum longevity were positively correlated with

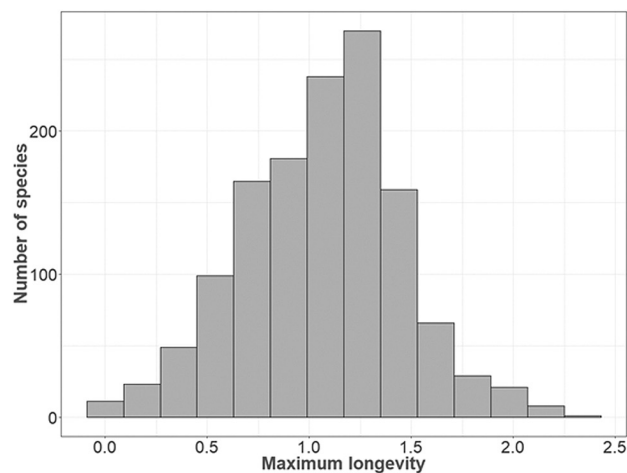
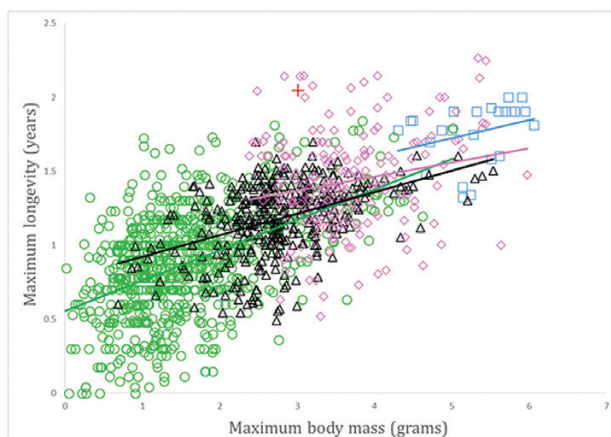


Figure 1. Distribution of the (\log_{10}) maximum longevity (in years) of the 1320 reptilian species.

Table 1. Longevity as a function of body mass for reptiles (phylogenetic analyses)

Confidence interval of slope	<i>P</i>	<i>N</i>	λ	Intercept \pm 1 SE	<i>t</i>	Slope \pm 1 SE	<i>R</i> ²	Group
0.161–0.218	< 0.0001	1305	0.800	0.739 \pm 0.182	14.6	0.190 \pm 0.013	0.14	Reptilia
0.241–0.298	< 0.0001	746	0.644	0.448 \pm 0.094	14.8	0.270 \pm 0.012	0.23	Lacertilia
0.074–0.131	< 0.0001	351	0.784	0.852 \pm 0.144	5.6	0.103 \pm 0.014	0.08	Serpentes
0.006–0.233	0.004	183	0.561	0.918 \pm 0.202	2.8	0.120 \pm 0.041	0.04	Testudines
–0.126 to 0.372	0.140	24	0.000	1.109 \pm 0.427	1.5	0.123 \pm 0.080	0.09	Crocodylia

**Figure 2.** The relationship between maximum longevity (log-transformed) and body mass (log-transformed) of the major reptilian groups for the complete dataset (*N* = 1320): Lacertilia (green circles), Serpentes (black triangles), Testudines (purple diamonds) and Crocodylia (blue squares). *Sphenodon punctatus* is marked by a red cross.

the number of specimens on which they were estimated (slope = 0.082 ± 0.007). While these results are in agreement with our hypotheses, other factors (microhabitat, activity period, clutch size, elevation and origin of data) were non-significantly associated with longevity ($P > 0.05$), contradicting our predictions. The best model explained 22% of the variation in longevity, with body size (partial $R^2 = 37.2\%$) explaining the largest part of the overall variance in longevity ($\lambda = 0.79$, $N = 1061$, see Table 2 for effect sizes and other statistics). For the full model see Table A3 in Appendix S3.3. The minimum adequate model for species with longevity data originating only from the wild ($N = 227$ species) was qualitatively similar to that for all species (i.e. it contained most of the same significant predictors with the same signs; see Appendix 3.4). Consequently, we only refer to models using the full dataset (1320 species) below.

Analysing those species with large samples (> 30 specimens per species, 531 species), we obtained somewhat similar results, with two exceptions: temperature seasonality ($P = 0.106$) and insularity ($P = 0.093$) were not associated with longevity. Body mass explained the

largest part (~45%) of the overall variance in longevity in this dataset (see Appendix S3.5).

The three reptile orders were characterized by different models. The models for squamates were very similar to the full reptilian model (i.e. most of the same factors were significant, with similar signs, see Table 3 for effect sizes and other statistics, and Table A4 in Appendix S3.3 for the full model), with one exception: mean annual temperature had a marginally significant effect on longevity ($P = 0.03$). The large sample size database for squamates (> 30 specimens per species, 424 species) was likewise qualitatively the same as that for all reptiles (see Appendix S3.5).

In testudines, the minimum adequate model revealed a negative relationship between longevity and mean annual temperature, and a positive relationship between longevity and sample size. In contrast to our predictions, however, we found that terrestrial testudines ($N = 43$ species) live, on average, 34.5% longer than aquatic testudines ($N = 117$). This model explained 37% of the variation in longevity, with mean annual temperature (15.8%) explaining the largest part (see Table 4 for effect sizes and other statistics,

Table 2. The minimal adequate model for the full reptile dataset and tree

Partial R^2 (%)	P	t	SE	Estimate	Factor
NA	< 0.0001	5.3	0.182	0.0982	Intercept
37.2	< 0.0001	9.3	0.013	0.124	Body mass (log grams)
1.3	0.0051	-2.7	0.002	-0.006	Mean annual temperature
1.3	0.0054	2.7	0.001	0.001	Temperature seasonality
2.1	0.001	3.2	0.026	0.083	Insularity
5.4	< 0.0001	10.7	0.007	0.082	Sample size (\log_{10})

Estimates for body mass, mean annual temperature, temperature seasonality and sample size are slopes, while the estimate for insularity is an intercept. The first row is the intercept for mainland species. For species living on islands the intercept is calculated by adding the estimate value in the corresponding row to this value (0.982). t and P values for insularity refer to differences from species living on the mainland. $R^2 = 0.22$, $N = 1061$, $\lambda = 0.798$, $P < 0.0001$.

Table 3. The minimal adequate model for Squamata only

Partial R^2 (%)	P	t	SE	Estimate	Factor
NA	< 0.0001	5.0	0.095	0.485	Intercept
31.0	< 0.0001	11.3	0.016	0.186	Body mass (log grams)
6.9	< 0.0001	5.3	0.003	0.002	Temperature seasonality
3.5	0.001	3.1	0.026	0.083	Insularity
9.1	< 0.0001	9.9	0.008	0.081	Sample size (log)

Estimates for body mass, mean annual temperature, temperature seasonality and sample size are slopes, while the estimate for insularity is an intercept. The first row is the intercept for terrestrial species living on the mainland. For species that feed in the water and living on islands the intercept is calculated by adding the estimate value in the corresponding row to this value (0.485). t and P values for insularity refer to differences from species living on the mainland. $R^2 = 0.25$, $N = 885$, $\lambda = 0.715$, $P < 0.0001$.

Table 4. The minimal adequate model for Testudines

Partial R^2 (%)	P	t	SE	Estimate	Factor
NA	< 0.0001	14.5	0.128	1.872	Intercept
8.3	0.0005	-3.5	0.056	-0.199	Microhabitat (aquatic)
12.1	< 0.0001	-4.8	0.005	-0.024	Mean annual temperature
5.1	0.004	2.6	0.094	0.250	Insularity
18.6	< 0.0001	4.9	0.020	0.101	Sample size (log)

Estimates for body mass, mean annual temperature and sample size are slopes, while estimates for microhabitat and insularity are intercepts. The first row is the intercept for terrestrial species living on the mainland. For species that feed in the water and living on islands the intercept is calculated by adding the estimate value in the corresponding row to this value (1.872). t and P values for microhabitat refer to differences from species feeding only on the ground. $R^2 = 0.35$, $N = 157$, $\lambda = 0.000$, $P < 0.0001$.

and [Table A5](#) in [Appendix S3.3](#) for the full model). Insular testudine species live longer, on average, than their mainland counterparts (17.7% longer lifespan; corrected for size). The phylogenetic signal was zero in this particular analysis, and seasonality ($P = 0.984$) did not affect longevity as it did for Squamata and for reptiles in general. The large sample size database for testudines resulted in a qualitatively similar model (see [Appendix S3.5](#)), with two exception: terrestrial testudines live longer than aquatic ones, but this result is not very strong ($P = 0.02$). Sample size was uncorrelated with longevity ($P = 0.159$). For crocodylians,

the phylogenetic signal was likewise zero and no predictors were significantly associated with longevity ($P > 0.05$ for all predictors), but note that sample size was much smaller (all 24 extant species). We found the same (negative) results in the large sample-size dataset ($N = 10$ species) of crocodylians. For a summary of all results for all reptile groups see [Appendix S3.6](#).

Snake longevity was not associated with possessing venom ($\lambda = 0.769$, $N = 347$, $P = 0.02$ for the contrast between non-venomous and rear-fanged species, and $P = 0.78$ for non-venomous vs. fully venomous species). Interestingly, when we tested (using PGLS) the

differences in longevity between testudines and other reptile groups, we did not find differences. A non-phylogenetic analysis (corrected for sample size) revealed that small testudines species live longer than other reptile species, but the difference diminishes with increasing sizes, and are reversed for reptiles >63 kg ($R^2 = 0.490$, $N = 1077$, $P = 0.003$). For effect sizes and other statistics see [Appendix 3.7](#).

A paired *t*-test revealed no intraspecific differences in longevity between captive and wild individuals ($N = 352$ species; average longevity in the wild: 20.8 ± 1.2 years, in captivity: 20.8 ± 1.1 years, $t = 0.01$, $P = 0.99$, see [Appendix S3.8](#)).

DISCUSSION

Our comparative analysis of lifespans of 1320 species across all reptilian orders supports some predictions derived from the evolutionary theories of senescence, but for others, the results are contradicting or equivocal. Reptile longevity is enhanced for large species, those living on islands, and those exposed to lower ambient and highly seasonal temperatures. Other factors, however, such as activity period, venomousness or captivity did not affect longevity either in reptiles in general or within any order.

Across most of our models, body size was positively correlated with lifespan (except for the low-power crocodile models), consistent with previous studies (e.g. [Austad & Fischer, 1991](#); [Healy *et al.*, 2014](#); [Scharf *et al.*, 2015](#); [Holm *et al.*, 2016](#); [Stark & Meiri, 2018](#)). Large species have a slower metabolism, which translates to slower growth ([Speakman, 2005](#)). This is associated with a reduction in the rate of accumulation of metabolic by-products and oxidative damage ([Sohal, 1986](#)). Consequently, large size can result in lower exposure to extrinsic mortality factors.

Body mass, however, explained little of the variance in reptile longevity ($R^2 = 14\%$). This may be because ectotherms are less affected by metabolic by-products because of their lower metabolic rates ([Bronikowski & Vleck, 2010](#)). Additionally, strong effects of temperature on ectotherms may mean that size has less variation to affect, but we did not find such a strong thermal signal in our analyses.

For a given increase in body mass, the lifespans of testudines species (slope: 0.11 ± 0.03) increase slowly. Small-bodied testudines thus live much longer than similar-sized squamates, but the differences diminish with increasing size, and are reversed for the largest squamates (> 63 kg). This is probably due to the shell playing a highly beneficial role in reducing predation on small testudines, but it may be less effective, and more costly to carry and maintain, at larger sizes. Thus, a

~600-g *Chrysemys dorsalis* turtle can live to 20.6 years compared to the similar-sized (575-g) *Leiolepis guttata* lizard that reaches 13 years (examples chosen from species close to their respective regression lines). Larger testudines, however, seem to have a similar lifespan to other large reptiles (although admittedly such large sizes are rare in squamates). This is despite the fact that some of the largest testudines are herbivorous, insular, land tortoises ([Itescu *et al.*, 2014](#)); these are additional factors that could promote longevity.

The relationships among the ecological variables we examined and lifespan differed among and within reptilian clades. Temperature was negatively related to reptilian longevity, a pattern that was shown in other ectothermic invertebrate and vertebrate groups such as crustaceans, gastropods, fish and amphibians ([Munch & Salinas, 2009](#); [Stark & Meiri, 2018](#)). Furthermore, lifespan is longer in more seasonal regions. This may be the result of a faster growth rate in climatically stable regions, leading to a faster accumulation of harmful metabolic by-products. Such a relationship has been linked to the rate-of-living theory, which posits that lifespan is dependent upon the exhaustion of a fixed quantity of a vital substance at a rate proportional to the metabolic rate ([Sohal, 1986](#)). A similar link is predicted in the oxidative damage theory of ageing, which posits that animals that produce more free radicals suffer more molecular damage, which in turn should lead to short lives ([Bryson *et al.*, 2007](#)). Additionally, in colder, more seasonal environments reptiles are active for shorter periods of the year ([Johnston & Dunn, 1987](#); [Meiri *et al.*, 2013](#)), thereby reducing their predation risk and risk of food shortages ([Turbill *et al.*, 2011](#)).

The longer lifespans of insular reptilian species support a model suggesting slower life-history traits on islands (often called 'island syndrome'; [Adler & Levins, 1994](#); [Grant, 1998](#); [Novosolov *et al.*, 2013](#)). Higher longevity on islands can be the result of lower exposure to fewer predator species and pathogens, which may result in lower extrinsic mortality ([Jordana *et al.*, 2012](#)).

Sample size was positively correlated with longevity in most of our analyses. It appears that increasing sample size strongly increases the probability of finding older individuals. We urge that sample size be controlled for in future comparative analyses of maximum longevity.

It seems the different microhabitats influenced longevity in testudines, but not in other reptile groups. Consequently, we suggest that the different microhabitats do not help reduce predation rates (lower extrinsic mortality). Surprisingly, however, even fossorial species, which we reasoned must enjoy relaxed predation pressures ([Williams & Shattuck, 2015](#)), did not have longer lifespans. Thus, either this assumption

is incorrect (e.g. if species are frequently preyed upon in the short periods they spend above ground, or even hunted below ground) as shown for mammals (when corrected for phylogeny and sociality; Healy *et al.*, 2014), or the metabolic costs associated with burrowing can cancel out the advantages of lower predation pressures. Activity period was likewise not related to lifespan in reptile species, refuting our initial prediction. It may be that high daytime temperatures in the regions inhabited by nocturnal reptiles (Vidan *et al.*, 2017) may increase their metabolic rates when they are not active, and that solar radiation is of little effect. Alternatively (but less parsimoniously), increased predation rates at night (Daly *et al.*, 1992) may offset lower metabolic rates and solar radiation experienced by nocturnal species. It may even be that cellular repair mechanisms are less efficient at the lower temperatures at which nocturnal reptiles operate. We have no direct data on predation rates, radiation effects or the efficacy of cellular repair mechanisms to allow us to test any of these hypotheses.

Interestingly, and in contradiction to the results of both Scharf *et al.* (2015) for squamates and for Stark & Meiri (2018) for amphibians, captivity did not influence the recorded longevity within species. We cannot easily explain this discrepancy. We tentatively suggest that factors such as stress, poor keeping conditions and disease may cause premature deaths in captivity, offsetting the positive effects of reducing predation and hunger (Robinson *et al.*, 2015).

We expected short-lived species to produce more offspring per clutch in order to maintain long-term persistence of the species. However (and in contradiction to the results of Scharf *et al.*, 2015), this expectation was not met by our results. We suggest that by analysing a more diverse assemblage of reptiles together, multiple reproductive strategies mask such a relationship.

The use/possession of venom did not help to decrease extrinsic mortality in snakes. Hossie *et al.* (2013) showed a similar pattern to ours with a smaller sample ($N = 102$). This may suggest that producing venom is costly (McCue, 2006; Smith *et al.*, 2014), negating beneficial effects of reduced predation. Alternatively, predators may suffer from the same misconceptions that many humans have, and may be unable to distinguish between potentially venomous and non-venomous snakes. Moreover, it may be that by mimicking the warning colours of venomous snakes some non-venomous species can avoid predators such as birds (Brodie & Janzen, 1995), which will help to reduce extrinsic mortality, and hence species that do not possess venom may evolve longer lifespans. Finally, venom, basically a mechanism used to obtain prey, may simply not be an effective mechanism to deter potential predators.

Our dataset enabled us to perform the largest (albeit still only ~12% of known reptilian diversity) comparative study of ectotherm longevity carried out to date. The large sample size, great spatial scope and the broad taxonomic sampling enabled us to observe patterns that would not have been feasible with small-scale studies. This type of study, however, can only suggest mechanisms based on correlations and not experimentally support (or refute) them. Experimental manipulations are not feasible at this scale, or with lifespans that can span decades. It is, of course, unethical to perform such manipulations, even if they had been possible. Thus, comparative methods may be the best way of conducting such studies (e.g. Wilkinson & South, 2002; Magalhães *et al.*, 2007; Healy *et al.*, 2014; Valcu *et al.*, 2014). The low explanatory power we achieve, however, could reflect issues with underlying data (see discussion in Scharf *et al.*, 2015), or with the nature and coarseness of our predictor variables.

In conclusion, some of our results support the evolutionary hypotheses of senescence that were proposed to explain the variation in longevity for different animal species (Medawar, 1952; Hamilton, 1966; Kirkwood, 1977; Kirkwood and Austad, 2000). Large size, insularity, low temperatures and high seasonality all promote reptile longevity. Some factors related to both extrinsic and intrinsic mortality rates, such as use of venom for defense and activity period, however, emerged as not affecting longevity in reptiles. We think that obtaining more direct measures of extrinsic mortality generators may prove illuminating regarding the merit of the evolutionary theory of senescence in reptiles and in ectotherms in general.

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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

Additional Supporting Information may be found in the online version of this article at the publisher's web-site.

Appendix S1. Longevity database.

Table S1.2. Longevity references.

Appendix S2. Crocodylia tree reconstruction.

Appendix S3. Full models and sensitivity analysis results.

Appendix S3.1. Body size and longevity.

Appendix S3.2. Island area.

Appendix S3.3. Full models.

Appendix S3.4. Models with data from wild individuals only.

Appendix S3.5. Well-sampled analysis – Minimum Adequate Model (MAM).

Appendix S3.6. Summary of results.

Appendix S3.7. Models for snakes and turtles.

Appendix S3.8. Origin of data - *t*-test.