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RESEARCH PAPER

Late bloomers and baby boomers: ecological drivers of longevity in squamates and the tuatara

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ABSTRACT

Aim Longevity is an important life-history trait, directly linked to the core attributes of fitness (reproduction and survival), yet large-scale comparative studies quantifying its implications for the ecology and life history of ectotherms are scarce. We tested the allometry of longevity in squamates and the tuatara, and determined how longevity is related to key environmental characteristics and life-history traits. Predictions based on life-history theory are expected to hold true for ectotherms, similarly to mammals and birds.

Location World-wide.

Methods We assembled from the literature a dataset of the maximum longevities of more than a thousand squamate species, representing *c.* 10% of their known species diversity, their phylogenetic relationships and multiple life-history and ecological variables. Correcting for phylogeny, we modelled the link between squamate longevity and both key life-history traits, such as body mass and age at first reproduction, and important environmental factors, such as latitude and primary productivity within species distributional ranges.

Results Large-bodied species live for longer than small ones, but body size explains far less of the variance in longevity than it does in mammals and birds. Accounting for body size, squamate brood frequency is negatively correlated with longevity, while age at first reproduction is positively correlated with longevity. This points to a continuum of slow-to-fast life-history strategies. Squamates in high latitudes and cold regions live for longer, probably because a shorter season of activity translates to slower development, older age at first reproduction and hence to increased longevity. Individuals live longer in captivity than in the wild. Herbivorous and omnivorous squamates live for longer than carnivorous ones. We postulate that low-quality nutrition reduces growth rates, promotes a relative decline in reproductive rates and thus prolongs life.

Main conclusions Our results support key predictions from life-history theory and suggest that reproducing more slowly and at older ages, being herbivorous and, plausibly, lowering metabolism, result in increased longevity.

Keywords
Body size, fast-slow continuum, lifespan, NPP, phylogenetic comparisons, reproduction, reptiles, temperature, trade-off.

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Table 1 Summary of predictions for the link between different intrinsic and extrinsic variables and lepidosaur longevity. For more detailed explanation, please see the text.

Variable	Prediction	Justification
Body size	+	Growing to a large size postpones reproduction
Latitude	+	Rate of life (metabolism), hibernation
NPP	–	Rate of life, postponing reproduction
Data origin	Captive > wild	Abundant food, veterinary treatment, no predators
Age at first reproduction	+	Many arguments, e.g. the mutation accumulation theory
Mode of reproduction	Viviparous > oviparous	Rate of life and reproduction intensity
Body temperature	–	Rate of life
Diet	Herbivores > carnivores	Predation risk, metabolic rate
Activity time	Nocturnal > diurnal	Rate of life, predation risk

'+' and '–' stand for a positive and a negative correlation, respectively.

their diet. This would lead, according to the ageing theory, to reduced longevity of carnivores (Hughes & Reynolds, 2005; Williams *et al.*, 2006).

We analyse the interplay between longevity in lepidosaurs (Lepidosauria, Haeckel, 1866: a clade including Rhynchocephalia and Squamata, i.e. the tuatara, snakes, amphisbaenians and lizards) and other life-history traits, in light of the theories of ageing explained above, testing seven predictions (Table 1). (1) we predict a positive relationship between lepidosaur longevity and both body mass and age at first reproduction. It takes larger species longer to start reproducing, and hence ageing should start at a later stage than for smaller species. (2) we predict longevity to be positively correlated with latitude, and negatively correlated with mean annual temperature. High temperature should lead to a high metabolic rates, and thus to a fast rate of living that could shorten life (Sohal, 1986). The opposite holds true in cold environments where animals often hibernate. High temperature can also lead to faster growth in ectotherms and to a smaller adult size ('the temperature–size rule'; Kingsolver & Huey, 2008), and consequently to shorter life span.

(3) we predict that lepidosaurs in regions of low NPP require more time to reach maturity. Resource scarcity could also lead to slower metabolic rates, to longer development times and to the postponement of reproduction in favour of growth and somatic maintenance; this combination should result in longer life. (4) following Meiri *et al.* (2013), we predict a negative relationship between longevity and body temperature. This also leads us to predict that nocturnal species live for longer than similar-sized diurnal species. Both lower body temperature and nocturnal activity time may lead to a longer life span, owing to a slower rate of living, expressed in slower activity, metabolism, growth and reproduction. (5) we expect a negative correlation between longevity and reproduction intensity (number of broods per year and clutch or litter size), based on the predicted trade-off between reproduction and longevity, either due to pleiotropic effects or to accumulation of harmful mutations. (6) viviparous lepidosaurs are expected to mature later, to have slow reproduction and hence to live longer than oviparous species and species having multiple, small offspring. While oviparous females can have multiple clutches, viviparous females are often limited to a single litter or less each season (Shine, 2005; Meiri *et al.*, 2012). (7) we test for a link between lizard diet (carnivorous, herbivorous and omnivorous) and longevity. While all snakes are carnivorous, lizards have diverse diets; most species are carnivorous, but some are omnivorous or herbivorous (Pough, 1973). Similar to Wasser & Sherman (2010), we expect higher longevity in herbivorous lizards after correcting for size, because they may develop more slowly, leading to delayed reproduction, and have reduced extrinsic mortality, because of the lower risks involved in foraging.

METHODS

Data collection

We assembled a dataset on the maximum longevity of 1014 species (672 lizards, 336 snakes, five amphisbaenids and the tuatara, *Sphenodon punctatus*), belonging to 50 of the 67 lepidosaur families currently recognized world-wide (taxonomy follows Uetz, 2014). Data are from the literature, supplemented by data on animals born or kept at the Meier Segals Garden for Zoological Research, and now residing in the Steinhardt Museum of Natural History, Tel Aviv University (Tables S1–S3 in Supporting Information). Longevity data are the maximum age (in years) reported for each species. For captive animals that were caught as adults, we calculated longevity by adding the minimum age at first reproduction to those data. For example, Montanucci (1983) reported that an adult *Phrynosoma douglasii* was kept for 5.25 years in captivity; as the species takes 2 years to reach adulthood we used a conservative longevity value of 7.25 years. In some cases, reported life spans are shorter than the time other sources report it takes a species to reach maturity [e.g., Carey & Judge (2000) report the longevity of *Cyclura pinguis* as 3.2 years, whereas Iverson *et al.* (2004) report that this species takes 4–9 years to reach sexual maturity]. We omitted such cases from the dataset.

For each species, we collected literature data on body size, earliest age at first reproduction, field body temperature of

twice, once with the dated Pyron & Burbrink (2014) 897-species tree and once with the inclusive (1014 species) tree, for which we did not have data on branch lengths. Because the results of the two sets of analyses are, for the most part, qualitatively similar, we focus on the outcome of the analysis of the dated tree, and discuss the results obtained with the 1014-species tree only when they are qualitatively different.

In all statistical tests 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.*, 2012). Pagel's λ represents the magnitude of the phylogenetic signal in the data or, for regression models, the model residuals, and ranges between zero (no signal) and one (a signal consistent with Brownian motion).

Statistical analysis

We $\log_{10}$ transformed data on body mass, longevity, age at first reproduction, clutch or litter size, the number of broods per year and NPP in order to normalize residuals and reduce heteroscedasticity. All statistical tests were performed using R 2.15.2 (R Development Core Team, 2013).

To test for a link between body mass and longevity we regressed longevity on body mass. To investigate the interclade differences we repeated this test (longevity versus mass, not corrected for phylogeny) for seven lepidosaur clades: Acrodontia, Anguimorpha, Gekkota, Iguania, Laterata, Scincomorpha and Serpentes (snakes). Amphisbaenia, Scolecophidia and Rhynchocephalia were not included in these analyses because of the small sample size (Table 2). We used a phylogenetic ANCOVA to test for differences between clades in the relationship between mass and longevity. We did not test for mean annual temperature as it was tightly correlated with latitude ($R^2 = 0.70$), and latitude explained more of the variance in longevity. We had data on the mass, diet, mode of reproduction, latitude and NPP of all species. For activity time we lacked data for four species: *Eryx tataricus*, *Myrrophis chinensis*, *Lygophis anomalus* and *Sphaerodactylus pimienta*. To be able to use these species in our multivariate models we classify the first two as nocturnal and the latter two as diurnal, based on the behaviour of closely related species. For 31 species we cannot tell whether longevity data are from captive specimens or relate to longevity in the wild. Because data from captive individuals are much more common (818 species versus 165 from the wild in the rest of the dataset), and because data from the wild are usually well flagged as such, we arbitrarily ascribe the origin of the data for these 31 species as derived from captive individuals. Analyses omitting these species give qualitatively similar results (not shown).

We first conduct ANCOVA to test which of these seven variables [mass, latitude, NPP, captivity versus nature, diet, activity time and mode of reproduction (with two levels, oviparous versus viviparous; species with mixed reproductive strategies were assigned to the predominant mode, e.g. viviparity for *Zootoca vivipara*)] are related to longevity, using a backwards stepwise elimination procedure (based on *P*-values at $\alpha = 0.05$). We then examine the other variables (clutch size, hatchling/neonate size, number of broods per year, age at first reproduction, and body temperature) by adding them to the minimum adequate model of the previous step, one at a time (because the database for each comprises a different subset of species).

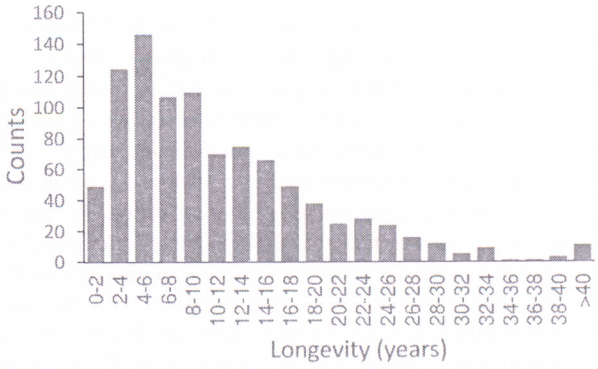


Figure 1 Frequency distribution of the maximum longevity of the 1014 species in the dataset.

RESULTS

The frequency distribution of lepidosaur longevities is depicted in Fig. 1. The lepidosaur clades differ significantly ($F_{9,1003} = 17.0$, $P < 0.0001$) in the intercept and slopes of their body mass versus longevity (Table 2). Although the slope is always positive, the clades can be divided into two groups: low slopes from 0.11 to 0.14 (Amphisbaenia, Anguimorpha, Laterata and Serpentes) and high slopes from 0.26 to 0.31 (Acrodontia, Scincomorpha, Iguania and Gekkota; Table 2). The scaling exponent between longevity and body mass for all lepidosaurs is 0.202 ± 0.009 (95% CI = 0.185–0.219).

We found that mass, latitude, NPP, data source (captivity versus wild) and diet are related to longevity, whereas activity time ($P = 0.22$) and mode of reproduction ($P = 0.12$) are not. Larger lepidosaurs and those inhabiting higher latitudes and regions with low NPP live for longer (Table 3), in accordance with our first three hypotheses. Omnivorous lepidosaurs live for *c.* 20% longer than carnivorous ones (corrected for the other six factors), and herbivorous lepidosaurs live for *c.* 20% longer than omnivores (Table 3). Finally, longevity is longer in captive individuals than in those studied in the wild by *c.* 13% (species for which we do not know whether records are from captivity or from the wild live even longer than captives, but are considered captive in all subsequent analyses). This five-predictor model explains 23.2% of the variation in longevity ($\lambda = 0.69$, $n = 897$; Table 3).

Hatchling size and age at first reproduction are positively correlated with longevity when added to the five-predictor model (Table 4). Clutch size and the number of broods per year were negatively correlated with longevity when added to this

Table 5 The minimum adequate model for the full 1014-species dataset and tree.

	Slope/ intercept	SE	*t*	*P*
Body mass	0.204	0.014	14.8	< 0.0001
Latitude	0.007	0.001	7.9	< 0.0001
Carnivorous species, captive	0.412	0.082	5.1	< 0.0001
Carnivorous species, in the wild*	0.371	0.024	−1.7	0.084
Herbivorous species†	0.590	0.049	3.7	0.0002
Omnivorous species†	0.506	0.025	3.8	0.0001

$n = 1014$ species, $\lambda = 0.461$, $R^2 = 0.247$.
Body mass and latitude estimate are slopes, all other are intercepts.
*SE, *t* and *P*-values are for difference from captive individuals.
†SE, *t* and *P*-values are for difference from carnivorous species; intercept is for captive individuals.

versus longevity trade-off is a common life-history feature which has been mainly measured within species (e.g. Seigel *et al.*, 1987; Stearns, 1992; Scharf *et al.*, 2013). Tinkle (1969), however, showed an interspecific trade-off between total offspring number per season and annual survivorship of 18 lizard species, explaining that reproduction entails some risk which affects survivorship.

Ectotherm development and body size are strongly influenced by temperature ('the temperature-size rule'; e.g. Kingsolver & Huey, 2008). Longevity is often shorter in warmer conditions, a phenomenon usually studied intraspecifically under controlled conditions (e.g. Valenzano *et al.*, 2006). The reason could be faster growth rate, leading to faster accumulation of harmful metabolic by-products and also earlier reproduction. Recent studies have differentiated between the habitat temperature and the actual body temperature of lizards (Meiri *et al.*, 2013), and the latter may have a higher impact on ectotherm survival (Conti, 2008). Latitude explains more of the variance in longevity than annual temperatures because it is correlated with additional climate components, such as precipitation, day length and season length. It has already been suggested that lizards at higher altitudes and latitudes live longer (e.g. Tomašević-Kolarov *et al.*, 2010). The latitude–longevity link may not be solely and directly related to temperature but to season length, and to lepidosaurs being inactive during longer periods of the year (e.g. Arribas & Galan, 2005). Inactivity is helpful in cold seasons when food supply is insufficient to support physiological body maintenance. Metabolism is further lowered on cold nights when animals are not foraging even during the active season when days are hot, reducing predation risk and intrinsic drivers of ageing. All these factors result in delayed growth and hence delayed reproduction, and longer life. The same factors may drive the correlation between NPP and longevity: animals having access to plenty of food would require a shorter development time and could start reproducing earlier, leading to reduced longevity. In spite of the statistical significance, NPP explained little of the variance in longevity. Moreover, the link between NPP and longevity disappeared when using the inclusive tree, requiring further caution with respect to this result.

Herbivores live for longer than carnivores of a similar size. Ingestion of a protein-rich diet (meat) may lead to faster growth, earlier and more intense reproduction and hence to shortened longevity (i.e. a faster life). This explanation was evoked by Fisher *et al.* (2001) while interpreting their results that herbivorous marsupials live for longer, have smaller litters and grow slowly. This pattern, however, is not supported by studies on birds. While it is difficult to evaluate the quality of food, African granivorous birds had shorter lives than insectivorous and nectarivorous birds consuming food with a lower fat content (Peach *et al.*, 2001). It is tempting to suggest a connection between poor nutrition and longevity through caloric restriction. The latter is a well-known factor, extending longevity in various organisms (e.g. Mair & Dillin, 2008). Although we have only indirect support for that, we see it as a fruitful direction for future research. Notably, in some species, no dietary effect on survival has been detected (e.g. bats; Wilkinson & South, 2002).

The longevity of lepidosaurs is greater in captivity, where predators are absent, food is in excess, veterinary care is available, movement is reduced and few risks are present (Mason, 2010). This is, however, not always the case, because the conditions required for animals in captivity are not always met.

Our dataset provides the first large-scale comparative study of longevity in ectotherms. However, a few words of caution are in order. We used the maximum known longevity for each species. Maxima are problematic because they are often based on very few individuals, usually kept in captivity, and they imply little about ageing processes. Furthermore, maxima are extremely sensitive to sample size, and we often found that a new literature source more than doubled a previous maximum estimate of a species' longevity. This is not easy to account for, as sample sizes are not recorded for most species [see Valcu *et al.* (2014) for an attempt to correct maximum longevity for how many times a species is mentioned in scientific publications as a proxy for how well known it is]. Most field guides and reptile care books simply state that members of a species can live to a certain age (e.g. Brown, 2012). Other reports are often anecdotal, for example for a marked specimen to have been found after a certain time (e.g. Bringsøe, 1998) without reference to the number of individuals originally marked; or a compilation will only state the age of a living or a dead individual (e.g. Slavens & Slavens, 1999). Such large compilations often cite one another, but little attention seems to be paid to obvious problems (such as maximum longevities apparently below the age at first reproduction). While we avoided such blatant errors here, undoubtedly some poor-quality data still remain.

Some of the data, both from captivity and from the wild, relate to individuals that were still alive when their longevity was reported (studies based on skeletochronology usually obtain longevity estimates from dead individuals). The often low quality of the data may explain why we only found a weak relationship between longevity and some factors that are often

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