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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INTRODUCTION

Longevity in animals is a highly variable trait, influenced by 'intrinsic' and 'extrinsic' environmental factors. There are three common intrinsic explanations for animal longevity.

1. The mutation accumulation theory suggests that the strength of natural selection decreases with age, because most reproduction occurs when animals are young. Thus, ageing is not under strong natural selection because the animal has already completed most of its reproduction (Hughes & Reynolds, 2005).

2. The antagonistic pleiotropy theory states that some genes encode phenotypes that are beneficial early in life but encode other traits that are harmful in advanced age (Ljubuncic & Reznick, 2009).

3. The 'rate of living theory', postulates that metabolic rate is negatively correlated with longevity because animals with high metabolic rates accumulate harmful metabolic by-products faster than those with lower metabolic rates (Sohal, 1986; Wilkinson & South, 2002; but see Møller, 2008, for an opposite reasoning).

All theories of ageing emphasize the trade-off between somatic maintenance and reproduction (often termed 'the disposable soma theory'; Kirkwood, 2001; Ljubuncic & Reznick, 2009), leading to a negative correlation between reproductive investment and longevity.

The most important environmental component affecting longevity is extrinsic mortality caused by various ecological pressures such as predation, famine and parasites (Healy et al., 2014; Valcu et al., 2014). Such extrinsic mortality is expected to lead to reproduction at an early age, and here intrinsic causes of ageing come into play. Animals reproducing early are exposed to the accumulation of age-specific harmful mutations or mutations with a pleiotropic effect, benefiting young animals but harming older ones (Stearns, 1992; Partridge & Gems, 2006). Mutations that are expressed late in life will mostly escape selection in animals that reproduce at a young age, but will be strongly selected against in animals that reproduce at older ages. Empirical evidence for faster ageing in populations suffering from a high predation threat compared with species/populations enjoying a low threat is mixed (summarized in Williams et al., 2006; but see also Valcu et al., 2014). Differences also exist in the specific process of senescence: while most species show either a gradual or abrupt decrease in performance with age, some appear not to age, such as some hydras and sea urchins (Kirkwood, 2001; Ebert, 2008).

A number of interspecific studies of birds and mammals have observed prolonged longevity with increasing body size (e.g. Lindstedt & Calder, 1976, 1981; Wilkinson & South, 2002; Speakman, 2005a; Healy et al., 2014; Valcu et al., 2014). Correcting for body mass, different key traits, such as age at first reproduction and level of sociality, also correlate with longevity (e.g. Prothero, 1993; Wasser & Sherman, 2010). In general, early, frequent and/or intensive reproduction is associated with decreased longevity (e.g. Kirkwood, 2001). Such life-history trade-offs have been termed the 'fast–slow continuum' (e.g. Bielby et al., 2007; de Magalhães et al., 2007).

There has been much experimental work on the longevity of several invertebrate species in order to study theories of ageing and the cost of reproduction (e.g. the reproduction–longevity trade-off; Kirkwood, 2001; Flatt, 2011; Scharf et al., 2013). Comparative interspecific studies of ectotherm longevity, however, are very rare (but see, e.g., Hutchings & Morris, 1985). In reptiles, comparative studies that include longevity do exist, but they are limited to a few, closely related species (e.g. Werner et al., 1993; Bauwens & Díaz-Uriarte, 1997; Bronikowski, 2008). Therefore there is a strong need to test whether large groups of ectotherms follow the same trade-offs described for the insect model organisms, and whether the emerging patterns resemble those of other vertebrates. In addition, the 'fast–slow continuum' could be particularly interesting with respect to reptile ecology, as reptile lineages show fundamental differences in their mode of reproduction, i.e. viviparity and oviparity, with differential investment in the offspring (Shine, 2005), clutch or litter size (e.g. Seigel & Fitch, 1984; Kratochvíl & Kubička, 2007) and the frequency of laying clutches (e.g. Andrews & Rand, 1974; Meiri et al., 2012). Such differences in life history are predicted to be correlated with longevity.

Climate and environmental gradients are known to affect the life history of ectotherms (Shine, 2005) and could, therefore, be an important factor linked to reptile longevity. At higher latitudes, reptile activity seasons are shorter, probably bringing about slower growth, older age at maturation and increased longevity, as suggested for some squamate species (Blouin-Demers et al., 2002; Arribas, 2004; Tomašević-Kolarov et al., 2010). Conversely, animals at higher latitudes, especially those with a complex life cycle, sometimes 'hurry up' to complete their development before winter arrives (e.g. Gotthard et al., 1999). Furthermore, higher latitudes are associated with cooler temperatures and, consequently, a slower rate of living, as shown for various animals such as fish and flies (Valenzano et al., 2006; Conti, 2008). In cold areas animals often hibernate. During hibernation predation is minimal and metabolism is much reduced, lowering mutation rates and oxidative damage. Both extrinsic and intrinsic mortality are therefore reduced in cold and high-latitude regions, which could lead to prolonged life spans.

Net primary productivity (hereafter NPP) could influence longevity, since animals in regions of low NPP may be more food-restricted. Therefore, they are likely to grow more slowly and, consequently, mature later and live for longer. Diet may also affect longevity through differences in the nutritive value of the food or the danger in obtaining it. Wilkinson & South (2002) suggested that predatory bats should have shorter lives than bats feeding on fruits or nectar, but failed to demonstrate such an association. In contrast, evidence for differences in longevity between granivorous, frugivorous and insectivorous birds is mixed. Examining hundreds of bird species, Wasser & Sherman (2010) demonstrated that herbivorous birds live for longer than their omnivorous and carnivorous counterparts. They reasoned that herbivorous birds have a lower extrinsic mortality than carnivorous ones. The latter may also become injured while pursuing prey and are more likely to acquire parasites through

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

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.

'+' 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

Table 2 Longevity as a function of body mass for the different lepidosaur clades (non-phylogenetic analyses). The effects of mass ($F_{1,996} = 500.9$), infraorder ($F_{9,996} = 17.42$) and their interaction ($F_{7,996} = 4.55$) are all significant ($P < 0.0001$ for all).

Clade	n	Longevity (mean; range)	R^2	Slope ± 1 SE	t	P	λ	Intercept ± 1 SE
Acrodontia	93	7.6; 0.5–33	0.224	0.236 ± 0.046	5.1	< 0.0001	0.548	0.373 ± 0.130
Amphisbaenia	5	10.7; 1.8–16	0.050	0.110 ± 0.277	0.4	0.717	0	0.744 ± 0.481
Anguimorpha	48	15.9; 2.5–62	0.195	0.161 ± 0.048	3.3	0.002	0.234	0.656 ± 0.153
Gekkota	171	9.3; 1.1–50	0.142	0.254 ± 0.048	5.3	< 0.0001	0.514	0.606 ± 0.109
Iguania	113	9.7; 1–60	0.355	0.327 ± 0.042	7.81	< 0.0001	0.278	0.187 ± 0.102
Laterata	95	7.6; 0.9–28	0.224	0.222 ± 0.045	4.9	< 0.0001	0.363	0.443 ± 0.110
Rhynchocephalia	1	91	–	–	–	–	–	–
Sauria	672	9.4; 0.5–62	0.22	0.257 ± 0.019	13.8	< 0.0001	0.628	0.443 ± 0.114
Scincimorpha	152	9.6; 1.25–44	0.076	0.318 ± 0.041	7.8	< 0.0001	0.624	0.357 ± 0.121
Serpentes	336	15.8; 3.4–47.5	0.073	0.097 ± 0.019	5.1	< 0.0001	0.409	0.840 ± 0.080

active individuals, reproductive mode (viviparous versus oviparous), clutch or litter size and brood frequency, diet (herbivorous, omnivorous or carnivorous) and activity time (diurnal, nocturnal or cathemeral; see Table 2 for sample sizes and Tables S1–S3 for data and references). We further recorded whether data were from captive or wild individuals. While animals in captivity usually get better access to food and medical treatment, the specific requirements of each species are sometimes difficult to fulfil (Mason, 2010). Furthermore, many records of captive animals, but fewer records of animals in the wild, are based on animals that were still alive at the time data were collected (e.g. many species in Slavens & Slavens 1999); the *Heloderma suspectum* specimens at the Meier Segals Garden for Zoological Research, Tel Aviv University is, likewise, still alive and well, at the age of at least 40).

Body size data for lizards are based on maximum snout–vent length (SVL, in mm) of individual species, because this is the commonest measure of lizard size reported in the literature. For snakes, body size is mainly based on maximum total length (TL, in mm). We converted body lengths to masses using clade-specific allometric relationships from Meiri (2010) (for lizards and amphisbaenians) and Feldman & Meiri (2013) (for snakes). Body masses better reflect the true size of animals than body length when examined over animals with highly different shapes, such as lizards and snakes. We updated these equations for some clades as required by taxonomic changes, or when better data became available. Thus, we used equations developed by Pincheira-Donoso *et al.* (2011) for *Liolaemus* and *Phymaturus*, Novosolov *et al.* (2013) for Gekkonidae *sensu stricto*, Sphaerodactylidae, Eublepharidae and *Anolis*, and Meiri *et al.* (2013) for limbed Anguidae. For the gekkotan clades Carphodactylidae, Diplodactylidae and Phyllodactylidae, for the Tropiduridae (*sensu stricto*) (Uetz, 2014) and for the snake clades Colubridae (*sensu stricto*) Dipsadidae, Natricidae, Pythonidae and Typhlopidae, we developed new allometric equations (Tables S4–S6).

Age at first reproduction can vary considerably across individuals, depending on a number of factors such as the climatic conditions within a species' range or the time in the year an individual hatched (i.e. whether an individual hatched from an early or a late clutch). We thus use the average age at first reproduction. For clutch or litter size and brood frequency we use species means, if available, or midpoints (e.g. the average between the largest and smallest known clutches) if means are not reported. Similarly, we use a midpoint of the largest and smallest mean if multiple means were reported. Diet is treated as a trichotomy with carnivorous lepidosaurs defined as those that do not take a substantial amount of plants (i.e. only occasionally and irregularly feed on plant material, or take < 10% of plants in the diet, if quantitative data are available). Species feeding mainly on plant material (> 50% of the diet) are treated as herbivorous and those between the two extremes (10–50% plants in the diet) are considered omnivorous. Some lizards shift their diet from carnivory to herbivory during ontogeny (see, e.g., Pough, 1973). However, because most of these species are large and long lived, we think that the adult diet, as used here, is most representative of their diet.

We mapped the global distribution of each species using published maps and locality data, museum records and expert-drawn maps (see http://www.gardinitiative.org/index.html). For each species we determined the latitudinal range centroid in ArcGIS10 (ESRI, 2013) and used the absolute value of latitude. For the calculation of environmental parameters we intersected species maps with average mean annual temperature within 0.16° × 0.16° grid cells from Hijmans *et al.* (2005), and recorded the average temperature of the species range. In a similar fashion, we intersected species ranges with NPP data (in g C m⁻² year⁻¹) from Imhoff *et al.* (2004).

Phylogenetic analyses

For the phylogenetic comparative analyses we mainly relied on the recently published and dated phylogeny of over 4000 lepidosaur species by Pyron & Burbrink (2014) which has 897 of the 1014 species in our dataset. We repeated all analyses for all 1014 species by adding the other 117 species to this tree, according to phylogenetic data available in other works, or according to taxonomic affiliation (Tables S1 & S3). We repeated each test

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
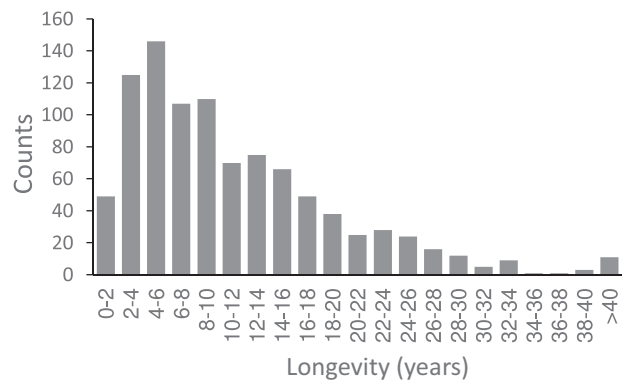

Figure 1 Frequency distribution of the maximum longevity of the 1014 species in the dataset.

Zootoca vivipara)] are related to longevity, using a backwards stepwise elimination procedure (based on *P*-values at α = 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).

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 ($λ = 0.69$, $n = 897$; 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

model, but adding body temperature to the model revealed no correlation between temperature and longevity (Table 4).

Analysing the full 1014-species dataset, we obtain qualitatively very similar results (i.e. the same factors were significant, with the same sign; Table 5), with two main differences: (1) NPP and data type were dropped from the full model (i.e. only mass, diet and latitude were retained); (2) in addition to the effects of age at first reproduction, the number of broods per year, clutch size and hatchling/neonate size, body temperature had a significant, negative relationship with longevity ($n = 437$, slope -0.005 ± 0.002, $t = -2.1$, $P = 0.033$, $\lambda = 0.423$, $R^2 = 0.379$). Interestingly, when adding the life-history factors to this model, data origin (wild or captive) regained significance (with captive specimens living longer) in all models (Table 5).

DISCUSSION

Our comparative study, including more than a thousand species across all major lepidosaur groups (except dibamid lizards), supports central predictions derived from the evolutionary theory of ageing (Hughes & Reynolds, 2005). Our results suggest that lepidosaur species exhibit a spectrum of life-history strategies, bounded by two extremes of fast and slow growth and reproduction rates. We found that long-living lepidosaurs are generally characterized by 'slow' life-history traits: delayed and infrequent reproduction, smaller clutches, larger hatchlings and colder body temperatures. As expected, the environment has a strong impact on longevity, and lepidosaurs at higher latitudes, and perhaps in less productive regions, live longer. Captive individuals live for longer than individuals in the wild, plausibly because of the absence of predators and the availability of veterinary care.

As predicted by theory, larger lepidosaur species live for longer. This logical pattern derives from the trade-off between growth and reproduction: growing to a large size delays reproduction because development takes longer, and it selects for longer life. Similar patterns have long been known for mammals and birds (e.g. Austad & Fischer, 1991; Healy *et al.*, 2014). Our results fit the expectation for a scaling exponent between longevity and body mass of 0.15 to 0.33 (calculated for mammals and birds; e.g. Speakman, 2005a). Nevertheless, we demonstrate large differences among clades, with gekkotans and iguanians having steeper slopes, and anguimorphs, snakes and members of the Laterata (lacertids, teiids, gymnophthalmids) having relatively shallow slopes. Furthermore, the generally accepted slope of 0.25 lies above the confidence interval exhibited by all lepidosaurs.

It is accepted that ageing is caused by the accumulation of free radicals and oxidants, both by-products of metabolism (Barja, 2004; Buttemer *et al.*, 2010). Yet the exact mechanism leading larger animals to live longer remains unclear, as many physiological traits correlate with body size (discussed in Speakman, 2005b). Body mass alone explained much less of the variance in lepidosaur longevity than in birds and mammals (e.g. 14 and 16% using the partial and full dataset versus over 60% in endotherms; de Magalhães *et al.*, 2007). Because mass explains little variation other life-history, environmental and clade-specific traits are likely to have a stronger effect on lepidosaur longevity than on endotherm longevity. We suggest that body temperatures of both active and inactive lepidosaurs, through their effects on metabolic rates, could also be major determinants of reptile longevity (see below).

Several components of fecundity were correlated with longevity. High investment in reproduction, expressed in frequent, large clutches is correlated with short life. The reproduction

Table 3 The basic model, with the five variables included in all analyses [body mass, latitude, net primary productivity (NPP), captive/wild and diet].

Factor	Estimate	SE	t	P
Intercept (carnivorous species, in captivity)	1.209	0.333	3.6	0.0003
In the wild	−0.058	0.024	−2.4	0.019
Diet (herbivorous species)	0.166	0.056	3.0	0.003
Diet (omnivorous species)	0.083	0.026	3.1	0.002
Body mass	0.198	0.015	13.4	< 0.0001
Latitude	0.005	0.001	5.3	< 0.0001
NPP	−0.060	0.026	−2.3	0.021

Estimates for body mass, latitude and NPP are slopes; estimates for diet and captive/wild individuals are intercepts. The first row is the intercept for carnivorous species in captivity. For species measured in the wild, for herbivores and for omnivores the intercept is calculated by adding the estimate value in the corresponding row. t and P-values for these categories refer to differences from specimens measured in captivity, and from carnivorous species.

Table 4 The relationship between longevity and life history factors, when these are added independently to a model containing diet, status (captive/wild), body mass, latitude and NPP.

Factor	Slope ± 1 SE	t	P	n	R^2 with factor	R^2 without factor	λ
Hatchling size	0.171 ± 0.033	5.3	< 0.0001	714	0.291	0.241	0.61
Age at first reproduction	0.479 ± 0.049	9.8	< 0.0001	378	0.540	0.390	0.46
No. of yearly broods	−0.172 ± 0.053	3.3	0.001	512	0.333	0.311	0.57
Clutch size	−0.139 ± 0.041	3.4	0.0007	849	0.254	0.241	0.71
Body temperature	−0.004 ± 0.003	1.5	0.128	402	0.379	0.357	0.42

	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, λ = 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 off-spring 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

assumed to affect it. The relatively low amount of variance explained by body size, and the often substantial differences found between closely related species, may, in part, be an artefact of often poor data quality. That said, maximum longevity is the commonest metric of longevity in comparative studies (Prothero, 1993; Wilkinson & South, 2002; de Magalhães *et al.*, 2007; Valcu *et al.*, 2014; Healy *et al.*, 2014, among others). The strengths of this study are its large scope and broad taxonomic sampling. The sources of error in such macroecological studies tend to average out (Brown, 1995). Nevertheless, as with other comparative studies (see discussion in Scharf & Meiri, 2013), we can only suggest a mechanism but not experimentally support it.

In summary, our results support fundamental predictions of life-history theory by showing a link between age at first reproduction, rate of reproduction and longevity. Moreover, environmental variables, related to season length and availability of food, are suggested to delay reproduction and increase longevity, in accord with our expectations. Body temperature and mean latitude of the distributional range are independently correlated with longevity (they are only loosely intercorrelated; Meiri *et al.*, 2013), and animals in captivity live for longer than wild ones. We also found a difference in longevity between herbivorous and carnivorous lepidosaurs with respect to reproductive age: herbivorous lepidosaurs probably consume poorer food, hence reach maturity later and thus live longer. Future experiments could test this by feeding a set of lepidosaur species with different diets and exploring the consequences for growth and time to maturity. This study presents for the first time longevity patterns of a large dataset of ectotherms and opens many avenues for further research on the attributes that govern longevity in ectotherms.

ACKNOWLEDGEMENTS

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Additional references to data sources used in this study can be found in Tables S2, S3 & S7.

SUPPORTING INFORMATION

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

Table S1 Data for all species included in the analysis.
Table S2 References for longevity data.
Table S3 References for the phylogenetic tree.
Table S4 Mass equations and methods.
Table S5 Lizard data for the mass equations.
Table S6 Snake data for the mass equations.
Table S7 References for the mass equations.

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