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Effects of Climate and Latitude on Age at Maturity and Longevity of Lizards Studied by Skeletochronology

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Synopsis Longevity and age at maturity are key life-history traits, directly linked to fitness attributes such as survival and reproductive output. It has been proposed that these traits are strongly influenced by environmental factors, such as temperature, seasonality, and precipitations, which determine the existence of a continuum of life-histories that goes from the “slow” life histories characterized by late maturity and high longevity of cold and highly seasonal climates to the “fast” life histories characterized by early maturity and low longevity, typical of the tropical climates. However, large-scale studies that address these topics in lizards are scarce and most of them are based on heterogeneous data, which may overlook the real patterns. Using skeletochronology, we studied age at maturity and longevity of two species of *Phymaturus* lizards, *Phymaturus aguanegra* from the Andes and *Phymaturus zapalensis* from the Patagonian steppe (Argentina). Then, we confronted longevity and age at maturity in these species with published skeletochronology-based data on 46 other lizard species to examine possible association of these life-history traits with latitude and mean annual temperature, thermal amplitude, and precipitations. Both *Phymaturus* species showed late sexual maturity (7 and 8–9 years, respectively) and high longevity (16 and 14–15 years, respectively) in coincidence with the other species of the genus studied up to date. The phylogenetic comparative analysis revealed that the most important variable in the determination of longevity patterns in the species studied was latitude: at higher latitudes lizards tend to live longer. In contrast, age at sexual maturity was dependent on mean annual temperature most, especially in males, as lizards from hotter climates mature earlier than lizards from cold sites.

Introduction

Environmental gradients of temperature, thermal amplitude (TA), precipitation, and photoperiod are known to affect many life-history traits of ectotherms (Shine 2005) such as longevity and age at sexual maturity (ASM). Specifically, temperature has a great influence over physiological performance (Huey and Stevenson 1979; Pinch and Claussen 2003; Angilletta 2006; among others) and, consequently, growth rates (Zug et al. 2001), age and size at sexual maturity (Adolph and Porter 1996; Niewiarowski 2001), reproductive frequency (Olsson and Shine 1999; Iburgüengoytía and Casalins 2007), and the number and size of offspring (Winkler et al. 2002; Shine 2005; Angilletta 2009). However, in cold-climate species which undergo long periods of brumation, activity times also become of paramount importance in the determination of life-history traits (Adolph and Porter 1993; Sears

and Angilletta 2004; Horváthová et al. 2013). For example, at high latitudes, lizards' activity seasons are short, and populations characterized by slow growth, late sexual maturity, and high longevity (Piantoni et al. 2006; Kubisch et al. 2012). Furthermore, high latitudes are associated with cool environmental temperatures and, consequently, a slow pace-of-life, as shown for diverse ectotherms such as fishes and flies (Valenzano et al. 2006; Conti 2008). Besides, other climatic factors such as precipitations can also affect indirectly life-history traits through their effects over food availability (Dunham et al. 1988).

The ASM is one of the most important life-history traits because it is correlated with fitness and it is usually more sensitive to natural selection than any other life-history trait (Stearns 2000). Life-history theory predicts that late sexual maturity at a greater size is favored by an increase in fecundity or survival

of offspring (Roff 1992; Kozłowski et al. 2004; Arendt 2011). This is a common pattern in lizards inhabiting cold climates, as low environmental temperatures reduce the metabolic rate, retarding growth, and age at maturity (Andreone and Guarino 2003). Ecological factors such as predation pressure can also affect age at maturity (Scharf et al. 2015), and in environments with high predation pressures it is expected that natural selection would favor the early reproduction at lower ages in order to avoid mortality before procreation.

Longevity is a highly variable trait, influenced by intrinsic and extrinsic factors (Scharf et al. 2015). Among the intrinsic factors, the most important are the accumulation of mutations (Hughes and Reynolds 2005), the pleiotropic genes that encode phenotypes that are beneficial early in life but encode other traits that are harmful later in life (Ljubuncic and Reznick 2009), and the generation of harmful metabolic by-products (Sohal 1986; Wilkinson and South 2002). However, the effects of these intrinsic factors in species that experience indeterminate growth like reptiles have been questioned with the findings of the existence of negative senescence, which states that mortality rate declines with age in adult individuals (Vaupel et al. 2004), in some lizards species (Tinkle and Ballinger 1972; Tinkle et al. 1993; Heulin et al. 1997), posing more importance to extrinsic factors in the determination of longevity patterns. The most influential extrinsic factor on longevity is mortality, either caused by predation, starvation, and/or parasites and diseases (Healy et al. 2014; Valcu et al. 2014). Mortality associated with predation and competition would be lower at high latitudes, since it has been demonstrated that biotic interactions such as predation and competition are significantly reduced at high latitudes (Schemske et al. 2009). Also, at high latitudes, seasonality is strong, shortening the annual activity times which has been shown to have positive effects on survival rate (Adolph and Porter 1993). Moreover, in highly seasonal climates lizards hibernate and during this period metabolism decreases significantly, reducing mutation rates and oxidative damage. Hence, both intrinsic and extrinsic mortality are reduced in cold regions and high latitudes, which would lead to prolonged life cycles (Scharf et al. 2015).

In order to describe the life-history of a species, it is essential to estimate two pivotal life-history traits—ASM and longevity. In this sense, skeletochronology is a reliable and robust histological technique for the determination of individual ages in reptiles and amphibians (Castanet 1994; Smirina 1994). Lizards, in particular, are the most studied

group as they have a simple bone structure with low vascularization [except for large varanids that exhibit bone vascular canals (De Buffrénil et al. 2008)] in addition to low intracortical remodeling and infrequent supplementary marks (Castanet 1994). Specifically, lizards from cold-temperate regions are better study models than those inhabiting the tropics, since their growth rings are more evident as a result of the reduction in metabolic activity produced by the low temperatures during cold seasons (Castanet et al. 1993).

In this study, we present original age and growth data of two species of *Phymaturus* lizards (Liolaemidae) from high altitudes in the central Andes (*Phymaturus aguanegra* from the *palluma* phylogenetic group) and high latitudes in the Patagonian steppe (*Phymaturus zapalensis* from the *patagonicus* phylogenetic group) of Argentina. *Phymaturus* is a genus of viviparous, saxicolous, and predominantly herbivorous lizards which includes species that live along a latitudinal and altitudinal gradient in the Andes and Patagonia of Argentina and central Chile (Ceï 1986; Debandi et al. 2012; Morando et al. 2013). The species studied up to date present slow life histories characterized by high ASMs (6–9 years old) and medium to high longevities (12–20 years old; Piantoni et al. 2006; Boretto et al. 2015, 2018; Cabezas-Cartes et al. 2015), which suggest that, among lizards, liolaemids present extraordinary high longevities and ASMs in relation to their body size. The results obtained for these *Phymaturus* species are integrated with data of wild populations of 46 lizard species, also studied by skeletochronology, in order to discuss the influence of environmental conditions in two pivotal life-history traits such as ASM and longevity, and compare these life-history traits between liolaemids and others saurians.

Materials and methods

Age and growth of *P. aguanegra* and *P. zapalensis*

Specimens

For the present study we used museum specimens of the herpetological collection of the Department of Zoology at the Centro Regional Universitario Bariloche (CRUB), Universidad Nacional del Comahue. Specifically, we analyzed 2 offspring, 14 juveniles, 11 adult females, and 11 adult males of *P. aguanegra* collected during the activity season (November–April) in 2005, 2006, and 2007 in the locality of Agua Negra (30°23'S, 69°34'W; 2900 m asl), Iglesia Department, San Juan province, Argentina; and 2 offspring, 12 juveniles, 17 adult

females, and 12 adult males of *P. zapalensis* collected during the activity season (September–March) in 2004, 2005, and 2007 in rocky outcrops near Laguna Blanca National Park (39°04'S, 70°22'W; 824–1312 m asl), Zapala Department, Neuquén province, Argentina.

Environmental characteristics of sampling sites

Phymaturus aguanegra's habitat is included within the Altoandina phytogeographic region, characterized by cold and dry climates with a mean annual temperature between 8 and 12°C, and year-round frosts (Cabrera 1994). It is an arid-semiarid region that presents valleys with rocky slopes and low vegetation cover, composed mainly by xerophilous grasses, annual plants, and cushion plants (Cabrera 1994). Specifically, Agua Negra locality is characterized by a remarkable glacial activity and rocky landslides in spring and summer, resulting in a dynamic and unstable mountain ecosystem (Aguado 1983).

The habitat of *P. zapalensis* is located within the Patagonian phytogeographic region, characterized by a landscape of low-elevation mountains, plateaus, and plains. The area presents a cold-temperate and sub-humid climate, with strong winds from the west (especially in summer), snow in winter, and temperatures below 0°C most of the year (Cabrera 1976). The mean temperatures range from 22°C in summer (with maximum temperatures higher than 40°C) and 5°C in winter (with minimum temperatures as low as –20°C). Annual precipitations are concentrated in winter and vary between 150 and 200 mm (Ramilo et al. 1993). The vegetation of the area corresponds to the Payunia district of the Patagonian Phytogeographic province (Cabrera 1978; Movia et al. 1982) and is characterized by a low and spiny shrub steppe.

Size, body mass, and reproductive data of the specimens studied

Data on snout–vent length (SVL, digital gauge ± 0.02 mm, CA-01, Lee Tools, Guangzhou, Guangdong, China), sex, and body mass (100 g spring scale ± 0.5 g; Pesola AG, Baar, Switzerland) of each specimen were registered before euthanasia. Size Dimorphism Index (SDI) was estimated by taking the ratio of female to male SVL and subtracting one ($SVL_{\text{female}}/SVL_{\text{male}} - 1$; Lovich and Gibbons 1992). The index has been widely used in many previous studies because of its intuitive appeal for both direction and degree of sexual size dimorphism and other advantages (Fairbairn et al. 2007). The minimum SVL at sexual maturity and the reproductive stages of the individuals used for this study had been

previously determined for *P. aguanegra* in Cabezas-Cartes et al. (2010) and for *P. zapalensis* in Boretto and Ibarquengoytía (2009), based on morphological and histological analysis of gonads.

Histological technique of skeletochronology

The right femur of each specimen was removed and left in 7% nitric acid for 2–7 h for decalcification; then the femur was dehydrated through a series of increasing concentrations of ethanol solutions, cleared with toluene, and embedded in paraplast for 24 h at 60°C. Cross-sections at mid-diaphyseal level were stained with Hematoxylin–Eosin (Martoja and Martoja-Pierson 1970).

Determination of growth rate, individual age, age at maturity, and longevity

The histological preparations were analyzed with an optic microscope (Olympus BX40, America Inc., New York, NY, USA) equipped with a Pro-Series High Performance CCD Camera. Digital images were measured using an Image-Pro Plus analyzer (Media Cybernetics, Inc., Rockville, MD, USA). To avoid under- or overestimating the age of lizards, the presence of the endosteal bone and the first bone zone (next to the medullar cavity or to the endosteal bone) were considered. The five best sections of each bone were selected to estimate the following variables, according to the methodology of Leclair and Castanet (1987): (1) minimum and maximum medullar radius from the center of the medullar cavity, (2) minimum and maximum diaphyseal diameter, (3) minimum and maximum estival ring thickness, (4) number of lines of arrested growth (LAGs; Fig. 1). We assumed LAGs correspond to annual arrested winter growth and thus, the lizard's age. The average of the minimum and maximum radius of each variable was calculated to minimize the asymmetry of the bone sections and medullar cavity. When endosteal resorption of LAGs was present, the estimated age was calculated using the size of the marrow cavity of newborns in order to back-calculate the number of rings resorbed (Piantoni et al. 2006; Boretto et al. 2015, 2018; Cabezas-Cartes et al. 2015). The number of resorbed rings was added to the number of observed rings. To calculate the age in years, the last LAG was only considered in the count when the date of death of the specimen occurred between February and April considering that births in *P. aguanegra* and *P. zapalensis* occur from February to March, and the beginning of the brumation period starts in April to May (Boretto and Ibarquengoytía 2009; Cabezas-Cartes et al. 2010). Individuals younger than 1 year of age were

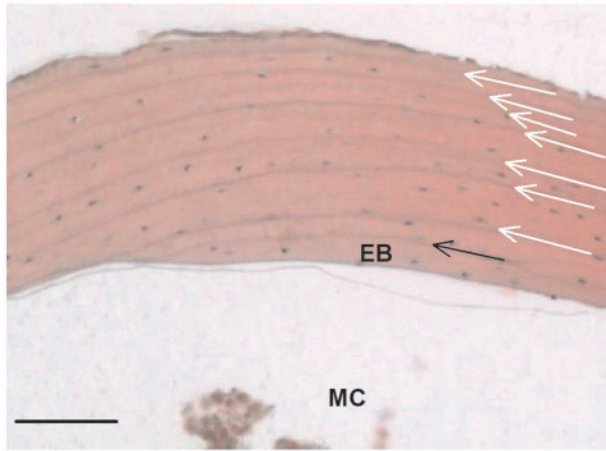


Fig. 1 Microphotograph of the diaphyseal cross section of the femur of an adult male of *P. aguanegra* of 10 years. White arrows indicate the LAGs, and the black arrow indicates the resorption line. EB, endosteal bone; MC, medullary cavity. Black scale bars are equivalent to 50 μm .

considered age class 0. The ASM was determined considering the youngest adult of each sex with reproductive activity, according to previous studies of reproductive biology carried out in the same specimens used for the present study (Boretto and Iburgüengoytia 2009; Cabezas-Cartes et al. 2010).

Comparative analysis of the influence of environmental variables in ASM and longevity in Sauria

Data collection

We assembled a dataset on the maximum longevity and ASM (of males and females, when available) of 48 lizard species belonging to 14 of the 41 saurian families currently recognized world-wide (taxonomy follows Uetz [2017]). Data are from the literature (Supplementary Information S1) and we only included the information of wild populations obtained from skeletochronological studies considering that this methodology to estimate individual ages in lizards has proven accurate, highly reliable, and robust (Castanet 1994). Longevity data are the maximum age (in years) reported for each species, and ASM was considered as the age at which individuals start reproducing. Whenever more than one entry of longevity or ASM of a given species were available, as a rule, we considered the highest for longevity and the lowest for the ASM.

Besides, for each species we collected literature data on body size (SVL), latitude, longitude, and altitude of the populations studied. When more than a population per species was available, we prioritized the elevation, latitude, and longitude from

the population that showed the maximum longevity and if populations still present the same longevity we chose the population with the lowest ASM. This criterion was adopted in order to neither underestimate longevity nor overestimate ASM using a mean value.

Environmental variables

We obtained the values of the following environmental parameters of each species' locality from the NASA database (<http://power.larc.nasa.gov/>) for the period between January 1983 and December 2016: Average air temperature at 2 m (TME), minimum air temperature at 2 m (TMIN), maximum air temperature at 2 m (TMAX), from which we calculated TA (calculated as TMAX–TMIN). Also, we obtained Precipitation (PREC) values from the same database but for the period available, from January 1997 to December 2014.

Phylogenetic hypothesis

For the phylogenetic comparative analyses we mainly relied on the phylogenies of Pyron et al. (2013). However, some species studied were not included in Pyron et al. (2013) so we added them manually using Mesquite 3.2 (Maddison and Maddison 2017) and placed them in accordance to the phylogenies of Guo et al. (2011), Bauer et al. (2013), and Morando et al. (2013). The final tree is showed in Fig. 2.

Phylogenetic signal

Prior to conducting our statistical analyses, we determined whether the traits exhibited a phylogenetic signal, that is, the consistency in trait values with the phylogeny. We estimated values for Pagel's λ (Pagel 1999; Freckleton et al. 2002). We used the package phytools (Revell 2012) to generate values of λ conducted in the R statistical environment (R Development Core Team 2017).

Phylogenetic comparative analyses

We employed multiple regression analysis using a phylogenetic generalized least squares (PGLS) model (Martins and Hansen 1997; Garland and Ives 2000) to determine the dependence of longevity and ASM on latitude, elevation, TME, TMIN, TMAX, TA, and PREC, adjusting the strength of phylogenetic non-independence using the maximum-likelihood value of the scaling parameter value λ (Pagel 1999). Because we did not have branch length information, all branches were arbitrarily set to a branch length of 1. PGLS incorporates phylogenetic information into the error structure of generalized linear models by specifying the expected variance and co-variances

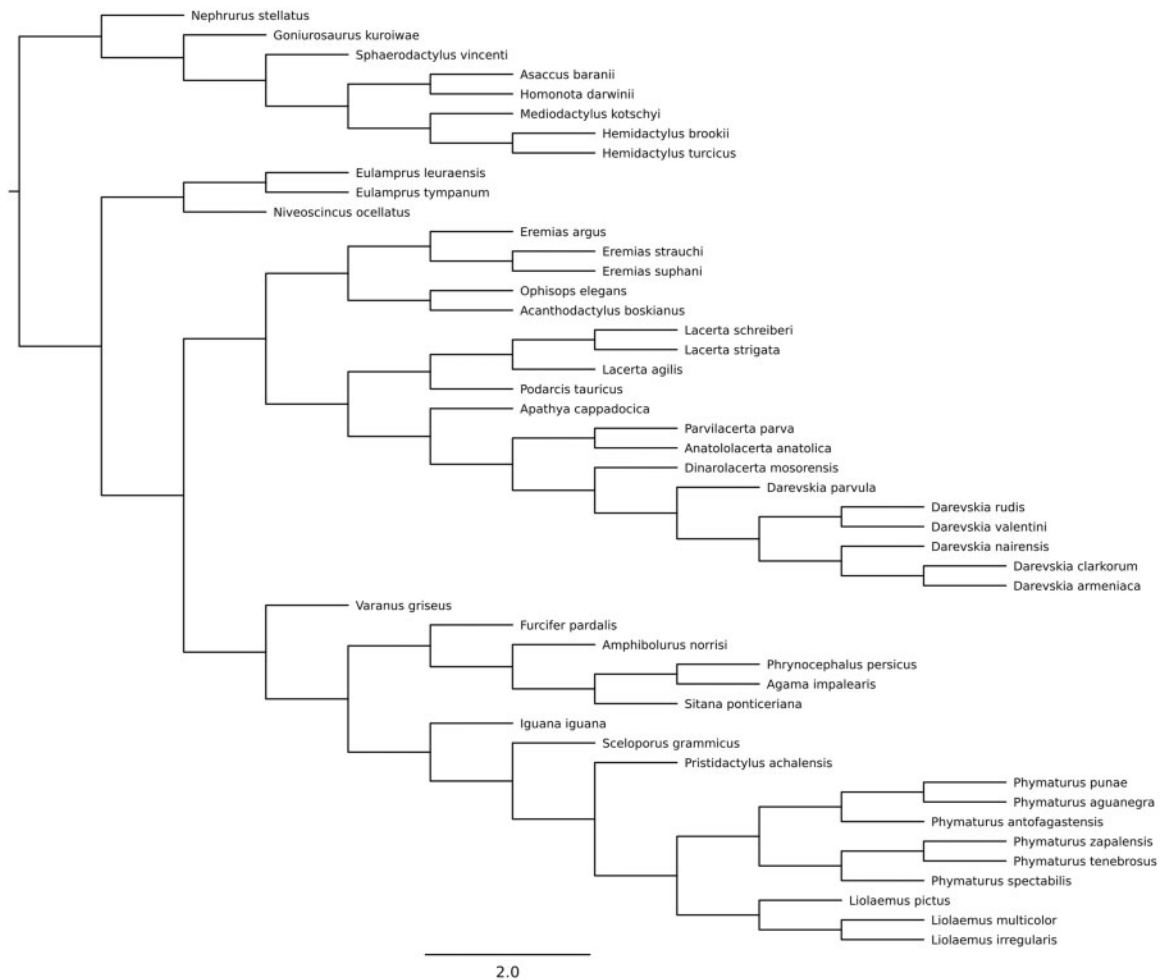


Fig. 2 Molecular-based phylogeny depicting the relationships among the species of Sauria analyzed in the present study (based on Guo et al. [2011], Bauer et al. [2013], Morando et al. [2013], and Pyron et al. [2013]) Branch lengths are set to unity.

among related species using an explicit model of evolution. Thus, PGLS controls for the non-independence that is inherent in the analysis of species that are phylogenetically related. We implemented PGLS analyses using the package *caper* (Orme et al. 2013) in R.

In order to compare the longevity of liolaemids versus the rest of the species of our database adjusting for phylogeny and body size we performed a Phylo ANCOVA using mean SVL of each species as a covariate and longevity as the response variable. This test was run using the packages *caper* (Orme et al. 2013) and *phytools* (Revell 2012) in R.

Statistical analyses

We used the statistical software Sigma Plot 11.0[®] to perform Linear Regressions to estimate the relationship between SVL and age in juveniles, and adult males and females of *P. aguanegra* and *P. zapalensis*. Also, *t*-tests were used to compute differences between two groups. ANCOVA was used for

computing size differences between adults of both sexes controlling the effect of age.

For phylogenetic analyses we used R 3.1.1 (R Development Core Team 2017) and Mesquite 3.2 (Maddison and Maddison 2017). Because the variables did not conform to a normal distribution, we used log 10 transformations to ensure the variables met the assumptions of the parametric statistics, which also reduced skew and homogenized variances (Zar 2009). We also conducted standard regression diagnostics to determine whether the data exhibited multicollinearity considering variance inflation factors (VIFs). We found no evidence of multicollinearity, being all VIF values below the threshold VIF value of 10, indicative of multicollinearity (Montgomery and Peck 1992). In order to select the model of best fit among the candidate models we used the corrected Akaike information criterion (AICc). This parameter modifies standard AIC with a correction for small sample sizes (Hurvich and Tsai 1989). Also, we calculated the values of $\Delta AICc$,

which is the difference between the AICc of a given model and the lower AICc (Burnham and Anderson 2002). Differences higher than 2 in ΔAICc were considered as significant (Burnham and Anderson 2002).

Results

Age and growth of *P. aguanegra* and *P. zapalensis*

In both species SDI was female-biased resulting in 0.055 in *P. zapalensis* and 0.022 in *P. aguanegra*. However, when considering age as a covariate females presented larger size than males only in *P. zapalensis* (ANCOVA, $F_{1,29} = 8.037$, $P = 0.009$), whereas in *P. aguanegra* males and females were similar in size (Table 1).

Within species, adult males and females showed similar mean ages (t -test; *P. aguanegra*: $t_{20} = -0.915$, $P = 0.371$; *P. zapalensis*: $t_{27} = -0.144$, $P = 0.886$; Table 1). *Phymaturus zapalensis* reach sexual maturity later than *P. aguanegra*; however, *P. aguanegra* presented a higher longevity than *P. zapalensis* (Table 1).

Comparative analysis of the influence of environmental variables in longevity and ASM in Sauria

When comparing liolaemids versus the rest of the species, we found that liolaemids presented significantly higher longevity than the rest of the species of our database when using mean SVL as a covariate (PhyloANCOVA, $F_{4,48} = 20.55$, $P < 0.001$; Fig. 3).

Longevity and ASM of both females and males showed significant phylogenetic signals (Table 2). Hence, PGLS were carried out and the results indicate that the environmental variables affected the life-history traits studied differently in males and females. In males, the candidate models show that longevity presented a strong positive influence of latitude and, to a lesser extent, negative effects of precipitation and TA (Table 2). On the other hand, in females, longevity was marginally influenced by latitude only in the best candidate model ($P < 0.07$; Table 2). However, when considering the longevity of the species regardless the sex, latitude was the variable that best explained the variation in all the candidate models (Table 2).

ASM was negatively influenced by mean air temperature in males in all the candidate models (Table 2), while in females this effect of TME was marginally significant ($P < 0.07$) in the three best models (Table 2).

Discussion

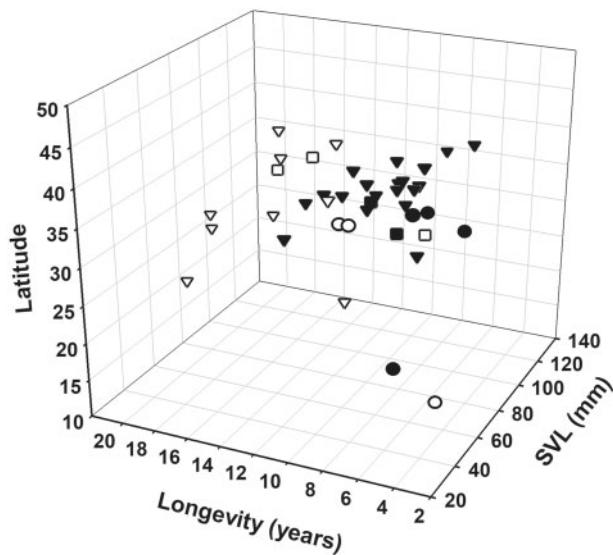
The cold temperate environments of the highlands of the Andes and the Patagonian steppe of Argentina have a strong influence on the physiology of the endemic lizards of genus *Phymaturus*, resulting in the occurrence of slow life-history patterns, characterized by late sexual maturity and high longevity. Accordingly, the comparative analysis presented here evidences the significant effect of environmental conditions over ASM and longevity in wild populations of many lizards around the world. Our results indicate that latitude is the most influential environmental variable in the determination of longevity patterns in lizards. In contrast, ASM in males and females is mostly influenced by the mean annual temperature of the habitat.

Phymaturus lizards live under harsh environmental conditions in the highlands of the Andes and tablelands of central Patagonia. In these environments, low temperatures with high annual and daily TA prevail, constraining the time for activity (Kubisch et al. 2016; Vicenzi et al. 2017). In accordance to this, we found that *P. aguanegra* and *P. zapalensis* developed life histories characterized by delayed sexual maturity and high longevity. Considering all the species studied in this genus, sexual maturity is reached between 6 and 9 years old (Piantoni et al. 2006; Boretto et al. 2015, 2018; Cabezas-Cartes et al. 2015; and present study). As a result, *Phymaturus* present the highest ASMs when compared with many other lizards around the world (Mesquita et al. 2016b). Besides, herein we observed longevity of 15 years for *P. zapalensis* and 16 years for *P. aguanegra*. Taking into consideration the longevity of *P. tenebrosus* (16 years; Piantoni et al. 2006), *P. punae* (20 years; Boretto et al. 2015), *P. spectabilis* (12 years; Cabezas-Cartes et al. 2015), and *P. antofagastensis* (20 years; Boretto et al. 2018), the longevity of the liolaemids in general is significantly higher in relation to the longevity of the other families studied in the present work when controlling the effect of phylogeny and body size, suggesting that liolaemids, in general, and *Phymaturus* in particular would be among the most long-lived lizard genus in spite of presenting body sizes smaller than many other species (Fig. 3).

Environmental constrains, like high TAs, low air temperatures, and short activity seasons in combination with a predominant herbivorous diet in *Phymaturus* species might be determinant for the occurrence of late sexual maturity and high longevity. However, the similarity among ASMs contrasts with the differences in longevity within *Phymaturus*

Table 1 Sex, juvenile or adult condition, sample size, SVL, number of LAGs, estimated age, SVL at sexual maturity, ASM, and longevity of the individuals studied of *Phymaturus aguanegra* and *Phymaturus zapalensis*

Sex and juvenile or adult condition (n)	SVL±SEM (mm)	LAGs±SEM	Estimated age±SEM (years)	SVL at sexual maturity (mm)	ASM (years)	Longevity (years)
<i>P. aguanegra</i>						
Juvenile males (6)	68.70±5.26 (51.93–82.70)	3.33±0.99 (0–6)	4±0.53 (0–8)	–	–	–
Juvenile females (8)	62.01±2.76 (50.27–71.98)	2.00±0.38 (0–3)	2.25±0.53 (0–4)	–	–	–
Adult males (11)	93.37±6.71 (83.48–104.5)	8.27±0.84 (4–13)	11.00±0.85 (7–16)	83.5	7	16
Adult females (11)	95.46±5.67 (82.42–101.78)	9.54±0.78 (6–13)	11.82±0.87 (7–16)	82.4	7	16
<i>P. zapalensis</i>						
Juvenile males (5)	65.80±2.44 (60.62–72.64)	5.00±0.45 (4–6)	5.00±0.45 (4–6)	–	–	–
Juvenile females (7)	63.10±4.29 (47.48–76.00)	2.86±0.77 (0–5)	2.57±0.78 (0–5)	–	–	–
Adult males (12)	82.19±1.26 (75.66–90.50)	8.08±0.53 (6–13)	11.67±0.62 (8–15)	75.6	8	15
Adult females (17)	86.71±1.21 (79.02–96.60)	7.59±0.34 (5–11)	11.76±0.37 (9–14)	79.0	9	14

**Fig. 3** Three-dimensional scatter plot of longevity (years) on Y-axis, SVL (mm) on the X-axis, and latitude on the Z-axis. Black circles indicate species of the family Agamidae, white circles species of Gekonidae, black triangles species of Lacertidae, white triangles species of Liolaemidae, black squares species of Phyllodactylidae, and white squares species of Scincidae.

genus, since the species of *palluma* group seems to be more long-lived than the *patagonicus* group. Although the genus *Phymaturus* is highly conservative in many ecological, physiological, and behavioral aspects (Cruz et al. 2009; Debandi et al. 2012; Halloy et al. 2013), they show certain differences associated with environmental conditions that could affect growth and survivorship, resulting in the differences observed in longevity. For example, there are higher TAs and lower precipitations in the habitats of the *palluma* group species compared with those of *patagonicus* group (Boretto et al. 2018) which not only

could affect the availability of food (Andrews 1982; Henle 1989; Smith and Ballinger 1994), but also the timing of activity (Ragland and Kingsolver 2008), two variables related to high longevities (Scharf et al. 2015). In addition, the strictly herbivorous diets of *palluma* group species (Videla 1983; Espinoza et al. 2004; Acosta et al. 2008; Castro et al. 2013; Corbalán and Debandi 2014; Córdoba et al. 2015) in comparison with the herbivorous–insectivorous diet of some species of the *patagonicus* group like *P. zapalensis* (Boretto et al. Forthcoming), and *P. spectabilis* (F. Cabezas-Cartes 2013, unpublished data), could also contribute to the higher longevities of the *palluma* members as it has been shown for other species (Fisher et al. 2001; Scharf et al. 2015). Moreover, there are differences in the female reproductive cycles being strictly biennial in *palluma* species (Boretto and Iburgüengoytía 2006; Boretto et al. 2007; Cabezas-Cartes et al. 2010; Castro et al. 2018), and annual–biennial in *patagonicus* species (Boretto and Iburgüengoytía 2009; Boretto et al. 2014). The differences in reproductive frequency could translate into differences in the energy devoted to reproduction and growth, and it is expected that the higher reproductive frequencies of *patagonicus* species would demand a higher expenditure on reproduction to the detriment of the allocation to growth, reducing longevity (Roff 1992). Besides, increased frequency of reproduction of *patagonicus* species might make the parents more visible and hence more vulnerable to predation, affecting longevity negatively (Roff et al. 2006).

Among ectotherms, variations in life-history traits, such as ASM and longevity, are usually highly geographically variable and heavily dependent on the local climate (Bauwens and Verheyen 1987; Sorci

Table 2 Results from PGLS models for factors that best predict variations in longevity and ASM in 48 saurian species

Trait	λ	Best models	Par	$\Delta AICc$	Coefficients (β)					R^2
					LAT	ALT	PREC	TA	TME	
Longevity	0.687**	LAT	2	0	0.52**	–	–	–	–	0.15
		LAT+TA	3	0.68	0.65**	–	–	–0.16	–	0.15
		LAT+PREC+TA	4	0.87	0.65**	–	–0.16	–0.29	–	0.16
		LAT+ALT	3	0.98	0.60**	–0.03	–	–	–	0.15
		LAT+PREC	3	1.86	0.50*	–	–0.04	–	–	0.13
		LAT+TME	3	1.96	0.50*	–	–	–	–0.03	0.13
Male longevity	0.945***	LAT+PREC+TA	4	0	1***	–	–0.30*	–0.38*	–	0.32
		LAT+TME+PREC+TA	5	1.48	0.94***	–	–0.31*	–0.41*	–0.1	0.31
		LAT+ALT+PREC+TA	5	1.92	1.01***	–0.01	–0.30*	–0.37(*)	–	0.30
Female longevity	0.616**	LAT	2	0	0.39(*)	–	–	–	–	0.07
		TME	2	0.76	–0.28	–	–	–	–	0.05
		LAT+TA	3	1.18	0.52*	–	–	–0.15	–	0.06
		LAT+TME	3	1.36	0.28	–	–	–	–0.15	0.06
		LAT+ALT	3	1.48	0.46*	–0.02	–	–	–	0.05
		LAT+PREC	3	1.54	0.43*	–	0.07	–	–	0.05
ASM males	0.706***	TME	2	0	–	–	–	–	–0.66**	0.22
		ALT+TME	3	1.86	–	–0.01	–	–	–0.69**	0.20
		TME+TA	3	1.87	–	–	–	–0.06	–0.69**	0.20
		TME+PREC	3	1.90	–	–	–0.04	–	–0.66**	0.20
		LAT+TME	3	1.94	0.09	–	–	–	–0.63*	0.20
ASM females	0.791***	TME	2	0	–	–	–	–	–0.36(*)	0.06
		LAT+TME	3	1.26	–0.24	–	–	–	–0.23(*)	0.06
		TME+TA	3	1.61	–	–	–	–0.11	–0.42(*)	0.05
		TME+PREC	3	1.95	–	–	0.03	–	–0.36	0.04
		ALT+TME	3	1.96	–0.01	–	–	–	–0.38	0.04

Notes: The models took into account latitude (LAT), altitude (ALT), precipitation (PREC), thermal amplitude (TA), and mean air temperature at 2 m (TME). The best-fit, most parsimonious models (Best models) are shown for the different life-history traits. The estimate of Pagel's lambda values (λ), the number of parameters (Par), and the R^2 across the 31 models tested is shown for the best-fit models. $\Delta AICc$ shows the change between the best and the other candidate models. The coefficients (β) are shown for factors in the candidate models, and asterisks denote the P -values for the coefficients and lambda values. (*) $P < 0.07$; * $P < 0.05$; ** $P < 0.01$; *** $P < 0.001$.

et al. 1996). In agreement with the pattern observed for most ectotherms (e.g., Adolph and Porter 1996; Miaud et al. 1999; Karl and Fischer 2009; Scharf et al. 2015), the present comparative study confirms that longevity in lizards increases with latitude. At higher latitudes, reptile activity seasons are shorter, probably bringing about slower growth, older ASM, and increased longevity, as suggested for some squamate species (Piantoni et al. 2006; Kubisch et al. 2012). In particular, the higher longevity might be related to the fact that survival rate is inversely correlated to annual activity times, which depend on latitude (Adolph and Porter 1993). Besides, the harsh climates of high latitudes are related to lower intensities of predation and competition (Schemske et al.

2009), which would result in higher survival rates (Angilletta et al. 2004) and, hence, higher longevity. Also, in cold areas, lizards often hibernate, and metabolic activity is considerably reduced, lowering mutation rates and oxidative damage (Sohal 1986; Wilkinson and South 2002).

In addition, in higher latitudes and colder areas, as hibernation periods are much longer, individuals should invest more into energy storage and self-maintenance (Jönsson et al. 2009). Allocations of energy into self-maintenance and energy reserves should also trade-off against investments into other traits, such as reproduction and growth, as the growth season gets shorter, which would further affect growth. Hence, growth is comparatively costlier

for lizards that live in environments where activity time is a limited resource, favoring not only late sexual maturity but also high longevity.

Present results show that, in males of Sauria, longevity was also negatively affected by precipitations and TA. This can be a consequence of the fact that precipitations are in general positively correlated with food availability (Andrews 1982; Henle 1989; Smith and Ballinger 1994), and its nutritional content translates into changes in the growth rates (Lagarde et al. 2003). Hence, lizards that present higher availability of food resources as a result of higher precipitations would require lower growth times and would be able to start reproducing sooner, resulting in reduced longevity (Scharf et al. 2015). In addition, TA, as well as mean air temperature, varies with altitude and latitude (Taylor 1981); and it also plays an important role in the physiology of lizards (Ragland and Kingsolver 2008). High TAs imply that extreme temperature values can be reached during a single day, restraining the activity of lizards not only because of the lack of heat, but also to avoid overheating (Sinervo et al. 2010; Kubisch et al. 2016; Vicenzi et al. 2017). Restriction of hours of activity would limit the possibilities of lizards reaching optimal body temperatures for physiological performance (e.g., locomotion, foraging, gut-passage rate; Avery 1971; Van Damme et al. 1991). Besides, in high-TA habitats, metabolism is reduced significantly at night, decreasing the oxidative damage produced by free radicals and, in consequence, increasing longevity (Scharf et al. 2015).

Temperature, precipitation, and their effects on hours of activity and energy income, respectively, can greatly mold the growth and alter the evolution of life histories since their combination affects the physiological performances (Adolph and Porter 1996), such as energy assimilation, which constrains the age and size at maturity, the frequency and magnitude of reproduction, and the size and the number of offspring (Angilletta 2009). In the present study, in males of the different saurian species, ASM was mostly influenced by mean air temperature; however, in females, this influence was only marginally significant. Specifically, lizards from hotter places reach sexual maturity at lower ages. In ectotherms, subtle differences in temperature (i.e., 2°C) can largely increase metabolic rate (Dillon et al. 2010) and hence, energetic needs. When juveniles can compensate for this increased metabolism by foraging more, it should lead to a faster body growth rate with subsequent consequences on their entire life-history. For example, in the lacertid lizard *Zootoca vivipara*,

warm climatic conditions had a strong positive impact on juvenile body growth, but affected survival negatively, reducing longevity (Bestion et al. 2015).

In general, all the regressions of the comparative analysis performed herein showed low values of R^2 , indicating extensive unexplained variation in the data. Many species of different regions of the world (South America, Europe, Africa, Asia, and Australia) compose our data set and, in consequence, it is expected to present a great amount of sampling error. In fact, a large number of unexplained variation is not uncommon in ecological studies with large data sets (Jongman et al. 1995; Guisan and Zimmermann 2000; Gilbert and Bennett 2010). However, other studies that analyzed life-history of a large number of species included data of captive individuals and diverse methodologies of age determination (Scharf et al. 2015; Mesquita et al. 2016a, 2016b; among others). In contrast, in the present study, only data from wild populations obtained by skeletochronology were used; hence, we have reduced the “noise” of our data set in comparison to other studies. Our results reinforce the ideas that, in lizards, latitude, and consequently season length, are major determinants of longevity patterns, and that air temperature has a great influence in the timing of sexual maturity.

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Supplementary data

Supplementary data available at ICB online.

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