



Slow life histories in lizards living in the highlands of the Andes Mountains

Jorgelina M. Boretto¹ · Facundo Cabezas-Cartes¹ · Nora R. Ibargüengoytía¹

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Abstract

In the highlands of the Andes, lizards must balance precisely the allocation of energy for growth and reproduction to ensure their survival. We studied the individuals' age, growth rates, age at sexual maturity, and maximum life span of the viviparous lizard *Phymaturus antofagastensis*, endemic of cold and harsh environments at high altitudes in the Andes Mountains of Catamarca province, Argentina. We also estimated key life history parameters like reproductive effort, lifetime reproductive effort, net reproductive rate, and relative reproductive time in *P. antofagastensis* as well as in other *Phymaturus* to compare the interplay among growth, maintenance, and reproduction in species that live across a latitudinal and altitudinal gradient. We found that females and males of *P. antofagastensis* mature late in life, at 6–7 years old, respectively, and some individuals reached 20 years of age. Adult females showed higher specific growth rates than males and an adult life span of 9 years which, due to their biennial reproduction, results in an estimated production of only four litters in life. This species exhibits one of the highest lifetime reproductive efforts described for lizards. Our results indicate the existence of a tradeoff between the number of reproductive events throughout life and reproductive effort devoted to each event in *Phymaturus*, related to the phylogenetic group. The *palluma* group shows low reproductive effort but high number of reproductive events throughout their lives, whereas the *patagonicus* group shows high reproductive efforts in low number of reproductive events.

Keywords Age at sexual maturity · Longevity · *Phymaturus* · Reproductive effort · Skeletochronology

Introduction

Life history is generally defined as a set of evolved traits including behavior, physiological demands and anatomical adaptations which directly influences survival and reproductive success (Ricklefs and Wikelski 2002). The theory of natural selection predicts that life history traits have been selected, giving adaptive advantages to organisms that maximize their biological adaptation or fitness (Moreno-Klemming 2002). Variations in these traits depend largely

on tradeoffs between different vital functions such as growth, maintenance, and reproduction (Duvall et al. 1982; Roff 1992), and limit the expression of the specific genetic variability of each lineage (Stearns 2000).

In reptiles, like in others organisms, the tradeoff concept is commonly used in the analysis of the interactions between physiological performance and different life history traits (Bogert 1949; Dunham et al. 1988; Stearns 1992). Two types of tradeoffs have been proposed (Angilletta 2009): the “acquisition tradeoff”, which occurs when an organism is exposed to a high risk of mortality associated with the acquisition of a particular resource like food, courtship, or suitable microenvironments for activities or refuge; and the “allocation tradeoff”, which occurs whenever an organism divides a finite amount of resources between competing demands like growth or reproduction. The interrelationship between the acquisition and allocation of resources, and biotic (e.g., inter- and intraspecific competition, predation pressure) and abiotic environmental factors (e.g., food availability, nutrients, temperature, photoperiod and availability of shelters) determine further variations in different aspects

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✉ Facundo Cabezas-Cartes
facundo.cabezas.cartes@gmail.com

¹ INIBIOMA (CONICET–Universidad Nacional del Comahue), San Carlos de Bariloche, Río Negro 8400, Argentina

of the life history of species (Angilletta 2009). Accordingly, it has been shown that growth rates in lizard species can change according to variations in food availability and nutrient content (Andrews 1976; Dunham 1978; Schoener and Schoener 1978). For example, juvenile individuals tend to have higher growth rates than adults, reaching sexual maturity at an earlier age, when food resources are abundant (Niewiarowski 2001). In addition, in adult female turtles, the deficiency of certain minerals, such as calcium, can affect the vitellogenesis (Lagarde et al. 2003).

Furthermore, the body temperature (T_b) in lizards is one of the main factors affecting the evolution of life history traits due to its close relationship with the biochemical reactions that influence the physiological performance (Bogert 1949; Huey and Stevenson 1979; Huey et al. 2003; Angilletta 2006, 2009). In particular, T_b affects behavior (Huey and Pianka 1977; Prosser and Brown 1991; Zug et al. 2001), growth rates (Zug et al. 2001; Kubisch et al. 2012), age and size at sexual maturity (Adolph and Porter 1993; Niewiarowski 2001; Gutiérrez et al. 2013), reproductive rates (Olsson and Shine 1999; Boretto and Ibarquengoytía 2009), and the number and size of offspring (Barbraud and Weimerskirch 2001; Shine 2005; Angilletta 2009). Thus, it is expected that lizard species with high availability of thermal environments for thermoregulation can reach T_b that results in high metabolism rates, locomotion, digestion and growth (Shine 2004).

In environments with cold–temperate climate, lizards present low T_b and short periods of annual activity that restrict their somatic growth, which results in distinctive life history traits as late sexual maturity and high longevity (Tinkle et al. 1970; Dunham et al. 1988; Wapstra et al. 2001). Accordingly, several authors have proposed the existence of a continuum between “slow” life histories with low reproductive rate, slow development, and long life span in species living in cooler environments, and “fast” life histories in species living in tropical climates (Ricklefs and Wikelski 2002; Shine 2005; Bielby et al. 2007; de Magalhães et al. 2007). The cold and harsh environments of the highlands of the Andes Mountain and the Patagonian steppe of Argentina and Chile are inhabited by the lizard genus *Phymaturus* (Cei 1986; Etheridge 1995; Díaz Gómez 2009; Debandi et al. 2012; Morando et al. 2013). *Phymaturus* species share morphological characteristics and life history traits like flat and robust bodies, preference for rocky microhabitats, predominantly herbivorous diets, viviparous reproductive mode (Cei 1986; Espinoza et al. 2004; Debandi et al. 2012), and prolonged female reproductive cycles (annual–biennial or strictly biennial; Habit and Ortiz 1996; Ibarquengoytía 2004; Boretto and Ibarquengoytía 2006, 2009; Boretto et al. 2007, 2014a; Cabezas Cartes et al. 2010). This genus consists of two major clades (Etheridge 1995; Morando et al. 2013), the *palluma* and *patagonicus* groups. The *palluma* group is

distributed mainly in the northern range of the genus and it is characterized by larger body sizes, strongly spiny caudal scales, sexual dimorphism with males larger than females, and strictly biennial female reproductive cycles (only 1 litter every 2 years; Habit and Ortiz 1996; Boretto and Ibarquengoytía 2006; Boretto et al. 2007; Cabezas-Cartes et al. 2010). The *patagonicus* group, distributed in the southern range of the genus in the north and central Patagonia, is characterized by smaller body sizes, larger females than males, and annual or biennial female reproductive cycles (only 1 litter every 1 or 2 years; Ibarquengoytía 2004; Boretto and Ibarquengoytía 2009; Boretto et al. 2014a, b).

In the genus *Phymaturus*, the age and growth dynamics have been studied only in *P. tenebrosus* (Piantoni et al. 2006) and *P. spectabilis* (Cabezas-Cartes et al. 2015), both species belonging to the *patagonicus* group that inhabits the Patagonian steppe, and in *P. punae* (Boretto et al. 2015) that belongs to the *palluma* group from the highlands of the Andes in central Argentina. In addition, other studies have been performed in the species of the sister genus *Liolaemus* that inhabit in cold environments at high altitudes in the Puna (Valdecantos et al. 2007) and in the forests of Patagonia, Argentina (Gutiérrez et al. 2013). All of these studies were developed using the histological technique of skeletochronology, which has been widely used in many species of reptiles from temperate and tropical habitats, resulting in a reliable method to estimate the age of individuals (Castanet 1978, 1979; Castanet and Roche 1981; Smirina and Ananjeva 2007). Specifically, lizards are the most suitable group for skeletochronology because of their simple bone structure with low vascularization (except varanids) which results in the absence of intracortical remodeling, and few supplementary marks (Castanet 1994). Moreover, lizard species that inhabit cold–temperate regions constitute better study models than tropical species, given that their growth rings are more evident (Cagle 1950; Enlow 1969). Skeletochronological studies performed to date show that *Phymaturus* species acquire sexual maturity at 6–9 years and can live up to 20 years (Piantoni et al. 2006; Boretto et al. 2015; Cabezas-Cartes et al. 2015).

Herein we used skeletochronology to determine the individuals' age, growth rates, age at sexual maturity, and maximum life span of *Phymaturus antofagastensis* Pereyra (1985), a species included within the *palluma* group, endemic of cold and extreme environments at 4200 m asl in the Andean highlands of Catamarca Province, Argentina. We also combined the information of the female reproductive cycle and litter size obtained from the same sample of individuals and published in Boretto and Ibarquengoytía (2006) to estimate key life history parameters such as reproductive effort, lifetime reproductive effort, net reproductive rate and relative reproductive time. Finally, we estimated the same life history parameters in other species of *Phymaturus* to

discuss the interplay among growth and reproduction in species that lives across a latitudinal and altitudinal gradient.

Materials and methods

Specimens

We analyzed 4 newborns (born in captivity from captured pregnant females), 6 juveniles, 12 adult females, and 10 adult males of *P. antofagastensis* from the collection of the Department of Zoology, Universidad Nacional del Comahue. Specimens were collected during spring, summer and early autumn of 2001, 2003, and 2005, near ‘‘Paso Internacional San Francisco’’ (27°02’S, 68°04’W; 4200 m asl), in the northwest of Catamarca Province, Tinogasta Department, Argentina. These specimens had been previously used for studies in reproductive biology (Boretto and Ibargüengoytía 2006) and endocrinology (Boretto et al. 2010).

Environmental characteristics of sampling sites

The sampling sites are located within the Andean–Patagonian phytogeographical domain, Altoandino Quichua District, characterized by cold climates with broad daily thermal amplitude, high solar radiation and irregular precipitation occurring mostly in summer (103–324 mm). The maximum and minimum mean annual temperatures are between 21 and – 3 °C, respectively, and the maximum and minimum absolute temperatures are approximately between 30 and – 18 °C, respectively (Cabrera 1994). In winter, there are impenetrable snow barriers (Belver, personal communication), and in summer the weather is unstable, with harsh weather conditions, and periods of very cold days with snow and intense ‘‘white winds’’ even in mid-summer (January; Acosta, personal communication). Temperature and wind intensity change very suddenly and storms are frequent. The landscape is characterized by high plains known as the ‘‘Puna’’ or ‘‘Altiplano’’ of Andean Mountains in central and northern Argentina. The soil is sandy and rocky and the vegetation is dominated by herbaceous steppes, mostly composed of *Poa* and *Festuca* grasses (Cabrera 1994).

Morphometrical variables and reproductive data

Data of 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 for previous studies before euthanasia and used in the present study. The minimum SVL at sexual maturity and the reproductive stages of the individuals were determined in Boretto and

Ibargüengoytía (2006), based on morphological and histological analysis of gonads.

Histological technique of skeletochronology

A 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 sexual maturity and maximum life span

The histological preparations were analyzed with an optic microscope (Olympus BX40, America Inc., New York, USA) equipped with a Pro-Series High-Performance CCD Camera. Digital images were measured using Image-Pro Plus analyzer (Media Cybernetics, Inc., Maryland, USA). To avoid under or overestimating the age of lizards, the presence of endosteal bone and the first bone zone (next to the medullar cavity or to the endosteal bone) was considered. The five best sections of each bone were selected to estimate the following variables according to Leclair and Castanet (1987) methodology: (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). 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 to back-calculate the number of rings reabsorbed (Piantoni et al. 2006; Boretto et al. 2015; Cabezas Cartes et al. 2015). The number of reabsorbed 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 specimen was euthanized between February and April considering that births in *Phymaturus antofagastensis* occur in February–March, and the beginning of the brumation period starts in April (Boretto and Ibargüengoytía 2006). Individuals with less than 1 year of age were considered age class 0. The age at sexual maturity of each individual was determined considering the youngest adult of each sex that showed reproductive activity, according to previous studies of reproductive biology based on histology and morphology of gonads on the same sample used in the present study (Boretto and Ibargüengoytía 2006). The

maximum life span for males and females was determined as the age of the oldest individual of each sex.

Life history parameters related to growth and reproduction

We used data from the present study and from Boretto and Ibarquengoytía (2006) like: (1) period of time between age at sexual maturity and maximum life span for males and females; (2) litter size; (3) frequency of female reproduction; (4) offspring body mass; and (5) post-partum females body mass. With these data we estimated dimensionless numbers (*sensu* Charnov 2002, 2005), each one representing a benefit–cost ratio summarizing the reproductive timing (relative reproductive time, $RT = E/\alpha$, where E is the maximum adult life span, α is age at sexual maturity) and the reproductive investment (reproductive effort, $RE = R/m$, where R is the average of offspring mass per female per unit of time [1 year], and m is the average mass of adult females). We also calculated the lifetime reproductive effort ($LRE = \text{litters/year} \times \text{litter size} \times \text{average adult life span} \times [\text{average SVL of offspring at born} / \text{SVL of the smallest sexually mature female}]^3$), and the net reproductive rate (R_0), which represents the average number of offspring produced over a mother's lifetime (*sensu* Charnov 2002; Charnov et al. 2007), as the product of litter size \times reproductive frequency \times relative reproductive time.

For comparative purposes, we also obtained these life history parameters either using data from bibliography or calculating them in the present study (see details in Table 3), using published data of *P. tenebrosus* (Ibarquengoytía 2004; Piantoni et al. 2006), *P. spectabilis* (Boretto et al. 2014a, b; Cabezas-Cartes et al. 2015), and *P. punae* (Boretto et al. 2007, 2015). In addition, we obtained the values of the following climatic parameters of each species' locality from the NASA database (<http://power.larc.nasa.gov/>) for the period between January 1983 and December 2016: average daily air temperature at 2 m (TME), minimum daily air temperature at 2 m (TMIN), maximum daily air temperature at 2 m (TMAX), from which we calculated thermal amplitude (TA, calculated as $TMAX - TMIN$). Besides, we obtained precipitation (PREC) values from the same database but for the period available which goes from January 1997 to December 2014. With these data we estimated the annual means of TME, TMIN, TMAX and TA, and the total annual precipitation (Fig. 3).

Statistical analysis

We used the statistical software Sigma Stat 3.5[®] (Systat Software Inc., Chicago, Illinois, USA), and Sigma Plot 11.0[®] (Systat Software Inc., Chicago, Illinois, USA), Table Curve 2D v. 5.01 (SYSTAT Software Inc., 2002), and R v. 3.1.1 (R

Core Team 2014). We performed linear regressions to estimate the relationship between SVL and medullar radius, and between SVL and age in juveniles, adult males and females. As the assumptions of normality and/or homogeneity of variance were not fulfilled, we used Mann–Whitney rank sum tests to compare adult ages, the number of rings reabsorbed, and the specific growth rates between sexes, and between juveniles and adults. ANCOVA was used for computing size differences between adults of both sexes controlling the effect of age. To compute the best age–growth curve and calculate the growth rates, we used the software Table Curve and chose the three best fitted models sorted by the highest Degree of Freedom Adjusted Coefficient of Determination (DOF r^2). Then, we calculated the corrected Akaike information criterion (AICc) of the three best models to decide which growth model provided the best fit among them (Angilletta 2006). The AICc modifies the standard AIC with a correction for small sample sizes (Hurvich and Tsai 1989). We also calculated the differential AICc (Δ_i), which is the difference between a given model's AICc and the lowest AICc, and the Akaike weight (ω_i), as a measure of strength of evidence for each model, indicating the probability that a given model is the best among a set of candidate models (Burnham and Anderson 2002). Also, we adjusted the von Bertalanffy model with the Package FSA (Ogle 2011) in R. Asymptotic SVL (L_∞) and growth constant (K) were calculated for male and female samples of the studied population. Following the conservative approach of Schoener and Schoener (1978) we considered as significant the observed differences between simple estimates of growth curve parameters only if their 95% bootstrapped confidence intervals did not overlap. Growth rates were calculated as the derivative of the curve of SVL in relation to age (obtained with Table Curve 2D v. 5.01) of the growth model chosen. Specific growth rates were obtained by dividing the growth rates by the SVL of each specimen. To analyze the climatic differences among localities of the *Phymaturus* species studied we used Kruskal–Wallis one-way analysis of variance on ranks and Tukey tests as multiple comparison procedures to isolate the locality or localities that differ from the others.

Assumptions of normality and homogeneity of variance were tested with the one-sample Kolmogorov–Smirnov test and with the Levene test, respectively. Means are given \pm standard error (SE).

Results

Bone histology

The individuals of *Phymaturus antofagastensis* exhibited bone growth patterns of lamellar bone. The diaphysis sections were circular and the cartilage was absent. The

mid-diaphyses of femur examined showed a layer of periosteal bone with abundant rounded osteocytes, and a medullar cavity that becomes larger in diameter with age. The periosteal bone exhibited lines of arrested growth (LAGs) as stripes strongly stained by hematoxylin, following the ellipsoidal bone shape. Endosteal bone was characterized by elongated osteocytes and delimited by an irregular resorption line.

Estimation of age

Lines of arrested growth (LAGs), which correspond to the winter period, appeared between lighter and thicker zones, which correspond to summer growth periods. LAGs were absent in the newborns ($n=4$; $SVL_{\text{range}} = 47.8\text{--}50.1$ mm), but the rest of the specimens showed up to 13 LAGs ($n=28$; $SVL_{\text{range}} = 55.1\text{--}100.4$ mm; Table 1).

Medullar radius showed a significant increment with SVL (Linear regression, $F_{1,31} = 297.452$, $r^2 = 0.908$, $P < 0.001$). Medullar resorption removed a maximum of two growth rings in juveniles, and from two to seven growth rings in adults (Table 1). Adult males and females did not exhibit significant differences in the number of rings removed by medullar resorption (Mann–Whitney, $U = 121.0$, $P = 0.800$). The estimated age, adjusted for reabsorbed growth rings, ranged from 1 to 6 years for juveniles, from 6 to 15 years in adult females and from 7 to 20 years in adult males (Table 1). Adult males and females did not exhibit differences in the mean age (t test, $t_{20} = 1.623$, $P = 0.120$).

Growth rates

Snout–vent length of adult males and females exhibited a significant relationship with the estimated age ($F_{\text{males}} = 60.010$, $r^2 = 0.882$, $n = 10$, $P < 0.001$; $F_{\text{females}} = 16.067$, $r^2 = 0.617$, $n = 12$, $P = 0.002$), but considering the estimated age as a co-variable, the SVL were not different between adult males and females (ANCOVA, $F_{1,22} = 3.422$, $P = 0.080$). Table 2 shows the models fitted for the age-at-length data of *P. antofagastensis* males, females and overall. In both males and females, the logarithmical, logistic and sigmoidal equation fitted the data, but considering the Akaike weights (ω_i , Table 2) the growth curve was best fitted by a logarithmic

Table 2 Growth models of *P. antofagastensis* fitted to the age-at-length data with Table Curve 2D and R package FSA

Model	K	AICc	Δ_i	ω_i	Iterations to convergence
Total sample ($n=32$)					
Logarithmical	4	36.73409	0	0.33339	7
Logistic	4	36.73420	0.0001	0.33337	8
Sigmoidal	4	36.73512	0.0010	0.33322	100
Von Bertalanffy	2	166.99887	130.2648	~0	5
Gompertz	3	170.72702	133.9929	~0	7
Females ($n=16$)					
Logarithmical	4	23.75750	0	0.33359	58
Logistic	4	23.75751	0	0.33359	40
Sigmoidal	4	23.76228	0.0048	0.33280	100
Von Bertalanffy	2	86.88696	63.12945	~0	7
Gompertz	3	90.61137	66.85387	~0	7
Males ($n=16$)					
Logarithmical	4	22.86086	0	0.33341	8
Logistic	4	22.86101	0.00015	0.33339	7
Sigmoidal	4	22.86221	0.00135	0.33319	11
Von Bertalanffy	2	80.73478	57.87391	~0	8
Gompertz	3	82.65045818	59.78959	~0	4

The number of parameters (K), the corrected Akaike Information criterion (AICc), the differential AICc (Δ_i), the Akaike weight (ω_i) and the number of iterations to convergence are presented

equation (Fig. 1): $SVL = a + b/(1 + \exp(-(t - c)/d))$, where a is the SVL at birth of the species, b is the length difference between SVL at birth and asymptotic SVL, t is the age (in months), c is the age (in months) at the inflection point of the curve, and d is the characteristic growth rate. Thus, growth rates were calculated from the logarithmic equation.

The specific growth rates of juvenile males and females were similar (Mann–Whitney, $U = 8$; $n_{\text{females}} = 4$, $n_{\text{males}} = 6$, $P = 0.476$), but the specific growth rates of juveniles were significantly higher than those of adults (Mann–Whitney, $U = 60$; $n_{\text{juveniles}} = 10$, $n_{\text{adults}} = 22$, $P = 0.044$). Adult females

Table 1 Sex, juvenile or adult condition, mean \pm SE and range of SVL (mm), number of LAGs, number of reabsorbed rings, and estimated age (years) of a sample of *Phymaturus antofagastensis*

Sex and condition (n)	SVL	Number of LAGs	Number of reabsorbed rings	Estimated age
Juveniles males (6)	57.87 \pm 4.84 (47.80–76.88)	0.83 \pm 0.40 (0–2)	0.50 \pm 0.34 (0–2)	1.17 \pm 0.65 (0–4)
Juvenile females (4)	68.39 \pm 7.02 (49.22–79.78)	2.25 \pm 1.03 (0–4)	1.25 \pm 0.48 (0–2)	3.50 \pm 1.50 (0–6)
Adult females (12)	89.50 \pm 1.59 (79.32–97.32)	7.42 \pm 0.62 (4–10)	2.92 \pm 0.36 (2–5)	10.17 \pm 0.83 (6–15)
Adult males (10)	94.88 \pm 1.45 (86.92–100.35)	8.70 \pm 0.86 (5–13)	4.40 \pm 0.64 (2–7)	12.70 \pm 1.39 (7–20)

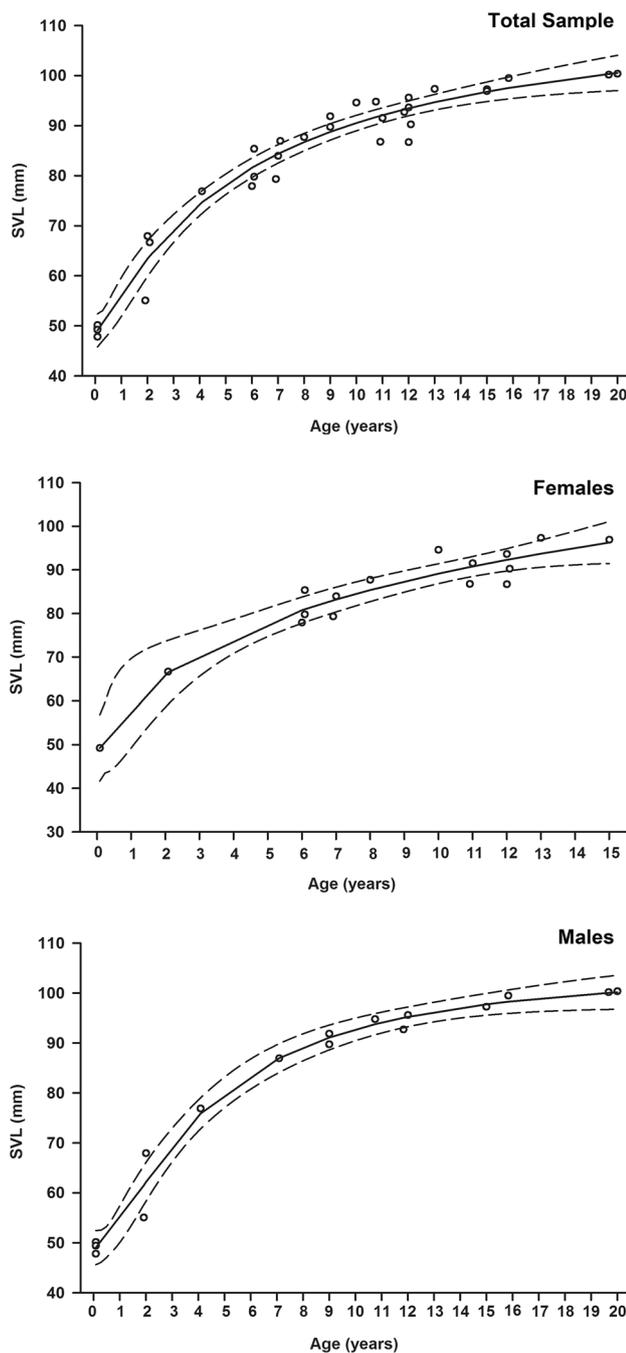


Fig. 1 Logarithmic curves relating SVL with age (years) considering the total sample, females, and males of *P. antofagastensis*. The dotted lines represent the confidence intervals of 95%

showed specific growth rates higher than those of adult males (t test, $t_{20} = -2.374$, $P = 0.028$; Fig. 2). Asymptotic SVL (L_{∞}) and growth constant (K) of the von Bertalanffy growth model were similar between males and females of *P. antofagastensis* ($L_{\infty \text{ females}} = 98.95 \pm 3.70$, $n = 16$; $L_{\infty \text{ males}} = 102.64 \pm 2.17$, $n = 16$; $K_{\text{females}} = 0.014 \pm 0.002$; $K_{\text{males}} = 0.014 \pm 0.001$).

Life history parameters related to growth and reproduction

The youngest adult male of the sample of *P. antofagastensis* was a specimen of 7 years, and the youngest adult female was a specimen of 6 years of age. The maximum estimated age was 20 years old for males and 15 years old for females. Considering these data, the average adult life span (E) was of 13 years for males and 9 years for females, and the estimated relative reproductive time (RT) was 1.86 for males and 1.5 for females. The estimated net reproductive rate (R_0) was 9 offspring over a reproductive female life span, considering the frequency of reproduction of 0.5 years (given that the female reproductive cycle is biannual) and the litter size of two offspring (Boretto and Ibargiengoytia 2006). The reproductive effort (RE) of *P. antofagastensis* was 0.16 and the lifetime reproductive effort (LRE) was 2.16. The proportion of adult life (%) in relation to the maximum estimated age for males and females vary from 65 to 60% in *P. antofagastensis* (Table 3).

Interspecific comparison of life history parameters and climatic conditions within the genus *Phymaturus*

For comparative purposes, we present in Table 3 the life history parameters of *P. antofagastensis*, *P. punae*, *P. tenebrosus*, and *P. spectabilis*, previously published, or estimated for the present study. Compared to others *Phymaturus* species, *P. antofagastensis* exhibited the higher average adult life span (E) in males, whereas *P. punae* exhibited the higher average adult life span (E) in females. The highest relative reproductive time (RT) and the highest proportion of adult life (%) in relation to the maximum estimated age were exhibited in both males and females of *P. antofagastensis*. The highest net reproductive rate (R_0) was exhibited by *P. antofagastensis* and *P. tenebrosus*, the highest reproductive effort (RE) was exhibited by *P. tenebrosus*, and the lifetime reproductive effort (LRE) was higher in species from the *palluma* group, *P. antofagastensis* and *P. punae* (Table 3).

The high-altitude environment in which *P. antofagastensis* inhabit exhibited the lowest mean annual temperature, mean annual minimum temperature and total annual precipitation, and the highest thermal amplitude (Fig. 3; for statistical results see Table 1 of Supplementary Material). In the same way, the environment of *P. punae*, which also belongs to the *palluma* clade, presented similar amount of precipitation and values of thermal amplitude than the habitat of *P. antofagastensis* (Fig. 3; Table 1 of Supplementary Material). The precipitations are significantly higher in the environments in which species of *patagonicus* group live, and thermal amplitudes are significantly lower than in the

Fig. 2 **a** Linear regressions of specific growth rates versus age of juvenile females (white circles), juvenile males (black circles), adult females (white triangles) and adult males (black triangles) of *P. antofagastensis*. **b** Detail of the linear regression lines of specific growth rates versus age of adult females (white triangles) and adult males (black triangles) of *P. antofagastensis*

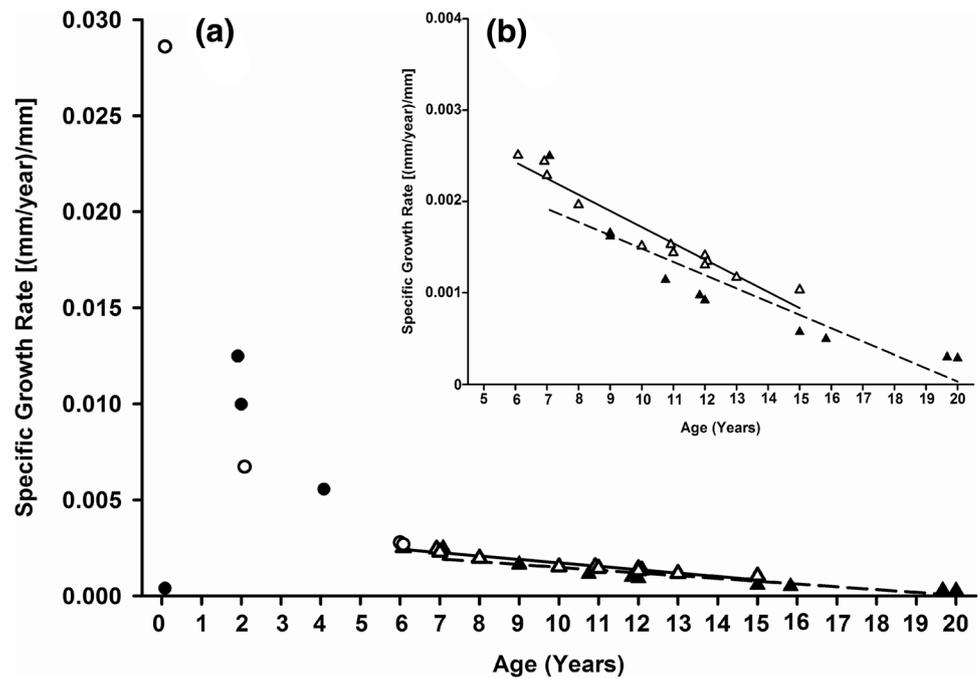


Table 3 Life history parameters of *Phymaturus* species

Species	Litter size	Reproductive frequency	Age at first reproduction	Maximum estimated age	<i>E</i>	<i>RT</i>	%	<i>R</i> ₀	<i>RE</i>	<i>LRE</i>
<i>P. antofagastensis</i>	2 ^a	0.5 ^a	♂ = 7 ♀ = 6	♂ = 20 ♀ = 15	♂ = 13 ♀ = 9	♂ = 1.86 ♀ = 1.50	♂ = 65 ♀ = 60	9	0.16	2.16
<i>P. punae</i>	1–2 ^b	0.5 ^b	♂ = 9 ^c ♀ = 8 ^c	♂ = 20 ^c ♀ = 18 ^c	♂ = 11 ^c ♀ = 10 ^c	♂ = 1.22 ^c ♀ = 1.25 ^c	♂ = 55 ♀ = 56	7.5 ^c	0.14	1.85
<i>P. tenebrosus</i>	2 ^d	0.5 ^d	♂ = 9 ^e ♀ = 7 ^e	♂ = 13 ^e ♀ = 16 ^e	♂ = 7 ^c ♀ = 9 ^c	♂ = 0.44 ♀ = 1.29 ^c	♂ = 31 ♀ = 56	9 ^c	0.31	1.36
<i>P. spectabilis</i>	1–3 ^{f,g}	0.5–1 ^{f,g}	♂ = 6 ^h ♀ = 7 ^h	♂ = 11 ^h ♀ = 12 ^h	♂ = 5 ♀ = 5	♂ = 0.83 ^h ♀ = 0.71 ^h	♂ = 45 ♀ = 42	7.5	0.25	1.26

We present the litter size, reproductive frequency (litters per year), age at sexual maturity (years), maximum estimated age (years), the average adult life span in years (*E*), the relative reproductive time (*RT*), the net reproductive rate (*R*₀), the reproductive effort (*RE*), and the lifetime reproductive effort (*LRE*; *sensu* Charnov 2002, 2005; Charnov et al. 2007), and we add the estimation of the proportion of adult life (%) in relation to the maximum estimated age for males and females. Some of the data presented were obtained from published data, and are indicated by a superscript, the rest of the data were calculated in the present study. (a) Boretto and Ibarquengoytía (2006); (b) Boretto et al. (2007); (c) Boretto et al. (2015); (d) Ibarquengoytía (2004); (e) Piantoni et al. (2006); (f) Boretto et al. (2014a); (g) Boretto et al. (2014b); (h) Cabezas-Cartes et al. (2015)

environments where species of *palluma* group live (Fig. 3; Table 1 of Supplementary Material).

Discussion

Phymaturus antofagastensis inhabits the highlands of the Andes where low environmental temperatures prevail, the daily and annual time for activities are constrained, and growth demands are costly enough to favor the development of “slow” life histories. Under this scenario we found that *P. antofagastensis* developed a life history characterized by slow growth rate, high rates of bone resorption, delayed

sexual maturity, and high longevity. Similar traits were exhibited by *P. punae*, another species of the *palluma* group that inhabit harsh environments in the Andes Mountains of San Juan Province at 3650 m asl (Boretto et al. 2015). *Phymaturus* species have shown similarity in the bone growth rates and in the patterns of juvenile growth that could be explained by the highly conservative eco-physiology proposed for the genus (Espinoza et al. 2004; Ibarquengoytía et al. 2008; Boretto and Ibarquengoytía 2009; Cruz et al. 2009; Debandi et al. 2012; Corbalán et al. 2013), since bone growth dynamics are influenced by phylogenetic and functional factors (e.g.: bone structure and biomechanical demands; Cubo et al. 2008).

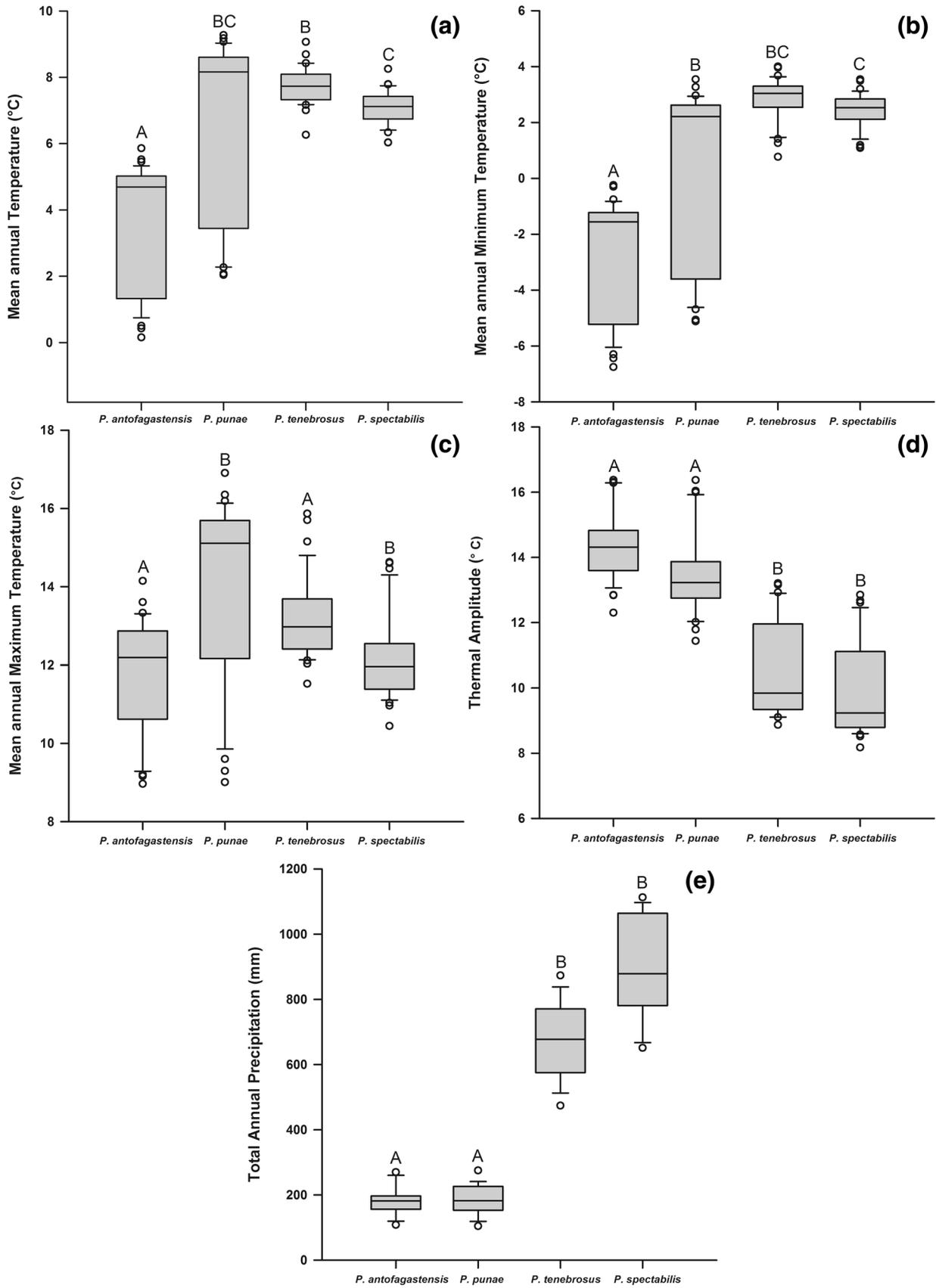


Fig. 3 Box plots diagrams of the environmental variables. **a** Mean annual temperature; **b** mean annual minimum temperature; **c** mean annual maximum temperature; **d** thermal amplitude; **e** total annual precipitation of the habitats of *P. antofagastensis* (27°2′ 0.0″S, 68°4′ 11.0″W; 4200 m asl), *P. punae* (29°2′ 0.0″S, 69°17′ 0.0″W; 3650 m asl), *P. tenebrosus* (41°3′ 44.7″S, 70°52′ 30.0″W; 913 m asl) and *P. spectabilis* (41°26′ 3.6″S, 69°45′ 7.0″W; 1030 m asl). The medians, 10%, 25%, 75% and 90% percentiles are indicated. Different letters (A, B, C) indicate significant differences among habitats ($P < 0.05$)

Males and females of *P. antofagastensis* exhibited the same type of growth curve, as other *Phymaturus*. The logarithmic function characterized the growth of *P. antofagastensis*, as in *L. irregularis* and *L. multicolor* that inhabit similar environments in the Puna of Argentina (Valdecantos et al. 2007), while in other *Phymaturus* growth was better adjusted to a logistic (Boretto et al. 2015) or sigmoidal curve (Piantoni et al. 2006; Cabezas-Cartes et al. 2015). Despite the differences in the best fitted model, *Phymaturus* species showed a growth pattern that reflects different allocation of energy, biased to growth in juveniles and to reproduction in adults, due to the high growth rates in juveniles and an asymptotic and undetermined growth observed after the acquisition of sexual maturity. Reproduction would entail higher energy requirements in females than in males (Saint Girons 1985), and in consequence, lower growth rates would be expected in females. However, adult females of *P. antofagastensis* presented higher growth rates than males, as in *P. punae* (Boretto et al. 2015), and in *P. spectabilis* (Cabezas-Cartes et al. 2015). In some reptiles the energetic requirements for spermatogenesis are comparable to those required for courtship, copulation and defense of the territory (e.g., *Vipera berus* snake; Olsson et al. 1997), which would reduce growth rates in males as well. Besides, the high growth rates of adult females of *P. antofagastensis* could result in an increment of the body size and weight in offspring, rather than increasing fecundity, due to the fixed and low litter size of two offspring (Boretto and Ibarguengoytia 2006). Accordingly, *Phymaturus* females performed a high parental energetic allocation in newborns as they were born with abundant fat reserves and large amounts of intrabdominal yolk (Boretto et al. 2007, 2014a; Boretto and Ibarguengoytia 2009; Cabezas-Cartes et al. 2010). These reserves could enhance the survival of the offspring even when the parental investment in the offspring negatively affects the future reproduction of the females (Boretto et al. 2007, 2014a; Boretto and Ibarguengoytia 2009; Cabezas-Cartes et al. 2010).

The interplay among reproduction, social and feeding activities that lizards perform, in addition to the environmental conditions, can also impact on bone growth and remodeling pattern. The rates of bone resorption in liolaemids are higher than in other lizards of the world of similar body size and longevity (e.g., Roitberg and Smirina 2006; Guarino et al. 2010). In *Phymaturus*, bone resorption varied between

2 and 7 reabsorbed rings in adults of *P. antofagastensis* (present study), 1–8 rings in *P. punae* (Boretto et al. 2015), 2–6 rings in *P. tenebrosus* (Piantoni et al. 2006), and 1–4 rings in *P. spectabilis* (Cabezas-Cartes et al. 2015). The great bone remodeling could be attributed, in part, to the biomechanical demands on locomotion imposed by the rocky environments (Curtin et al. 2009) with steep slopes where *Phymaturus* species live (Cabezas-Cartes et al., 2014). In *Liolaemus*, although they present smaller body sizes than *Phymaturus*, similar rates of bone resorption were observed (1–6 rings in adults of *L. pictus argentinus*, Gutiérrez et al. 2013; 1–7 in *L. irregularis*, and 2–14 in *L. multicolor*; Valdecantos et al. 2007). In contrast, in the sand lizards *Lacerta agilis boemica* and *L. a. strigata*, species of medium body sizes that inhabit cold–temperate environments, significantly lower resorption rates were observed (1–2 rings; Roitberg and Smirina 2006; Guarino et al. 2010), probably because these species present lower biomechanical demands on locomotion imposed by their sandy environments with low vegetation. However, taking into account the environmental constraints of the Andean environments, it is more likely that the high bone resorption in *Phymaturus* and *Liolaemus* species is due to the effect of harsh environments on the individual physiology. In this sense, the adverse environmental conditions would impose higher physiological demands on liolaemids, than the European cold–temperate environments in which *Lacerta* species live. The long periods of inactivity (brumation) and the probably lower food availability of the Andes and the Patagonian steppe would favor a relocation of the minerals deposited in the bones to other regions of the body, producing the high rate of bone resorption registered in *Liolaemus* and *Phymaturus*. Another possible explanation is that the high rates of bone resorption observed in liolaemids might be an ancestral character of all members of the group. Further studies of age and growth dynamics of other members of this clade and phylogenetic comparative analysis are being developed to shed light on these issues.

The age at sexual maturity is a pivotal trait since it is correlated with fitness and is often more sensitive to natural selection than any other life history trait (Stearns 2000). The liolaemids, and particularly the genus *Phymaturus*, present the highest ages at sexual maturity when compared with many other lizards around the world (Mesquita et al. 2015), probably because under harsh and cold environmental conditions, the low temperatures affect negatively the metabolic rate, retarding growth (Castanet and Báez 1991; Martori et al. 1998; Andreone and Guarino 2003). Consequently, in *Phymaturus*, the climatic restrictions of their habitats might have driven the development of slow life cycles with late maturity at 6–9 years (Piantoni et al. 2006; Boretto et al. 2015; Cabezas-Cartes et al. 2015; and present study). Similar high ages at sexual maturity have been described in liolaemids living in similar environments than *Phymaturus*, at

high altitudes in the Andes Mountains, or at high latitudes in the harsh and cold Patagonia of Argentina (mean 7.1 years, Valdecantos et al. 2007; Gutiérrez et al. 2013).

The comparative analysis in *Phymaturus* showed that the cost–benefit ratio between the time required to growing enough to reach the size for sexual maturity and the life span spent in reproduction (*sensu* Charnov 2002) was different among species. *Phymaturus punae* from the highlands of the Andes and *P. tenebrosus* from the steppe plateaus of Patagonia exhibited the highest age at sexual maturity, and their environments exhibited similar low mean annual minimum temperature (Fig. 3). Nevertheless, females of *palluma* group, *P. antofagastensis* and *P. punae*, exhibit higher adult life span, relative reproductive time, and proportion of adult life than species of the *patagonicus* group, *P. tenebrosus* and *P. spectabilis*, probably because of the influence of a diet strictly herbivorous in species from the *palluma* group in contrast to omnivorous diet in species from the *patagonicus* group, over lifespan of adult individuals. In addition, females of *P. antofagastensis* acquire sexual maturity at a younger age than males, as also do females of *P. tenebrosus* (Piantoni et al. 2006) and *P. punae* (Boretto et al. 2015), probably because an earlier age at maturity allows longer relative reproductive time (*RT*) that could compensate the low (biennial) reproductive frequency. In contrast, females of *P. spectabilis* have higher reproductive frequency (annual–biennial, Boretto et al. 2014a), and mature later and at bigger sizes than males (Cabezas-Cartes et al. 2015) and thus, counteract the delay in the age at which they begin to reproduce, probably favoring an increase in size and/or number of offspring. These results are in agreement with the statements that adult female body size may represent a compromise between selection for increased litter size accomplished by increasing body size, and selection for increased reproductive frequency accomplished by decreasing body size (Beaupre and Duvall 1998).

Phymaturus antofagastensis produces approximately only 4 litter in all their life, due to the relatively short adult life span of females, and the biennial female reproductive cycle, compensated by a high lifetime reproductive effort (*LRE*: 2.16), compared with those described for lizards in general (*LRE*: 1.43; Charnov et al. 2007), and for *P. punae*, in particular (1.85; Table 3). Lifetime reproductive effort (*LRE*) is a key life history parameter due to its influence on fitness, since it includes key concepts of life history theory like reproductive investment, body size of females at sexual maturity, body size of newborns at birth, and adult life span (Charnov et al. 2007). In this sense, the lifetime reproductive effort of *P. antofagastensis* compensates the low reproductive effort of 0.16 per female per year. In contrast, those *Phymaturus* species of the *patagonicus* group that live at lower altitude in the steppe plateaus of Patagonia, which present lower thermal amplitude and higher precipitations than

environments where species from the *palluma* group inhabit (Fig. 3), exhibit low lifetime reproductive effort as a result of the lower proportion of life span that species allocate to reproduction. However, this low lifetime reproductive effort is counteracted by the higher frequency of reproduction and litter size, resulting in a similar production of newborns throughout life in all *Phymaturus* (Table 3).

The production of litters has a cost (“cost of reproduction”, Williams 1966; Shine 1980, 2005) usually estimated by the reproductive effort (*RE*: proportion of biomass allocated to reproduction per unit of time; Charnov et al. 2007). Species with high longevity frequently exhibit low reproductive effort (Shine and Schwarzkopf 1992; Stearns 2000; Charnov et al. 2007), like *P. antofagastensis* and *P. punae* from *palluma* group that presented a high maximum estimated age of 20 years, high number of reproductive events throughout the life, but low reproductive effort. In contrast, *P. tenebrosus* and *P. spectabilis* from *patagonicus* group, presented lower maximum estimated age (16 and 12 years, respectively) than species from the *palluma* group, but high reproductive effort in fewer number of reproductive events in life. These results indicate the existence of a physiological compromise between the number of reproductive events throughout the life and the reproductive effort devoted to each event. Comparing with other groups of reptiles, it has been stated that *Phymaturus* exhibited the lowest rate of specific productivity, defined as the total offspring mass produced per year in relation to the mother mass (*sensu* Meiri et al. 2012). In agreement with Meiri et al. (2012), species from *palluma* group, like *P. antofagastensis* and *P. punae*, present low reproductive effort, but our results show that *patagonicus* species like *P. tenebrosus* and *P. spectabilis* allocated 31% and 25%, respectively, of their biomass in reproduction per year, which represents a reproductive effort by unit of time higher than the median for viviparous lizards (21%; Meiri et al. 2012).

Physiological demands can have a constraining role in life history tradeoffs (Wikelski and Ricklefs 2001). In ectotherms living in cold–temperate environments, slow growth rates and late sexual maturity at greater body sizes are observed (Tinkle et al. 1970; Dunham et al. 1988; Angilletta et al. 2004) since environmental harshness constrains the activity times of the species and, hence, the possibilities to reach body temperatures that allow an optimal physiological performance. Lizards living at low latitudes or altitudes can be active most of the year and have growing seasons that are longer compared to those species that inhabit at high latitudes or altitudes (Adolph and Porter 1993). Environmental constrains in combination with an herbivorous diet in *Phymaturus* may explain the existence of slow life histories characterized by late sexual maturity and high longevity, especially in species of the *palluma* group. Within *Phymaturus*, the similarity among ages at sexual maturity

contrasts with the differences in longevity, since the species of *palluma* group are more long lived than the *patagonicus* species. Although the genus *Phymaturus* is highly conservative in many ecological, physiological and behavioral aspects (Cruz et al. 2009; Debandi et al. 2012; Corbalán et al. 2013), it is possible that certain differences in diet, like a strictly herbivory in the *palluma* group (Espinoza et al. 2004; Videla 1983; Acosta et al. 2008; Castro et al. 2013; Corbalán and Debandi 2014; Córdoba et al. 2015), and an herbivorous–insectivorous diet in some species of the *patagonicus* group (like *P. zapalensis*, Boretto and Ibarquengoytía 2009, Boretto, 2009 and *P. spectabilis*, Personal Observations), reproductive plasticity (strictly biennial in *palluma*, and annual–biennial in *patagonicus*; Boretto et al. 2014a), and environmental conditions (higher thermal amplitude and lower precipitations in *palluma*; lower thermal amplitude and higher precipitations in *patagonicus*, this study), would affect physiological and metabolic processes of the species resulting in the different longevity observed. In the same way, present study shows that the physiological tradeoffs between growth and reproduction evidences two distinctive patterns: on the one hand, the *palluma* group species invest more time of their lives in reproduction but less amount of energy and biomass in each reproductive event; on the other hand, the *patagonicus* species present lower reproductive times which are compensated by higher reproductive frequencies and higher investment in energy and biomass in each reproductive event. The results and conclusions of our study are important for the conservation of these species, reinforcing the vulnerability that presents the genus, since a deep knowledge of life histories of *Phymaturus* enables the planning of management strategies to ensure the sustainability of the populations of this interesting group of lizards.

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