Herpetological Journal

Age, growth and life-history parameters of an endemic vulnerable lizard from Patagonia, Argentina

Facundo Cabezas-Cartes, Jorgelina M. Boretto & Nora R. Ibargüengoytía

[1]INIBIOMA (CONICET – Universidad Nacional del Comahue). Bariloche, Río Negro, Argentina

For ectotherms like lizards, temperature plays a key role in shaping life history traits such as age and size at sexual maturity, longevity and growth. In cold, temperate habitats like Patagonia, balancing the energy expended to growth and reproduction is vital for persistence. In the present study, age and growth of the lizard *Phymaturus spectabilis* were studied using skeletochronology. We estimated individual ages, growth rates and life history parameters related to growth and reproduction. Juveniles were up to five years old. The youngest adult male was six years and the youngest adult female was seven years of age; females reached a higher longevity, and the oldest specimen was a female of 12 years. Resulting from the short activity season of Patagonia, *P. spectabilis* were characterised by delayed sexual maturity and medium longevity. Considering the rather short reproductive lifetime and small clutch size, *P. spectabilis* is characterised by the lowest net reproductive rate documented for liolaemids so far. This suggests that the capability to demographically recover from disturbances is low.

Key words: age, life-history, Liolaemidae, sexual maturity, skeletochronology

INTRODUCTION

The life history of a species comprises several traits related to growth and reproduction, such as age and size at sexual maturity, clutch size, frequency of reproduction, and longevity (Tinkle et al., 1970; Dunham et al., 1988; Stearns, 2000; Gotthard, 2001). One of the most influential environmental variables for the life history of a species is temperature. This is especially true for ectotherms such as reptiles, given the high thermal dependence of many aspects of their physiology and behaviour that affect survival and fecundity (Angilletta et al., 2002; 2004). In lizards however, it has been proposed that selection on life history traits imposed by the thermal environment could also arise through its effect on activity times rather than body temperature per se (Adolph & Porter, 1993; Sears & Angilletta, 2004; Olalla-Tárraga et al., 2006; Horvathova et al., 2013). Considering that the rate and duration of somatic growth determine when sexual maturity is reached, lizards with a longer activity period should grow more per year and may mature sooner at a smaller size (Adolph & Porter 1993). In cold temperate climates, short active seasons result in less opportunity for growth, reflected in distinctive life history traits such as late maturity and increased longevity (Tinkle et al., 1970; Dunham et al., 1988; Wapstra et al., 2001).

In cold climates, lizards must be efficient thermoregulators in order to reach body temperatures included in their set point range (T_{set}: interquartile of T_{pref},

Barber & Crawford, 1977; Firth & Turner, 1982). Lizards present behavioural mechanisms of thermoregulation, usually consisting of basking on exposed rocks during the morning and evening, and moving under bushes or inside crevices during noon (Bauwens et al., 1996). Behavioural thermoregulation requires energy expenditure, and increases mortality risk and missed opportunities for feeding or reproduction (Angilletta, 2009). Organisms moving between microclimates will spend more energy, attract more predators, and alarm more possible prey compared to organisms that remain still (Huey, 1974; 1982; Huey & Slatkin, 1976). Energy expended for moving between thermal microsites to thermoregulate cannot be used to grow or reproduce, which could prolong the time needed to reach sexual maturity (Angilletta, 2009).

Seasonal extremes in climates, with long cold winters and short summer breeding seasons, are common at high altitudes in the Andes of Argentina and Chile, and at high latitudes, in Patagonia, Argentina, where many liolaemid lizards live (Cei, 1986; Pincheira-Donoso et al., 2008, Díaz-Gómez, 2009, Morando et al., 2013). The climatic restrictions of these habitats poses significant limitations for growth. For example, in the Argentinean Puna, at 3478 m asl, *Liolaemus multicolor* males mature at 12 years and females at 9 years, attaining longevities of up to 20 years (Table 1; Valdecantos et al., 2007). However, the sympatric *L. irregularis* matures earlier and attains a significantly lower longevity, which has been explained by a different reproductive behaviour (Table 1; Valdecantos et al., 2007, see also Scharf et al., 2014).

Correspondence: Facundo Cabezas-Cartes (facundo.cabezas.cartes@gmail.com)

Table 1. Age and size at sexual maturity, longevity, net reproductive rate (R_0), thermoregulatory efficiency (E), altitude (m asl), and mean±standard error or median, and (range) of air temperatures (T_a), preferred temperatures (T_{pref}), operative temperatures (T_e) and body temperatures (T_b) of *L. multicolor, L. irregularis, L. pictus argentinus, P. tenebrosus* and *P. spectabilis*. [a] Valdecantos et al. (2007); [b] Valdecantos et al. 2013; [c] Gutierrez et al., 2013; [d] Gutierrez et al., 2010; [e] Piantoni et al., 2006a; [f] unpublished data.

Species	Age at Sexual maturity	Size at Sexual maturity	Longevity	R_0	E	Altitude	T_a	T_{pref}	T_e	T_b
Liolaemus multicolor [a,b]	♂=12 ♀=9	♂=53.9 mm ♀=55.6 mm	♂=16 ♀=19	-	0.94	3478	32.66±4.81 (20.9–42.6)	35.2±0.5	32.2±10.5	36.5±1.3 (33.7–39.1)
Liolaemus irregularis [a,b]	♂=7 ♀=8	♂=61.7 mm ♀=62.1 mm	♂=10 ♀=8	-	0.88	3478	32.66±4.81 (20.9–42.6)	36.2±1.8	32.2±10.5	36.6±1.4 (33.1–39.3)
Liolaemus pictus argentinus (high altitude) [c,d]	♂=4 ♀=3	♂=51.4 mm ♀=50.4 mm	♂=8 ♀=8	9	0.40	1692	22.8±1.0 (14.3–37.2)	36.2±2.08	24.9 (20.6–37.9)	28.9±4.38 (22.7–37.0)
Liolaemus pictus argentinus (low altitude) [c,d]	♂=4 ♀=4	♂=49.8 mm ♀=51.7 mm	♂=9 ♀=7	9	0.24	771	23.2±0.9 (16.6–36.0)	35.6±2.74	31.3 (17.7–59.5)	32.6±5.17 (22.3–43.5)
Phymaturus tenebrosus [e,f]	♂=9 ♀=7	♂=87.2 mm ♀=90.2 mm	♂=13 ♀=16	9	0.71	902	-	36.03±2.64	12.87 (-0.9–45.4)	28.95±0.83 (22.0–35.0)
Phymaturus spectabilis [f]	♂=6 ♀=7	♂=79 mm ♀=83 mm	♂=11 ♀=12	6.7	0.45	1023	21.51±4.39 (14.8–30.0)	33.54±2.34	24.41	30.01±4.68 (16–35.8)

Liolaemus pictus argentinus, an insectivorous species of the template forests (770–1770 m asl), mature relatively early and live up to 9 years (Table 1; Gutierrez et al., 2013), whereas *Phymaturus tenebrosus* (previously known as *Phymaturus patagonicus;* Lobo & Quinteros, 2005), a herbivorous species of steppe rocky habitats (575–1230 m asl), presents delayed maturity and high longevity (Table 1; Piantoni et al., 2006a). The genus *Phymaturus* is characterised by a viviparous reproductive mode, a strictly saxicolous life style, predominantly herbivorous diets and conserved thermal preferences (Cei, 1986; Espinoza et al., 2004; Scolaro, 2005; 2006; Ibargüengoytía et al., 2008; Pincheira-Donoso et al., 2008, Cruz et al., 2009; Corbalán et al., 2013). While the reproductive biology of the genus has been the focus of several studies (Ibargüengoytía, 2004; Boretto & Ibargüengoytía, 2006; 2009; Boretto et al., 2007; 2014a; Cabezas-Cartes et al., 2010), little is known about the age and growth of the species of the genus.

Skeletochronology is a technique for age and growth estimation that has been widely used in many species of reptiles from temperate and tropical habitats (Castanet, 1978, 1979; Castanet & Roche, 1981; Castanet et al., 1988; Patnaik & Behera, 1981; Smirina & Ananjeva, 2007). Lizards are the best studied group because of their simple bone structure with low vascularisation (except varanids) and thus no intracortical remodelling and few supplementary marks (Castanet, 1994). Lizards from temperate regions appear better study models than tropical species, given that their growth rings are more evident (Cagle, 1950; Enlow, 1969). In the present study,

we used skeletochronology as a tool for age estimation in *Phymaturus spectabilis*. In addition, we determined age at sexual maturity and other life history parameters relating to reproduction. Considering the homogeneity of life history traits within genus, we predict that *P. spectabilis* will present a growth pattern similar to *P. tenebrosus*. We provide novel information regarding the life history of this vulnerable and endemic species (Abdala et al., 2012) essential for conservation and management.

MATERIAL AND METHODS

Study area and sampling
The studied specimens were collected from a population of *P. spectabilis* located 25 km south of Ingeniero Jacobacci, Río Negro Province, Argentina (41°26' S and 69°45' W, 983 to 1064 m asl). This biotope is included within the occidental district of the Patagonian steppe, a steppe showing open ground, with gravel and effusive rocks. The dominant landscape is barren steppe, with shrubby, low herbaceous coverage, and bare soil percentages above 50%. The dominant vegetation is composed by cushion bushes and sparse large clumps, and the Floristic Physiognomy Dominions are low shrubby steppes, and mean shrubby-grass steppes (Cabrera, 1971). The outcrops of Patagonia are characterised by a diverse, regionally varied flora. The predominant plant families are Poaceae followed by Asteraceae (Speziale & Ezcurra, 2012). According to data obtained from the National Meteorological Service of the Argentinean Air Force station Maquinchao (87 km northeast of the
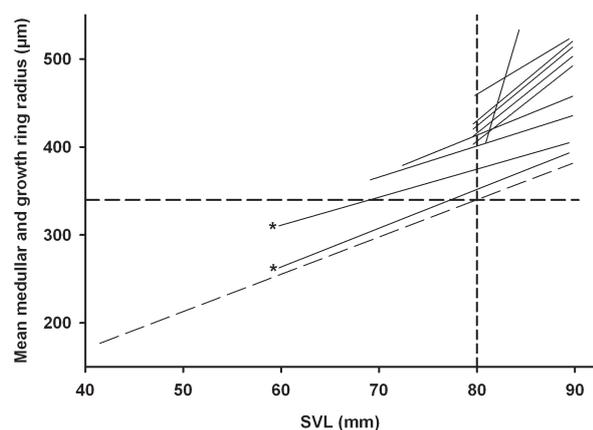
Fig. 1. Estimation of medullar resorption. Regression lines of the observed medullar radius versus SVL (long dashed line) and radius of LAGs versus SVL (continuous lines) in *P. spectabilis*. Medullar resorption was calculated placing a vertical line on a particular SVL (in this case 80 mm) and a horizontal line on the intersection between the vertical line and the medullar radius regression line. The number of reabsorbed rings at a certain SVL corresponds to the number of regression lines that are under the horizontal line mentioned above (in this case for a individual of 80 mm, two reabsorbed rings; methodology used in Piantoni et al., 2006 a, b, and Gutiérrez et al., 2013). Asterisks illustrate the regression lines below the horizontal line.

study site), the mean maximum temperature in the area reaches 27°C in late January, and the mean minimum temperature reaches -5°C in late July. Precipitation reaches an annual mean of 185 mm, with a peak in winter.

We captured 5 juveniles, 16 males and 10 females of *P. spectabilis*, during the active season (late September to late March) between 2006 and 2012. We further included five juvenile specimens (ages 0 to 5) from the J.A. Scolaro-Diagnostic Collection, CENPAT-CONICET, Puerto Madryn, Argentina, sampled from the same population in 2006. Specimens were captured by slipknot, and transported to the laboratory of the Department of Zoology at the Centro Regional Universitario Bariloche, Universidad Nacional de Comahue, San Carlos de Bariloche, Argentina. For histological studies, the specimens were euthanised with an overdose of thiopental sodium, fixed in a Bouin solution for 24 hours, and transferred to a solution of 70% ethanol. Snout-vent length (SVL) of each lizard was measured using a digital vernier caliper (SVL

±0.01 mm). The reproductive stages of the individuals used in the present study were obtained from Boretto et al. (2014a), based on morphological and histological analysis of gonads. We deposited the specimens in the collection of the Centro Regional Universitario Bariloche of the Universidad Nacional del Comahue.

Histological techniques and age determination
Our skeletochronological techniques were adapted from the standard procedures of Piantoni et al. (2006a) and Gutierrez et al. (2013). The left femur of each specimen was removed for decalcification and placed in 5–7% nitric acid; the smaller femurs for 3 hours and the larger ones for 6 hours. Bones were then dehydrated through a series of increasing concentrations of ethanol solutions, cleared with toluene, and then embedded in paraplast for at least 24 hours at 60°C. Cross-sections at mid-diaphysial level were stained with Hematoxylin and Eosin according to Martoja & Martoja Pierson (1970).

The histological preparations were analysed and photographed using an Olympus BX40 microscope equipped with a Pro-Series High Performance CCD Camera. Digital images were taken at different magnifications (x40, x100, x200 and x400) and measurements made using an Image-Pro Plus analyser. The five best sections of each bone were selected from an approximated total of 50 slices per specimen, to estimate the following variables proposed by Leclair & Castanet (1987): (i) the minimum and maximum radius from the centre of the medullar cavity, (ii) minimum and maximum diaphysial diameter, (iii) growth rings thickness, and (iv) the number of lines of arrested growth (LAGs). We assume LAGs correspond to annual arrested winter growth and thus, lizard age. The average of the minimum and maximum radius of each variable was calculated to minimise the asymmetry of the bone sections and medullar cavity.

When endosteal resorption of LAGs was present, estimated age was calculated using the size of the marrow cavity of newborns in order to back-calculate the number of rings reabsorbed. Medullar resorption was calculated graphically in a plot of mean medullar and growth rings radius versus SVL (Fig. 1). The estimation of the growth rings reabsorbed by an individual was calculated by placing a vertical line on its value of SVL and a horizontal line on the intersection between the vertical line and the medullar radius regression line. The number of reabsorbed rings corresponds to the

Table 2. Sex, reproductive state, and mean±SE, and range of SVL (mm), number of LAGs and estimated age (years) of *P. spectabilis*.

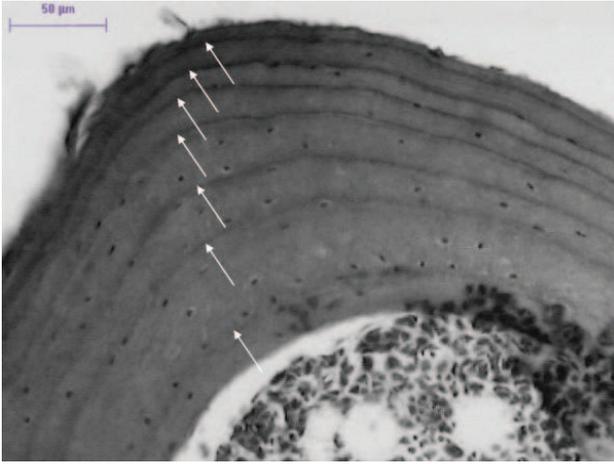| Sex and reproductive state (*n*)	SVL	Number of LAGs	Estimated age
Juveniles males (2)	46.12±1.20 (44.92–47.33)	0±0 (0)	0±0 (0)
Juvenile females (8)	58.91±3.78 (41.5–72.4)	1.62±0.53 (0-4)	1.87±0.66 (0–5)
Adult females (10)	86.51±2.50 (83.13–89.76)	9.1±1.10 (7–11)	10.3±1.70 (7–12)
Adult males (16)	82.91±2.28 (79.62–86.91)	8.62±1.41 (6–11)	9.25±1.39 (6–11)

Fig. 2. Diaphysial cross-section of an 11 year old female of *P. spectabilis* with 3 reabsorbed LAGs. Arrows indicate the lines of arrested growth (LAGs).

number of regression lines under the horizontal line for that size (Fig. 1; methodology used in Piantoni et al., 2006a, b, and Gutiérrez et al., 2013). In those cases, the number of reabsorbed rings was added to the number of observed rings to estimate age. The outer rings were only considered for age estimation when the date of death of the specimen corresponded to the period from February to April when lizards start brumation, considering that births occur in February in this species (Boretto et al., 2014a). Specimens younger than 1 year were considered as age class 0. Age at maturity was determined considering the youngest adult specimen of each gender that presented reproductive activity following Boretto et al. (2014a).

Growth models and life history

To determine the relationships between individual SVL and age (in months), we obtained the three best fitted curves for males, females and the total of specimens using the software Table Curve 2D v.5.01 (SYSTAT Software Inc., 2002). The best models were chosen according to the corrected Akaike information criterion (AICc; Hurvich & Tsai, 1989; Angilletta, 2006). Growth rates were calculated as the first derivative of the curve of SVL versus age for the model chosen. Specific growth rates were obtained by dividing the growth rates by the SVL of each individual.

For comparative purposes we also estimated the growth curve according to von Bertalanffy's (1938) equation: ($L_t = L_\infty[1 - e^{-k(t-to)}]$), where L_t is the body size at time t, L_∞ is the asymptotic body size that correspond to the estimated maximum mean SVL that can be reached, and the growth coefficient (K) is the rate at which asymptotic SVL is reached and determines the shape of the curve. The curve was fitted to length-at-age (in months) data, with separate readings for males and females.

We estimate the following life history parameters related to growth and reproduction following Charnov (2002, 2005): (i) relative reproductive time (*T*), considering the average adult life span and the age at first reproduction of males and females, and (ii) the net reproductive rate (R_0), which is the number of offspring

produced over an individual's life span, estimated as the product of: clutch size x reproductive frequency x relative reproductive time. Clutch size and frequency of reproduction were obtained from Boretto et al. (2014a).

Statistical analysis

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 for 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 models chosen to decide which growth model provided the best fit among them (Angilleta, 2006). The AICc modifies the standard AIC with a correction for small sample sizes (Hurvich & 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 (w_i), as a measure of strength of evidence for each model, indicating the probability that a given model is the best among a series of candidate models (Burnham & Anderson, 2004).

The von Bertalanffy model was adjusted with the Package FSA (Ogle, 2011) in R. Asymptotic SVL (L_∞), and growth constant (K) of the von Bertalanffy growth model were calculated for male and female samples of the studied population. Following the conservative approach of Schoener & Schoener (1978) we considered as significant the observed differences between sample estimates of growth curve parameters only if their 95% bootstrapped confidence intervals did not overlap.

Assumptions of normality and homogeneity of variance were tested with the one-sample Kolmogorov-
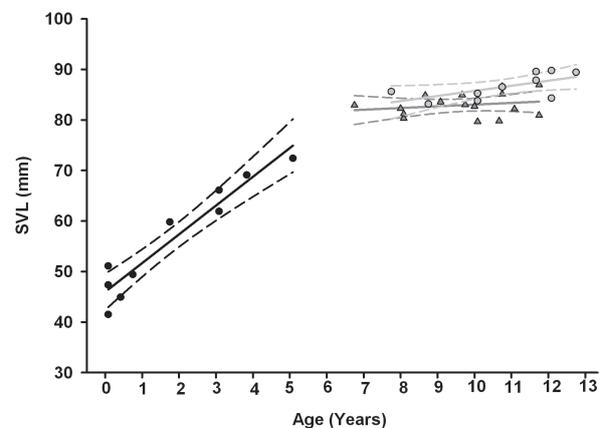

Fig. 3. Regressions of SVL versus age of juveniles (black line and full circles), females (light grey line and circles), and males (dark grey line and triangles). The discontinued lines indicate the 95% confidence intervals.

Smirnov test and with the Levene test, respectively (Sokal & Rohlf, 1969). Means are given±standard error (SE). We used the statistical software Sigma Stat 3.5® (Systat Software Inc., Chicago, Illinois, U.S.A.), Sigma Plot 10.0® (Systat Software Inc., Chicago, Illinois, U.S.A.), Table Curve 2D v. 5.01 (SYSTAT Software Inc., 2002), and R v. 3.1.1 (R Core Team, 2014).

RESULTS

Bone growth patterns and age

The individuals exhibited similar bone growth patterns of lamellar bone. Most of the mid-diaphyses examined showed periosteal bone with an abundant number of rounded osteocytes, and a larger medullar cavity diameter was observed in older specimens. Lines of arrested growth (LAGs) were strongly stained by Hematoxylin and appeared between lighter and thicker growth zones which correspond to growth rings (Fig. 2). Endosteal bone was characterised by elongated osteocytes and delimited by an irregular resorption line. Periostium and endostium were observed as layers of osteoblasts surrounding the femur and the medulla, respectively.

Medullar radius showed a significant increment with SVL (Linear Regression, $F_{1, 35}$=63.236, r^2=0.650, p<0.001). Medullar resorption removed a maximum of one growth ring in juveniles, and from one to four growth rings in adults. The number of rings removed was significantly higher in females than males (Mann-Whitney, U=43.5, p=0.010; median $_{females}$=2.5 rings, median $_{males}$=2 rings). The estimated age, adjusted for reabsorbed growth rings, ranged from one to five years for juveniles (Table 2). Age did not differ between females and males (Mann-Whitney, U=47.5, p=0.084; Table 2).

Body size and growth

Females were significantly larger than males treating estimated age as the covariate (ANCOVA, $F_{1, 26}$=9.175, p=0.006; range $_{males}$=79.62 to 86.91 mm; mean SVL $_{males}$=82.91 mm; range $_{females}$=83.13 to 89.76 mm; mean SVL
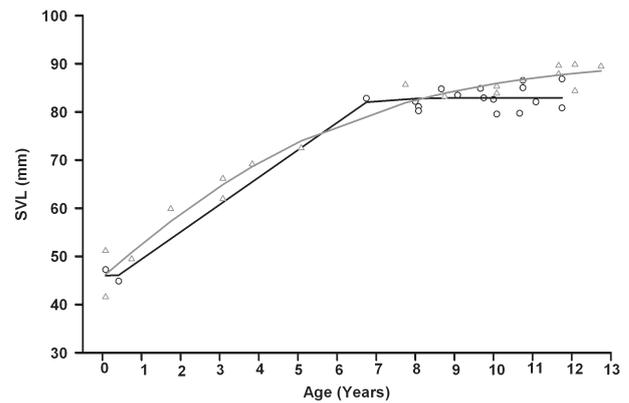

Fig. 4. Sigmoidal relationships between SVL and age in males (black line and circles) and females (grey line and triangles) of *P. spectabilis*.

$_{females}$=86.51 mm). Body length was positively correlated to age in juvenile specimens (Fig. 3; Linear Regression, $F_{1, 9}$=85.168, r^2=0.914, p<0.001). Age was not significantly related to the SVL in males (Linear Regression, $F_{1, 15}$=0.662, r^2=0.045, p=0.429). However, in females age positively affected SVL (Fig. 3, Linear Regression, $F_{1, 9}$=5.782, r^2=0.420, p=0.043).

Table 3 shows the models fitted for the age-at-length data of *P. spectabilis* males, females and overall. In both males and females, the function that best fitted the data was a sigmoidal equation (Fig. 4): y=a+b/(1+exp(-(x-c)/d)). In males, due to the lack of data of juveniles, Table Curve was only able to fit the sigmoidal function. When considering males and females together the growth curve was best fitted by a logarithmic equation (Fig. 5). However, the differences between models adjusted by Table Curve are minimal, as reflected by the AICc differential (Δ_i) and the Akaike weights (w_i, Table 3). Thus, growth rates were calculated from the sigmoidal equation, which allows comparison with the other liolaemids studied in Patagonia.

Growth rates of juveniles were significantly higher than those of adults (Mann-Whitney, U=21, p<0.001).

Table 3. Growth models fitted to the age-at-length data with Table Curve 2D and R package FSA. The number of parameters (K), the corrected Akaike Information criterion (AICc), the differential AICc (Δ_i), the Akaike weight (w_i) and the number of iterations to convergence are presented.

	Model	K	AICc	Δ_i	w_i	Iterations to convergence
Overall (*n*=36)						
	Logarithmical	4	40.79917	0	0.3333622	7
	Logistic	4	40.79924	0.00007	0.3333506	8
	Sigmoidal	4	40.79962	0.00045	0.3332872	10
	Von Bertalanffy	3	184.1859	143.38673	~0	7
Females (*n*=18)						
	Sigmoidal	4	24.61101	0	0.3333839	11
	Logistic	4	24.61138	0.00037	0.3333222	11
	Logarithmical	4	24.61155	0.00054	0.3332939	9
	Von Bertalanffy	3	91.62219	67.01118	~0	7
Males (*n*=18)						
	Sigmoidal	4	25.08113	0	~1	60
	Von Bertalanffy	3	92.37324	67.29211	~0	13

Table 4. Summary of the estimated parameters, growth coefficient (K) and asymptotic SVL (L_∞) for each von Bertalanffy growth curve for the population of *P. spectabilis*. The sample size (*n*), the 95% bootstrapped Lower Confidence interval (LCI), the 95% bootstrapped Upper Confidence Interval (UCI), and the standard error (±SE) are also indicated.

	K	LCI - UCI of K	Asymptotic SVL (L_∞)	LCI - UCI of L_∞
Overall (*n*=36)	0.014±0.002	0.011-0.018	92.031±2.611	88.480-97.909
Females (*n*=18)	0.013±0.002	0.009-0.016	96.350±3.674	90.342-104.203
Males (*n*=18)	0.024±0.008	0.014-0.045	85.432±2.437	82.587-91.437

Additionally, the specific growth rates of adult females were significantly higher than those of adult males (Mann-Whitney, *U*=6, *p*<0.001). The observed differences between males and females' growth curve parameters of the von Bertalanffy equation were not significant (Table 4).

Life history parameters

The youngest adult male of the sample was a specimen of six years, and the youngest adult female was a specimen of seven years. Based on LAGs, the maximum estimated age was 11 years for males and 12 years for females. Considering these data, the estimated relative reproductive time (*T*) was 0.83 for males and 0.71 for females. The net reproductive rate (R_0) estimated was 6.7 offspring over a reproductive female life span, considering the frequency of reproduction of 1.5 years (given that the female reproductive cycle is annual-biannual) and the mean clutch size of two offspring (Boretto et al., 2014a).

DISCUSSION

Phymaturus spectabilis showed the ring bone pattern typical of species that inhabit highly seasonal environments characterised by thick zones of spring-summer growth interrupted by thin lines that correspond to the periods of arrested growth during winter. The bone resorption estimation resulted in one to four growth rings reabsorbed, similar to that observed in the slightly larger *P. tenebrosus* (maximum of six rings reabsorbed, Piantoni et al., 2006a). However, in *Liolaemus*, despite being smaller in size, the resorption is significantly higher: 1–4 and 2–6 rings reabsorbed in juveniles and adults of *L. pictus argentinus*, respectively (Gutierrez et al., 2013), 1–7 rings reabsorbed in *L. irregularis*, and 2–14 rings reabsorbed in *L. multicolor* (Valdecantos et al., 2007).
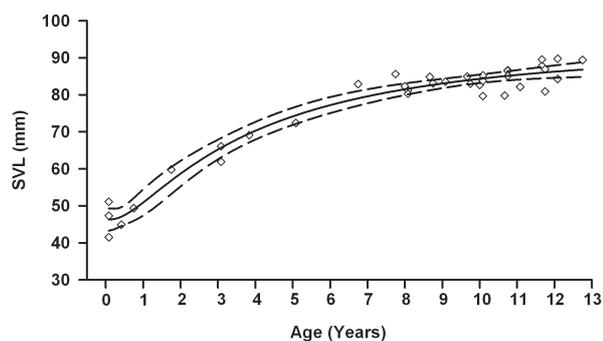

Fig. 5. Logarithmic relationship between SVL and age considering the whole sample of *P. spectabilis*.

Bone resorption is generally considered as the consequence of mechanical constraints and physiological demands (Castanet et al., 1993). Liolaemids resorption rates are high when compared to other similar-sized lizards inhabiting cold temperate habitats (for example *Lacerta agilis* shows 1–2 LAGs partially or completely removed, Roitberg & Smirina, 2006; Guarino et al., 2010). The environmental harshness of the Andes and Patagonian steppe might impose greater physiological demands over liolaemids than the environments where other cold-temperate lizards inhabit. The large periods of inactivity and limited food availability might favour a relocation of minerals deposited in bones to other regions of the body.

As in *P. tenebrosus* and *L. pictus argentinus* (Piantoni et al., 2006a; Gutiérrez et al., 2013; respectively), a sigmoid curve fitted best to the age-length relationship for *P. spectabilis* males and females, thus appearing typical for Patagonian liolaemids. In many other species of lizards, growth fits a logistic model (e.g., Tinkle, 1967; Andrews, 1976, 1982; Dunham, 1978; Schoener & Schoener, 1978; Castanet et al., 1988; El Mouden et al., 1999) or the von Bertalanffy model (James, 1991; Wapstra et al., 2001; Roitberg & Smirina, 2006; Guarino et al., 2010). When considering males and females together, the best fitted equation was the logarithmic function, similar to other liolaemids from Argentinean Puna (*L. irregularis* and *L. multicolor*, Valdecantos et al., 2007). Growth trajectories, however, are generally expected to differ between sexes, given their contrasting energetic demands (Olsson et al., 2002; Cox et al., 2003).

Like most other reptiles, juvenile *P. spectabilis* grow faster than adults, due to an allocation of energy primarily toward growth in juveniles and toward reproduction in adults (Kusano et al., 1995; Measey, 2001; Wapstra et al., 2001; Bruce et al., 2002): sexual maturity is associated with the energy demands of gonadal maturation and other costs associated with reproduction (Andrews, 1982; Shine & Schwarzkopf, 1992; Bernardo, 1993). Females grew faster than males, translating into larger sizes. This contrasts with for example *P. tenebrosus* (Piantoni et al., 2006a), *Homonota darwini* (Piantoni et al., 2006b; Kubisch et al., 2012), *L. irregularis*, *L. multicolor* (Valdecantos et al., 2007), *Iguana iguana* (Zug & Rand, 1987) and *Tupinambis rufescens* (Fitzgerald et al., 1993).

Life-history theory predicts that late maturity at a larger size is favoured by the increment in fecundity or survivorship (Tinkle et al., 1970; Roff, 1992; Kozlowski et al., 2004; Arendt, 2011). The harsh environmental

conditions of Patagonia might have favoured the development of a late maturity life cycle in *P. spectabilis* females. Even when we have to be cautious because of the limited sample size due to working with a vulnerable species, present results showed that *P. spectabilis* females mature later and at a larger size than males. This statement is also sustained by the great heterogeneity in age that was observed for the same body size in both males and females which indicates that sexual maturity might be more dependant of reaching a certain body size as has been found in other lizard species (Zug & Rand, 1987; Leclair & Castanet, 1987; Fitzgerald et al., 1993; Ibargüengoytía & Cussac, 1996; Valdecantos et al., 2007). Particularly, in *Phymaturus* a larger size would increase the survivorship of the offspring by allowing them to reach a greater size at birth rather than increase the fecundity, a common pattern when brood size is small (Olsson et al., 2002). The abundant fat reserves observed in the offspring of *P. spectabilis* (Boretto et al., 2014a), as well as the high parental investment per offspring denoted by large fat bodies and intra-abdominal yolk reserves found in the offspring of *P. punae* (Boretto et al., 2007), *P. antofagastensis* (Boretto, 2009), *P. aguanegra* (Cabezas-Cartes et al., 2010) and *P. zapalensis* (Boretto & Ibargüengoytía, 2009), reinforces this prediction. These reserves could enhance offspring survival, traded against higher investment in offspring which might impede future reproduction for females (Boretto et al., 2007; Boretto & Ibargüengoytía, 2009; Cabezas-Cartes et al., 2010).

Delayed maturity and larger sizes at maturity are common in lizards inhabiting cold climates (Martori et al., 1998; Castanet & Baez, 1991; Andreone & Guarino, 2003). Growth patterns are determined by reaching and maintaining preferred body activity temperatures required for an optimum metabolism (e.g., sprint speed, prey encounter rate, gut-passage rate, food digestion, Avery 1971; Van Damme et al., 1991; Arribas & Galán, 2005; Scharf et al., 2014). In environments with constrained activity periods, thermoregulation efficiency should be under strong selection. The effectiveness of thermoregulation (*E*, *sensu* Hertz et al., 1993) is higher in *P. tenebrosus* than *P. spectabilis* (Table 1), in line with a larger size at sexual maturity. *Phymaturus tenebrosus* appears more efficient in thermoregulating, which might enhance its capabilities for feeding and growing before reaching sexual maturity. In *L. pictus argentinus*, for example, high altitude populations seem to compensate the lower temperatures and shorter active season by enhancing thermoregulation efficiency, which results in similar ages at sexual maturity, reproductive lifespan and fecundities in both low and high altitude populations (Table 1; Gutiérrez et al., 2010, 2013).

Reduced activity seasons correlate with other ecological variables that select for delayed maturation, large body size and higher longevity (Arribas & Galán, 2005; Horvathova et al., 2013; Scharf et al., 2014). It is expected that lizards living in habitats with long activity seasons may benefit from longer growth opportunities at however higher predation risk (Werner & Anholt, 1993). Given that low mortality is associated with higher longevity, females living in cold environments can thus compensate the delayed sexual maturity and lower frequency of reproduction by reaching a higher longevity and thus a larger body size (Kubisch et al., 2012). This could explain the higher longevity registered for *P. tenebrosus* (Piantoni et al., 2006a)*.* The risk of predation in turn might be higher for *P. spectabilis,* as a result of a longer active season and a higher abundance of predators (Scolaro et al., 2008; Cabezas-Cartes, 2013).

A longer reproductive life could mitigate the negative effects of delayed maturity, prolonged reproductive cycles and small clutch sizes over the net reproductive rate (R_0). R_0 is higher in *P. tenebrosus* than in *P. spectabilis* (Table 1), due to a longer relative reproductive lifetime (0.71 versus 1.28 years; Piantoni et al., 2006a). In the same way, R_0 of *L. pictus argentinus* is higher than for *P. spectabilis* due to its bigger clutch size (Table 1; Ibargüengoytía & Cussac, 1996). As a result, *P. spectabilis* has the lowest value of net reproductive rate across *Liolaemidae* so far. This suggests that population declines for example caused by bushfires, prolonged drought and volcanic ashfall (see Cabezas-Cartes et al., 2014; Boretto et al., 2014b) can only be followed by rather slow demographic recoveries (Dubey et al., 2013). Considering that *P. spectabilis* has recently been categorised as Vulnerable (Abdala et al., 2012), future studies should focus on the population dynamics of the species.

ACKNOWLEDGEMENTS

REFERENCES

Abdala, C.S., Acosta, J.L., Acosta, J.C., Alvarez, B., et al. (2012). Categorización del estado de conservación de los lagartos de la República Argentina. *Cuadernos de Herpetología* 26, 215–248.

Adolph, S.C. & Porter, W. (1993). Temperature, activity, and lizard life histories. *American Naturalist* 142, 273–295.

Adolph, S.C. & Porter, W. (1996). Growth, seasonality, and lizard life histories: age and size at maturity. *Oikos* 77, 273–295.

Andreone, F. & Guarino, F.M. (2003). Giant and long-lived? Age structure in *Macroscincus coctei*, an extinct skink from Cape Verde. *Amphibia-Reptilia* 24, 459–470.

Andrews, R.M. (1976). Growth rate in island and mainland anoline lizards. *Copeia* 1976, 477–482.

Andrews, R.M. (1982). Patterns of growth in reptiles. In *Biology of the Reptilia. Volume 13, Physiology: D. Physiological ecology*, 273-320. Gans, C. & Pough, F.H. (eds.). New York: Academic Press.

Angilletta, J.M. Jr. (2006). Estimating and comparing thermal

performance curves. *Journal of Thermal Biology* 31, 541–545.

Angilletta, J.M. Jr. (2009). *Thermal adaptation. A theoretical and empirical synthesis*. Oxford: Oxford University Press.

Angilletta, J.M. Jr., Hill, T. & Robson, M.A. (2002). Is physiological performance optimized by thermoregulatory behavior? A case study of the eastern fence lizard, *Sceloporus undulatus*. *Journal of Thermal Biology* 27, 199–204.

Angilletta, J.M. Jr., Steury, T.D. & Sears, M.W. (2004). Temperature, growth rate, and body size in ectotherms: Fitting pieces of a life-history puzzle. *Integrative and Comparative Biology* 44, 498–509.

Arendt, J.D. (2011). Size-fecundity relationships, growth trajectories, and the temperature-size rule for ectotherms. *Evolution* 65, 43–51.

Arribas, O.J. & Galan, P. (2005). Reproductive characteristics of the Pyrenean high-mountain lizards: *Iberolacerta aranica* (Arribas, 1993), *I. aurelioi* (Arribas, 1994) and *I. bonnali* (Lantz, 1927). *Animal Biology* 55, 163–190.

Avery, R.A. (1971). Estimates of food consumption by the lizard *Lacerta vivipara* Jacquin. *Journal of Animal Ecology* 40, 351–365.

Barber, B.J. & Crawford, E.C. (1977). A stochastic dual-limit hypothesis for behavioural thermoregulation in lizards. *Physiological Zoology* 50, 53–60.

Bauwens, D., Hertz, P.E. & Castilla, A.M. (1996). Thermoregulation in a lacertid lizard: the relative contributions of distinct behavioral mechanisms. *Ecology* 77, 1818–1830.

Bernardo, J. (1993). Determinants of maturation in animals. *Trends in Ecology and Evolution* 8, 166–173.

Boretto, J.M. (2009). *Ecofisiología reproductiva del género Phymaturus (Liolaemidae): estudio histológico, ultraestructural y bioquímico*. Ph.D Thesis. Argentina: Universidad Nacional del Comahue.

Boretto, J.M. & Ibargüengoyía, N.R. (2006). Asynchronous spermatogenesis and biennial female cycle of the viviparous lizard *Phymaturus antofagastensis* (Liolaemidae): reproductive responses to high altitudes and temperate climate of Catamarca, Argentina. *Amphibia-Reptilia* 27, 25–36.

Boretto, J.M. & Ibargüengoytía, N.R. (2009). *Phymaturus* of Patagonia, Argentina: Reproductive biology of *Phymaturus zapalensis* (Liolaemidae) and a comparison of sexual dimorphism within the genus. *Journal of Herpetology* 43, 96–104.

Boretto, J.M., Ibargüengoytía, N.R., Acosta, J.C., Blanco, G.M., Villavicencio, J. & Marinero, J.A. (2007). Reproductive biology and sexual dimorphism of a high-altitude population of the viviparous lizard *Phymaturus punae* from the Andes in Argentina. *Amphibia-Reptilia* 28, 427–432.

Boretto, J.M., Cabezas Cartes, F., Tappari, F., Méndez-De la Cruz, F., Sinervo, B., Scolaro, J.A. & Ibargüengoytía, N.R. (2014a). Reproductive biology of *Phymaturus spectabilis* (Liolaemidae): females skip reproduction in cold and harsh environments of Patagonia, Argentina. *Herpetological Conservation and Biology* 9, 170–180.

Boretto, J.M., Cabezas-Cartes, F., Kubisch, E.L., Sinervo, B. & Ibargüengoytía, N.R. (2014b). Changes in female reproduction and body condition in an endemic lizard, *Phymaturus spectabilis*, following the Puyehue volcanic ashfall event. *Herpetological Conservation and Biology* 9,

181–191.

Bruce, R.C., Castanet, J. & Francillon-Vieillot, H. (2002). Skeletochronological analysis of variation in age structure, body size and life history in three species of desmognathine salamanders. *Herpetologica* 58, 181–193.

Burnham, K.P. & Anderson, D.R. (2004). Multimodel inference: understanding AIC and BIC in model selection. *Sociological Methods and Research* 33, 261–304.

Cabezas-Cartes, F. (2013). *Phymaturus spectabilis* (NCN). Predation. *Herpetological Review* 44, 679.

Cabezas-Cartes, F., Kubisch, E.L. & Ibargüengoytía, N.R. (2014). Consequences of volcanic ash deposition on the locomotor performance of the *Phymaturus spectabilis* lizard from Patagonia, Argentina. *Journal of Experimental Zoology Part A: Ecological Genetics and Physiology* 321A, 164–172.

Cabezas-Cartes, F., Boretto, J.M., Acosta, J.C., Jahn, G.A., et al. (2010). Reproductive biology of *Phymaturus cf. palluma*: A vulnerable lizard from the highlands of the Andes, San Juan, Argentina. *Herpetological Conservation and Biology* 5, 430–440.

Cabrera, A.L. (1971). Fitogeografía de la República Argentina. *Boletín de la Sociedad Argentina de Botánica* 14, 1–42.

Cagle, F.R. (1950). The life history of the slider turtle, *Pseudemys scripta troosti* (Holbrook). *Ecological Monographs* 20, 31–54.

Castanet, J. (1978). Les marques de croissance osseuse comme indicateurs de l'age chez les lezards. *Acta Zoologica* 59, 35–48.

Castanet, J. (1979). Donées comparatives sur la minéralisation des marques de croissance squelettique chez les Vertébrés. *Comptes Rendus de l'Académie des Sciences de Paris* 289, 405–408.

Castanet, J. (1994). Age estimation and longevity in reptiles. *Gerontology* 40, 174–192.

Castanet, J. & Báez, M. (1991). Identificación de dos especies de lagartos de un yacimiento sub-fósil de la isla de Hierro (Islas Canarias) con histología ósea. *Revista Española de Herpetología* 5, 43–49.

Castanet, J. & Roche, E. (1981). Détermination de l'âge chez le lézard des murailles, Lacerta muralis (Laurenti, 1768) au moyen de la squelettochronologie. *Revue Suisse de Zoologie* 88, 215–226.

Castanet, J., Newman, D.G. & Saint Girons, H. (1988). Skeletochronological data on the growth, age and population structure of the tuatara, *Sphenodon punculatus*, on Stephens and Lady Alice Islands, New Zeland. *Herpetologica* 52, 160–171.

Castanet, J., Francillon-Vieillot, H., Meunier, F.J. & de Ricqlès, A. (1993). Bone and individual aging. In *Bone growth*, 245–283. B.K. Hall (ed.). Boca Raton, CRC Press.

Cei, J.M. (1986). *Reptiles del centro, centro-oeste y sur de la Argentina. Herpetofauna de las zonas áridas y semiáridas*. Torino: Museo Regionale di Scienze Naturali.

Charnov, E.L. (2002). Reproductive effort, offspring size and benefit–cost ratios in the classification of life histories. *Evolutionary Ecology Research* 4, 749–758.

Charnov, E.L. (2005). Reproductive effort is inversely proportional to average adult life span. *Evolutionary Ecology Research* 7, 1221–1222.

Corbalán, V., Debandi, G. & Kubisch, E. (2013). Thermal ecology of two sympatric saxicolous lizards of the genus *Phymaturus*

from the Payunia region (Argentina). *Journal of Thermal Biology* 38, 384–389.

Cox, R.M., Skelly, S.L. & John-Alder, H.B. (2003). A comparative test of adaptative hypotheses for sexual size dimorphism in lizards. *Evolution* 57, 1653–1669.

Cruz, F.B., Belver, L., Acosta, J.C., Villavicencio, H.J., et al. (2009).Thermal biology of *Phymaturus* lizards: evolutionary constraints or lacks of environmental variation. *Zoology* 112, 425–432.

Díaz-Gómez, J.M. (2009). Historical biogeography of *Phymaturus* (Iguania: Liolaemidae) from Andean and Patagonian South America. *Zoologica Scripta* 38, 1–7.

Dubey, S., Sinsch, U., Dehling, M.J., Chevalley, M. & Shine, R. (2013). Population demography of an endangered lizard, the blue mountains water skink. *BMC Ecology* 13, 4.

Dunham, A.E. (1978). Food availability as a proximate factor infuencing individual growth rates in the iguanid lizard *Sceloporus merriami*. *Ecology* 59, 770–778.

Dunham, A.E., Miles, D.B. & Reznick, D. (1988). Life history patterns in squamate reptiles. In *Biology of the Reptilia*, 443–511. Gans, C. & Huey, R. (eds). New York: Alan R. Liss.

El Mouden, E.H., Znari, M. & Brown, R.P. (1999). Skeletochronology and mark–recapture assessments of growth in the North African agamid lizard (*Agama impalearis*). *Journal of Zoology* 249, 455–461.

Enlow, D.H. (1969). The bone of reptiles. In *Biology of the Reptilia: 1A*, 45–80. Gans, C. & d'A Bellairs, A. (eds). London: Academic Press.

Espinoza, R.E., Wiens, J.J. & Tracy, C.R. (2004). Recurrent evolution of herbivory in small, cold-climate lizards: breaking the ecophysiological rules of reptilian herbivory. *Proceedings of the National Academy of Sciences USA* 101, 16819–16824.

Firth, B.T. & Turner, J.S. (1982). Sensory, neural, and hormonal aspects of thermoregulation. In *Biology of the Reptilia, vol. 12: Physiology C, Physiological and Ecology*, 213–274. Gans, C. & Pough, F.H. (eds). New York: Academic Press.

Fitzgerald, L., Cruz, F.B. & Perotti, G. (1993). The reproductive cycle and the size at maturity of *Tupinambis rufescens* (Sauria: teiidae) in the dry Chaco of Argentina. *Journal of Herpetology* 27, 70–78.

Gotthard, K. (2001). Growth strategies of ectothermic animals in temperate environments. In *Environment and Animal Development: Genes, Life Histories, and Plasticity*, 287–303. Atkinson, D. & Thorndyke, M. (eds). Oxford: BIOS Scientific Publishers.

Guarino, F.M., Di Già, I. & Sindaco, R. (2010). Age and growth of the sand lizards (*Lacerta agilis*) from a high Alpine population of north-western Italy. *Acta Herpetologica* 5, 23–29.

Gutiérrez, J.A., Krenz, J.D. & Ibargüengoytía, N.R. (2010). Effect of altitude on thermal responses of *Liolaemus pictus argentinus* in Argentina. *Journal of Thermal Biology* 35, 332–337.

Gutiérrez, J.A., Piantoni, C. & Ibargüengoytía, N.R. (2013). Altitudinal effects on life history parameters in populations of *Liolaemus pictus argentinus* (Sauria: Liolaemidae). *Acta Herpetologica* 8, 9–17.

Hertz, P.E., Huey, R. & Stevenson, R.D. (1993). Evaluating temperature regulation by field-active ectotherms: the fallacy of the inappropriate question. *American Naturalist* 142, 796–818.

Horvathova, T., Cooney, C.R., Fitze, P.S., Oksanen, T.A., et al. (2013). Length of activity season drives geographic variation in body size of a widely distributed lizard. *Ecology and Evolution* 3, 2424–2442.

Huey, R.B. (1974). Behavioral thermoregulation in lizards: importance of associated costs. *Science* 184, 1001–1003.

Huey, R.B. (1982). Temperature, physiology, and the ecology of reptiles. In *Biology of the Reptilia*, 25–91. Gans, C. & Pough, F. H. (eds). New York: Academic Press.

Huey, R.B. & Slatkin, M. (1976). Cost and benefits of lizard thermoregulation. *Quarterly Review of Biology* 51, 363–384.

Hurvich, C.M. & Tsai, C.L. (1989). Regression and time series model selection in small samples. *Biometrika* 76, 297–307.

Ibargüengoytía, N.R. (2004). Prolonged cycles as a common reproductive pattern in viviparous lizards species from Patagonia, Argentina: reproductive cycles of *Phymaturus patagonicus*. *Journal of Herpetology* 38, 73–79.

Ibargüengoytía, N.R. & Cussac, V.E. (1996). Reproductive biology of *Liolaemus pictus* (Tropiduridae): a biennial viviparous lizard? *Herpetological Journal* 6, 137–143.

Ibargüengoytía, N.R., Acosta, J.C., Boretto, J.M., Villavicencio, H.J., et al. (2008). Field thermal biology in *Phymaturus* lizards: comparisons from the Andes to the Patagonian steppe in Argentina. *Journal of Arid Environments* 72, 1620–1630.

James, C.D. (1991). Growth rates and ages at maturity of sympatric scincid lizards (*Ctenotus*) in Central Australia. *Journal of Herpetology* 25, 284–295.

Kozłowski, J., Czarnołęski, M. & Dańko, M. (2004). Can optimal resource allocation models explain why ectotherms grow larger in cold? *Integrative and Comparative Biology* 44, 480–493.

Kubisch, E., Piantoni, C., Williams, J., Scolaro, A., et al. (2012). Do higher temperatures increase growth in the nocturnal gecko *Homonota darwini* (Gekkota: Phyllodactylidae)? A skeletochronological assessment analyzed in temporal and geographic scales. *Journal of Herpetology* 46, 587–595.

Kusano, T., Fukuyama, K. & Misshayita, N. (1995). Age determination of the stream frog *Rana sakuraii* by skeletochronology. *Journal of Herpetology* 29, 625–628.

Leclair, R. & Castanet, J. (1987). A skeletochronological assessment of age and growth in the frog *Rana pipiens* Schreber (Amphibia, Anura) from southwestern Quebec. *Copeia* 1987, 361–369.

Lobo, F. & Quinteros, S. (2005). A morphology-based phylogeny of *Phymaturus* (Iguania: Liolaemidae) with the description of four new species from Argentina. *Papéis Avulsos de Zoologia* 45, 143–177.

Martoja, R. & Martoja Pierson, M. (1970). *Técnicas de histología animal*. Barcelona: Toray-Masson.

Martori, R., Cardinale, L. & Vognolo, P. (1998). Growth in a population of *Liolaemus wiegmannii* (Squamata: Tropiduridae) in central Argentina. *Amphibia-Reptilia* 19, 1–9.

Measey, G.J. (2001). Growth and ageing of feral *Xenopus laevis* (Daudin) in South Wales, UK. *Journal of Zoology* 254, 547–555

Morando, M., Avila, L.J., Perez, C.H.F., Hawkins, M.A. & Sites, J.W. Jr. (2013). A molecular phylogeny of the lizard genus

223

Phymaturus (Squamata, Liolaemini): implications for species diversity and historical biogeography of southern South America. *Molecular Phylogenetics and Evolution* 66, 694–714.

Ogle, D.H. (2011). FSA: fisheries stock analysis. R package version 0.4.30. Available from: <http://www.rforge.net/FSA/>.

Olalla-Tárraga, M.A., Rodríguez , M.A. & Hawkins, B.A. (2006). Broad-scale patterns of body size in squamate reptiles of Europe and North America. *Journal of Biogeography* 33, 781–793.

Olsson, M., Shine, R., Wapstra, E., Ujvari, B. & Madsen, T. (2002). Sexual dimorphism in lizard body shape. The roles of sexual selection and fecundity selection. *Evolution* 56, 1538–1542.

Patnaik, B.K. & Behera, H.N. (1981). Age-determination in the tropical agamid garden lizard, *Calotes versicolor* (Daudin) based on bone histology. *Experimental Gerontology* 16, 295–307.

Piantoni, C., Ibargüengoytía, N.R. & Cussac, V.E. (2006a). Age and growth of the Patagonian lizard *Phymaturus patagonicus*. *Amphibia-Reptilia* 27, 385–392.

Piantoni, C., Ibargüengoytía, N.R. & Cussac, V.E. (2006b). Growth and age of the southernmost nocturnal gecko *Homonota darwini*: a skeletochronological assessment. *Amphibia-Reptilia* 27, 393–400.

Pincheira-Donoso, D., Scolaro, J.A. & Sura, P. (2008). A monographic catalogue on the systematics and phylogeny of the South American iguanian lizard family Liolaemidae (Squamata, Iguania). *Zootaxa* 1800, 1–85.

R Core Team (2014). *R: A language and environment for statistical computing*. Vienna, Austria: R Foundation for Statistical Computing. Available: <http://www.R-project.org/>.

Roff, D.A. (1992). *The evolution of life histories: theory and analysis*. New York: Chapman & Hall.

Roitberg, E.S. & Smirina, E.M. (2006). Age, body size and growth of *Lacerta agilis boemica* and *L. strigata*: a comparative study of two closely related lizard species based on skeletochronology. *Herpetological Journal* 16, 133–148.

Scharf, I., Feldman, A., Novosolov, M., Pincheira-Donoso, D., et al. (2014). Late bloomers and baby boomers: ecological drivers of longevity in squamates and the tuatara. *Global Ecology and Biogeography*. doi: 10.1111/geb.12244.

Schoener, T.W. & Schoener, A. (1978). Estimating and interpreting body-size growth in some *Anolis* lizards. *Copeia* 1978, 390–405.

Scolaro, A. (2005). *Reptiles Patagónicos Sur: Una guía de campo*. Trelew: Universidad Nacional de la Patagonia.

Scolaro, A. (2006). *Reptiles Patagónicos Norte: Una guía de campo*. Trelew: Universidad Nacional de la Patagonia.

Scolaro, J.A., Ibargüengoytía, N.R. & Pincheira-Donoso, D. (2008). When starvation challenges the tradition of niche conservatism: On a new species of the saxicolous genus

Phymaturus from Patagonia Argentina with pseudoarboreal foraging behaviour (Iguania, Liolaemidae). *Zootaxa* 1786, 48–60.

Sears, M.W. & Angilletta, M.J. Jr. (2004). Body size clines in *Sceloporus* lizards: proximate mechanisms and demographic constraints. *Integrative and Comparative Biology* 44, 433–442.

Shine, R. & Schwarzkopf, L. (1992). The evolution of reproductive effort in lizards and snakes. *Evolution* 46, 62–75.

Smirina, E.M. & Ananjeva, N.B. (2007). Growth layers in bones and acrodont teeth of the agamid lizard *Laudakia stoliczkana* (Blanford, 1875) (Agamidae: Sauria). *Amphibia-Reptilia* 28, 193–204.

Sokal, R.R. & Rohlf, F. (1969). *Biometry. The Principles and Practice of Statistics in Biological Research*. USA: W.H. Freeman and Co.

Speziale, K. & Ezcurra, C. (2012). The role of the outcrops in the diversity of the Patagonian vegetation: relicts of glacial paleo-flora? *Flora* 207, 141–149.

Stearns, S.C. (2000). Life history evolution: successes, limitations, and prospects. *Naturwissenschaften* 87, 476–486.

Tinkle, D.W. (1967). The life and demography of the side-blotched lizard, *Uta stansburiana*. *Miscelaneous Publications Museum of Zooloogy University of Michigan* 132, 1–182.

Tinkle, D.W., Wilbur, H.M. & Tinlley, S.G. (1970). Evolution strategies in lizard reproduction. *Evolution* 24, 55–75.

Valdecantos, S., Lobo, F. & Martínez, V. (2007). Estimación de edades, tamaño corporal y adquisición de la madurez sexual en dos especies de *Liolaemus* (Iguania: Liolaemidae). *Cuadernos de Herpetología* 21, 31–44.

Valdecantos, S., Martínez, V., Lobo, F. & Cruz, F.B. (2013). Thermal biology of *Liolaemus* lizards from the high Andes: Being efficient despite adversity. *Journal of Thermal Biology* 38, 126–134.

Van Damme, R., Bauwens, D. & Verheyen, R.F. (1991). The thermal-dependence of feeding-behavior, food-consumption and gut-passage time in the lizard *Lacerta vivipara* Jacquin. *Functional Ecology* 5, 507–517.

von Bertalanffy, L. (1938). A quantitative theory of organic growth. *Human Biology* 10, 181–213.

Wapstra, E., Swain, R. & O´Reilly J.M. (2001). Geographic variation in age and size at maturity in a small Australian viviparous skink. *Copeia* 3, 646–655.

Werner, E.E. & Anholt, B.R. (1993). Ecological consequences of the trade-off between growth and mortality rates mediated by foraging activity. *American Naturalist* 142, 242–272.

Zug, G.R. & Rand, A.S. (1987). Estimation of age in nesting female *Iguana iguana*: testing skeletochronology in a tropical lizard. *Amphibia-Reptilia* 8, 237–250.