

Altitudinal effects on life history parameters in populations of *Liolaemus pictus argentinus* (Sauria: Liolaemidae)

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Abstract. We used skeletochronology to assess the age structure, body size and sexual maturity in two populations of *Liolaemus pictus argentinus* from San Carlos de Bariloche, Argentina. The species occupies a wide altitudinal range within the Patagonian Lake District which enabled us to choose populations from two climatic extremes: 771 m a.s.l. and 1615-1769 m a.s.l. Age of sexual maturity in both populations of *L. p. argentinus* is achieved with a minimum body size of 49 mm. However, at the high-altitude site, lizards matured between the ages of three to six years and had a lifespan of eight years limiting some individual's reproductive life to only two years. Lizards from the low-altitude site achieved maturity at the age of four and lived until the age of nine years old. Despite the environmental variations between sites populations' growth curves' patterns were similar represented by a rapid initial growth rate of 10.3 mm/year in youngest juvenile which slowed considerably to 4.9 mm/year after attaining sexual maturity, as energy is reallocated towards reproduction, to finally grow at a rate of 0.1 mm/year in the oldest adults. Present results show intraspecific differences in *L. pictus*, whether it results from adaptive polymorphism or physiological plasticity remains uncertain.

Keywords. Age estimation, altitudinal range, Patagonia, populations, skeletochronology.

INTRODUCTION

Lizards require an external source of heat to initiate activities in order to obtain resources to grow, reproduce and maintain their physiological functions. The allocation of energy to each of these three processes decreases the amount of energy available for the other two. A disproportionate allocation to only one or two of these functions can affect individual fitness in a given environment (Kubacka and Kratochvil, 2009). Therefore, an

optimal allocation will depend on complex trade-offs among resource availability, physiological and behavioral traits and the environmental conditions (Sears and Angilletta, 2004). For example, individual's maximal growth can be affected when resources, such as food or water, diminish or when predators, which may limit foraging, become more numerous (Sears and Angilletta, 2004). On the other hand, fast growth reduces the cost of maintenance, and can be enhanced by a more efficient digestion (Sears and Angilletta, 2004), as well as by longer activity hours (Shine, 2005). Besides, faster growing lizards are more exposed to predators and can result in higher mortality than slower growing lizards (Sears and Angilletta, 2004). In particular, the short activity seasons in the

* We remember here our friend Joel Antú Gutierrez who passed away during the revision of the manuscript, for his comradeship and passion for science.

cold-temperate lands of Patagonia, impose severe trade-offs among thermoregulation, reproduction and foraging, since energy storage and a rapid growth of newborns becomes necessary to afford the brumation period and next spring reproduction (Ibargüengoytía and Cussac, 1996, 2002; Boretto and Ibargüengoytía, 2009).

In addition, differences in the spectrum of variation of the life-history traits associated to growth (e.g., growth rates, longevity, age at sexual maturity, and fecundity) between and within populations can vary with daily thermal conditions and the length of the activity season (Sinnero and Adolph, 1989; Niewiarowski and Roosenburg 1993; Wapstra et al., 2001). For lizards, the extent of daily and seasonal duration of activity can be more relevant than the variation in body temperatures (T_b) that can be experienced during activity (Sears and Angilletta, 2004; Angilletta, 2009). For example, differences in the activity regime can happen, as in *Sceloporus merriami* populations, along an altitudinal gradient (Smith and Ballinger, 2001), and lizards that have longer periods of activity are expected to grow quicker and to reach sexual maturity sooner than lizards that have a shorter activity period (Adolph and Porter, 1993; Niewiarowski, 2001). Likewise, intra- and inter-specific differences in daily metabolic rates were found in two species of the genus *Pristidactylus* that inhabit different thermal areas, being higher in the forest than in the sunnier and warmer shrublands areas (Labra and Rosenmann, 1992).

The activity and brumation periods of lizards from temperate regions like Patagonia are defined by the strong seasonality between winter and summer. Moreover this pattern generates cyclical growth, characterized by an alternation between fast growth in spring-summer and slow growth in autumn-winter (Leclair and Castanet, 1987; Wake and Castanet, 1995). Previous studies confirmed that femurs of *Phymaturus tenebrosus* (Piantoni et al., 2006a) and the geckonid *Homonota darwini* (Piantoni et al., 2006b; Kubisch et al., 2012) exhibited growth marks associated to periods of high and low growth rates. The same pattern was found in *Liolaemus multicolor* and *L. irregularis* (Valdecantos et al., 2007) from the highlands of Salta, Argentina, and in the amphibian *Pleurodema thaul* (Iturra-Cid et al., 2010) from central and southern Chile.

Here we compare growth, longevity, and fecundity of two populations of *Liolaemus pictus argentinus*, located at approximately the same latitude and longitude (41°15'S, 71°17'W) but at different altitudes: 771 m a.s.l. in Melipal beach, and 1615-1769 m a.s.l. in the Challhuaco mountain. The following questions were addressed: (1) Is there an intra-specific variation in bone growth patterns related to altitude? (2) Do growth related life history traits vary in relation to habitat air temperature (T_a) in *L. p. argenti-*

nus? Results are discussed based on the differences in the length of the daily and seasonal duration of activity and in the efficiency of thermoregulation observed in previous studies on the same populations (Gutiérrez et al., 2010).

MATERIAL AND METHODS

Study area

Two populations of *Liolaemus pictus argentinus* were sampled at two sites in northwestern Patagonia, Argentina: a) 13 juveniles, seven males and 11 adult females were captured in the area of Challhuaco mountain, in the surroundings of San Carlos de Bariloche, Province of Río Negro, ("high-altitude site", 41°15'57.9"S, 71°17'57.4"W; 1615-1769 m a.s.l.); and b) eight juveniles, 10 males and 11 adult females were collected in Melipal beach by the lake Nahuel Huapi ("low-altitude site", 41°07'41.53"S, 71°20'44.87"W; 771 m a.s.l.). Lizards were captured during activity season 2005 to 2007. Field work was carried out with authorization from the Wild Life Service of the Province of Río Negro and National Park Service.

Capture and autopsy

Specimens were captured by hand or noose, then transported to the Department of Zoology laboratory at the Centro Regional Universitario Bariloche, Universidad Nacional de Comahue, San Carlos de Bariloche, Argentina. For histological studies the specimens were euthanized with an overdose of thiopental sodium, fixed in a Bouin solution for 24 hours, and finally transferred to a solution of 70% ethanol. Lizards' snout-vent length (SVL) was measured using a caliper (SVL \pm 0.02 mm).

Histological technique

One femur of each specimen was removed for decalcification. The pieces were left in 5-7% nitric acid; the smaller pieces for 5 h and the larger ones for 17 h. Bones were then dehydrated through a series of increasing concentrations of ethanol solutions, cleared with toluene, and then embedded in paraplast for 24 h at 60 °C. Cross-sections at mid-diaphyseal level were stained with Hematoxylin and Eosin, according to Martoja and Martoja Pierson (1970).

Determination of growth rate, age, and longevity

The histological preparations were analyzed 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 and X200) and measurements made using an Image-Pro Plus analyzer. The ten best sections of each bone were selected to estimate the following variables proposed by Leclair and Castanet (1987): the

Table 1. Data obtained from bibliography and adapted for comparative purposes. Sexual maturity, longevity and reproductive frequency are expressed in years.

Species	Geographic coordinates and altitude (m a.s.l.)	Sexual maturity	Longevity	Reproductive frequency	Litter size	Fecundity
<i>Holbrookia maculata</i> ^a	41°34'N, 99°43'W; 1170	0.5	4	0.5	4.5	31.7
<i>Homonota darwini</i> ^{b, c}	41°0.8'S, 71°0.8'W; 930	3	9	2	1	4
<i>Hoplodactylus duvauceli</i> ^d	41°0.6'S, 174°25'E; 0	7	36	2	2	29
<i>Woodworthia</i> "Otago/Southland" (formerly <i>Hoplodactylus maculatus</i>) ^{d, f, g}	45°28'S, 170°28'E; 300–700	4	36	2	1.7	22.4
<i>Phymaturus tenebrosus</i> ^{g, h, j}	41°0.8'S, 71°0.8'W; 575–1230	7	16	2	2	9

^aJones and Ballinger, 1987; ^bKubisch et al., 2012; ^cIbargüengoytía and Casalins, 2007; ^dCree, 1994; ^eCree and Guillette, 1995; ^fHare and Cree, 2005; ^gIbargüengoytía, 2004; ^hPiantoni et al., 2006b.

minimum and maximum radius from the center of the medullar cavity (1) minimum and maximum diaphyseal diameter, (2) estival-layers or ring thickness, and (3) the number of lines of arrested growth (LAGs) which corresponds to the winter growth. 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 had taken place, estimated age was calculated using the size of the first growth marks of juveniles in order to back-calculate the number of rings removed following Piantoni et al. (2006a). In those cases the number of reabsorbed rings was added to the number of observed rings.

To determine the relationship between individual SVL and the number of rings, the best fitted curve using the highest r^2 was selected using Table Curve 2D software. Growth rates were calculated as the derivative of the curve of SVL vs. age. Specific growth rates were obtained by dividing the growth rates by the SVL of each estimated age group.

Relationship between growth and reproduction

To estimate fecundity the following variables were taken into consideration: (1) period between age at maturity and longevity, (2) litter size, and (3) frequency of reproduction according to Ibargüengoytía and Cussac (1996). For comparative purposes the fecundity of other reptiles was calculated extracting bibliographical data of age at sexual maturity, longevity, litter size and frequency of reproduction (Table 1).

RESULTS

Body size

The populations did not show differences in body size (Mann-Whitney, $T_{1, 31+29} = 950$, $P = 0.384$; range_{high-altitude} = 23.5 to 62.1 mm; median SVL_{high-altitude} = 50.8 mm; range_{low-altitude} = 24.8 to 64.3 mm; median SVL_{low-altitude} = 56.3 mm; Table 2).

Bone growth patterns

Both populations exhibited similar bone growth patterns of lamellar bone. Most of the mid-diaphyses examined showed periosteal bone with an abundant number of osteocytes and a larger medullar cavity diameter was observed in older specimens. Lines of arrested growth (LAGs), which in *L. p. argentinus* correspond to the winter period, were strongly stained by Hematoxylin and appeared between lighter and thicker growth zones which correspond to summer growth periods (Fig. 1).

Bone resorption and estimated individual age

Medullar radius showed a significant increment with the SVL in femurs of both populations (Regression, $F_{\text{high-altitude } 1, 30} = 40.39$, $P < 0.001$; $F_{\text{low-altitude } 1, 28} = 9.38$, $P < 0.05$). Medullar resorption in both populations removed from one to four rings in juveniles and from two to six in adults (Fig. 2, Table 2).

The estimated age, adjusted for reabsorbed rings, ranged from one to six years for juveniles at high-altitude. Adults, at this site, ranged from three to eight years old in females and from four to eight years old in males (Fig. 3A). At the low-altitude site juveniles' age ranged from one to four years, and in adults from four to seven years in females and from four to nine years in males (Fig. 3B). The relationship between estimated age and SVL in both populations fitted a sigmoid regression ($F_{\text{high-altitude } 3, 30} = 28.45$, $r^2 = 0.76$, $P < 0.0001$; $F_{\text{low-altitude } 3, 28} = 29.26$, $r^2 = 0.78$, $P < 0.0001$; Fig. 4A).

Growth rates and reproductive life

Specific growth rates of juveniles and adults were significantly different within populations (High-altitude site: Mann-Whitney, $T = 283.0$, $P = 0.003$, $n = 31$; Low-

Table 2. Comparison between juveniles, females, and males of *Liolaemus pictus argentinus* populations from Challhuaco mountain and Melipal beach concerning snout-vent length (SVL; mm), marrow radius (MRA; mm), number of reabsorbed rings (RR), measured rings (MR), and estimated age (years).

	Challhuaco mountain (High-altitude site)					Melipal beach (Low-altitude site)					
	SVL	MRA	RR	MR	Age	SVL	MRA	RR	MR	Age	
Juveniles	23.5	0.11	0	0	1	24.8	0.14	0	1	1	
	24.7	0.15	0	0	1	27.2	0.14	0	2	2	
	25.5	0.13	0	0	1	28.7	0.18	1	2	3	
	26	0.13	0	0	1	29.6	0.13	0	2	2	
	30.5	0.15	0	1	1	30.9	0.12	0	2	2	
	34.9	0.2	2	2	4	31	0.15	0	2	2	
	40.4	0.17	1	4	5	43.1	0.22	2	2	4	
	42.4	0.18	1	2	3	44.4	0.16	1	3	4	
	42.9	0.14	0	3	3						
	44.3	0.15	0	4	4						
	46.8	0.15	0	4	4						
	48.7	0.2	2	4	6						
	48.8	0.18	1	2	3						
Females	50.4	0.19	1	2	3	51.7	0.18	2	3	5	
	50.6	0.19	1	2	3	52.3	0.14	0	5	5	
	50.8	0.15	0	3	3	54.6	0.2	2	3	5	
	53	0.18	1	2	3	55.8	0.21	2	3	5	
	55.4	0.2	2	3	5	56.3	0.18	2	4	6	
	54.8	0.17	1	3	4	57	0.19	2	4	6	
	56.5	0.21	3	3	6	57.3	0.2	2	2	4	
	60.5	0.22	3	2	5	57.4	0.17	1	3	4	
	60.7	0.22	3	5	8	57.7	0.19	2	2	4	
	60.8	0.21	3	2	5	57.8	0.18	2	5	7	
	62.1	0.23	3	4	7	64.3	0.14	0	6	6	
	Males	51.4	0.2	2	3	5	49.8	0.14	0	4	4
		56	0.21	3	5	8	54.7	0.17	1	5	6
58.7		0.25	4	3	7	57.8	0.18	2	4	6	
60.2		0.19	1	3	4	58.9	0.15	0	5	5	
60.8		0.16	1	5	6	60.8	0.21	2	5	7	
60.9		0.23	3	3	6	60.2	0.16	0	7	7	
62		0.19	1	4	5	60.1	0.16	1	6	7	
						61.4	0.21	2	2	4	
						61.9	0.19	2	4	6	
					63.2	0.28	6	3	9		

altitude site Mann-Whitney, $T = 199$, $P < 0.001$, $n = 29$; Table 3; Fig. 4B). No differences were found between the specific growth rates of male and female adults in either population (High-altitude site: Mann-Whitney, $T = 50.5$, $P = 0.152$, $n = 18$; Low-altitude site: Mann-Whitney, $T = 89$, $P = 0.138$, $n = 21$; Table 3). The specific growth rates of juveniles and adults from high and low-altitudes were

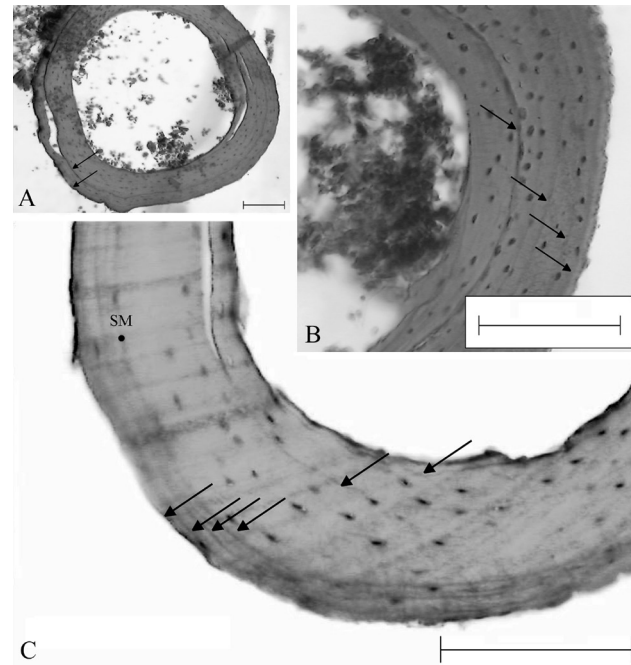


Fig. 1. Diaphysal cross-section of three (A), five (B) and seven (C) year-old specimens of *Liolaemus pictus argentinus*. Arrows indicate the lines of arrested growth (LAGs). SM: first LAG after attaining sexual maturity. Scale bars: 100 mm.

also compared and showed no significant differences (Mann-Whitney, $T_{\text{juveniles}} = 105$, $P = 0.229$, $n = 21$; $T_{\text{adults}} = 347.0$, $P = 0.723$, $n = 39$, Table 3).

Considering the youngest and the oldest adults of both populations, sexual maturity was attained at the age of three and the maximum longevity was nine years. Populations did not show differences in the number of years during which they are reproductively active. The reproductive life, considering the youngest adult male or female, was of five years. Females reproductive cycle in *L. p. argentinus* can be biennial or triennial (reproduction occurs every two or three years) with a mean litter size of 4.5 offspring (Ibargüengoytia and Casalins, 2007). Hence, the annual reproductive output results in 1.8 and a mean fertility of 9 offspring.

DISCUSSION

During the activity season, in the *Nothofagus* forest near the summit of Challhuaco Mountain, the monthly mean air and median operative temperatures ($T_a = 22.8 \pm 1.0$ °C; $T_e = 24.9$ °C) resulted overall lower than at the Melipal beach ($T_a = 23.2 \pm 0.9$ °C; $T_e = 31.3$ °C; Gutiérrez et al., 2010). Possibly due to a greater radiation index, from mid-November to mid-January, *Liolaemus pictus argentinus*

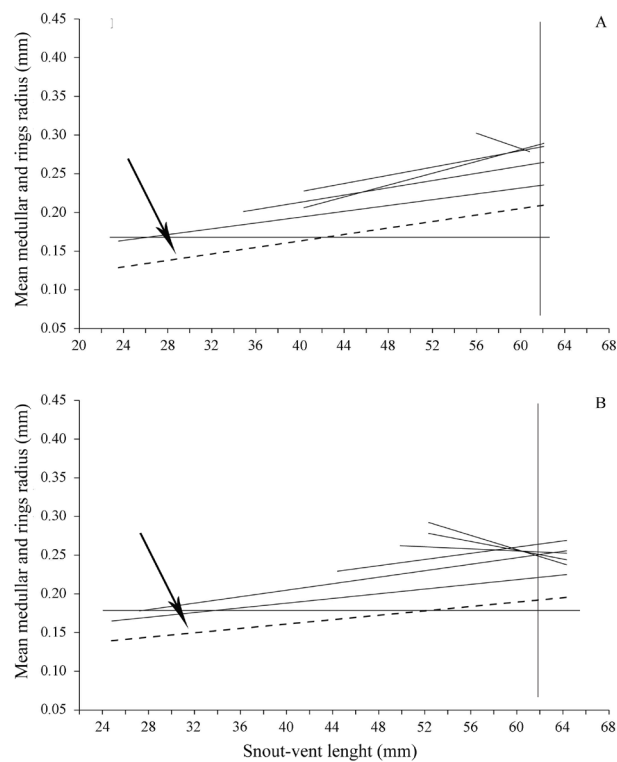


Fig. 2. Estimates of medullar resorption. The lines of lineal regression of the observed medullar radius (arrow and dashed line) and the radius of growth rings (continuous lines) vs. snout-vent length (SVL; mm) in *Liolaemus pictus argentinus* at the high (A) and low (B) altitude sites. Medullar resorption can be calculated placing the vertical line on a particular SVL and the horizontal line on the intersection between the vertical line and the medullar radius regression line. The number of reabsorbed rings would correspond to the number of regression lines under the medullar radius line for that size (methodology used in Piantoni et al., 2006a,b).

experienced warmer T_a s at high-altitude (Gutierrez et al., 2010), while at the beach T_a was buffered by the effect of the lake (Koeppen, 1948). Nevertheless, the winter snow, hence brumation, lasted one month more in the mountains than at the beach reducing the lizards' activity season at the high-altitude site (September, Gutierrez et al., 2010). At high-altitude, *L. p. argentinus* behaved as a moderate thermoregulators (*sensu* Hertz et al., 1993), compensating the fewer warm microenvironments, and the shorter activity season showing low body temperatures ($T_b = 28.97 \pm 0.8$ °C), while at the low altitude site, in a more benign environment, they behaved as thermoconformers, achieving a mean T_b of 32.67 ± 0.9 °C (Gutiérrez et al., 2010). These intra-specific differences among different thermal-ecological environments could have been driven by local selection on fitness through the phenotypes or could also be due to behavioral plasticity associated to its thermal physiology.

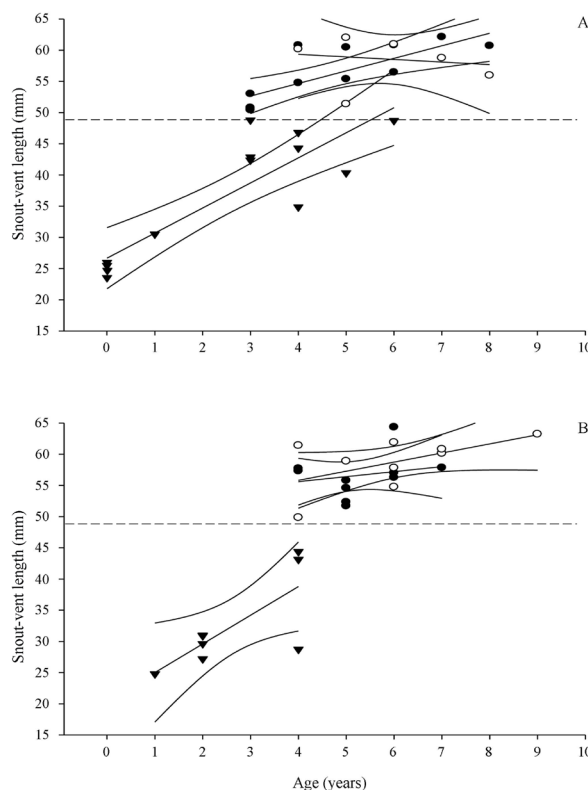
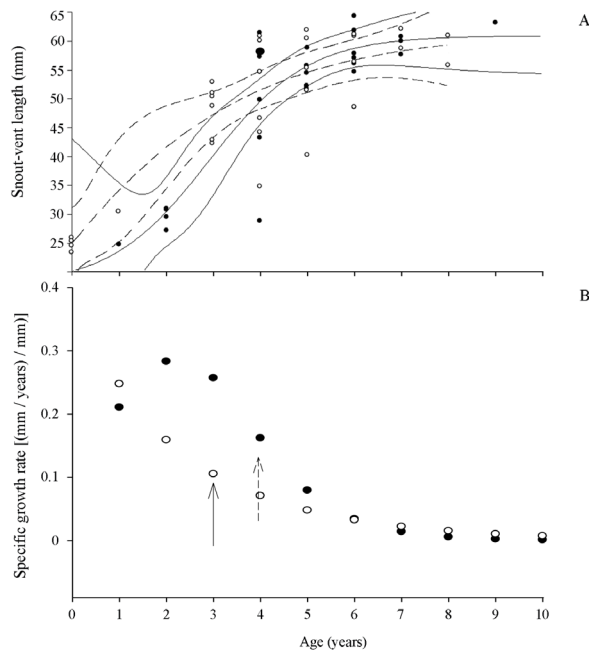


Fig. 3. Growth lines of juveniles (black triangles), females (black dots), and males (empty dots) at the high (A) and low (B) altitude sites (the curve and 95% confidence intervals are indicated). The discontinued line indicates the maximum juvenile size of *Liolaemus pictus argentinus* according to Ibagüengoytia and Cussac (1996).

Behavioral plasticity may counteract the effects of the harsh environmental conditions at high-altitudes, and partially explain the similarities in the growth patterns and SVL of the studied populations. Pincheira-Donoso and Tregenza (2011) discussed how a stronger fecundity selection can direct relative adjustments for optimization of fecundity in species of *Liolaemus* from cold areas. They also suggest that variation in T_a along a geographical gradient alone would poorly explain the real outcome of fecundity selection on reproductive maximization. In support of their conclusions, sexual maturity of *L. p. argentinus* at the high-altitude site was attained earlier in life compensating the shorter lifespan and resulting in the same fecundity output than at the low-altitude. Further tests are needed to determine the real cause of these inter-population differences.

As other ectotherms, growth of *L. p. argentinus* is indeterminate, considerably different in juveniles and adults, and can be assessed by studying the femur's cross sections where growth bands become progressively thin-



ner as the animal grows, especially after reaching sexual maturity. This growth pattern that relates age with SVL can be represented by sigmoidal (Pielou, 1977; Castanet et al., 1988; Measey, 2001; Bruce et al., 2002), logarithmic (Valdecantos et al., 2007) or logistic (Mouden et al., 1999) curves. Growth of *L. p. argentinus* was better modeled by a sigmoidal curve characterized by a greater growth rate in juveniles and an asymptotic phase in adults related to a typical re-allocation of the energy from growth to reproduction (Castanet et al., 1988; Zug and Glor, 1998; Mouden et al., 1999; Wapstra et al., 2001; Roitberg and Smirina, 2006; Guarino et al., 2010). The sigmoidal curve has also characterized the growth of *P. tenebrosus*

(Piantoni et al., 2006a), while the best fitted curve for the growth in other liolemids, *L. irregularis*, and *L. multicolor*, was represented by logarithmic equation (Valdecantos et al., 2007).

Individuals living in warmer areas are predicted to mature earlier, whereas co-specifics from colder environments can sometimes delay maturity, investing available energy into present growth and future reproduction (Roitberg and Smirina, 2006). Based on our results and in agreement with Ibarzüengoytía and Cussac (1996), sexual maturity in *L. p. argentinus* appeared to be body size dependant. Accordingly, a great heterogeneity in age was observed for the same body size (Fig. 3) particularly in juveniles at the high-altitude site. However, in contrast with our prediction, *L. p. argentinus* at higher altitudes achieved sexual maturity earlier, at the age of three years in females and at four to six years in males (Fig. 3A), but longevity in both sexes was of eight years. On the other hand, at low-altitude both, males and females, reached sexual maturity at the age of four years, and longevity was extended to nine years (Fig. 3B).

Sexual maturity brings along secondary sexual characters and sometimes sexual dimorphism in SVL, which may result in larger and more successful males (Devender, 1978; Anderson and Vitt, 1990; Verrastro, 2004), but most importantly, larger females that could produce larger and/or more numerous litters (Tracy, 1999; Smith, 2002; Pincheira-Donoso and Tregenza, 2011). This could be an important adaptive trait especially in cold-temperate environments where higher thermal inertia relative to size can determine survival, mostly in newborn. These secondary sexual characters and behavior can determine the amount of energy that will be allocated to reproduction which can vary within species and populations (Olsson et al., 2002). Growth will depend on the remaining

Table 3. Comparison between juveniles, females and males of *Liolaemus pictus argentinus* at the high- and the low-altitude sites with respect to: mean snout-vent length (SVL) and SVL range (mm), estimated age as number and range of rings (years), growth rate range [(mm x year)⁻¹], and mean specific growth rate and specific growth rate range [mm x (year x mm)⁻¹].

Populations	Challhuaco mountain (High-altitude site)				Melipal beach (Low-altitude site)			
	Juveniles (13)	Females (11)	Males (7)	Total adults (18)	Juveniles (8)	Females (11)	Males (10)	Total adults (21)
SVL (mean; range; mm)	36.9; 23.5-48.8	55.9; 50.4-62.1	58.6; 51.4-62	48.5; 23.5-62.1	32.5; 24.8-44.4	56.6; 37.5-47.1	59; 36.2-44.1	57.7; 49.8-64.3
Estimated age (mean; range; years)	2.8; 1-6	4.7; 3-8	5.8; 4-8	5.1; 3-8	2.5; 1-4	5.2; 4-7	6.1; 4-9	5.6; 4-9
Growth rate range (mm x year ⁻¹)	8.395-1.825	4.952-0.880	3.621-0.880	4.952- 0.880	10.279- 4.948	7.996-0.823	7.996-0.128	7.996- 0.128
Specific growth rate {mean and range; [mm x (year x mm) ⁻¹]}	0.179; 0.357- 0.0375	0.0593; 0.0983- 0.0145	0.0357; 0.0602- 0.0157	0.0501; 0.0838- 0.0983	0.260; 0.358-0.180	0.0784; 0.140- 0.0142	0.0512; 0.160- 0.00202	0.0654; 0.160- 0.00202

energy and therefore is expected to vary as well. Sexual dimorphism with respect to SVL and growth rates were absent in both high- and low-altitude populations. This is also a common pattern in southern South American squamates like *P. tenebrosus* (Piantoni et al., 2006a), *H. darwini* (Piantoni et al., 2006b; Kubisch et al., 2012), *L. irregularis*, *L. multicolor* (Valdecantos and Lobo, 2007), *Iguana iguana* (Zug and Rand, 1987) and *Tupinambis rufescens* (Fitzgerald et al., 1993).

The relationship between growth and elevation in *L. p. argentinus* could be explained by differences in the hours of activity. High-altitude stands for shorter time of activity (Gutierrez et al., 2010) which restricts foraging, hence energy intake (Sears and Angilletta, 2004; Shine, 2005). This has a negative effect on certain traits associated to growth: in the mountains, juveniles usually hatch or are born later and go into hibernation earlier than those in lower altitudes (Roitberg and Smirina, 2006; Gutiérrez et al., 2010). An earlier achievement of sexual maturity in the high-altitude population of *L. p. argentinus* can compensate for the shorter lifespan and ensure enough reproductive years, similar to the ones in the low-altitude site. Similarly to *L. p. argentinus* female growth rates of *H. darwini* and *P. tenebrosus* are also greater during the juvenile stage (Piantoni et al., 2006a,b; Kubisch et al., 2012) which allows them to reach the minimum body size for reproduction and attain sexual maturity earlier, and in this way extend their reproductive life (Piantoni et al., 2006a). This characteristic of life-history is especially advantageous in Patagonia where lizards face periods of restrictive growth due to hibernation (Ibargüengoytía and Casalins, 2007).

In comparison to most lizards *L. p. argentinus* exhibits low growth rates, a reduced reproductive life and, as a consequence, low fertility, but compensates with early sexual maturity in females. This pattern is commonly found in other Patagonian species although sexual maturity tends to be reached later. Females of *P. tenebrosus* achieve late sexual maturity at the age of seven years old and males at the age of nine years old. Fecundity in this lizard is reduced to nine offspring, possibly due to its prolonged reproductive cycle (Piantoni et al., 2006a). Despite the differences observed in the thermal microenvironments, both populations of *L. p. argentinus* exhibited a reproductive life-span of five years. Considering that the *L. p. argentinus* females reproduce every two or three years (Ibargüengoytía and Cussac, 1996) the total reproductive output (five years) would be among the lowest reported for lizards (Table 1).

In conclusion we agree with Ferguson and Brockman (1980) and Sinervo and Adolph (1989) in that both environmental and body temperatures (Gutiérrez et al., 2010) as well as effectiveness in thermoregulation, are fundamental factors affecting metabolism and growth, and this

can determine the time of sexual maturity and life-span. Thermal constraints in cold-temperate environments like Patagonia restrict some aspects of the life history of *L. p. argentinus*, such as growth, sexual maturity, reproductive frequency and fertility, when compared, in a general context, to lizards from temperate or tropical climates (Ibargüengoytía and Casalins, 2007).

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In memory of our friend and colleague, Joel, we dedicate this work to his wife Florencia Cuassolo and son Lautaro Gutierrez.

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