
REPRODUCTIVE BIOLOGY OF *PHYMATURUS CF. PALLUMA*: A VULNERABLE LIZARD FROM THE HIGHLANDS OF THE ANDES, SAN JUAN, ARGENTINA

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Abstract.—Viviparous liolaemids that inhabit cool and harsh environments of Patagonia and the highlands of the Andes exhibit distinctive life-history traits to synchronize births with benign environmental conditions. We studied the reproduction of *Phymaturus cf. palluma*, a viviparous species that inhabits rocky outcrops in cool environments of the Andean highlands of San Juan, Argentina, and discuss our results in relation to the conservation status of this poorly known species. We determined male and female reproductive cycles, male testosterone cycle, allometry of morphometric variables and sexual size dimorphism, minimum adult size, clutch size, and mean annual reproductive output. Females of *Phymaturus cf. palluma* exhibited a biennial reproductive cycle, with a litter size of one to two offspring, resulting in a low mean annual reproductive output of 0.75 offspring/female/year. The male spermatogenic cycle was asynchronous among individuals. We observed males with sperm in the epididymis and high values of serum testosterone concentrations throughout the activity season. The sexual dimorphism and allometric analyses revealed that legs are wider in males than in females throughout the life span, and not linked to sexual maturity. In contrast, the head size in males and the trunk size in females are developed after sexual maturity, suggesting that they have arisen through sexual selection. Our study confirmed a pattern of prolonged female reproductive cycles and low mean annual reproductive output in the genus *Phymaturus*, resulting in this species having one of the lowest values of mean annual reproductive output for lizards in the world.

Key Words.—allometry; conservation; cool environments; *Phymaturus*; reproductive cycles; sexual dimorphism; testosterone

INTRODUCTION

Reptiles inhabiting cool and harsh environments are constrained by the need to reproduce during short activity seasons from mid spring to early autumn because they hibernate the rest of the year. During this hibernation period, the physiological activity is almost nil (Saint Girons 1985; Gotthard 2001). Cold climate lizards often show reproductive styles that favor male/female encounters, nourishment by viviparity, birth in warmer periods of the activity seasons, and larger offspring (e.g. Saint Girons 1985; Cree and Guillette 1995; Olsson and Shine 1999; Edwards et al. 2002; Ibargüengoytía and Casalins 2007). Distinctive life-history traits include the retention of eggs in the oviducts during most of embryogenesis (Packard et al. 1977; Blackburn 1982; Guillette 1993) and plasticity in the relative timing of female reproductive events (Cree and Guillette 1995; Olsson and Shine 1998, 1999; Edwards et al. 2002) to synchronize births with benign environmental conditions (Olsson and Shine 1999). The viviparous liolaemids that inhabit the Patagonia and the Andean highlands show different

adaptations to these particular cool and harsh environments, such as prolonged biennial to triennial reproductive cycles in females, evolutionary transitions from oviparity to viviparity (Ibargüengoytía and Cussac 1996, 1998, 1999; Boretto and Ibargüengoytía 2009) and high interspecific differences in male reproductive cycles showing different paths to coordinate with female cycles (Ibargüengoytía and Cussac 1999; Ibargüengoytía 2004; Boretto 2009). For example, the viviparous lizard *Liolaemus elongatus* lays eggs buried in the soil, and the embryos break the eggshell with the egg tooth between 15 minutes and 12 hours after egg laying (Crocco et al. 2008). The offspring of *L. elongatus*, like several species of the viviparous genus *Phymaturus*, show intra-abdominal yolk storage after birth (Boretto et al. 2007; Boretto 2009; Boretto and Ibargüengoytía 2009). Males of *Liolaemus pictus* (Ibargüengoytía and Cussac 1999) and *Phymaturus antofagastensis* (Boretto and Ibargüengoytía 2006) store sperm in epididymides for fertilization throughout the activity season. In contrast, males of *L. elongatus* (Ibargüengoytía and Cussac 1999),

Phymaturus punae (Boretto et al. 2007), *Phymaturus vociferator* (Habit and Ortiz 1996), *Phymaturus tenebrosus* (Ibargüengoytia 2004), and *Phymaturus zapalensis* (Boretto and Ibargüengoytia 2009) show annual and seasonal reproductive cycles with sperm present in the epididymides only during a brief period of the activity season. The common pattern of prolonged female cycles observed in liolaemids suggests the existence of a causal relationship between cool environments, low frequency of reproductive females in populations (male biased operational sex ratio as a result of biennial female cycles), and sexual dimorphism represented in the genus *Phymaturus* by larger and more robust males (Ibargüengoytia 2008; Boretto and Ibargüengoytia 2009). These patterns could be a result of sexual selection, which includes male-male rivalry (Olsson et al., 2002), and females having wider bodies and a proportionally greater interlimb length than males (Boretto and Ibargüengoytia, 2009). However, there are few studies that analyze the relationship of dimorphic traits with the snout-vent length during ontogeny, which could lead to a better understanding of the dimorphic variables that are linked to sexual maturity, and hence to reproduction (Ibargüengoytia and Cussac 1996).

All species in the genus *Phymaturus* are viviparous and predominantly herbivorous, and inhabit the cool and harsh environments of the Andean highlands of Argentina and Chile and the Patagonian steppe of Argentina (Ceï 1986, 1993). *Phymaturus cf. palluma* is found above 2000 m in elevation in a restricted area of valleys and cliffs of San Juan province. The only data known about *P. cf. palluma* relates to the rock-dwelling habits, the herbivorous-insectivorous diet and the viviparous type of reproduction (Ceï 1986).

The aim of this work is to study the reproductive biology of *P. cf. palluma* in order to increase our knowledge about reproductive patterns of the genus *Phymaturus*, and to better understand the relationship between environment and reproduction in the Squamata. Preliminary studies revealed that the genus *Phymaturus* is especially vulnerable to global warming and that populations are showing retraction and some may have become extinct, probably because of their viviparous condition (Ceï 1986), their preference for low body temperatures (Ibargüengoytia and Casalins 2007) and their high-altitude habitats in the Andes (Sinervo et al. 2010). In the present study, we provide the first data on the reproductive biology of *P. cf. palluma* and comment on the possible conservation status of this species. Specifically, we studied the minimum adult size, sexual dimorphism, allometric growth, clutch size, male and female reproductive cycles, male testosterone cycle, and mean annual reproductive output.

MATERIALS AND METHODS

Specimens used and capture site.—We captured 22 male *P. cf. palluma* during November ($n = 4$),

December ($n = 4$), February ($n = 8$) and April ($n = 6$) in 2005, 2006, and 2007. We captured 22 females during November ($n = 4$), December ($n = 11$), February ($n = 3$) and April ($n = 4$) in 2005, 2006, and 2007. The captures were made by hand or noose in rocky outcrops of the locality Agua Negra, Iglesia Department, San Juan Province, Argentina. We also used data from a subset of male ($n = 13$) and female ($n = 14$) *P. cf. palluma* from the Museo de Ciencias Naturales of Salta province, Argentina, captured from 1 February to 6 March 2002, in the same locality. We used the museum sub-sample in the sexual dimorphism statistical analyses and in the descriptions of reproductive cycles, discriminating them in the figures of the cycles, but not including them in the statistical analysis of the reproductive cycles because the exact collection dates were not available.

Phymaturus cf. palluma inhabits the Puna and Altoandina phytogeographic provinces, which are characterized by cold and dry climates with a mean annual temperature from 8° C to 12° C and almost permanent frost (Cabrera 1994). This species lives in a semiarid to arid region, where solar radiation is very high and intense. The landscape is characterized by valleys with dry slopes mostly composed of *Senecio oreophyton*, *Artemisia mendozana*, *Tetraglochin alatum*, *Lycium fuscum*, *L. Chanar*, *Ephedra breana*, and rock outcrops (Cabrera 1994). Specifically, the collection site of Agua Negra is an area with marked glacial activity and rocky landslides in temperate seasons, providing a dynamic and unstable environment in this mountain ecosystem (Aguado 1983). Access to this species is limited due to the extensive snow accumulation in the winter months, allowing the collection of specimens only during the months of peak runoff, from spring until late summer or early autumn.

Autopsy procedures and blood extraction.—As a consequence of the large distance between the lizards' capture site and the laboratory, we extracted blood 3–5 days postcapture. During this period, each animal was kept in an individual container, thereby protecting them from external stimulus and stressor agents. We brought all captured lizards to the laboratory and weighed them (body mass, BM, 10 g spring scale \pm 0.5 g; Pesola AG, Baar, Switzerland). We separated a representative subsample of adult males of each capture date ($n = 14$) for blood extraction. The rest of the lizards were immediately killed by a lethal intraperitoneal (i.p.) dose of sodium thiopental and fixed in Bouin's solution for 24 h.

For blood extraction, we anesthetized males with an i.p. dose of sodium thiopental (0.03 mm³ / 10 g of body weight) and immediately took a blood sample from the tail artery with an insulin syringe (1 mm³). We clotted blood samples in a microtube at ambient temperature, spun them at 1500 rpm for 15 min, and stored them at -20° C until analysis. After blood extraction, we injected males with a lethal dose of

sodium thiopental and fixed them in Bouin's solution for 24 h. After fixation, we preserved all captured lizards in 70% ethanol, and deposited them in the Department of Zoology, Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, Río Negro, Argentina.

Assessment of sexual maturity, female reproductive cycle, and clutch size.—We determined the minimum snout vent length (SVL) at sexual maturity using the smallest female containing vitellogenic follicles, uterus morphology, or pregnancy. We measured follicular sizes, estimated as the diameter of the largest ovarian follicle, using vernier callipers on camera lucida schemes (± 0.02 mm) using an Olympus SZ-PT40 stereoscopic microscope. We characterized the uteri into three categories: (1) Uterus type 1: folds, if present, were small, and never spread over all the uterus, similar to the thread-like oviduct typical of juveniles reported by Van Wyk (1991); (2) Uterus type 2: medium size folds spread all over the uterus, indicative of the distended oviducts of adulthood *sensu* Vitt and Caldwell (1993), and generalized hypertrophy of the oviducts associated with vitellogenic recrudescence (Ramírez-Pinilla 1992); and (3) Uterus type 3: with conspicuously more stretched oviducts than uterus type 2, characteristic of recent parturition (Flemming and Van Wyk 1992; Ramírez-Pinilla 1992).

Clutch size was determined by counting the embryos in each uterus, the number of offspring born in captivity, and relationship between the largest oocyte present in the right and left ovaries (Fig. 1). We classified developmental stages of embryos following Leyton et al. (1980), as *early* (from cleavage to somitic embryos), *middle* (curvate trunk to limbs with five fused fingers, outlines of ears and eyes, and abundant yolk), and *late* (from gonadal differentiation to active foetal movements, scales and pigmented skin); which correspond to *Lacerta vivipara* stages 1 to 20, 21 to 31, and 32 to 40, respectively (Dufaure and Hubert 1961). We calculated the mean annual

reproductive output by averaging the annual number of offspring per female (*sensu* Cree 1994).

Assessment of sexual maturity, male reproductive cycle and operational sex ratio.—For males, we determined the minimum SVL at sexual maturity using the smallest male showing spermatogenesis. We measured testicular sizes, estimated as the antero-posterior diameters of both testes, using vernier callipers on camera lucida schemes (± 0.02 mm) using an Olympus SZ-PT40 stereoscopic microscope. For testicular histology, we removed and dehydrated the right testis and epididymis of captured males ($n = 22$) in an ethanol series, and subsequently embedded samples in paraffin. We stained sections (7 μ m) with Haematoxylin and Eosin and examined them using an Olympus BX40 microscope. We used the most advanced cell type present at the luminal margin of the seminiferous tubule, following Mayhew and Wright (1970), to determine stages of spermatogenesis. The stages corresponded to: (1) only spermatogonia and Sertoli cells (juvenile male), without lumen; (2) primary/secondary spermatocytes; (3) spermatids; (4) spermatozoa in the tubular lumen and in the epididymis; (5) early testicular regression with scarce spermatozoa and cellular debris in tubular lumen and spermatozoa in the epididymis; and (6) advanced regression, with only spermatogonia, scarce cellular debris, and ample tubular lumen, and with few or no spermatozoa in the epididymis. We based cell type recognition on Pudney (1995), and classified presence either as scarce or abundant or as the absence of spermatozoa in the epididymis. Development of interstitial tissue (IT) lying between seminiferous tubules was qualitatively classified as scarce, medium, or highly developed. We did not use males obtained from the museum for the histological analysis, and juvenile males and females were not included in the statistical analysis of reproductive cycles. We calculated the operational sex ratio of reproductive females to males considering only adult females with uterus type 2 (characteristic of vitellogenic activity) and adult males showing spermiation or spermatozoa in the epididymis.

Testosterone measurements.—We defrosted frozen serum samples ($n = 14$), and used aliquots (50 μ l) to determine testosterone concentration in sera extracted with 100% ethanol. We mixed serum aliquots (50 μ l) with 500 μ l of 100% ethanol and separated the precipitated proteins by centrifugation at 1000 x g for 15 min. The precipitate was re-extracted with 250 μ l of 100% ethanol, centrifuged, and the pooled supernatants evaporated overnight at 36° C. Then, we dissolved 150 μ l of the residues in PBS gelatin by incubating for 60 min at 37° C in a Dubnoff shaker. We used aliquots (25 μ l) for testosterone determination by Radioimmunoassay (RIA). We performed RIA using the commercial kit DSL-4100

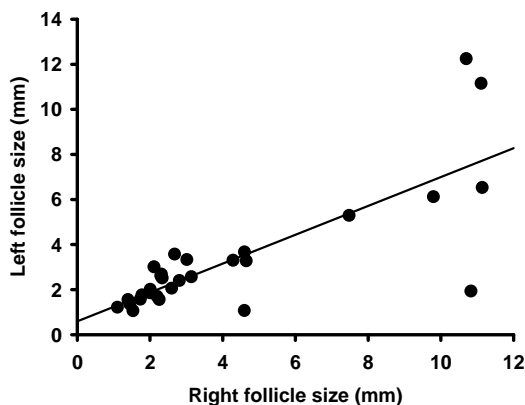


FIGURE 1. The relationship between the sizes of right and left follicles of *Phymaturus cf. palluma* females.

Testosterone double antibody RIA (Diagnostic Systems Laboratories, Inc., Webster, Texas, USA).

Extraction efficiency was greater than 95% for the concentrations assayed, that was 2 and 50 ng/ml testosterone added to the charcoal extracted serum. Serial dilutions of one sample each from males in spring, early and late summer were parallel to the standard curve. All samples were measured in the same assay and the intra-assay coefficient of variation was 7%. The minimum detectable concentration for the assay was 0.75 pg/tube. Equivalent volumes of PBS gelatin added to reference and standard curve tubes did not interfere with binding. Cross reactivity, as informed by the manufacturer was 6% with 5alpha dihydrotestosterone, 2% with 5-androstane-3beta, 17beta diol and 11-oxotestosterone, and < 1% or nondetectable with all other assayed androgens, corticoids, estrogens, or progesterone.

Sexual dimorphism and allometry.—We made morphological descriptions of preserved adult specimens ($n = 46$) to assess sexual dimorphism of *P. cf. palluma* using the following variables: SVL, head length (HL), head width (HW), neck width (NW), width of the tail base at the vent (WTV), maximum body width (BW, pregnant individuals not included), diameter of the front leg (FLD), and hind leg (HLD) at the insertion to the pectoral and pelvic girdles, respectively, distance between the front and hind limbs (interlimb length, IL; *sensu* Olsson et al. 2002), and hip width (HipW) measured as the body width at the insertion of the hind legs. We took each of these measurements using a vernier calliper (± 0.2 mm). We also analyzed the allometric relationships between the morphometric variables and the SVL of males and females and juveniles and adults by regression scatters of the logarithms of these variables.

Statistical analyses.—We used the statistical software SigmaStat 3.5[®] (Systat Software Inc., Chicago, Illinois, U.S.A.), Sigma Plot 10.0[®] (Systat Software Inc., Chicago, Illinois, U.S.A.), and SPSS 17.0[®] (Chicago, Illinois, U.S.A.). We used analysis of covariance (ANCOVA) to test the differences in testicular size between the spermatogenic stages and to test for sexual dimorphism. We used linear regression to test the relationship between follicular size and body mass, and between follicular size and the date of capture in females. We also used linear regression to analyze the relationship between testicular size and SVL in males. We used Spearman correlations to test the significance of the relationship between the testicular size and the spermatogenic stage, between the testicular size and the interstitial development, the spermatogenic stages and date, and between the serum testosterone concentration and the spermatogenic stages. Assumptions of normality and homogeneity of variance were tested using one-sample Kolmogorov-Smirnov tests and Levene tests, respectively (Sokal

and Rohlf 1969). We used $\alpha = 0.05$ to assess statistical significance.

RESULTS

Follicle size and female reproductive cycle.—The minimum adult size showing reproductive activity was 82.42 mm SVL in a vitellogenic female with type 2 uteri. The follicle sizes of vitellogenic females exhibited a positive and significant relationship with body mass ($r^2 = 0.82$, $F_{1,6} = 23.22$, $P = 0.005$) and with date ($r^2 = 0.67$, $F_{1,11} = 20.08$, $P = 0.001$; Fig. 2A). Adult females exhibited a gradual increase in follicle size, with small sizes in late spring (November), the largest sizes in late summer (February), and the lowest values in March and April, which belong to postpartum females. All gravid females ($n = 4$), each possessing two embryos, were found with increasing developmental stages of the embryos throughout the summer, simultaneously with the presence of non-pregnant females with follicles showing advanced vitellogenesis ($n = 10$). We captured postpartum females with type 3 uteri ($n = 6$) only in late summer and early autumn (Fig. 2A). These data lead us to classify the female reproductive cycle of the species as biannual due to the simultaneous presence of reproductive females (with follicles showing advanced vitellogenesis and type 2 uteri) and pregnant females during the summer. Juvenile females ($n = 14$), were captured throughout the activity season and showed transparent oocytes and type 1 uteri (Fig. 2A).

We kept one pregnant female in captivity that was captured in late February and she gave birth on 4 March to two offspring of 51.30 mm SVL (5.5 g) and 51.38 mm SVL (5.5 g). While in captivity, the female refused to eat. The offspring born in captivity appeared in good condition and both showed large fat bodies and a remnant of intra-abdominal yolk with two main blood vessels, an artery from the dorsal artery and a vein draining away. Considering the number of embryos found in the uterus of each pregnant female ($n = 4$ females), the number of offspring born in captivity, and the larger oocytes present in the right and left ovaries, the clutch size was one to two offspring. The mean annual reproductive output, considering the clutch size and the biennial female reproductive cycle, was 0.5 to 1 offspring per year (0.75).

Male reproductive cycle, operational sex ratio and serum testosterone concentrations.—The minimum adult size showing reproductive activity was 83.48 mm SVL in a male with spermatid testicular stage. The testicular size did not show differences among the spermatogenic stages, when using SVL as a significant co-variate in the model ($F_{4,20} = 1.83$, $P = 0.17$). The testicular size showed a significant and positive relationship with SVL ($r^2 = 0.49$, $F_{1,20} = 18.29$, $P < 0.001$). Consequently, we used the residuals of this regression (ResTS) for further analyses. The ResTS

did not show a significant relationship with the spermatogenic stages ($r^2 = -0.034$, $n = 21$, $P = 0.88$) or the interstitial development ($r^2 = -0.076$, $n = 21$, $P = 0.742$).

The spermatogenic stages did not show a significant relationship with date ($r^2 = 0.40$, $n = 21$, $P = 0.070$; Fig. 2B). Males with spermatid, spermatozoa, or regression stages were present throughout the activity season, from spring to autumn, resulting in an asynchronous spermatogenic cycle. We found males with the spermatocyte stage only at the beginning of autumn ($n = 2$). In mid-summer, we captured one juvenile male with testes smaller than 3.87 mm, a transparent epididymis, and at stage 1 of spermatogenesis (spermatogonia; Fig. 2B). The histological analysis of the epididymis showed that throughout the activity season males with spermatozoa stored in the epididymis were continually available;

72.7% of the total sample of adult males captured exhibited spermatozoa storage in the epididymis, corresponding to 50% of males captured in spring, 75% of males captured in summer, and 83% of males captured in autumn. The operational sex ratio of the population resulted in 1.75 reproductive males to 1 reproductive female.

We captured males with high serum testosterone concentrations throughout the activity season (Fig. 3A). The values of serum testosterone concentrations ranged from 57 to 106 ng/ml in late spring, from 53 to 140 ng/ml in early summer, and from 40 to 199 ng/ml in late summer (Fig. 3A). All males with higher testosterone, captured during the summer, contained spermatozoa in the epididymis (Fig. 3A). There was not a significant relationship between serum testosterone concentration and the spermatogenic stages (Spearman Correlation, $r^2 = 0.508$, $n = 14$, $P =$

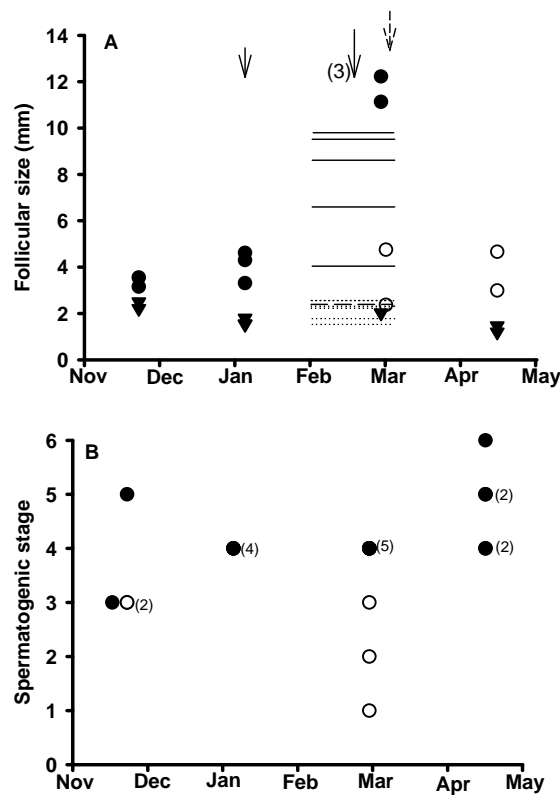


FIGURE 2. (A) Female reproductive cycle of *Phymaturus cf. palluma*. Follicle size of vitellogenic females (solid dots), post-reproductive females (empty dots) and juvenile females (solid triangles) in relation to collection date. Capture date of gravid females with embryos in middle stages of development (small arrow) and late development (big arrow), and the date of a birth in the lab (dashed arrow) are shown. The number of individuals is indicated in parentheses. Horizontal bars indicate the range of dates when some of the specimens were collected; date of death is not accurately known (continuous bars: vitellogenic females; dashed bars: post-reproductive females; dotted bars: juveniles). (B) Spermatogenic stage versus date. Solid circles indicate individuals that exhibited spermatozoa in the epididymis and open circles those that did not. The number of cases is in parentheses. Stage 1: spermatogonia, juveniles; stage 2: primary/secondary spermatocytes; stage 3: spermatids; stage 4: spermatozoa in tubular lumen and/or in epididymis; stage 5: early testicular regression; stage 6: advanced testicular regression).

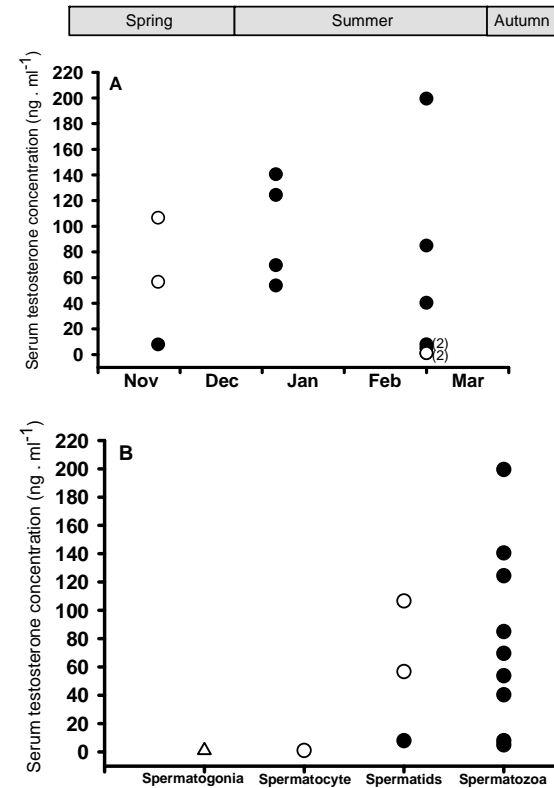


FIGURE 3. Testosterone cycle in males of *Phymaturus cf. palluma*. Serum testosterone concentration ($\text{ng} \cdot \text{ml}^{-1}$) versus date (A) or spermatogenic stage (B) of each male are presented. Adult males with abundant (solid dots) or absent (open dots) spermatozoa in the epididymis are differentiated. The triangle indicates a juvenile male with absence of spermatozoa in the epididymis. Parentheses indicate the number of observations.

0.061; Fig. 3B). Serum testosterone concentration in a juvenile male was low (1.11 ng/ml; Fig. 3B).

Sexual dimorphism and allometrical analyses.—*Phymaturus cf. palluma* varied in SVL from 82.42 to 101.78 mm in adult females ($n = 18$) and from 83.48 to 104.50 mm in adult males ($n = 28$). Juvenile SVL varied between 52.76 and 82.70 mm ($n = 21$). Adult males and females did not show significant differences in body mass or SVL ($P = 0.30$; Table 1). Sexual dimorphism resulted in greater HL, HW, FLD, and HLD in males and greater IL and BW in females ($P < 0.05$, Table 1) with SVL as a significant co-variate.

Regressions of the allometric relationships between HW, HL, BW, and IL with SVL showed a difference between juvenile and adult lizards, consistent with the minimum adult size determined for females (SVL = 82.42 mm) and males (SVL = 83.48 mm; Fig. 4). The HW and HL showed a significantly higher growth rate in adult males than in females, while females showed a significantly larger BW and IL than males after sexual maturity ($P < 0.05$). Although both sexes were similar in HW, HL, BW and IL as juveniles, HLD and FLD were significantly larger in males throughout life ($P < 0.05$).

DISCUSSION

Phymaturus cf. palluma showed a biennial female reproductive cycle performing either early vitellogenesis or mid pregnancy in early summer, or advanced vitellogenesis or advanced pregnancy in late summer, and exhibited a low mean annual reproductive output of 0.75. Biennial cycles have been also described for *P. vociferator* (Habit and Ortiz 1996), *P. tenebrosus* (Ibargüengoytía 2004), *P. antofagastensis* (Boretto and Ibargüengoytía 2006), *P. punae* (Boretto et al. 2007), whereas an annual-biennial cycle was described for *P. zapalensis* (Boretto

low mean annual reproductive outputs (0.75–1.12, Boretto 2009) that are among the lowest registered for reptiles (see Cree 1994; Ibargüengoytía and Casalins 2007). The prolonged cycles in the genus *Phymaturus* appear to be a consequence of the hormonal and physiological limitations observed in viviparous lizards and severe cool environments. The habitats of these lizards in the Andes highlands and in Patagonia (Argentina) prevent females from completing vitellogenesis, pregnancy, and fat storage within one activity season prior to hibernation (Boretto et al. 2007). The reproductive cycles in viviparous female lizards are physiologically constrained because vitellogenesis and pregnancy are mutually exclusive phenomena in squamates during most of the pregnancy (Duvall et al. 1982; Callard et al. 1992; Custodia-Lora and Callard 2002). Even though there is evidence that vitellogenesis can occur at the end of pregnancy in some New Zealand geckos, such as *Hoplodactylus maculatus* and *Naultinus gemmeus* (Wilson and Cree 2003), this is not the case for liolaemids. Previous studies of the reproductive biology of the Liolaemidae have shown that enlarged vitellogenic follicles and pregnancy do not occur simultaneously in the same female, as shown for *Liolaemus pictus* (Ibargüengoytía and Cussac 1996), *Liolaemus elongatus* (Ibargüengoytía and Cussac 1998), *Phymaturus tenebrosus* (Ibargüengoytía 2004), *Phymaturus antofagastensis* (Boretto and Ibargüengoytía 2006), *Phymaturus vociferator* (Habit and Ortiz 1996), *Phymaturus punae* (Boretto et al. 2007), *Phymaturus zapalensis* (Boretto and Ibargüengoytía 2009), and *Liolaemus lineomaculatus*, *L. boulengeri* and *L. bibronii* (Medina and Ibargüengoytía 2010). Four reproductive features have been pointed out to cause multiennial reproductive cycles in lizards: (1) prolonged vitellogenesis (Van Wyk 1991; Cree et al. 1992; Cree and Guillette 1995); (2) prolonged pregnancy (Vial and Stewart 1985; Cree and Guillette 1995; Habit and Ortiz 1996); (3) allocation of

TABLE 1. Analysis of sexual dimorphism in adult *Phymaturus cf. palluma* taking into account SVL and body mass ($P = 0.30$), and results of covariance analysis of sexual dimorphism in relation to seven other variables. The asterisk (*) indicates the variables that presented significant differences between males and females: Head length (HL), head width (HW), neck width (NW), width of the tail base at the vent (WTV), diameter of the front leg (FLD) and hind leg (HLD) at the insertion to the shoulders and pelvic girdles respectively, right and left distance between front and hind limbs (interlimb length, IL). The degree symbol (°) indicates the adjusted means.

Variable	$F_{1,49}$	P	$\bar{x}_{\text{males}} \pm \text{SE}$	$\bar{x}_{\text{females}} \pm \text{SE}$
SVL (mm) ($t_{48} = 1.04$)	---	---	93.74 ± 1.00	95.30 ± 1.13
BM (g) ($t_{18} = 0.69$)	---	---	26.53 ± 1.66	24.40 ± 1.71
WTV (mm)	1.401	0.243	12.58 ± 0.18°	12.25 ± 0.20°
NW (mm)	2.640	0.111	24.75 ± 0.33°	23.95 ± 0.37°
FLD (mm)	4.424	0.041*	7.91 ± 0.12°	7.52 ± 0.14°
HLD (mm)	26.353	<0.001*	9.16 ± 0.10°	8.37 ± 0.11°
HW (mm)	56.261	<0.001*	18.39 ± 0.13°	16.92 ± 0.15°
HL (mm)	4.382	0.042*	17.08 ± 0.22°	16.37 ± 0.25°
IL (mm)	25.500	<0.001*	47.60 ± 0.39°	50.58 ± 0.44°

and Ibargüengoytía 2009), showing a pattern in the genus characterized by prolonged female cycles and

vitellogenesis and pregnancy in separate breeding seasons (Ibargüengoytía and Cussac 1996;

Ibargüengoytía 2004; Boretto and Ibargüengoytía 2006; Boretto et al. 2007); and (4) skipping a year (Van Wyk 1991; Boretto and Ibargüengoytía 2009).

In addition, annual cycles in lizards can be discarded because of a high ratio of non reproductive females during the breeding season (Aldridge 1979; Van Wyk 1991), the simultaneous presence of females with reproductive conditions non-adjacent in the cycle sequence (Cree and Guillette 1995), as was found herein for *P. cf. palluma*, and its corollary, the simultaneous presence of vitellogenic and pregnant females in the population (Ibargüengoytía and Cussac 1996).

The simultaneous presence of females with pre-ovulatory follicles and gravid females with embryos showing medium to advanced stages of development

during the summer indicates that females invest in vitellogenic processes one year, and in embryonic development the next year. Females of *P. cf. palluma* exhibited a biennial reproductive cycle, requiring two years to complete one reproductive cycle. The lack of data on vitellogenic and pregnant *P. cf. palluma* during early spring and late autumn prevented us from confirming the mating period and the length of pregnancy. Nevertheless, the presence of males with spermatozoa in the epididymis during summer and early autumn and the higher serum testosterone concentration found in males captured in late summer suggests that in *P. cf. palluma*, mating occurs in late summer-early autumn, as in *P. antofagastensis* (Boretto et al. 2010) and *P. punae* (Boretto 2009). Pregnancy could last approximately one year until the

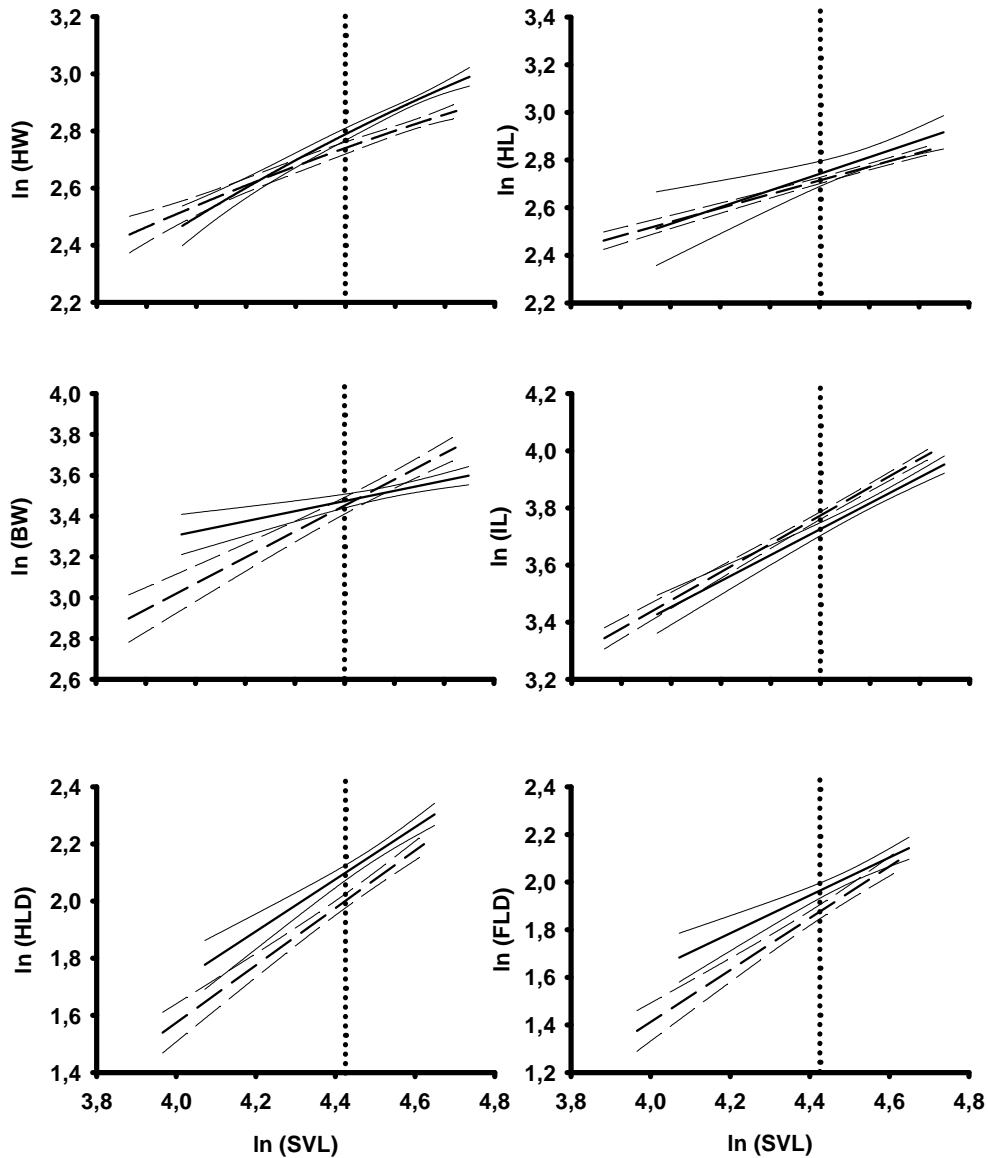


FIGURE 4. Allometric relationship of the natural logarithms of HW, HL, BW, IL, HLD and FLD with SVL for male and female *Phymaturus cf. palluma*. Regression and confidence intervals are indicated (solid: males; dashed: females). Vertical dotted line indicates SVL = 81.16 mm.

following summer as happens in reptiles from cold temperate environments in the Southern Hemisphere, where winter is the harsher season and lizards hibernate (for example: *P. vociferator*, Habit and Ortiz 1996; *Niveoscincus metallicus*, Swain and Jones 1994; Jones and Swain 1996; and *Niveoscincus ocellatus*, Jones et al. 1997). The other possibility is that ovulation takes place during the following spring, with sperm stored in females' reproductive tracts during winter, as was proposed for *P. antofagastensis* (Boretto and Ibarquengoytia 2006) and *P. punae* (Boretto et al. 2007). A displacement of the mating period from spring to autumn, with prolonged gestation over winter and birth in the next spring, has been proposed for viviparous species of the genus *Liolaemus* (Leyton et al. 1977, 1982; Ramirez-Pinilla 1991, 1992) and in the genus *Sceloporus* (Méndez-de la Cruz et al. 1998). However, this reproductive model mostly occurs in populations at high altitudes in tropical latitudes, where the environmental temperatures during winter are more benign than in summer (Janzen 1967).

The male reproductive cycle of *P. cf. palluma* was asynchronous among individuals, because males from the same population and captured on the same day exhibited different spermatogenic stages and conditions of the epididymis, and the regression stages observed in males captured in early autumn and late spring suggest a resting period during hibernation. Additionally, the reproductive cycle could be considered continuous in terms of the presence of males with sperm in the epididymis throughout the activity season and with high serum testosterone concentrations throughout the activity season, increasing fertilization chances. This continuous male cycle could be an adaptation to intrasexual competition related to the low proportion of reproductive females in the population caused by a high proportion of non-receptive pregnant females during the activity season, as was observed in *L. pictus* (Ibarquengoytia and Cussac 1999), *P. antofagastensis* (Boretto and Ibarquengoytia 2006), and in *P. zapalensis* (Boretto 2009). In accordance, *P. cf. palluma* showed sexual dimorphism with males having more robust limbs and wider and longer heads than females. The allometric analyses revealed that wider legs in males than in females are present throughout life and this difference is not linked to sexual maturity. In contrast, the head size is developed after sexual maturity in males, suggesting that this dimorphic trait has arisen through sexual selection. Accordingly, the territorial *P. vociferator* (Habit and Ortiz 1994) shows a relatively larger head in males than in females attributed to a strong sexual selection toward male success under male-male rivalry, as has been reported for several lizard species (Olsson et al. 2002).

Lizards that inhabit cold climates commonly present delayed sexual maturity and an increase in minimum adult size because low ambient temperatures depress the metabolic rate and slow growth (Castanet and Baez

1991; Martori et al. 1998; Andreone and Guarino 2003). This is the case in *P. tenebrosus*, where females reach sexual maturity at seven years and males at nine (Piantoni et al. 2006). Females of *P. cf. palluma* instead reached sexual maturity at a smaller size than males, but the dimorphic and allometric analyses strongly suggest they compensate for this smaller SVL by enhancing body width and interlimb length. The reproductive life-history traits associated with viviparous species (Dunham et al. 1988) observed in *Phymaturus*, such as a relatively large body size and the abundant fat and yolk reserves of offspring (Boretto et al. 2007; Boretto and Ibarquengoytia 2009), probably helps compensate for the low reproductive output, enhancing offspring survival. Because of the restricted distribution of *P. cf. palluma* to the Puna and Altoandina phytogeographic provinces, the prolonged biennial female reproductive cycle and the low reproductive output, future studies should focus on population sizes and trends in order to estimate the conservation status of this unknown species.

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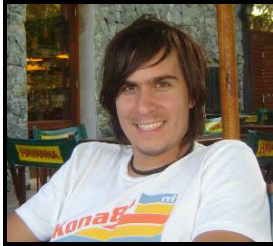
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