

MALE RESPONSE TO LOW FREQUENCY OF FEMALE REPRODUCTION IN THE VIVIPAROUS LIZARD *LIOLAEMUS* (TROPIDURIDAE)

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Female *Liolaemus elongatus* and *Liolaemus pictus* have biennial and triennial reproductive cycles respectively, with a low availability of reproductive females during the breeding season. Previous results have shown slight interspecific differences in sexual dimorphism between *L. pictus* and *L. elongatus*, coinciding with differential accessibility to females. Present results show major interspecific differences in the timing of spermatogenesis. Male *L. pictus* begin to reproduce during the first year of adulthood and remain active during a long breeding season. In contrast, male *L. elongatus* delay reproduction for one year and reproduce during a narrower period, in synchrony with the female reproductive cycle. Male *L. elongatus* showed an increasing testicular size during spermatogenesis, and a reduction in size when the first spermatozoa appear. *Liolaemus pictus* had spermatozoa in seminiferous tubules for the entire sampling period, from spring to autumn. The existence of severe thermal constraints for vitellogenesis and pregnancy set the following chain of causal events: environmental conditions - female cycle - male cycle and male dimorphic traits. This sequence of events shows how environmental cues can constrain the female cycle, and female availability, and thereby also affect the male cycle and the development of male dimorphic traits.

Key words: Sexual dimorphism, *Liolaemus*, male reproductive cycles

INTRODUCTION

The factors determining sexually dimorphic traits are complex and can involve natural or sexual selection (Mouton & van Wyk, 1993), and/or non-adaptive circumstances (Huang, 1996a). In the context of sexual selection (Harvey & Bradbury, 1991), sexual dimorphism may result from inter-sexual selection (e.g. female choice) or intra-sexual selection (e.g., male-male competition). Sexual dimorphism occurs frequently in lizards and is commonly reflected in differences in body size (Censky, 1995; Huang, 1996a), body proportions (Mouton & van Wyk, 1993), colour pattern and presence of pre-anal glands (Cei, 1986; 1993). It has been widely studied in many reptile groups (Mouton & van Wyk, 1993; Censky, 1995; Huang, 1996a), including *Liolaeminae* (Cei, 1986; 1993; Lobo & Laurent, 1995; Ibarquengoytia & Cussac, 1996; 1998; Vega, 1997).

Liolaemus pictus lives in temperate habitats up to moderate altitudes (520 to 1600 m), in leaf-mould and under logs and it is the most common lizard in the Andean-Patagonian forest of Nahuel Huapi National Park (Christie, 1984). *Liolaemus elongatus* lives on rock promontories in the steppe and in the transition rainforest-steppe where it may be seen in the understory as well as the rocks along the shores of lakes (Ibarquengoytia, Cussac & Ubeda, 1997). The species are sympatric in the transition rainforest-steppe (Ibarquengoytia *et al.*, 1997) of Northern Patagonia.

The sexual dimorphism found in *L. pictus* and *L. elongatus* corresponds to pre-anal glands present only in males (Cei, 1986) and to differences in body shape, particularly a bigger head and a larger vent width in males (Ibarquengoytia & Cussac, 1996; 1998). Sexual differences observed in *L. pictus* were due to an allometric increase in male head length relative to juveniles. In *L. elongatus* head width grows in a negative allometric way in juveniles and adult females, whereas in adult males head width is isometric. The vent width of *L. elongatus* grows in a positive allometric manner in juveniles and adult males, whereas in adult females growth is isometric. Differences between adult male and female body size, or between male and female maximum juvenile size, were not found in these species (Ibarquengoytia & Cussac, 1996; 1998).

Dimorphic head size can be a consequence of (a) resource partitioning between the sexes; (b) differential energy allocation for reproduction; or (c) a response to selective pressures due to the social structure (Mouton & van Wyk, 1993). Notwithstanding the need for further studies on the diet to test the first hypothesis, three phenomena make it worth considering the last two hypotheses:

(1) *Liolaemus pictus* and *L. elongatus* are viviparous, suggesting that females are the sex with higher investment in offspring (Bull & Shine, 1979; Krebs & Davies, 1993).

(2) Both species have a low frequency of female reproduction with biennial to triennial (*L. pictus*) and annual to biennial (*L. elongatus*) female reproductive cycles so, even though the relation between male and female captures is near 1:1, the calculated proportion of reproductive females ranges between 0.5 and 0.33 in *L.*

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pictus, and between 1 and 0.5 in *L. elongatus*. Reproductive females are therefore a limited resource (Ibargüengoytía & Cussac, 1996; 1998).

(3) In both species, the exponent of the allometric relationship of male head size is greater in adults than in juveniles (Ibargüengoytía & Cussac, 1996; 1998).

Bias in sex ratio and differential parental effort may affect the intensity of sexual selection, since male ability to acquire a mate becomes important (Krebs & Davies, 1993), increasing male-male competition (Dearing & Schall, 1994).

The male component of sexual dimorphism has its functional parallel in the male reproductive cycle. *Liolaemus pictus* shows high testicular diameters from the end of spring to early autumn, suggesting a prolonged reproductive activity period (Ibargüengoytía & Cussac, 1996). In contrast, *L. elongatus* shows the largest testicular size in mid-spring, a minimum in summer, and a clear gonadal recrudescence, reaching its peak value in autumn, suggesting a prolonged spermatogenic period of one year (Ibargüengoytía & Cussac, 1998). Testis mass and volume correlate with spermatogenic activity in some lizards, such as *Eumeces elegans* (Huang, 1996b), and three species of the genus *Uma* (Mayhew & Wright, 1970). However, the relationship between testicular size and male reproductive cycle is complex in species such as *Liolaemus gravenhorsti* (Leyton, Morales & Bustos Obregón, 1977), *L. alticolor*, *L. bitaeniatus*, *L. darwini*, *L. scapularis* (Ramírez-Pinilla, 1992), *L. aymaramum*, *Tropidurus peruvianus* (Leyton, Veloso & Bustos Obregón, 1982), *Platysaurus capensis* and *P. minor* (van Wyk & Mouton, 1996).

The existence of severe thermal constraints for vitellogenesis and pregnancy, and their effects on the female cycle (Ibargüengoytía & Cussac, 1996, 1998), suggest the existence of female influence on male cycle and male dimorphic traits. Differences between *L. pictus* and *L. elongatus* sexual dimorphism and male cycle (testicular size-based) seem to be related to distinct female reproductive cycles and different accessibility of females. In the present work we consider the male cycle as the functional counterpart of the male component of sexual dimorphism. We investigated major inter-specific differences in the reproductive biology of male *L. elongatus* and *L. pictus*, mainly based on spermatogenic traits, and explore the possible existence of differences in male life history. Particularly, we test the hypothesis of dependence between testicular size and spermatogenic processes, through a comparative study, in order to make use of this tool for studying the consequences of low frequency of female reproduction on male reproductive traits.

MATERIALS AND METHODS

SAMPLING PROTOCOL

The sample studied included four groups of specimens of both sexes: (A) *L. elongatus*, $n=39$, collected

from October to March (1981 to 1984) and *L. pictus*, $n=186$, collected from November to April (1982 to 1984) at Nahuel Huapi and Lanín National Parks; (B) *L. elongatus*, $n=35$, collected from November to March (1993 to 1995) and *L. pictus*, $n=30$, collected from October 1993 to April 1994 at San Carlos de Bariloche. Localities of samples A and B are situated between 39° and 41.5° S, and between 71.6° and 70.5° W, at altitudes of 500 to 1800 m high. Specimens are deposited in the Centro Regional Universitario Bariloche of the Universidad Nacional del Comahue. The third sample, included *L. elongatus*, $n=130$, collected from December to January in Neuquén (1963 to 1973) and Mendoza (1961 to 1994). These localities are situated at 32° to 41.1° S and 66.5° to 72° W, 1200-4000 m altitude, and specimens are deposited in the Instituto de Biología Animal of the Universidad Nacional de Cuyo. The fourth group, D, corresponded to a capture-recapture sample of *L. pictus*, $n=8$, and *L. elongatus*, $n=16$, caught along the shore of the Moreno Lake near San Carlos de Bariloche (41.2° S, 71.5° W, 760 m altitude) from September 1996 to April 1997 (see Ibargüengoytía *et al.*, 1997). Sample D was the only group originating from a single locality.

The morphological study was based on the four groups of specimens, but the histological study considered only 13 specimens of *L. elongatus* and five specimens of *L. pictus* from groups A and B. Adulthood criteria followed Ibargüengoytía & Cussac (1996, 1998). Therefore, maximum juvenile size (53.74 mm) in *L. elongatus* was determined by taking into account (a) the size of the smallest female with ovulated oocytes, or uterus with medium size folds spread all over the organ surface, and (b) the smallest male showing testicular growth during the breeding season. In *L. pictus* the maximum juvenile size was considered less than the size of the smallest vitellogenic female (49 mm).

AUTOPSY PROCEDURES AND HISTOLOGY TREATMENT

Lizards were killed by intraperitoneal administration of sodic thiopental, fixed in Bouin's solution for 24 hr, and preserved in 70 % ethanol. Male gonads were removed and dehydrated in ethanol series and embedded in paraffin. Sections of 4 to 7 μ m were stained with Masson tricromic or Hematoxylin and Eosin (Martoja & Martoja Pierson, 1970).

DATA RECORDED

In the case of samples A, B and C, capture dates (DATE) were considered as days of a single standard year. The following data were recorded: capture date (DATE), testicular size as antero-posterior diameter (TS), snout-vent length (SVL), maximum body perimeter (BP, only for sample D), and body weight (BW, only for sample D). Following Mayhew & Wright (1970), spermatogenesis stages (SS) were determined by the most advanced cell type present at the luminal margin of the seminiferous tubule: (1) for spermatogonia, (2) for spermatocytes, (3) for spermatids, and (4)

for spermatozoa. Cell type recognition was based on Pudney (1995). Light microscopy examination of left and right testis of two individuals of each species did not show differences in the SS, so gonads were considered equally in the subsequent analysis. The seminiferous tubule diameter (TD) and epithelium height (EH) was recorded for each testis from 16 slides. The TD and EH averages from each individual were used in the analysis. Female reproductive cycles, inferred from individuals of groups A, B and C, were taken from Ibartigüengoytia & Cussac (1996, 1998).

STATISTICAL ANALYSIS

Data were studied using regression, correlation, Student's *t*-test, cluster (CA, centroid and euclidean

distance as measures) and discriminant (Wilks' Lambda as method) analysis. Normality and variance homogeneity assumptions were tested comparing predicted and observed frequencies by means of the Kolmogorov-Smirnov test, and by analysis of residuals or Levene's test, respectively (Sokal & Rohlf, 1969; Norusis, 1986). Kruskal-Wallis, Kolmogorov-Smirnov and Mann-Whitney tests were used as non-parametric tests.

RESULTS

TESTICULAR SIZE AND SPERMATOGENESIS

Liolaemus elongatus. Testicular diameter (TS) and snout-vent length (SVL) were related (Fig. 1, upper left panel). A subset of males (*n*=12) analysed for SVL, TS,

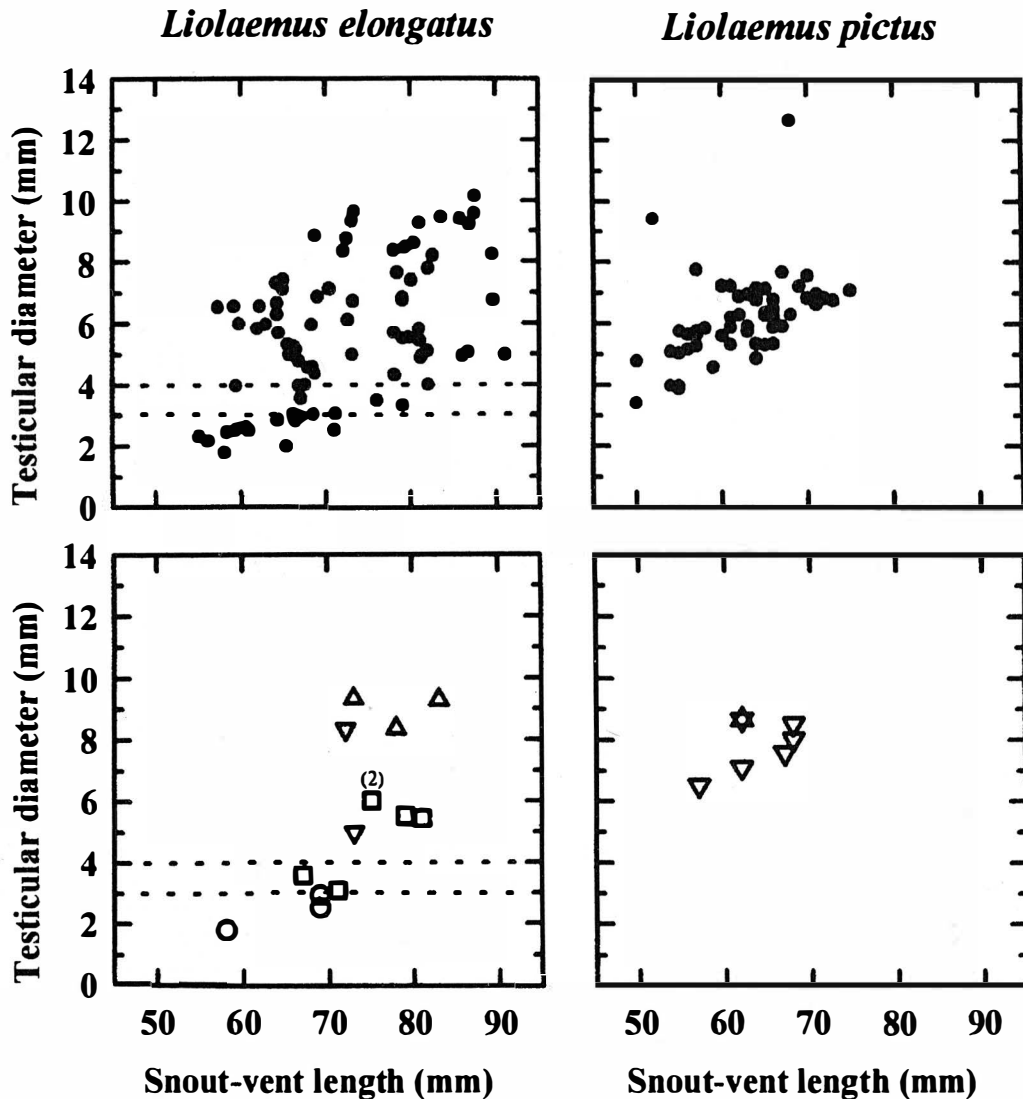


FIG. 1. Testicular diameter (TS) versus snout-vent length (SVL) of *L. elongatus* (left) and *L. pictus* (right). Lower panels show the spermatogenic stages (SS) resulting from the histological study (circles SS 1, squares SS 2, triangles SS 3, inverted triangles SS 4; numbers in parenthesis indicate coincident values). TS of *L. elongatus* was related to SVL (Regression, $F=28.33$, $df=82$, $P<0.0001$, upper left panel). The TS showed differences among SS (Kruskal-Wallis, $\chi^2=33.85$, $df=3$, $P<0.0001$, lower left panel). Dashed lines (left panels) indicate males with testes greater or smaller than 4 mm TS, which are significantly discriminated (Discriminant, $WL=0.330$, $n=14$, $P<0.0004$), and the cut-off point between males with and without spermatozoa in the testes (3 mm). Considering all the data, the SVL shows differences between male groups with TS smaller and greater than 3 mm (Mann-Whitney, $Z=4.4018$, $n=83$, $P<0.0001$, upper left panel). TS of *L. pictus* was related to SVL (Regression, $F=13.44$, $df=52$, $P<0.0001$, upper right panel). All the specimens, except one, have advanced SS (lower right panel), so the relationship between TS and SS could not be statistically analysed.

and SS (2 left and 12 right testes were considered) could be clustered into two groups (CA) and significantly discriminated on the basis of TS (Fig. 1, lower left panel), grouping males with testes greater ($n=9$) or smaller ($n=5$) than 4 mm TS. Particularly, histological observation showed that spermatocytes, spermatids, and spermatozoa are absent in testes smaller than or equal to 3 mm TS (i.e. stage 1), and no stage 1 male has testes greater than 3 mm TS. Considering all the data, the SVL showed significant differences between male groups with TS smaller and greater than 3 mm (Fig. 1, upper left panel).

The TS showed a significant relationship between SVL and DATE (1 in Table 1). However, analysis of variance among SS, taking into account SVL and DATE as covariates, was not possible due to lack of variance homogeneity. Spermatogenic stage 4 was found only at the end of spring and at the end of summer. The TS showed significant differences among SS (Fig. 1, lower left panel and Fig. 2): in particular, TS corresponding to spermatogenic stage 1 was significantly smaller than all others, and TS of spermatogenic stage 3 was significantly larger than those of spermatogenic stage 2 and 4.

A significant relationship was found between TD and EH (2 in Table 1). The TS showed a significant relationship with TD (3 in Table 1), and EH (4 in Table 1).

Liolaemus pictus. TS was related to SVL (Fig. 1, upper right panel). All the specimens, except one, have advanced SS (4) so, the relationship between TS and SS could not be statistically analysed (Fig. 1, lower right panel).

A significant relationship was found between TD and EH (5 in Table 1). The TS did not show a significant relationship either with EH (6 in Table 1), or with TD (7 in Table 1).

BODY SIZE

Liolaemus elongatus. Male SVL in samples A, B and C ranged from 55.06 mm to 90.9 mm ($n=84$). Male

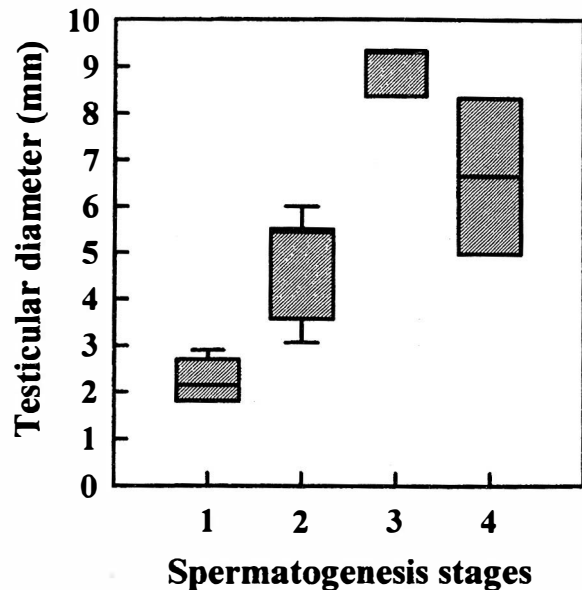


FIG 2. Testicular diameter versus spermatogenesis stages for male *L. elongatus*. Box plots indicate median, quartiles, and 10th and 90th percentiles (no data outside). The TS corresponding to spermatogenic stage 1 was significantly smaller than all others (Mann-Whitney, $Z_{1,2}=4.1033$, $n=28$, $P<0.0001$, $Z_{1,3}=3.5341$, $n=17$, $P<0.0004$, $Z_{1,4}=3.4427$, $n=16$, $P<0.0006$), and TS of spermatogenic stage 3 was significantly larger than those of spermatogenic stage 2 (Mann-Whitney, $Z=4.2797$, $n=29$, $P<0.0001$) and 4 (Mann-Whitney, $Z=3.5523$, $n=17$, $P<0.0004$).

SVL from capture-recapture sample (D) ranged from 57.3 mm to 77.1 mm ($n=15$). Female SVL from samples A, B and C ranged from 53.7 mm to 85.9 mm ($n=88$). Female SVL from sample D ranged from 63.7 to 76.8 mm ($n=8$). Male and female SVL distributions (all individuals) did not show significant differences (Fig. 3). In sample D, males and females show significantly different BP (8 in Table 1) but not different BW (9 in Table 1).

Liolaemus pictus. Male SVL ranged from 50 mm to 75 mm (samples A and B, $n=55$), while SVL of males from the capture-recapture sample (D) ranged from 53.5 mm to 61.8 mm ($n=5$). Female SVL from samples

TABLE 1. Summary of statistical analyses. TS, testicular size; SVL, snout-vent length; DATE, date of capture; TD, seminiferous tubule diameter; EH, epithelium height; BP, maximum body perimeter; BW, body weight.

Test	Variables	Statistic	df or n	P	
1	Multiple Regression	TS vs. SVL and DATE	$F=37.57$	df=44	$P<0.001$
2	Correlation	TD vs. EH	$r=0.95$	$n=14$	$P<0.0001$
3	Correlation	TS vs. TD	$r=0.91$	$n=14$	$P<0.0001$
4	Correlation	TS vs. EH	$r=0.84$	$n=14$	$P<0.0001$
5	Correlation	TD vs. EH	$r=0.94$	$n=7$	$P<0.002$
6	Correlation	TS vs. EH	$r=0.08$	$n=7$	$P>0.86$
7	Correlation	TS vs. TD	$r=0.09$	$n=7$	$P>0.84$
8	Student's <i>t</i>	BP, between sexes	$t=4.70$	df=19	$P<0.0001$
9	Student's <i>t</i>	BW, between sexes	$t=0.01$	df=11	$P>0.90$
10	Student's <i>t</i>	BP, between sexes	$t=0.58$	df=6	$P>0.58$
11	Student's <i>t</i>	BW, between sexes	$t=-0.40$	df=7	$P>0.70$

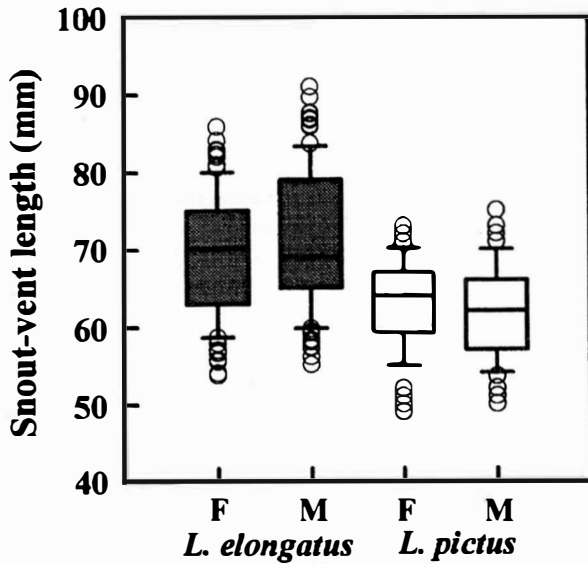


FIG. 3. Female (F) and male (M) snout-vent length of adult *L. elongatus* ($n=194$, samples A, B, C and D) and *L. pictus* ($n=143$, samples A, B and D). Box plots indicate median, quartiles and data outside 10th and 90th percentiles. No significant difference between sexes could be found (Kolmogorov-Smirnov, *L. elongatus*, $Z=1.042$, $n=194$, $P>0.22$, *L. pictus*, $Z=0.819$, $n=143$, $P>0.51$).

A and B ranged from 49 mm to 73 mm ($n=79$), while SVL of females from the capture-recapture sample (D), ranged from 55.8 mm to 68.9 ($n=4$). Male and female SVL were not significantly different (Fig. 3). In sample D, males and females did not show significantly different BP (10 in Table 1) nor different BW (11 in Table 1).

ADULT GROWTH

Liolaemus elongatus. Capture-recapture data from sample D (Fig. 4) show individual growth of two fe-

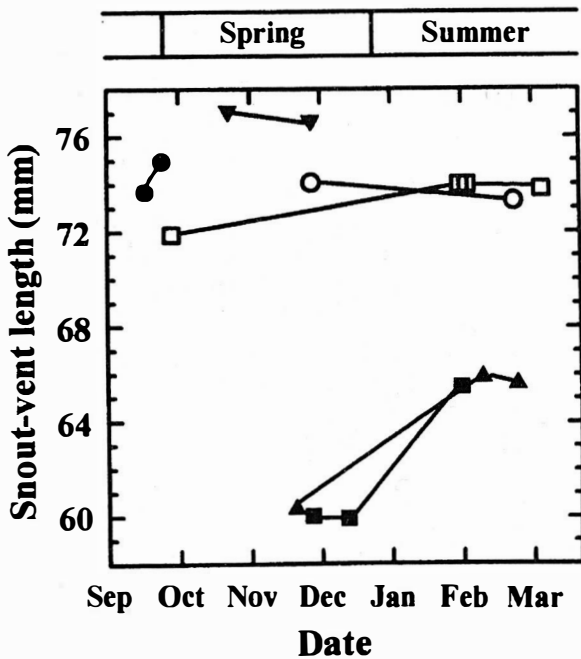


FIG. 4. Snout-vent length versus DATE recapture data of female (hollow symbols) and male (solid symbols) *L. elongatus*. Lines link records of the same animal.

males and four males and particularly, a notable growth of two males during summer.

Liolaemus pictus. Only one male lizard was recaptured (sample D), so no inter-sexual comparison was possible.

DISCUSSION

Reptile reproduction is considered to be cyclical in temperate zones. Pudney (1995) considered two patterns of spermatogenesis. In the typical "postnuptial" pattern the mating occurs in spring/early summer, followed by a period of testicular regression. Spermatogenic recrudescence is initiated in the late summer/autumn. For some species spermatogenesis is completed before winter, with spermatozoa stored in the epididymides (*sensu* Pudney, 1995) for the next breeding season. In the "prenuptial" pattern, spermatogenesis undergoes arrest in the winter (or proceeds at a very slow rate) to resume again in the spring, and is completed just before mating (Pudney, 1995). Most oviparous *Liolaemus* species can be ascribed to one of these patterns (Ramírez-Pinilla, 1991; Cruz & Ramírez-Pinilla, 1996; Vega, 1997). Viviparous *Liolaemus* species have "prenuptial" - for example *L. gravenhorsti* (Leyton *et al.*, 1977) - or "postnuptial" patterns - for example, *L. aymarae* - but also different reproductive patterns not clearly ascribed to "prenuptial" or "postnuptial" profiles such as those of *L. multiformis*, *L. jamesi* and *L. alticolor* (Leyton *et al.*, 1982). *Liolaemus gravenhorsti* has a yearly, continuous spermatogenesis, with a period of maximal activity in summer-autumn and minimal activity in spring-summer. Female *L. gravenhorsti* do not have a sperm reservoir and oocytes are ovulated in spring (Leyton *et al.*, 1977). *Liolaemus aymarae* has spermatozoa in the epididymides in mid- and late autumn and pregnancy in late spring. In *Liolaemus multiformis* and *L. jamesi* the availability of gametes is synchronized in males and females in autumn. Pregnancy takes place during winter and spring (Leyton *et al.*, 1982).

Male *L. elongatus* and *L. pictus* show two major inter-specific differences in their reproductive biology. First, we found a small group of non-reproductive adult male *L. elongatus* alongside reproductive lizards. Non-reproductive adult males lack germinal cells other than spermatogonia and have smaller testes and shorter SVL. The capability of TS to discriminate a group of small males, with testes poorly developed reinforces the relationship between TS and SS. This seems to be the case for *Platysaurus* (van Wyk & Mouton, 1996) in which young adult males, while entering the mature group may exhibit a delay in reproduction relative to larger individuals. It is tempting to consider stage 1 males as juveniles, but the presence of similar-sized males with large testes still supports the 53.74 mm SVL (Ibargüengoytia & Cussac, 1998) as maximum juvenile size. The non-reproductive character of small adult males would probably allow the coexistence of males with a wide range of body sizes, as can be seen in the

SVL distribution of sample D (see Results), instead of the spatial displacement of newly mature males by larger adult ones, as happens in *Anolis limifrons* (Andrews & Stamps, 1994). This delayed reproduction, probably for one year, reduces the reproductive cost over the entire life cycle by preventing male-male encounters (and indirectly, exposure to predators), and by allowing smaller males to allocate energy to growth. Such a strategy augments, in *Ameiva plei* (Censky, 1995), the possibilities of future mating and, ultimately, increases the reproductive success. Large *A. plei* males win intrasexual encounters, guard females and are the only males observed to mate (see also Sugg, Fitzgerald & Snell, 1995). We cannot ignore the fact that, curiously, this phenomenon was not observed in *L. pictus*, though the latter has lower availability of reproductive females (Ibargüengoytía & Cussac, 1996). Other factors, such as environmentally dependent differences in predation risk, probably change the final consequences of male-male encounters.

Secondly, the observed relationships between TS and SS also show two species-specific characteristics. As in *L. gravenhorsti* (Leyton *et al.*, 1977), male *L. elongatus* show an increasing TS during spermatogenesis and a decrease when the first spermatozoa occur. However, the positive relationship among TS, TD and EH in *L. elongatus* differs from *L. gravenhorsti*, where the tubules maintain a wide diameter even when testicular weight decreases. It is important to keep in mind, when considering similarities between these species, that the female reproductive cycle of *L. elongatus* closely resembles *L. gravenhorsti* (Leyton *et al.*, 1977; Leyton, Miranda & Bustos Obregón, 1980; Ibargüengoytía & Cussac, 1998).

Liolaemus elongatus had spermatozoa in the seminiferous tubules at the end of spring and at the end of summer. In a rather different way, *L. pictus* had spermatozoa in seminiferous tubules throughout the sampling period, from spring to autumn, and displayed no significant relationship between TS and EH and TD, suggesting a different male cycle. The absence of a relationship between testicular and tubular size would be related to interstitial hydration (Leyton *et al.*, 1977). Here, it seems that the same strategy is used in two different situations. Male neotropical lizards, such as *Tropidurus peruvianus*, encounter reproductive females throughout the year (Leyton *et al.*, 1982). Male *L. pictus* face, in a temperate environment, a low availability of reproductive females, due to the biennial to triennial female reproductive cycle (Ibargüengoytía & Cussac, 1996) and probably, a low and unpredictable encounter rate during the spring-autumn breeding season. For both species, males have a permanent supply of spermatozoa.

The absence of dependence between female reproductive condition and adult female body length in both species (Ibargüengoytía & Cussac, 1996; 1998), and female growth rates that are lower than males in *L. elongatus*, agree with the idea of female preferential in-

vestment in present reproduction (Smith, 1992; Sugg *et al.*, 1995). However, in *L. elongatus* and *L. pictus* (present results and Ibargüengoytía & Cussac, 1996; 1998), adult male and female mean body length showed neither intersexual differences nor differences in size at the time of sexual maturity. Different growth rates but similar adult size suggest a cause that remains to be tested - that of greater predation on larger males.

Past (Ibargüengoytía & Cussac, 1996; 1998) and present results point out slight interspecific differences in sexual dimorphism and major differences in male cycle between *L. pictus* and *L. elongatus*, coinciding with a differential accessibility to females. Male *L. pictus* begins to reproduce during its first year of adulthood and remains active during a long breeding season. In contrast, male *L. elongatus* delay reproduction for one year and reproduce during a narrower period, in synchrony with the female reproductive cycle.

The male cycle can be considered as the functional counterpart of the male component of sexual dimorphism. The causal relationships between female and male reproductive cycles are mutual but the existence of severe thermal constraints for vitellogenesis and pregnancy (Ibargüengoytía & Cussac, 1996, 1998) set the following chain of causal events: environmental conditions - female cycle - male cycle and male dimorphic traits. This sequence of events, compared for two species of *Liolaemus* in Patagonia, indicates how environmental cues can constrain female cycle and female availability, and in consequence affect male cycle and the development of male dimorphic traits.

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