

REPRODUCTIVE BIOLOGY OF THE VIVIPAROUS LIZARD, *LIOLAEMUS PICTUS* (*TROPIDURIDAE*): BIENNIAL FEMALE REPRODUCTIVE CYCLE?

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Viviparity has been reached independently by different genera of reptiles. Synchronization of the reproductive style with the environment facilitates offspring birth and survival. Several authors postulate a close relationship between reproductive mode and environmental conditions in these species. *Liolaemus pictus* is a viviparous medium-sized lizard that lives in temperate habitats up to moderate altitudes in the Andean-Patagonian forest. Sexual dimorphism, follicle number and size in relation to body size, date and locality, reproductive cycle and litter size were studied. In the light of our results we reject an annual reproductive cycle for female *Liolaemus pictus* in favour of a multiannual one. As a different reproductive style among viviparous lizards, biennial (or triennial) reproduction enlarges the known diversity of reptilian reproductive responses to short and cold activity seasons, such as those typical of the highlands of southern South America.

INTRODUCTION

Most lizards are oviparous, but squamate viviparity (Callard, Fileti, Pérez, Sorbera, Giannoukous, Klosterman, Tsang & McCracken, 1992; Guillette, 1993; Stewart, 1993) has evolved at a multitude of taxonomic levels, and within *Liolaemus* itself (Blackburn, 1982, 1985).

The relationship between reptilian reproductive styles (sensu Balon, 1990) and environment is complex (Vitt, 1992). In addition, it may be the consequence of inherited traits that evolved in the past (Guillette & Méndez de la Cruz, 1993). Optimization of offspring production implies not only present reproductive success but also parental survival and future reproductive success. Thus, we can expect that species will find an adequate balance between the age of first breeding, the annual number of broods, clutch size and duration of embryonic life, considering only the most important reproductive characteristics (Shine & Schwarzkopf, 1992). An appropriate co-ordination of the reproductive style with the environment (e.g. temperature, photoperiod, rainfall) allows offspring birth and survival.

The cold climate hypothesis (Shine, 1985, 1989) considers viviparity evolved in cold climates and this evolution is an adaptation to low temperature conditions, among other factors. Guillette (1993) contrasts this hypothesis with that of Tinkle & Gibbons (1977), who considered viviparity as a pre-adaptation to such conditions. Irrespective of the causal order of the events, there is a relationship between reproductive mode and environmental conditions in squamate reptiles. Viviparity is more common among cool-climate reptiles than among species living in warmer climates (Shine, 1995).

Probably, the strong relationship between embryonic developmental rate and temperature (Heulin, Oseneeg & Lebouvier, 1991) establishes the main con-

straint to reproduction in relation to the shortening of the activity season under cold climates. Recently, Shine (1995) proposed and tested successfully the idea that prolonged uterine retention directly enhances hatchling viability, because eggs incubated at maternal body temperatures produce 'better' hatchlings than do eggs incubated at normal nest temperatures. The phenotypic plasticity hypothesis (Shine, 1995) predicts that prolonged uterine retention might enhance offspring fitness in any environment in which maternal temperatures differ from nest temperatures.

Many of the extant reptiles of southern South America belong to the family *Tropiduridae* (sensu Frost & Etheridge, 1989), with three subfamilies. One of them, *Liolaeminae*, has three genera. The genus *Liolaemus*, with at least 50 known species in the centre and south of Argentina, is broadly distributed from the highlands of Perú and Bolivia to Tierra del Fuego and from the Pacific islands to Brazil (Cei, 1986). *Liolaemus pictus* (Duméril & Bibron) is a viviparous medium-sized lizard (23 to 75 mm snout-vent length) that lives in temperate habitats up to moderate altitudes (520 to 1600 m), in leaf-mould and under logs (Donoso-Barros, 1966). It is the most common lizard in the Andean-Patagonian forest of Nahuel Huapi National Park (Christie, 1984).

Several annual reproductive cycles have been described in the genus *Liolaemus* (Pearson, 1954; Ramirez Pinilla, 1991, 1992a, 1995; Leyton & Valencia, 1992; Duarte Rocha, 1992), but this genus has great variations in the timing of reproductive processes. Within viviparous *Liolaemus* species we can see two different ways of coping with high altitude conditions. As do most autumn/winter-breeding viviparous lizards (Flemming & van Wyk, 1992), *L. multiformis multiformis* (4600 m) and *L. huacahuasicus* (3700 m) exhibits autumn vitellogenesis and ovulation, followed by pregnancy over winter and parturition during spring (Pearson, 1954; Ramirez Pinilla, 1991). Three vivipa-

rous montane species (2500 m), *L. altissimus*, *L. leopardinus*, and *L. nigroviridis* (Leyton & Valencia, 1992), exhibit vitellogenesis from late summer to early spring, followed by pregnancy during spring and summer, and the same situation occurs in *L. gravenhosti*, a mid-elevation (700 m) viviparous lizard (Leyton & Valencia, 1992).

The aim of this work is to study the reproductive biology of *Liolaemus pictus*, in order to augment knowledge of the existing reproductive styles of the genus *Liolaemus*, and understanding of the relationship between environment and reproduction in reptiles.

MATERIALS AND METHODS

MATERIAL USED

Specimens preserved in 70% ethanol (Sample A, $n=186$), collected from November to April 1982, 1983, and 1984, during an extensive survey of Nahuel Huapi and Lanín National Parks (Christie, 1984) were used. Additional specimens (Sample B, $n=30$) were collected from October 1993 to April 1994 in the rain forest and at the shore of the Nahuel Huapi lake. As a result of weather, *L. pictus* was inactive during the winter and capture was not possible several months of the year.

AUTOPSY PROCEDURES

Lizards were killed by intraperitoneal administration of sodic thiopental, fixed in 4% formaldehyde (Sample A) or Bouin's solution (Sample B) for 24 h and preserved in 70% ethanol. Small lizards, undoubtedly juvenile, were not dissected.

Ovarian follicles, corpora lutea and uteri were characterized by morphological and histological observation. Follicular categories were defined on the basis of the follicular size and the absence (previtellogenic follicles), presence (vitellogenic follicles) or anomalous distribution (atretic follicles) of yolk.

Estimation of ovarian size was based on the diameter of the largest follicle (Duarte Rocha, 1992), recorded with a vernier calliper on camera lucida schemes. For testicular size the antero-posterior diameter was used. Litter size was estimated by counting the number of embryos in the uterus.

DATA RECORDED

Capture dates (DATE) were considered as the number of days after 21 September. Longitude and latitude of sampling sites were noted, and the following data were recorded for each lizard: sex, reproductive stage, gonadal size, snout-vent length (SVL), head length (HL), head width (HW) and width at vent (WAV). When needed, all original measures were transformed to natural logarithms to approximate multivariate normality and linear relationships, and corrected for SVL according to the following equation

(Reichow, Largiadèr, Kligerberg, Clemmesen, Froese & Ueberschär, 1991; Battini, Alonso & Cussac, 1995):

$$(a) AM = OML - (RC \times (\ln SVL - \text{Mean}(\ln SVL))),$$

where AM = adjusted measurement, OML = original measurement logarithm, RC = regression coefficient between the logarithm of the character and the logarithm of SVL, Mean(ln SVL) = overall mean of SVL logarithm.

STATISTICAL ANALYSIS

Data were analysed using analysis of variance (ANOVA), regression analysis (REGR), Kruskal-Wallis (KW), paired *t*-test (T-TEST) and discriminant analysis (DISCR). Normality and variance homogeneity assumptions were tested, comparing predicted and observed frequencies, by means of Kolmogorov - Smirnov (KS) and Runs test (RUN), and by means of Bartlett test, respectively (Sokal & Rohlf, 1969; Norusis, 1986).

RESULTS

JUVENILE PERIOD, SEXUAL DIMORPHISM, AND SEX RATIO

In agreement with Pflanz, Cusumano & Powell (1991), the maximum juvenile size was considered less than the size of the smallest vitellogenic female (49 mm, Fig. 1).

Temporal distribution of juveniles collected is presented in Fig. 2. Capture date was bimodal (KS, $Z=1.398$, $n=54$, $P<0.04$), with groups either side of

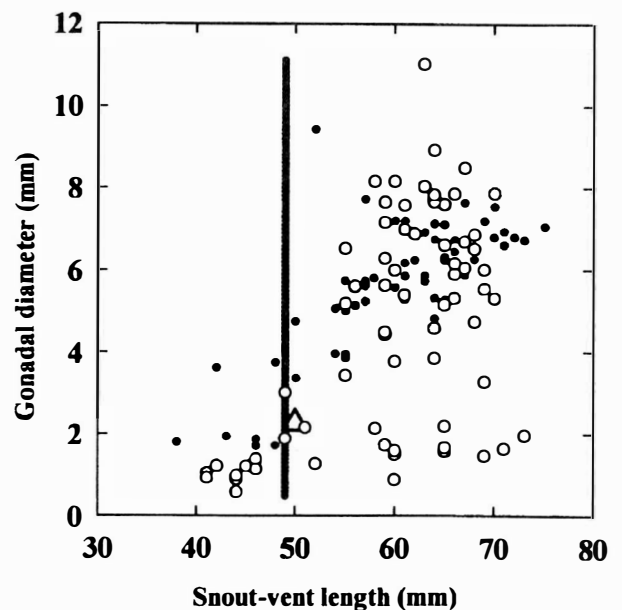


FIG. 1. Maximum juvenile size (vertical line) of male (filled circles) and female (hollow circles) *L. pictus* in relation to gonadal diameter and SVL. The triangle indicates the smallest vitellogenic female.

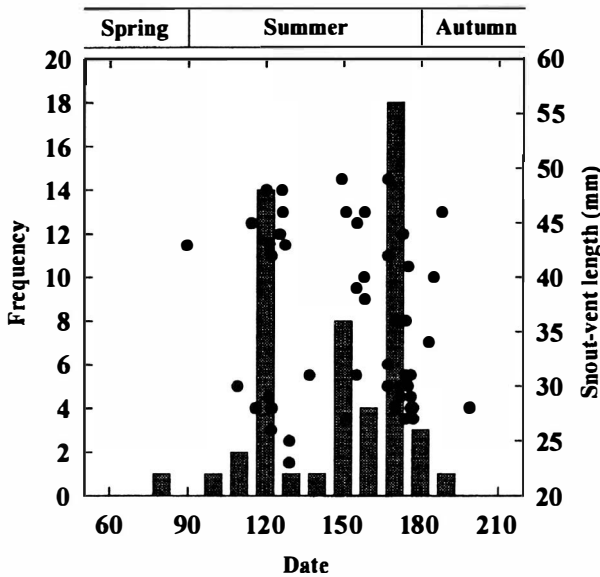


FIG. 2. Frequency (histogram) and SVL (filled circles) of juveniles against DATE (number of days after September 21).

DATE 140 (RUN, $Z=-2.30$, $n=54$, $P < 0.0001$), but DATE groups did not show different SVL (KW, $n=54$, $\chi^2=0.036$, $df=1$ $P > 0.84$). On the other hand SVL was also bimodal (KS, $Z=1.51$, $n=54$, $P < 0.02$) with groups of SVL (Fig. 2), less than and more than 35 mm (RUN, $Z=-7.14$, $n=54$, $P < 0.0001$).

Liolaemus pictus does not show notable differences between the sexes. Only males had pre-anal glands (sensu Antoniazzi, Jared, Pellegrini, & Macha, 1993), which were two to four in number. The SVL did not differ between males and females (ANOVA, $F=0.25$, $df=150$, $P > 0.61$) but body shape did (DISCR, Wilks' $\Lambda=0.487$, $n=147$, $P < 0.0001$, AM were used). The relative importance of the morphometric variables was WAV > HW > HL. Analysed separately, each of these variables was significantly larger in males (Table 1).

TABLE 1. (a) Standardised canonical discriminant function coefficients $P < 0.0001$; grouped cases correctly classified: 87.76%, (b) Pooled-within-groups Pearson correlations between discriminating variables and canonical discriminant function and (c) significance of the ANOVA between male and female lizards.

| Variable* | Canonical coefficient (a) | Correlation coefficient (b) | P (c) |
|-----------|---------------------------|-----------------------------|--------|
| HW | 0.3310 | 0.70509 | 0.0001 |
| HL | 0.2846 | 0.46990 | 0.0001 |
| WAV | 0.6875 | 0.92044 | 0.0001 |

* Adjusted measurements

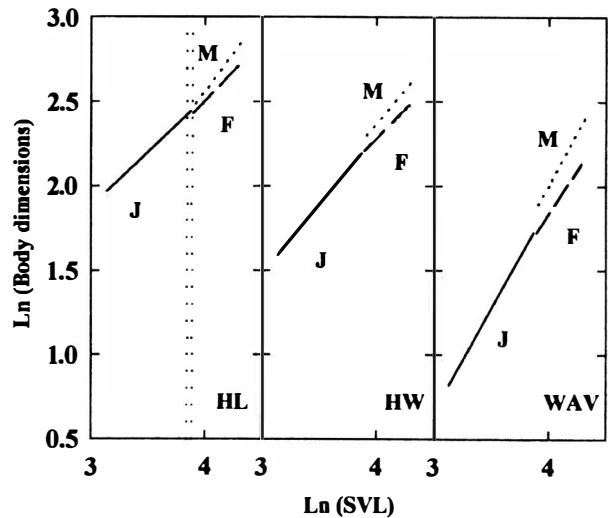


FIG. 3. Juvenile (J), male (M) and female (F) allometric relationship of HL, HW and WAV with SVL. Regression lines are indicated. Vertical dotted lines indicate SVL=46.6 mm and SVL=49 mm.

Comparison of 95% confidence intervals, for slopes and intercepts regression lines for adults and juveniles, showed that HL grew faster in adult males ($n=54$) than in juveniles ($n=52$). Other significant differences of slopes and intercepts between adults and juveniles were not found (Fig. 3).

Scatterplots of allometric relationships between HL, HW and WAV with SVL did not show a clear cut-off point between juvenile and adult lizards, but the intersection between juvenile and male HL lines (SVL=46.6 mm) is consistent with the assumed maximum juvenile size (SVL=49 mm, Fig. 3).

Amongst specimens collected (Sample A), the ratio of adult males to adult females was 0.86:1.

GONADS AND DUCTS

Male. The epididymis in adults males appeared convoluted and white, while in juveniles it was thinner and less conspicuous. Slight but significant differences were found between right and left testicular diameter ($t=6.68$, $df=58$, $P < 0.001$).

Female. Previtellogenic follicles were present in the ovaries of all examined juvenile females (smallest SVL=41 mm), while previtellogenic, vitellogenic or atretic follicles were found in adult females. Corpora lutea were seen only in gravid females, together with previtellogenic follicles. Large vitellogenic follicles were never recorded in gravid females.

The uterus of vitellogenic and postgravid female *L. pictus* was folded and pale white. Folds grow, in preovulatory individuals, with a notable thickening of the mucosa and proliferation of secretory glands. Juveniles had a transparent uterus without folds.

No significant differences were found between right and left follicle diameter ($t=0.30$, $df=69$, $P > 0.76$) nor

TABLE 2. Multiple regression analysis of standardised gonadal diameter versus locality coordinates, SVL and DATE. Latitude and Longitude are expressed in the Gauss-Kruger system.

| | Variable | Slope | <i>n</i> | <i>P</i> |
|-----------|-----------|-----------|----------|----------|
| Males | Longitude | 0.002033 | 50 | 0.5101 |
| | Latitude | -0.001345 | 50 | 0.1179 |
| | Altitude | -0.000073 | 38 | 0.7748 |
| | SVL | 0.002915 | 50 | 0.5952 |
| | DATE | -0.000208 | 50 | 0.8716 |
| Females | Longitude | 0.005302 | 46 | 0.3342 |
| | Latitude | -0.003325 | 46 | 0.0126 |
| | Altitude | 0.000203 | 36 | 0.7323 |
| | SVL | 0.003591 | 46 | 0.7531 |
| | DATE | 0.001182 | 46 | 0.6632 |
| Vit. Fem. | Longitude | -0.001025 | 30 | 0.7907 |
| | Latitude | -0.001027 | 30 | 0.2527 |
| | Altitude | 0.000181 | 25 | 0.6615 |
| | SVL | -0.009281 | 30 | 0.4052 |
| | DATE | 0.003821 | 30 | 0.0448 |

follicle number ($t=0.00$, $df=14$, $P=1$). Follicle growth (REGR multiplicative model, $F=5.63$, $df=42$, $P<0.023$) and follicle number (REGR, multiplicative model, $F=4.75$, $df=14$, $P<0.049$) in vitellogenic females showed a significant relationship with SVL. Thus, female gonadal diameters were adjusted according to equation (a) for further studies.

REPRODUCTIVE CYCLE

Male. No significant regression of male testicular diameter, adjusted to equation (a), ° latitude of localities was found (Table 2, $n=50$, $P<0.12$), even when relationships with SVL and DATE were considered into the analysis. In the same way, adjusted testicular diameter did not show variation in relation to DATE in the period considered (REGR, $n=60$, $\alpha=0.64$).

Female. A significant regression ($n=46$, $P<0.01$) of adjusted follicle diameter of all females ° latitude of localities was found (Table 2), but not for vitellogenic females only ($n=30$, $P<0.25$), even when relationships with SVL and DATE were considered in the analysis.

The number of non-reproductive adult females captured during summer and early autumn (Fig. 5) represented 20% of the total number of adult females.

The adjusted follicle diameter, from late spring to early autumn, keeps a linear and significant relationship with DATE (Fig. 4 and 5, REGR, $n=43$, $\alpha=0.0003$), (estimate \pm S.E.).

$$(b) Y = 0.0049 (\pm 0.0012) X + 1.0 (\pm 0.2)$$

Time span from the onset of vitellogenesis until peak vitellogenic activity occurred in preovulatory females, was 129 days.

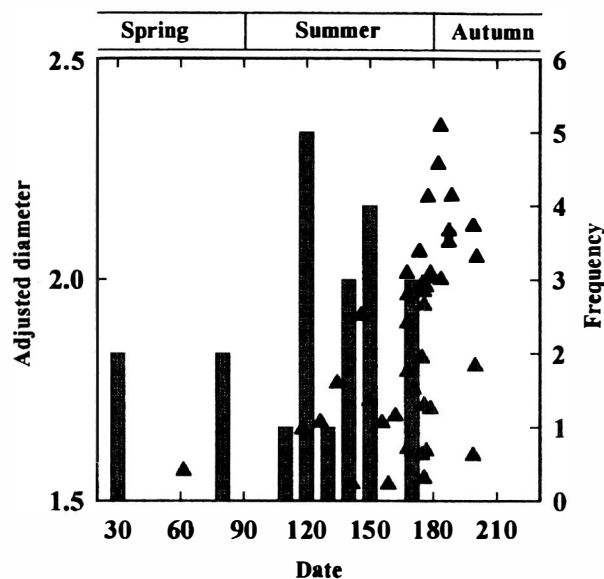


FIG. 4. Adjusted follicular diameter of vitellogenic females (filled triangles) and frequency of gravid females (histogram) against DATE (number of days after September 21).

Gravid females ($n=21$) were captured from late spring (December) to late summer (March, Figs. 4 and 5). The four females caught in spring contained in the uterus ovulated oocytes only, with no embryonic development apparent. Gravid females caught in summer (January to March) all contained advanced embryos. Litter size (LS) ranged between three and six foetuses in 62 to 74 mm SVL females ($LS_{media} = 4.08$, $n=12$).

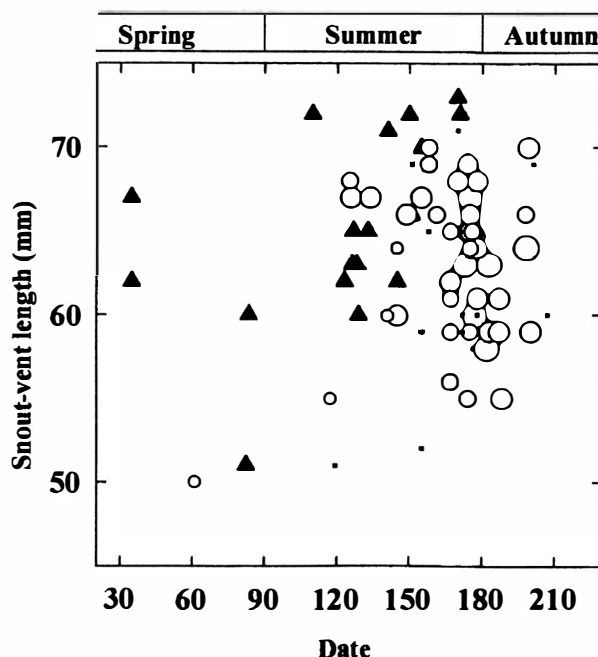


FIG. 5. SVL of non-vitellogenic females (small squares), vitellogenic females (hollow circles; sizes are proportional to the diameter of the largest ovarian follicles, ranging from 2.27 to 11.02 mm) and gravid females (triangles) against DATE (number of days after September 21).

DISCUSSION

The juvenile populations of *L. pictus* clearly show two cohorts. Modal grouping of juvenile by DATE or by SVL, as Christie (pers. com.) proposed, points to the unanswered question of the magnitude of juvenile growth from autumn to spring. In any case, sexual maturity would not be reached in less than one and a half years from birth. This is in agreement with observations of Sinervo & Adolph (1994) for mid-elevation *Sceloporus occidentalis* lizards from southern California (2200 m) and central Oregon (750 m).

Although brood size is associated with female body size, and a selective advantage to large female body size could be expected because of its immediate reproductive consequences (Vitt & Blackburn, 1991), we failed to record differences in SVL between male and female *L. pictus*.

Donoso-Barros (1966) noted a narrower female head in *L. pictus*. We noted a larger male head and, in addition, two to four pre-anal glands (three to four according to Cei, 1986) and a greater width at vent in males. Among the differences here observed, the last was found to be the best variable to identify the sex in the field, even before capture.

Sexual differences in head size could reflect divergence resulting from resource partitioning, or differential energy allocations for reproduction, or could be a response to selective pressures due to the social structure (Mouton & van Wyk, 1993). The observed sexual differences in the head size of *L. pictus*, however, are due to an allometric increase in male head size relative to juvenile head size. This phenomenon, differing from reports for other lizard species (Mouton & van Wyk, 1993), could be the result of sexual selection, given the sex ratio and that less than half of adult females seem to be ready to ovulate each year (see below).

Morphology and histology of male and female reproductive organs agree with the descriptions for *Iguana* (Cei, 1986) and *Liolaemus* Ramírez Pinilla, 1991, 1992b; Leyton & Valencia, 1992).

Data about the male cycle suggest a prolonged spermatogenetic period, from late spring to early autumn. An exhaustive histological study will be necessary to relate male and female cycles, particularly in relation to the possible storing of sperm in the epididymides (Pudney, 1995) or in the uterus-vagina transition (Ramírez Pinilla, 1991, 1992b).

Similar to other squamates (Schwarzkopf, 1992; Shine & Schwarzkopf, 1992; Méndez de la Cruz, Guillette & Villagran-Santa Cruz, 1993), female *L. pictus* showed positive relationships between the size and number of follicles and SVL, contrary to Leyton & Valencia (1992) who considered the follicle population to be stable in six *Liolaemus* species.

Females coming from southern localities showed a larger mean follicle size, when all females were considered in the analysis. Vitellogenic females did not show

this variation. Thus, an earlier onset of ovary growth in southern populations may be indicated, rather than a different energy allocation to reproduction as can be seen in other reptilian and vertebrate groups (Iverson, Balgooyen, Byrd & Lyddan, 1993).

The statements of Callard *et al.* (1992), that hepatic vitellogenin synthesis is down-regulated by progesterone and that the corpus luteum is responsible for the prolonged pattern of progesterone secretion common to viviparous species, point out vitellogenesis and pregnancy as two phenomena mutually exclusive in viviparous squamates.

If vitellogenesis and pregnancy cannot coexist, we would expect capture dates of vitellogenic and pregnant females to show a successive pattern. The almost complete temporal overlapping found between vitellogenesis and pregnancy (Figs. 4 and 5) is inconsistent with the hypothesis of an annual reproductive cycle in *L. pictus*. Plotting data as Pearson (1954) did shows that the presence of advanced vitellogenic females in almost all the range of DATE and SVL of pregnant females (Fig. 5) discards an artefact due to dependence with SVL.

The minimum time required by *L. pictus* to complete the reproductive cycle appears to be two years, as was also observed in *Cordylus giganteus* (van Wyk, 1991). However, the criterion used by van Wyk (1991) and previously by Aldridge (1979 cited in van Wyk, 1991) to determine biennial reproduction was, as we interpreted, the presence of ca. 50% of non-reproductive adult females during the breeding season. No temporal overlapping between vitellogenesis and pregnancy was described in *C. giganteus*; most females skip a year before starting the next vitellogenic cycle, probably due to the fact that parturition take place in autumn at the time when vitellogenesis starts. Therefore, the skipping of a cycle may be related to environmentally constrained access to energy.

We postulate that *L. pictus* vitellogenesis begins in late spring and is continued through the summer and autumn, being completed after a period of latency or low follicle growth over winter. Ovulation and mating would happen in the next spring, when the male gonads are already active. Such a lengthening of the ovarian cycle beyond the annual cycle was also shown by Cree, Cockrem & Guillette (1992) in *Sphenodon*. In the female tuatara, vitellogenesis of a single clutch usually begins in the first year after nesting, but often continues for several years before ovulation occurs. As well as having a prolonged period of vitellogenesis, female tuatara have an exceptionally long period of gravidity (6-8 months) compared with other oviparous reptiles (Cree *et al.*, 1992). In *Hoplodactylus maculatus* (from the Macraes-Middlemarch population) a biennial cycle is reached by means of a prolonged vitellogenesis of 10 months and a gestation of 14 months (Cree & Guillette, 1995). In this species, and in *Barisia monticola* (Vial & Stewart, 1985 cited in Cree & Guillette, 1995), the biennial cycles do not skip a year (Cree & Guillette,

1995). In *L. pictus* pregnancy occurs during late spring and summer. The advanced development of fetuses seen in gravid females of *L. pictus* caught in summer and the juvenile capture dates lead us to propose that parturition takes place from late summer to early autumn.

At the time of ovulation in a female group, we expect that another group of females starts a new vitellogenic cycle. However, we found many (20%) non-reproductive adult females during summer and early autumn (Fig. 5). This suggests that, after parturition, at least some females skip a year before starting the next vitellogenic cycle. These females will undergo vitellogenesis every third year.

Multiannual female reproductive cycles have also been observed in several snakes (Bonnet, Naulleau & Mauget, 1992), but the cause seems to be the time necessary to store lipids for future vitellogenesis. The evolution of viviparity in lizards has been related to low temperature conditions (Tinkle, Wilbur & Tilley, 1970; Tinkle & Gibbons, 1977; Shine, 1985, 1989), particularly in association with the time and the optimum temperature needed for development (Shine & Harlow, 1993; Shine, 1995). It seems that *L. pictus* responds to short and cold activity seasons in a new way, allocating vitellogenesis and development to separate years, and sometimes combining the lengthening of the ovarian cycle with the skipping of a year. The reproductive cycle of *L. pictus* enlarges the spectrum of reptilian responses to climate, and can be seen as a means of access to new niches, particularly in the cold highlands of southern South America.

ACKNOWLEDGEMENTS

We wish to express our gratitude to Adriana Albino and Oliver Pearson for their valuable suggestions and comments, and to Miguel Christie for the critical review of the manuscript. We also thank Daniel G. Blackburn and an anonymous reviewer who offered constructive and insightful comments on the manuscript.

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