REPRODUCTION OF THE VIVIPAROUS LIZARD *LIOLAEMUS ELONGATUS* IN THE HIGHLANDS OF SOUTHERN SOUTH AMERICA: PLASTIC CYCLES IN RESPONSE TO CLIMATE?

NORA R. IBARGÜENGOYTÍA AND VICTOR E. CUSSAC

Centro Regional Universitario Bariloche, Universidad Nacional del Comahue, Unidad Postal Universidad del Comahue, Bariloche, 8400, Río Negro, Argentina

Squamate viviparity has evolved on several occasions, and probably independently within the genus *Liolaemus* itself. Hypotheses about the origin of reptilian viviparity emphasize the advantage of providing an adequate thermal environment for the embryo. At the same time, high latitudes and altitudes limit the availability of heat to perform vitellogenesis and gestation. The genus *Liolaemus* includes both oviparous and viviparous modes of reproduction, as well as reproductive cycles with great variations in the timing of the events. In the present work maximum juvenile size, sexual dimorphism, gonadal cycle and litter size of viviparous *Liolaemus elongatus* were studied. Female lizards may have annual or biennial cycles, but males reproduce annually in synchronization with the female cycle. Phenotypic plasticity may be one way that allows the species to cope with environmental constraints, and may be a reproductive adaptation that *Liolaemus* has evolved in response to the the cold climate in the highlands of southern South America.

INTRODUCTION

Viviparity has arisen in the squamate reptiles on multiple occasions (Packard, Tracy & Roth, 1977; Blackburn, 1982; Guillette, 1993), and probably independently within the genus *Liolaemus* itself (Blackburn, 1985; Espinoza, 1996). The relationship between reptilian reproduction and the environment may be the consequence of ecological factors (Vitt, 1992) as well as inherited traits that evolved in the past (Guillette & Méndez la Cruz, 1993; Heulin, Osenegg & Lebouvier, 1991). The family Liolaeminae has been subject to the consequences of tertiary orogeny and glacial fluctuations (Cei, 1993) and probably many of its phenotypic characteristics are related to these events.

The cold climate hypothesis (Packard *et al.,* 1977; Shine 1983; Shine, 1985) considers viviparity to have evolved as an adaptation to low temperature conditions, among other factors. The strong relationship between embryonic developmental rate and temperature (Shine 1983; Heulin *et al.,* 1991; Van Damme, Bauwens, Braña & Verheyen, 1992; Shine & Harlow, 1993) establishes the main constraint to reproduction in relation to the shortening of activity season in high latitudes. Espinoza (1996) proposes this hypothesis to explain the origin of viviparity in the genus *Liolaemus*.

Van Damme *et al.* (1992), Shine & Harlow (1993), and Shine (1995) tested the idea that a given range of temperatures during embryogenesis directly enhances hatchling viability. 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. Evidence in support of this hypothesis is far from comprehensive (Heulin *et al.,* 1991; Sinervo & Adolph, 1994; Martín Vallejo, García

Fernández, Pérez Mellado & Vicente Villardón, 1995; Shine, 1995). A complementary approach is that of Charland (1995); (see also Charland & Gregory, 1990; Packard *et al.,* 1977), i.e. the advantage of viviparity lies in the acquisition of a narrow range of developmental temperatures.

We can expect that pregnant females thermoregulate to offer a stable thermal environment to developing embryos while vitellogenic females require an optimum body temperature to minimize vitellogenesis lapse. Both processes require adequate access to heat. Although thermoregulation in lizards is extensively described, how females respond during gametogenesis and pregnancy is little-known (Charland & Gregory, 1990; Charland, 1995; Ibargüengoytía & Cussac, 1996).

There are four responses that may result in multiannual cycles: (1) prolonged vitellogenesis (van Wyk, 1991; Cree & Guillette, 1995; Cree *et al.,* 1992); (2) prolonged pregnancy (Vial & Stewart, 1985; Cree & Guillette, 1995); (3) allocation of vitellogenesis and pregnancy in separate breeding seasons (Ibargüengoytía & Cussac, 1996); and (4) skipping of a year (van Wyk, 1991). Annual cycles can be tested by three criteria: (1) a high ratio of non reproductive females during the breeding season (Aldridge, 1979; van Wyk, 1991); (2) the simultaneous presence of individuals with reproductive conditions non adjacent in the cycle sequence (Cree & Guillette, 1995), and its corollary, (3) the simultaneous presence of vitellogenic and pregnant females in the population (Ibargüengoytía & Cussac, 1996).

The genus *Liolaemus* is distributed from the highlands of Perú and Bolivia to Tierra del Fuego and from Pacific islands to Brazil (Cei, 1986). *Liolaemus* include oviparous and viviparous modes. Viviparous species

show great variations in the timing of reproductive events. *Liolaemus multiformis multiformis* (4600 m), *L. alticolor, L. jamesi, L. aymararum* and *L. huacahuasicus* (3700 m) exhibit autumn vitellogenesis and ovulation, followed by pregnancy over winter and parturition during spring (Pearson, 1954; Leyton *et al.*, 1982; Ramírez Pinilla, 1991). Three mountain 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. gravenhorsti*, a mid-elevation (700 m) lizard (Leyton & Valencia, 1992). *Liolaemus pictus* responds to short and cold activity seasons by means of biennial or triennial cycles, allocating vitellogenesis and pregnancy in different years, and sometimes combining the lengthening of the ovarian cycle with the skipping of a year (Ibargüengoytía & Cussac, 1996).

Liolaemus elongatus has been always described as a saxicolous species dwelling in the steppe (Cei, 1986), but recently it has been recorded from the transition rainforest-steppe (41.2° S, 71.2° W, Ibargüengoytía *et al.*, 1997), overlapping with *L. pictus*, a typical rainforest lizard. The cycle of female *L. elongatus* from a Mendoza population (ca. 32.5° S, 69.3° W and 2700 m high) has been described (Ramírez Pinilla, 1992*b*) as annual and showing vitellogenesis from beginning of summer until end of spring. Females were noted to be gravid from late spring to late summer followed by a new cycle, without a period of rest. An annual male cycle has been described, for the same locality of Mendoza (Macola *et al.*, 1984; Ramírez Pinilla, 1992*b*). These results have the following problems: (1) authors do not differentiate adults from juveniles; (2) Macola *et al.* (1984) describe a rest period in summer and a "receso" (rest?) period in winter, while the same winter individuals are considered active (high testicular volumes) by Ramírez Pinilla (1992*b*); and (3) the latter author does not discuss the pregnant females caught in mid- and late summer (see Fig. 2, pp. 70).

The aim of this work is to describe the reproductive biology of *L. elongatus*, in order to increase the understanding of the effect of environment factors on the reproduction of *Liolaemus* lizards.

MATERIAL AND METHODS

COLLECTION OF SPECIMENS

Three set of specimens were used: Group A: $n = 39$, collected from October to March (1981 to 1984), in Nahuel Huapi and Lanín National Parks; Group B $n = 35$, collected from November to March (1993 to 1995), in San Carlos de Bariloche. Localities of groups A and B are situated between 39° to 41.5° S and 71.6° to 70.5° W, from 500 to 1800 m high. Specimens are deposited in the Centro Regional Universitario Bariloche of the Universidad Nacional del Comahue. Group C: $n = 130$, collected from December to January in Neuquén (1963

to 1973) and Mendoza Province (1961 to 1994). Localities are situated between 32° to 41.07° S and 66.52° to 71.97° W) and specimens are deposited in the Instituto de Biología Animal of the Universidad Nacional de Cuyo.

AUTOPSY PROCEDURES

Lizards were killed by intraperitoneal administration of sodic thiopental, fixed in 4% formaldehyde for 10 days (Groups A and C) or Bouin's solution (Group B) for 24 hr, and preserved in 70 % ethanol. Small lizards (SVL 23.1 to 29.66 mm), were not dissected.

The uteri were characterized by morphological observations into three categories: (1) Uterus type 1: folds, if present, are 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 & Caldwell (1993), and generalized hypertrophy of the oviducts associated with vitellogenic recrudescence (Ramírez Pinilla, 1992*a*); and (3) Uterus type 3: similar to type 2 but conspicuously more stretched with bigger folds. This type seems to be analogous to the stretched oviducts (Flemming & van Wyk, 1992) and to the post-reproductive uterus (Ramírez Pinilla, 1992*a*), in both cases an indication of recent parturition.

Ovarian size was estimated as the diameter of the largest follicle, recorded with a vernier calliper on camera lucida schemes. For testicular size the antero-posterior diameter was used.

The maximum juvenile size was determined taking into account the size of the smallest female with ovulated oocytes or Uterus type 2 (Van Wyk, 1991; Mouton & Van Wyk, 1993), and the smallest male showing testicular growth during the breeding season (Vitt & Caldwell, 1993; Censky, 1995). Litter size was estimated by counting the number of ovulated oocytes or embryos in uterus.

DATA RECORDED

Capture dates were considered as days counted from 21 September, in order to consider a standard year starting the first day of spring (Southern Hemisphere), approximately when lizards become active.

The following data were recorded for each lizard: sex, gonadal size, snout-vent length (SVL), head length (HL), head width (HW) and width at vent (WAV). When needed, all original measures were transformed using natural logarithms to approximate multivariate normality and linear relationships, and corrected for SVL according to the following equation (Reichow *et al.*, 1991):

$$AM = OML - (RC \times (\ln SVL - Mean\ (\ln SVL)))$$

where AM = adjusted measurement; OML = original measurement logarithm; RC = regression coefficient between the logarithm of the character and the loga-
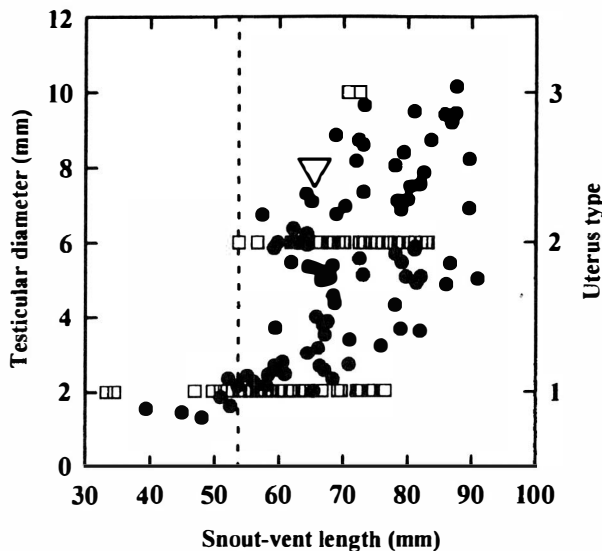
FIG. 1. Maximum juvenile size (SVL, vertical dashed line) in relation to the smallest gravid female (triangle), male testicular diameter (circles) and uterus type (squares).

rithm of SVL, *Mean (ln SVL)* = overall mean of SVL logarithm.

STATISTICAL ANALYSIS

Data were studied using analysis of variance (ANOVA), regression analysis, and the paired *t*-test. 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 the Levene test, respectively. When normality or variance homogeneity assumptions did not hold, Mann-Whitney and Runs tests were used instead (Sokal & Rohlf, 1969; Norusis, 1986).

RESULTS

JUVENILE PERIOD, SEXUAL DIMORPHISM AND SEX RATIO

The smallest female found with ovulated oocytes in the uterus was 65.44 mm SVL whereas Uterus type 2 appears at 53.74 mm SVL. The smallest male showing testicular growth was 57.26 mm SVL. Thus the maximum juvenile size (SVL) was considered less than 53.74 mm (Figs. 1 and 2).

Juveniles were caught from mid spring to late autumn. Although juvenile SVL frequency was normal (Kolmogorov Smirnov test: $Z = 1.28$, $n = 30$, $P > 0.07$), grouping SVL less than and more than 37.5 mm shows the existence of two groups (Fig. 3; Runs test: $Z = -4.71$, $n = 30$, $P < 0.0001$).

Juvenile and adult lizards show different allometric relationships between the three recorded body measurements (head length, head width and width at vent) and SVL. Comparison of 95 % confidence intervals for slopes of adults and juveniles showed that head length grew slower than SVL in juveniles ($n = 30$), adult males
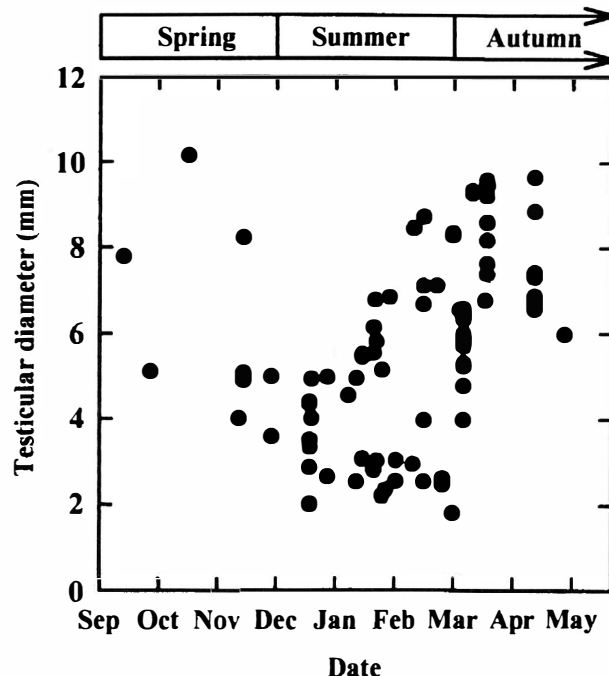

FIG. 2. Testicular diameter of adult males *versus* capture date.

($n = 84$), and females ($n = 87$). Particularly, the 95 % confidence interval for the slope was lower for juveniles than for adult males and females. At the same time, head width grew slower than SVL in juveniles ($n = 30$) and adult females ($n = 87$). In adult males, head width ($n = 84$) growth was isometric. Width at vent grew faster than SVL in juveniles ($n = 30$) and adult males ($n = 84$), while in adult females ($n = 87$) growth was isometric (Fig. 4).

SVL did not differ between adult males and females (Mann Whitney test: $n = 171$, $Z = 1.4708$, $P > 0.14$), but head length (Mann Whitney test: $n = 171$, $Z = 5.0935$,
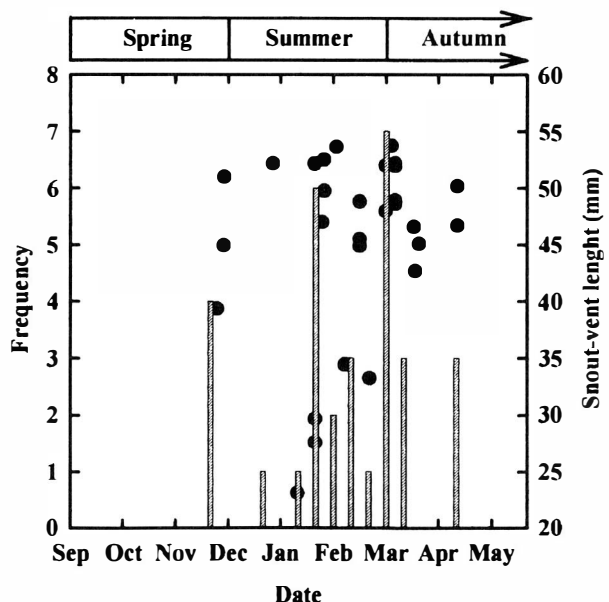

FIG. 3. Frequency (histogram) and SVL (circles) of juveniles *versus* capture date.
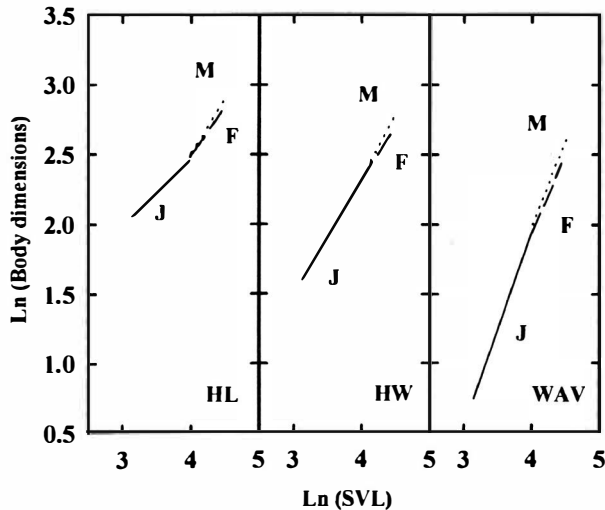
FIG. 4. Juvenile (J, solid line), adult male (M, dotted line), and adult female (F, dashed line) allometric relationship of head length, head width and width at vent with SVL. Regression lines are indicated.

$P<$ 0.0001), head width (Mann Whitney test: $n=171$, $Z=6.4484$, $P<$ 0.0001) and width at vent did (Mann Whitney test: $n=171$, $Z=6.2290$, $P<$ 0.0001; adjusted measurements used in all tests). The three variables had greater values for males (Fig. 4).

Amongst all the specimens collected, the ratio of adult males to adult females was 0.97:1.

GONADS AND REPRODUCTIVE CYCLE

Adult Males. A slight difference was found between right and left testicular diameter ($t = 4.45$, df = 83, $P<$ 0.0001), so values for the largest testicle (right) were used.
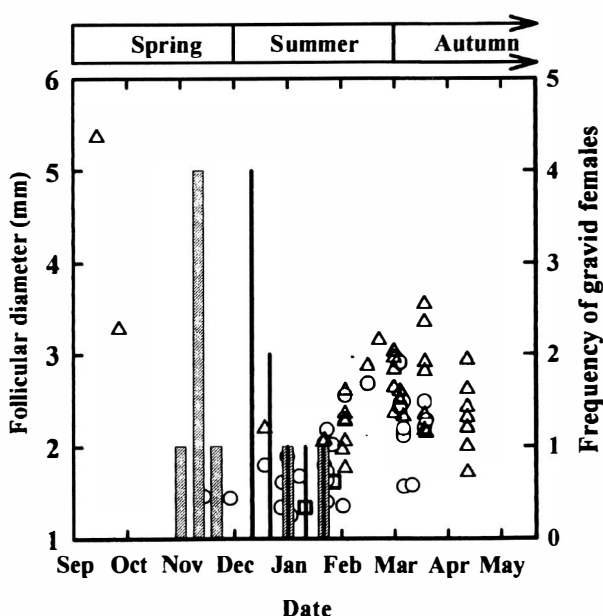

FIG. 5. Follicular diameter of adult females (circles: Uterus type 1, triangles: Uterus type 2 and squares: Uterus type 3) *versus* capture date. Frequency of gravid females, with early (dashed bars) and late developed embryos (black bars) are also indicated.

The relationship between testicular size and date of capture showed the biggest testicular size in mid-spring, a minimum in summer, and a clear gonadal recrudescence, reaching its peak value in autumn (Fig. 2). The relationship of Log (testicular size) with Log (SVL) was significant ($F = 30.46$, df = 79, $P<$ 0.0001, Fig. 1) and showed positive allometry (95 % confidence interval for slope > 1).

Adult Females. Differences between right and left follicle diameter ($t = 0.75$, df = 68, $P > 0.456$) were not found. Average follicle diameter showed an isometric relationship with SVL ($F = 11.15$, df = 66, $P<$ 0.002) and a linear relationship with date of capture ($F = 26.94$, df = 64, $P<$ 0.0001). Gravid females and the two advanced vitellogenic females caught in spring were excluded from the analysis (Fig. 5).

The span from the time the first adult female was caught in summer, until the record of the highest follicular diameter in autumn, was 124 days, with the gonadal diameter ranging from 1.25 mm to 3.55 mm. The size of the smallest oocyte found in the uterus was 9.17 mm (uterine wall included).

Gravid females ($n=17$) were captured from late spring (3 December) to mid summer (9 February). It must be noted that early and advanced pregnancy both occur in mid-summer (Fig. 5). The first female found with Uterus type 3 was captured on 27 January.

Litter size ranged between three and seven foetuses, from females that varied between 65.44 and 82.38 mm SVL ($n=5$, other gravid females underwent extraction of some embryos previously to this study).

In summary, female cycles showed vitellogenesis in summer through winter with ovulation in the following spring. Females were gravid throughout late spring and summer, birth possibly taking place from mid-summer to autumn.

DISCUSSION

A clear assessment of adulthood is necessary to analyse reproductive cycles, differentiating non-reproductive adults from juveniles (van Wyk, 1991; Flemming & Van Wyk, 1992; Vitt & Carvalho, 1992; Mouton & van Wyk, 1993; Vitt & Caldwell, 1993; Flemming, 1994; Censky 1995, Ibargüengoytía & Cussac, 1996). In *L. elongatus*, yolk deposition is not conspicuous in preserved ovaries. Nevertheless, the appearance of pregnancy, Uterus type 2, and the increase of testicular growth allows the assessment of a common size for attaining adulthood in both sexes. The juvenile population shows two cohorts. Capture dates of the lower SVL group suggest that birth takes place in summer. Modal grouping of juveniles by SVL shows that, as in *L. pictus* (Ibargüengoytía & Cussac, 1996) and *Sceloporus occidentalis* (Sinervo & Adolph, 1994) adulthood would not be reached before one and a half years after birth.

We failed to record differences between adult male and female SVL and also between maximum juvenile size. As in *L. pictus* (Ibargüengoytía & Cussac, 1996), male *L. elongatus* have larger heads and wider tail bases than females. Adult male and female head shape

differs from that of juveniles. Sexual selection may account for such dimorphism (Mouton & van Wyk, 1993; Censky, 1995.

Data on male cycles suggests there is gonadal recrudescence from summer to autumn. Spring adults indicate a prolonged spermatogenetic period of one year. These events show high synchrony with the female cycle. On the basis of the analysis of follicular diameters, we postulate that in *L. elongatus* vitellogenesis begins in summer and continues until the following spring when, as the difference between follicular and oviductal oocyte size suggests, it is suddenly completed.

Callard *et al.* (1992), point out that vitellogenesis and pregnancy are two phenomena that are mutually exclusive for a viviparous squamate female. If this is the case, capture dates of vitellogenic and pregnant females should show a sequential pattern within the population. In *L. elongatus,* the simultaneous presence of females showing early pregnancy and females initiating vitellogenesis strongly suggests an overlapping situation (see Ibargüengoytía & Cussac, 1996). In the same way, the co-occurrence of adult females with low and high gonadal size suggests a biennial cycle (van Wyk, 1991; Ibargüengoytía & Cussac, 1996). These hypotheses imply the presence of both vitellogenic and non vitellogenic adult females during autumn and winter but, due to the cool and snowy winter, capture is normally not possible. On the other hand, both females with Uterus type 3 and the advanced pregnant females caught in summer, seem to be able to begin a new vitellogenic cycle in the same season. We propose that *L. elongatus* populations consist of annual cycles in males, and annual and biennial cycles in females. This plasticity in reproductive strategy could be one of the conditions that allow its range to encompass a wide range of steppe and cold montane environments. Causal relationships between reproductive timing and access to heat may be complex since environmental temperature also influences food availability, and this constrains reproduction (Hahn & Tinkle, 1965; Greenberg & Gist, 1985, Bonnet, Naulleau & Mauget, 1992). Fat bodies and gut content studies will be necessary to estimate the relative importance of each factor.

The reproductive cycle of *L. elongatus* closely resembles that of *L. gravenhorsti* (Leyton, Miranda & Bustos Obregón, 1980; Leyton, Morales & Bustos Obregón, 1977), but an important difference must be noted. Overlap between early pregnant and early vitellogenic *L. elongatus* females implies that individuals may be at different stages of the reproductive cycle within the same population (Cree & Guillette, 1995; Ibargüengoytía & Cussac, 1996). However, overlap between preovulatory and early pregnant *L. gravenhorsti* females does not obviate an annual cycle. Increasing plasticity of reproductive responses can be envisioned by comparing *L. gravenhorsti, L. elongatus* and *L. pictus* (Leyton, Miranda & Bustos Obregón, 1980; Ibargüengoytía & Cussac, 1996). Reproductive patterns in these species appear to be correlated with their latitudinal and altitudinal distribution.

REFERENCES

Aldridge, R. D. (1979). Female reproductive cycles of the snakes *Arizona elegans* and *Crotalus viridis. Herpetologica* **35**, 256-261.

Blackburn, D. G. (1982). Evolutionary origins of viviparity in the Reptilia. I *Amphibia-Reptilia* **3**, 185-205.

Blackburn, D. G. (1985). Evolutionary origins of viviparity in the Reptilia. II Serpentes, Amphisbaenia, and Ichthyosauria. *Amphibia-Reptilia* **6**, 259-291.

Bonnet, X., Naulleau, G. & Mauget, R. (1992). Cycle sexuelle de la femelle de *Vipera aspis (Squamata, Viperidae),* importance des reserves et aspects metaboliques. *Bull. Soc. Zool. Fr.* **117**, 279-290.

Callard, I. P., Fileti, L. A., Pérez, L. E., Sorbera, L. A., Giannoukus G., Klosterman L., Tsang P. & Mc Cracken J. A. (1992). Role of the corpus luteum and progesterone in the evolution of vertebrate viviparity. *Am. Zool.* **32**, 264-275.

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

Cei, J. M. (1993). *Reptiles del noroeste, nordeste y este de la Argentina. Herpetofauna de las selvas subtropicales, Puna y Pampas.* Torino: Museo Regionale di Scienze Naturali, monografie XIV.

Censky, E. J. (1995). Mating strategy and reproductive success in the teiid lizard, *Ameiva platei. Behaviour* **132**, 7-8.

Cree A., Cockrem J. & Guillette L. (1992). Reproductive cycles of male and female tuatara (*Sphenodom punctatus*) on Stephens Island, New Zealand. *J. Zool., Lond.* **226**, 199-217.

Cree, A. & Guillette L. J. (1995). Biennial reproduction with a fourteen-month pregnancy in the Gecko *Hoplodactylus maculatus* from southern New Zealand. *J. Herpetol.* **29**, 163-173.

Charland, M. B. (1995). Thermal consequences of reptilian viviparity: thermoregulation in gravid and nongravid garter snakes (*Thamnophis). J. Herpetol.* **29**, 383-390.

Charland, M. B. & Gregory P. T. (1990). The influence of female reproductive status on thermoregulation in a viviparous snake, *Crotalus viridis. Copeia* **4**, 1089-1098.

Espinoza, R. E. (1996). Correlaciones ecológicas y evolutivas del viviparismo en lagartos del género *Liolaemus*, 276. IV Congreso Latinoamericano de Herpetología. Santiago, Chile.

Flemming, A. F. (1994). Male and female reproductive cycles of the viviparous lizard, *Mabuya capensis* (Sauria: Scinidae) from South Africa. *J. Herpetol.* **28**, 334-341.

Flemming, A. F. & van Wyk, J. H. (1992). The female reproductive cycle of the lizard *Cordylus p. polyzonus* (Sauria: Cordylidae) in the Southwestern Cape Province, South Africa. *J. Herpetol.* **26**, 121-127.

Greenberg, D. S. & Gist, D. H. (1985). Fat bodies and reproduction in female *Anolis carolinensis*. *J. Exp. Zool.* **233**, 277-283.

Guillette, L. J. (1993). The evolution of viviparity in lizards. *BioScience* **43**, 742-751.

Guillette, L. J. & Méndez de la Cruz, F. R. (1993). The reproductive cycle of the viviparous Mexican lizard *Sceloporus torquatus*. *J. Herpetol.* **27**, 168-174.

Hahn, W. E. & Tinkle, D. W. (1965). Fat body cycling and experimental evidence for its adaptive significance to ovarian follicle development in the lizard *Uta stansburiana*. *J. Exp. Zool.* **158**, 79-86.

Heulin, B., Osenegg, K. & Lebouvier, M. (1991). Timing of embryonic development and birth dates in oviparous and viviparous strains of *Lacerta vivipara*: testing the predictions of an evolutionary hypothesis. *Acta Oecologica* **12**, 517-528.

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

Ibargüengoytía, N. R., Cussac, V. E. & Ubeda, C. A. (1997). Simpatría de *Liolaemus elongatus* y *L. pictus* (Tropiduridae): una hipótesis reproductiva para explicar su distribución en relación con el gradiente ambiental, 91. VIII Congreso Iberoamericano de Biodiversidad y Zoología de Vertebrados, Concepción. Chile.

Leyton, V. C., Miranda, E. A. & Bustos Obregón, E. (1980). Gestational chronology in the viviparous lizard *Liolaemus gravenhorsti* (Gray) with remarks on ovarian and reproductive activity. *Arch. Biol.* **91**, 347-361.

Leyton V. C., Morales C. & Bustos Obregón E. (1977) Seasonal changes in testicular function of the lizard *Liolaemus gravenhorsti*. *Arch. Biol.* **88**, 393-405.

Leyton, V. & Valencia, J. (1992). Follicular population dynamics, its relation to the clutch and litter size in Chilean *Liolaemus* lizards. In *Reproductive Biology of South American Vertebrates*, 177-199. Hamlett, W. D. (Ed). New York: Springer-Verlag.

Leyton, V., Veloso, A. & Bustos Obregón, E. (1982). Modalidad reproductiva y actividad cíclica gonadal en lagartos iguánidos de distintos pisos altitudinales del interior de Arica (Lat. 18-10° S). In *El hombre y los*

ecosistemas de montaña 1. La vegetación y los vertebrados ectotérmicos del transecto Arica-Lago Chungará, Vol. 1, 293-301. Veloso A. and Bustos-Obregón E. (Eds). Montevideo: Proyecto MAB-6 Unep/ Unesco 110577-01.

Macola, G. S., Castro, L. P., Castro, M. P. & Mattiussi, M. B. (1984). Estudio comparativo del ciclo espermatogénico anual de las especies de una comunidad de saurios de altura, Uspallata - Las Heras - Mendoza *(Sauria-Iguanidae)*. *Rev. Mus. Cienc. Nat. "B. Rivadavia"* **13**, 139-145.

Martín Vallejo J., García Fernández J., Pérez Mellado V. & Vicente Villardón, J. L. (1995). Habitat selection and thermal ecology of the sympatric lizards *Podarcis muralis* and *Podarcis hispanica* in a mountain region of central Spain. *Herpetological Journal* **5**, 181-188.

Mouton, P. le F. N. & van Wyk, J. H. (1993). Sexual dimorphism in cordylid lizards: a case study of the Drakensberg crag lizard, *Pseudocordylus melanotus*. *Can. J. Zool.* **71**, 1715-1723.

Norusis, M. J. (1986). *Advanced statistics SPSS/PC+ for the IBM PC/XT/AT*. Chicago: SPSS inc.

Packard, G. C., Tracy, C. R. & Roth, J. J. (1977). The physiological ecology of reptilian eggs and embryos, and the evolution of viviparity within the class Reptilia. *Biol. Rev.* **52**, 71-105.

Pearson, O. P. (1954). Habits of the lizards *Liolaemus multiformis multiformis* at high altitudes in southern Perú. *Copeia* **1954**, 111-116.

Ramírez Pinilla, M. P. (1991). Estudio histológico de los tractos reproductivos y actividad cíclica anual reproductiva de machos y hembras de dos especies del género *Liolaemus* (Reptilia: Sauria: Iguanidae). Ph.D. Thesis. Universidad Nacional de Tucumán, Facultad de Ciencias Naturales e Instituto Miguel Lillo. Argentina.

Ramírez Pinilla, M. P. (1992a). Variaciones histológicas en los tractos reproductivos de hembras de algunas especies ovíparas de *Liolaemus* (Reptilia: Iguanidae) en diferentes estados de actividad reproductiva. *Acta Zool. Lilloana* **42**, 115-122.

Ramírez Pinilla, M. P. (1992b). Actividad reproductiva en tres especies simpátricas del género *Liolaemus* (Reptilia: Sauria: Tropiduridae). *Caldasia* **17**, 67-74.

Reichow, D., Largiadèr, C., Kligerberg, Ch., Clemmesen, C., Froese, R. & Ueberschär, B. (1991). The use of multivariate morphometrics to determine the nutritional condition of marine fish larvae. *Int. Coun. Exp. Sea* **1991**, 1-9.

Shine, R. (1983). Reptilian viviparity in cold climates: testing the assumption of an evolutionary hypothesis. *Oecologia* **57**, 397-405.

Shine, R. (1985). The evolution of viviparity in reptiles: an ecological analysis. In *Biology of Reptilia* vol. 15, 605-694. Gans, C. and Billet, F. (Eds.). New York: John Wiley & Sons.

Shine, R. (1995). A new hypothesis for the evolution of viviparity in reptiles. *Am. Nat.* **145**, 809-823.

Shine, R. & Harlow, P. (1993). Maternal thermoregulation influences offspring viability in a viviparous lizard. *Oecologia* **96**, 122-127.

Sinervo, B. & Adolph, S. C. (1994). Growth plasticity and thermal opportunity in *Sceloporus* lizards. *Ecology* **75**, 776-790.

Sokal, R. R. & Rohlf, F. J. (1969). *Biometry. The principles and practice of statistics in biological research.* USA: W. H. Freeman and Co.

Van Damme, V. R., Bauwens, D., Braña, F. & Verheyen R. F. (1992). Incubation temperature differentially affects hatching time, egg survival, and hatchling performance in the lizard *Podarcis muralis.* *Herpetologica* **48**, 220-228.

van Wyk, J. H. (1991). Biennial reproduction in the female viviparous lizard *Cordylus giganteus.* *Amphibia-Reptilia* **12**, 329-342.

Vial, J. L. & Stewart, J. R. (1985). The reproductive cycle of *Barisia monticola*: a unique variation among viviparous lizards. *Herpetologica* **41**, 51-57.

Vitt, L. J. (1992). Diversity of reproductive strategies among Brazilian lizards and snakes: the significance of lineage and adaptation. In *Reproductive Biology of South American Vertebrates*, 135-148. Hamlett W.C. (Ed). New York: Springer-Verlag.

Vitt, L. J. & Caldwell, J. P. (1993). Ecological observations on Cerrado lizards in Rondônia, Brasil. *J. Herpetol.* **27**, 46-52.

Vitt, L. J. & Carvalho C. M. (1992). Life in the trees: the ecology and life history of *Ketropyx striatus* (Teiidae) in the lavrado area of Roraima, Brazil, with comments on the life histories of tropical teiid lizards. *Can. J. Zool.* **70**, 1995-2006.