

## REPRODUCTIVE CYCLE IN A PYRENEAN OVIPAROUS POPULATION OF THE COMMON LIZARD (*ZOOTOCA VIVIPARA*)

by

JUAN MANUEL ROIG, MIGUEL ANGEL CARRETERO  
and GUSTAVO ADOLFO LLORENTE\*

(*Department de Biologia Animal (Vertebrats), Facultat de Biologia,  
Universitat de Barcelona, Av. Diagonal 645, 08028 Barcelona*)

### ABSTRACT

High altitude reptiles inhabit adverse environments that condition their reproductive biology. The reproductive and fat body cycles of a high altitude oviparous population of the Common lizard (*Zootoca vivipara*) in the central Pyrenees were analysed and compared with data on other oviparous and viviparous populations from lower altitudes found in the literature. The studied population shows an extremely short reproductive period. Males show a mixed-type spermatogenesis with very short, vernal spermiogenesis. They emerge from their winter burrows earlier than females and remain unfertile until females start activity and the breeding season begins. Large males release more sperm in copulations than small ones. Females synchronically lay a single clutch per year whereas other oviparous populations living at lower altitudes are iteroparous. Females invest more fat reserves from different compartments (liver, tail) than males, but later in the reproductive season. This major energetic stress seems to be due to the long period of oviductal egg retention. The main effect of altitude on oviparous *Zootoca vivipara* is the shortening of the reproductive period, which precludes the laying of a second clutch. However, no substantial differences (other than reproductive modality) have been detected between this high mountain oviparous population and viviparous ones. This suggests that not only viviparity but also oviparity is a suitable strategy in such environmental conditions.

KEY WORDS: reproduction, fat cycles, egg retention, high altitude, Pyrenees, *Zootoca vivipara*.

### INTRODUCTION

The Common Lizard, *Zootoca vivipara*, is a small ground-dwelling lacertid with a very wide distribution range (from northern Spain to Japan) living under different environmental conditions. Moreover, it is one of the few reptiles that exhibits reproductive bimodality (LANTZ, 1927; BRAÑA

---

\* E-mail: llorrente@porthos.bio.ub.es

& BEA, 1987) with oviparous populations restricted to the Cantabric Mountains, Pyrenees and Aquitaine (BEA, 1978; HEULIN, 1988; HEULIN & GUILLAUME, 1989). More recently, oviparous females have also been found in Slovenia and adjacent areas (BÖHME *et al.*, 1999; BÖHME, *pers.com.*). The female reproductive traits have been previously studied in both oviparous and viviparous populations (PANIGEL, 1956; AVERY, 1975; PILORGE & BARBAULT, 1981; MELLADO *et al.*, 1981; BAUWENS & VERHEYEN, 1985; BRAÑA, 1986; HEULIN *et al.*, 1994) and genetic control of reproductive modality has been demonstrated (HEULIN *et al.*, 1989; HEULIN, 1990; HEULIN *et al.*, 1992; ARRAYAGO *et al.*, 1996).

One important point is that the reproductive cycle has been studied only for oviparous females from low and medium altitudes (HEULIN *et al.*, 1994; BRAÑA, 1986). It would be of interest to analyse how such females face environmental conditions at high altitudes which would *a priori* be more suitable for viviparous lizards (SHINE, 1983). Furthermore, little is known about male reproductive traits in this species; only GAVAUD (1991) reports some data on spermatogenesis in a viviparous population. Finally, the cycles of fat body and other reserve organs are also poorly known.

Thus, this study aims 1) to analyse the reproductive cycle of oviparous females at high altitudes and to compare it with those located at medium and low altitudes as well as with viviparous populations, 2) to describe the male reproductive cycle emphasising the study of spermatogenesis, and 3) to analyse annual variation of the fat body reserves in both sexes.

## MATERIAL AND METHODS

The study area is an alpine meadow at a high plateau located at 1800 m in the central Pyrenees (Pla de Beret, Naut Aran, UTM grid 31T CH3434), with a dominance of heather (*Calluna vulgaris*) and, to a lesser extent, common juniper (*Juniperus communis*). The area has a high mountain Atlantic climate with a mean annual temperature of 9.7°C and a total annual precipitation of 918.9 mm (30 years means, PANAREDA & NUET, 1973). From April to October 1995, 76 males and 53 females of *Zootoca vivipara* were captured in field sampling carried out every 15 days.

Only animals with active gonads in the reproductive season were considered adults and minimum adult sizes were determined for each sex. Outside the reproductive period, only lizards larger than these minima were included in the adult class and the rest were considered immatures (CARRETERO & LLORENTE, 1997). A total of 38 adult males and 39 adult females were collected.

All lizards were sacrificed humanely and frozen. Once in the laboratory, they were dissected and several variables of sexual significance were

recorded: right testis weight and right epididymis weight for males; right ovary weight, number of ovocytes, diameter of ovocytes, right oviduct diameter and number of oviductal eggs for females; snout-vent length (SVL), liver weight, fat bodies weight and the surface area (A) of the tail base for both sexes. The tail base section was measured at the level of the 7<sup>th</sup> scale verticil, considering it an elliptic area:  $A = \Pi ab$ , where  $a$  represents the height and  $b$  the width. All weights were measured with a digital balance to the nearest 0.0001 g. Linear variables were measured to the nearest 0.01 mm using a digital calliper or a dissecting microscope with a micrometric eyepiece. Regression residuals between all variables and SVL (both log-transformed) were calculated to standardise for size.

In order to estimate the seasonal variation of the sexual cells, testis and epididymis extensions on microscope slides were coloured by the diff-quick method (BEA, 1979) and observed with an optic microscope (400 $\times$ ). Three microscopic fields were selected at random and the number of distinct sexual cells was counted. Cell counts in the three fields were pooled for each cell type and for each male lizard.

## RESULTS

Table 1 shows the sizes of the lizards collected throughout the activity period. Minimum SVL of adults were similar for males and females (43.18 and 43.81 mm, respectively). Adult females were larger than males (mean  $\pm$  se: males  $51.57 \pm 3.19$  females  $48.25 \pm 2.38$ ;  $T = 5.16$ , 75 d.f.,  $p = 2 \cdot 10^{-6}$ ).

### *Male cycle*

Adult males came out of their winter burrows in April, two weeks before females. The testis weight showed a high degree of seasonal variation (ANCOVA  $F_{(8,28)} = 13.81$ ,  $p < 0.00001$ ; fig. 1). After the winter diapause, testis size decreased gradually reaching a minimum during the first half of July. From then onwards, a significant increase in testis weight was found. The right testis was larger than the left ( $T$  test for paired data,  $T = 4.91$ ,  $p = 0.00002$ ). The epididymis also varied seasonally (ANCOVA  $F_{(8,28)} = 12.19$ ,  $p < 0.00001$ ; fig. 1) with high relative values during the reproductive period which lasted from early May to the end of June. Afterwards, it decreased reaching a minimum at the end of July and it remained constant until the diapause. In contrast to the testis, the epididymis were symmetric ( $T$  test).

Spermatogonia were the only cellular type which did not show variation throughout the year. The other cellular types varied seasonally and were

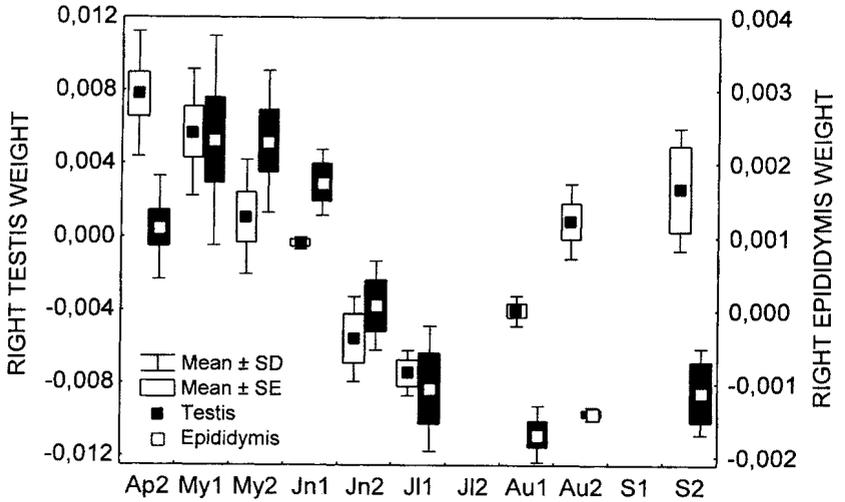


Fig. 1. Annual variation of the weight of the testis and the epididymis. Abscises show the regression residuals between each variable and the snout-vent length, SVL (both log-transformed).

TABLE 1

Number of individuals of *Zootoca vivipara* collected. \*minimum size of sexual maturity.

SVL(mm)	Sex	Ap2	My1	My2	Jn1	Jn2	JI1	JI2	Au1	Au2	S1	S2	O1
15-20	Males												
	Females										1		
20-25	Males		1	1						2	3	2	2
	Females									1		1	1
25-30	Males			2	1	2						1	1
	Females				4	1				1			
30-35	Males					1	2						
	Females						1						
35-40	Males						2	3					
	Females												
40-45*	Males	1	2		1			1	2	2	5	2	
	Females				1			1			2		
45-50	Males	6	4	4	2	2	2		3	2		2	
	Females												
50-55	Males	1		1		1	1		1	2			
	Females		1		2	4	3	4	4	2	3	2	
55-60	Males												
	Females						1	1		1			

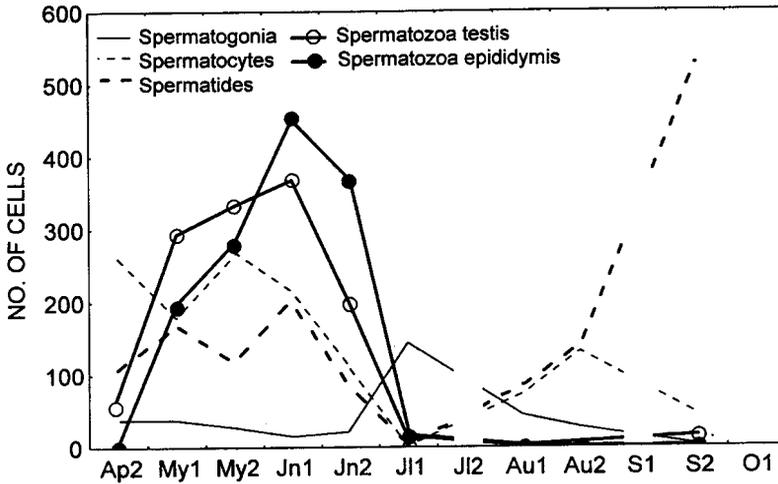


Fig. 2. Annual variation of the different types of sexual cells in testis and epididymis.

slightly out of phase with respect to each other (fig. 2). Spermatozoa were quite abundant from April to the beginning of June. Then the number decreased and remained constant but scarce during the rest of the active cycle (ANCOVA  $F_{(8,28)} = 3.85$ ,  $p = 0.004$ ). Spermatozoa also varied seasonally (ANCOVA  $F_{(8,28)} = 5.07$ ,  $p = 0.0006$ ) and were absent in the first half of July. It is noteworthy that there were more spermatozoa before than after the diapause. The variation in spermatozoa was significant in both testis and epididymis (ANCOVAs  $F_{(8,28)} = 8.66$ ,  $p < 0.00001$  and  $F_{(8,28)} = 16.45$ ,  $p < 0.00001$ , respectively). When males emerged from the winter diapause, spermatozoa were scarce in testes but almost completely absent in the epididymis. Afterwards, the number of spermatozoa increased progressively, earlier in testes than in the epididymis, and then both decreased again until mid-June. After this decrease, no spermatozoa were found until the following activity period. Only two males showed some spermatozoa in testes during the last week of September. During the mating period (May-June), the number of spermatozoa in testes was negatively correlated with SVL whereas in the epididymis this correlation was positive (fig. 3).

Epithelial cells were found in the epididymis from early July to late September, and their number increased throughout this period (ANCOVA  $F_{(8,28)} = 16.45$ ,  $p < 0.00001$ ).

#### Female cycle

Females left the winter diapause 15-20 days later than males. The ovary weight was larger in June than in the rest of the active period (ANCOVA

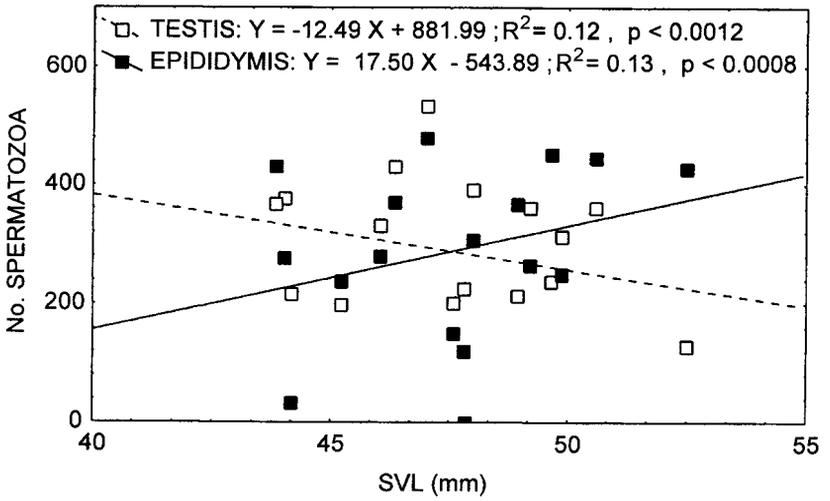


Fig. 3. Relationships between SVL and the number of spermatozoa in testis and epididymis, respectively.

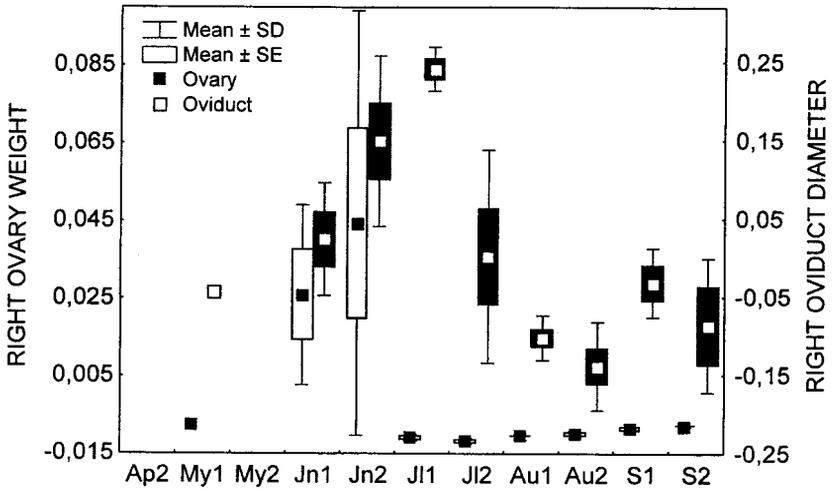


Fig. 4. Annual variation of the ovary weight and the oviduct diameter. Abscises show the regression residuals between each variable and the snout-vent length, SVL (both log-transformed).

$F_{(8,29)} = 4.67$ ,  $p = 0.001$ ) (fig. 4). No significant differences were observed between the left and right ovaries ( $T$  test). From the beginning of the activity period the oviduct showed a significant increase, in diameter

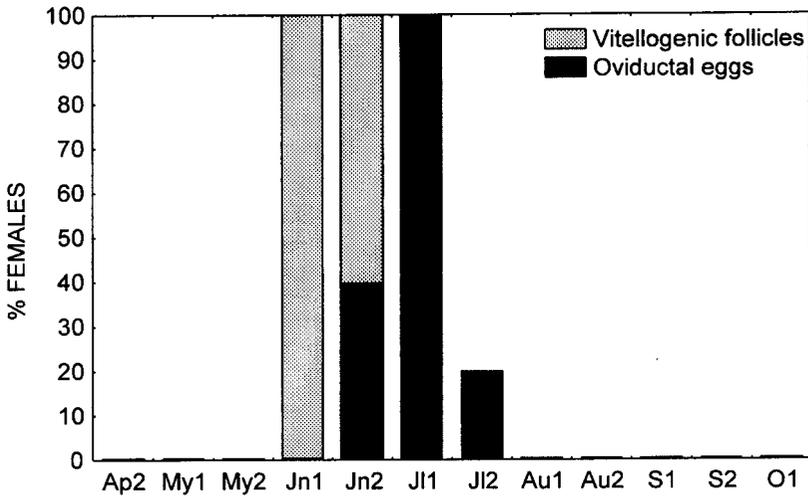


Fig. 5. Percentage of females with vitellogenic follicles and oviductal eggs throughout the active period.

reaching its maximum between the second half of June and the first half of July. In the second half of July the diameter of the oviduct decreased and remained constant throughout the rest of the active cycle (ANCOVA  $F_{(8,29)} = 12.02$ ,  $p < 0.00001$ ) (fig. 4).

Vitellogenic follicles were found in June and oviductal eggs were detected from the second half of June to July (fig. 5). The minimum diameter of vitellogenic follicles was 2.7 mm. No significant correlation between female SVL and either the number of oviductal eggs ( $R_{\text{Spearman}} = 0.46$ ,  $p = 0.24$ , n.s.) or the number of vitellogenic follicles ( $R_{\text{Spearman}} = 0.16$ ,  $p = 0.72$ , n.s.) were found. Since no differences in clutch size were found when comparing the number of vitellogenic follicles and oviductal eggs, both were pooled for subsequent analysis. The mean clutch size was  $5.86 \pm 0.38$  (3-8). The presence of oviductal eggs during this period (fig. 5) indicated that clutches were laid mainly in July. No evidence of *corpora lutea* was found. The first hatchlings were observed during the second half of August. The SVL of the smallest lizard found was 20.43 mm.

#### *Fat reserves*

Fat body weight showed significant variation throughout the active period in both males and females (ANCOVA  $F_{(8,28)} = 7.02$ ,  $p = 0.000045$  and ANCOVA  $F_{(8,29)} = 13.94$ ,  $p < 0.00001$ , respectively; fig. 6). In males, fat bodies attained a minimum weight in June and early July, whereas in

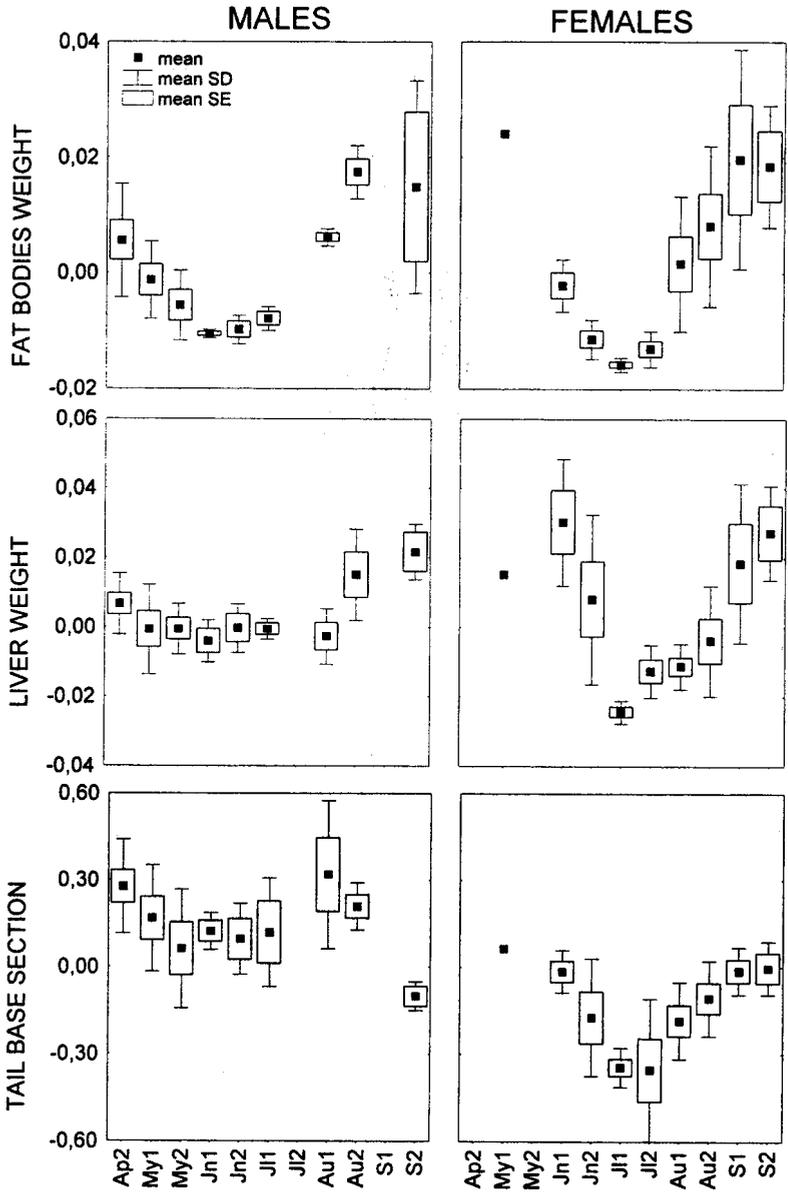


Fig. 6. Annual variation of the fat body and liver weight, and the area of the tail base section in males and females. Abscises show the regression residuals between each variable and the snout-vent length, SVL (both log-transformed).

females this occurred in July. Liver weight also varied seasonally in both sexes (ANCOVA  $F_{(8,28)} = 3.17$ ,  $p = 0.010800$  for males, and ANCOVA  $F_{(8,29)} = 11.15$ ,  $p < 0.00001$  for females; fig. 6). In males only the increase of liver weight between the first and the second half of August was significant. In contrast, the female pattern was similar to that of their fat bodies. Furthermore, the area of the tail base section showed seasonal variation in females (ANCOVA  $F_{(8,29)} = 3.42$ ,  $p = 0.006774$ ), but not in males (ANCOVA  $F_{(8,28)} = 1.50$ ,  $p = 0.200159$  n.s.) (fig. 6). In females the variation in tail section area was again very similar to the pattern of fat bodies and liver.

### DISCUSSION

Based on the sizes of the lizards collected (table 1), the high Pyrenean *Z. vivipara* reaches sexual maturity during the second calendar year in both sexes, since the cohort of immature lizards reached minimum adult size (43 mm) once the reproductive period has finished. These results are similar to other oviparous populations of this species (HEULIN *et al.*, 1994).

The most relevant trait used to distinguish the different male reproductive cycles in reptiles is the stage in which sexual cells remain, after the reproductive period (SAINT-GIRONS, 1963b; BONS & SAINT-GIRONS, 1982; SAINT-GIRONS, 1984). Male *Z. vivipara* shows mixed-type spermatogenesis since spermatocytes and spermatides are found almost immediately after the end of the breeding period and then throughout the year until the next reproductive season. Spermiogenesis is very short as found in other lizards living in cold climates (BRAÑA, 1983). However, at least for some individuals there is evidence of a second spermiogenic period which is interrupted at the beginning of September. Similar results have been observed in some Mediterranean lacertids such as *Podarcis sicula* (ANGELINI *et al.*, 1979) and *Psammodromus algirus* (BONS & SAINT-GIRONS, 1982; CARRETERO & LLORENTE, 1997). Furthermore, the number of spermatida is much lower at the beginning of the cycle than at the end suggesting abortive spermatogenesis (ANGELINI *et al.*, 1979).

As reported before, spermiogenesis is almost exclusively vernal (GAVAUD, 1991) and spermatozoa are already present at the beginning of the activity period but remain in testes. They are functional only when they pass to the epididymis about two weeks later. Thus, male *Z. vivipara* are infertile immediately after hibernation, this confirms the results reported by OLSON & MADSEN (1996) for *Lacerta agilis*. The relationship between the number of spermatozoa and body size indicates that the larger

the male, the greater the number of sperm cells found in the epididymis and the lower the number left in the testes during the breeding season. This suggests that large males do not produce more spermatozoa than small ones, but pass more sperm from the testes to the epididymis and probably release it in copulations. If this is true, large lizards have a higher probability of genome transmission.

This cellular variation matches reasonably well with the seasonal changes in size observed in testes and the epididymis. Epididymis weight is associated with the number of spermatozoa whereas testis weight is related with the overall number of sexual cells. Finally, the presence of epithelial cells in the epididymis from early July to the end of activity has been reported previously (GAVAUD, 1991) and has been attributed to the regeneration of the epididymis epithelium after reproduction.

The most remarkable trait found in females is that vitellogenic follicles and oviductal eggs are found very late and only during a very short period (June-July). As a result, reproduction becomes very synchronic, individual females apparently lay only one clutch per year and new-borns appear simultaneously and very late, in the year. These results are quite similar to those found in the oviparous population living at 1490 m in the Cantabric mountains (BRAÑA, 1986). In contrast, oviparous populations at medium (1100 m) or low altitudes (370-150 m) in Aquitaine and the Pyrenees have been reported to begin reproduction earlier, with females laying two or even three clutches per year and hatchlings being found over a wider period (HEULIN *et al.*, 1991; HEULIN *et al.*, 1994). Similar variation has also been observed in viviparous populations but they do not seem to be iteroparous in any case (see HEULIN *et al.*, 1991 and references therein). Thus, the clutch frequency of high-altitude oviparous populations are comparable to viviparous ones. However, parturition in viviparous females takes place before the hatching of oviparous clutches under the same environmental conditions (HEULIN *et al.*, 1991).

The climatic conditions at high altitudes tend to shorten the annual activity period and prevent females from laying a second clutch (BRAÑA, 1983). This is especially true for lizards such as the oviparous *Z. vivipara* which show long oviductal retention of eggs (BRAÑA *et al.*, 1991). In such environments egg retention in the oviduct is a system for reducing incubation time by buffering the environmental conditions by means of female thermoregulation (BLACKBURN, 1982; SHINE, 1983, 1985; QUALLS & SHINE, 1996).

The variation of body reserves during the activity period highlights interesting intersexual differences. Females invest more fat reserves than males but later in the reproductive season, as reported for other lacertid species (ARGÜELLO, 1990; CARRETERO & LLORENTE, 1991, 1995,

1997). Moreover, this investment implies more compartments in females than in males (*i.e.* tail fat, see fig. 6). Sperm production seems to be energetically cheap for lizards but not for some snakes (*Vipera berus*, OLSON *et al.*, 1997). Prenuptial spermatogenesis of many lizards extends for at least four months. In contrast, many snakes show postnuptial sperm production concentrated in one month (BONS & SAINT-GIRONS, 1982). This suggests that male lizards are less stressed than male snakes since energetic investment in sperm is distributed over a longer period. Furthermore, egg transport is an additional cause for energetic stress in females (SCHWARZKOPF, 1996). This may be especially important in those species with long egg retention such as the oviparous *Z. vivipara* (BRAÑA *et al.*, 1991).

In conclusion, the reproductive cycle of this population of *Zootoca vivipara* is quite similar to other mountain lacertids (ELVIRA & VIGAL, 1985; BRAÑA, 1986). In comparison with other oviparous populations of the same species living at low or medium altitudes, the reproductive period is shorter due to unfavourable climatic conditions, which prevent the laying of a second clutch. However, no substantial differences (other than reproductive modality) have been detected between this high mountain oviparous population and the viviparous ones. This suggests that viviparity and oviparity (with long egg retention) are both suitable strategies in such environmental conditions.

#### ACKNOWLEDGEMENTS

This study was carried out with the financial support of an ACOM grant (no. 1996ACOM 00074) given by CIRIT (Generalitat de Catalunya). Collection permits were provided by the Servei de Gestió de la Fauna, Departament d'Agricultura, Ramaderia i Pesca of the Generalitat de Catalunya. We would also like to thank the support of the Centre de Recerca d'Alta Muntanya (Universitat de Barcelona) and the Conselh Generau d'Aran (local Government).

#### REFERENCES

- ANGELINI, F., R. BRIZZI & C. BARONE, 1979. The annual spermatogenetic cycle of *Podarcis sicula campestris* De Betta (Reptilia Lacertidae). I. The spermatogenetic cycle in nature. *Monitore Zool. Ital. (N.S.)* **13**: 279-301.
- ARGÜELLO, J. A., 1990. Biología reproductiva de *Lacerta monticola* en una población de la Cordillera Cantábrica. *Graellsia* **46**: 253-261.
- ARRAYAGO, M. J., A. BEA & B. HEULIN 1996. Hybridation experiment between oviparous and viviparous strains of *Lacerta vivipara*: a new insight into the evolution of viviparity in reptiles. *Herpetologica* **52**(3): 333-342.

- AVERY, R.A., 1975. Clutch size and reproductive effort in the lizard *Lacerta vivipara* Jacquin. *Oecologia* **19**: 165-170.
- BAUWENS, D. & R.F. VERHEYEN, 1985. The timing of reproduction in the lizard *Lacerta vivipara*: differences between individual females. *J. Herpetol.* **19**: 353-364.
- BEA, A., 1978. Nota sobre *Lacerta vivipara* Jaquin, 1787, en la Península Ibérica. *Butll. Inst. Cat. Hist. Nat.* **42** (Sec. Zool. 2): 123-126.
- BEA, A., 1979. *Método rápido de preparación de testículo en anfibios y reptiles*. P. Dept. Zool. IV: 69-70.
- BLACKBURN, D.G., 1982. Evolutionary origins of viviparity in the Reptilia. I. Sauria. *Amphibia-Reptilia* **3**: 185-205.
- BONS, J. & H. SAINT-GIRONS, 1982. Le cycle sexuel des reptiles mâles au Maroc et ses rapports avec la répartition géographique et le climat. *Bull. Soc. Zool. Fr.* **107**(1): 71-86.
- BRAÑA, F., 1983. La reproducción en los saurios de Asturias (Reptilia: Squamata). Ciclos gonadales, fecundidad y modalidades reproductoras. *Revista de Biología de la Universidad de Oviedo* **1**(1): 29-50.
- BRAÑA, F., 1986. Ciclo reproductor y oviparismo de *Lacerta vivipara* en la Cordillera Cantábrica. *Rev. Esp. Herp.* **1**: 273-292.
- BRAÑA, F. & A. BEA, 1987. Bimodalité de la reproduction chez *Lacerta vivipara* (Reptilia, Lacertidae). *Bull. Soc. Herp. France* **44**: 1-5.
- BRAÑA, F., A. BEA & M.J. ARRAYAGO, 1991. Egg retention in lacertid lizards: relationships with reproductive ecology and evolution of viviparity. *Herpetologica* **47**(2): 218-226.
- BÖHME, W., B. HEULIN & W. BISCHOFF, 1999. First data on a second oviparous population of the viviparous lizard, *Zootoca vivipara* Jacquin, 1787 (Squamata, Lacertidae) from NW Slovenia. 10<sup>th</sup> Ordinary General Meeting Societas Europea Herpetologica. Irakleio, Crete. Abstract Book, pp. 35-35.
- CARRETERO, M.A. & G.A. LLORENTE, 1991. Reproducción de *Psammotromus hispanicus* en un arenal costero del nordeste ibérico. *Amphibia-Reptilia* **12**: 395-408.
- CARRETERO, M.A. & G.A. LLORENTE, 1995. Reproduction of *Acanthodactylus arthrurus* in its Northern boundary. *Russian Journal of Herpetology* **2**(1): 10-17.
- CARRETERO, M.A. & G.A. LLORENTE, 1997. Reproduction of *Psammotromus algirus* in coastal sandy areas of NE Spain. *Amphibia-Reptilia* **18**: 369-382.
- ELVIRA, B., & C.R. VIGAL, 1985. Further data on the reproduction of *Lacerta monticola cyreni* (Sauria, Lacertidae) in Central Spain. *Amphibia-Reptilia* **6**: 173-179.
- GAVAUD, J., 1991. Role of cryophase temperature and thermophase duration in thermoperiodic regulation of testicular cycle in the lizard *Lacerta vivipara*. *Journal of Experimental Zoology* **260**: 239-246.
- HEULIN, B., 1988. Données nouvelles sur les populations ovipares de *Lacerta vivipara*. *C. R. Acad. Sci. Paris* **306**, Série III: 63-68.
- HEULIN, B. & C. GUILLAUME, 1989. Extension géographique des populations ovipares de *Lacerta vivipara*. *Rev. Ecol. (Terre et Vie)* **44**: 39-45.
- HEULIN, B., M.J. ARRAYAGO & A. BEA, 1989. Expérience d'hybridation entre les souches ovipare et vivipare du lézard *Lacerta vivipara*. *C. R. Acad. Sci. Paris* **309**, Série III: 341-346.
- HEULIN, B., 1990. Étude comparative de la membrane coquillière chez les souches ovipare et vivipare du lézard *Lacerta vivipara*. *Can. J. Zool.* **68**: 1015-1019.
- HEULIN, B., K. OSENEGG & M. LEBOUBIER, 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**(4): 517-528.

- HEULIN, B., M.J. ARRAYAGO., A. BEA & F. BRAÑA, 1992. Caractéristiques de la coquille des oeufs chez la souche hybride (ovipare x vivipare) du lézard *Lacerta vivipara*. Can. J. Zool. **70**: 2242-2246.
- HEULIN, B., K. OSENEGG & D. MICHEL, 1994. Survie et incubation des oeufs dans deux populations ovipares de *Lacerta vivipara*. Amphibia-Reptilia **15**: 199-219.
- LANTZ, L.A., 1927. Quelques observations nouvelles sur l'herpetologie des Pyrenes Centrales. Rev. Hist. Nat. Appliq. **8**: 56-61.
- MELLADO, J., G. OLMEDO & C. FERNANDEZ QUIRÓS, 1981. Datos sobre la reproducción de *Lacerta vivipara* en la Cordillera Cantábrica. Doñana, Acta Vertebrata **8**: 300-302.
- OLSSON, M. & T. MADSEN, 1996. Cost of mating with infertile males selects for late emergence in female sand lizards (*Lacerta agilis* L.). Copeia **2**: 462-464.
- OLSSON, M., T. MADSEN & R. SHINE, 1997. Is sperm really so cheap? Costs of reproduction in male adders, *Vipera berus*. Proc. R. Soc. Lond. B **264**: 455-459.
- PANAREDA, J.M. & J. NUET, 1973. El clima i les aigües dels Països Catalans. In: Ketres (Ed.), *Geografia Física dels Països Catalans*.
- PANIGEL, M., 1956. Contribution à l'étude de l'ovoviviparité chez les reptiles: gestation et parturition chez le lézard vivipare *Zootoca vivipara*. Annales Sci. Nat. Zool. **18**: 569-668.
- PILORGE, T. & R. BARBAULT, 1981. La viviparité chez les lézards: Évolution et adaptation. Acta Oecologica **2**: 387-397.
- QUALLS, C.P. & R. SHINE, 1996. Reconstructing ancestral reaction norms: an example using the evolution of reptilian viviparity. Functional Ecology **10**: 688-697.
- SAINT-GIRONS, H., 1963. Spermatogenèse et évolution cyclique des caractères sexuels secondaires chez les Squamata. Ann. Sc. Nat. Zool. **12**(5): 462-476.
- SAINT-GIRONS, H., 1984. Les cycles sexuels des lézards mâles et leurs rapports avec le climat et les cycles reproducteur des femelles. Annales des Sciences Naturelles. Zoologie. Paris **6**: 221-243.
- SHINE, R., 1983. Reptilian viviparity in cold climates: testing the assumption of an evolutionary hypothesis. Oecologia **57**: 397-405.
- SCHWARZKOPF, L., 1996. Decreased food intake in reproducing lizards: A fecundity-dependent cost of reproduction? Australian Journal of Ecology **21**(4): 355-362.