*Animal Biology*, Vol. 56, No. 1, pp. 1-12 (2006)

# Spermatogenesis in two Iberian *Podarcis* lizards: relationships with male traits

MIGUEL A. CARRETERO [1,*], RAQUEL RIBEIRO [1], DIANA BARBOSA [1],
PAULO SÁ-SOUSA [2], D. JAMES HARRIS [1,3]

[1] *Centro de Investigação em Biodiversidade e Recursos Genéticos (CIBIO), Campus Agrário de Vairão, 4485-661 Vairão, Portugal*
[2] *Laboratório de Biologia da Conservação, Dep. Biologia, Univ. Évora, P-7002-544 Évora, Portugal*
[3] *Faculdade de Ciências da Unuversidade do Porto, 4499-002 Porto, Portugal*

**Abstract**—The spermatogenic cycles of *Podarcis bocagei* and *P. carbonelli*, two lacertids previously considered conspecific, were analysed in northwest Portugal. Monthly sampling was carried out at three sites: a zone of strict syntopy and two sites of allopatry for both species, all of them geographically close and harbouring similar habitats. The maritime Atlantic climate, which allows males to remain active most of the year, plays a determinant role on the variation of the mixed-type cycle, typical of lacertids in temperate regions. Comparison with other populations and species indicates that climate modifies the pattern of spermatogenesis by restricting the beginning (but not the end) of the activity period. Results also corroborate previous studies that report an agreement between the variations in the gonads observed at both microscopic and macroscopic scales in the reproductive period. Peaks for spermatozoa were delayed in sympatry but competition cannot be directly concluded. Furthermore, relationships between the number of spermatozoa and body size suggest sperm competition and possibly a reproductive interaction between the species.

*Keywords*: Reproduction; spermatogenesis; sperm competition; *Podarcis bocagei*; *Podarcis carbonelli*; Lacertidae.

## INTRODUCTION

Lizards are a classic model for studying intraspecific competition in natural communities (Toft, 1985; Schoener, 1986). When two ecologically similar species coincide in space and time, either exploitation of a common, restricted resource (Stamps and Tanaka, 1981; Leal et al., 1998) or direct interference (Hess and Losos, 1991) can reduce fitness components (growth, survivorship and fecundity) in members of one

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[*] Corresponding author; e-mail: carretero@mail.icav.up.pt

or both of the species concerned. Among lacertids, it has been demonstrated that behavioural interference between two *Podarcis* species affects thermal ecology and microhabitat use (Downes and Bauwens, 2002). It is likely that such shifts influence the biological traits of the species involved.

*Podarcis bocagei* and *P. carbonelli* are two lacertids previously considered to be conspecific (Harris and Sá-Sousa, 2001, 2002; Sá-Sousa and Harris, 2002). Ecologically, both are ground-dwelling inhabitants of bush areas with an Atlantic climate on the northwest Iberian Peninsula. Although most of their ranges do not adjoin, they overlap in a narrow contact zone in Douro Litoral (northern Portugal); this is thought to be a recent occurrence (Sá-Sousa, 2001). Such traits make them a good candidate for competitive interaction since it is unlikely that strong segregation will have taken place to minimise ecological interactions and affect fitness.

In contrast to previous opinion, spermatogenesis seems to be very energy expending in reptiles (Olsson et al., 1997) although this effect may be minimised in lacertids (see Roig et al., 2000). Nevertheless, if this cycle undergoes a critical period in any part of the year, it is vulnerable to any pressure that might affect the male's energy input. Previous studies have revealed substantial differences between both *Podarcis* in body size and reproductive parameters (phenology, sexual maturity, eggs and clutches) but failed to detect any variation in such traits attributable to the presence of the other species (Carretero et al., unpubl. data). Nonetheless, the presence of a sympatric species with similar ecology could still lead to a competition-mediated decrease in male condition in one or both species.

On the other hand, unstable developmental conditions (environmental or genetic), are related to a high degree of fluctuating asymmetry (Polak, 2003; for lacertids see Carretero, 2001; Crnobrnja-Isailovic et al., 2005). In fact, it has recently been demonstrated in lacertids, both by incubation experiments and environmental correlation analysis, that extreme temperatures produce more asymmetric individuals (Zhdanova and Zakharov, 2004). If suboptimal development has more permanent consequences (i.e. body condition in the adult stage), males would have a diminished sperm production. Similarly, accidents throughout life, such as tail autotomy, could also change metabolic priorities (Dial and Fitzpatrick, 1981; Fox and McCoy, 2000; Doughty et al., 2003), which could disrupt the spermatogenetic process. Such effects are to be distinguished from the indirect costs on survival, reproductive success and social interactions (see discussion).

Thus, this study aims: i) to describe and compare the spermatogenic cycles of both *Podarcis* species; ii) to assess if the presence of the congeneric species produces (negative) effects on the spermatogenic cycles; and iii) to assess the influences of male size and condition (asymmetry and tail shedding) on spermatogenesis.

## MATERIALS AND METHODS

Sampling was carried out in three coastal localities of northwest Portugal: a previously documented zone of strict syntopy between both species (Espinho-

Granja, UTM squares 29T NF24 and NF34, see Carretero et al., 2002), and two areas of allopatry (Torreira near Aveiro, 29T NF21, for *P. carbonelli*, and Mindelo-Vila Chã, 29T NF27, for *P. bocagei*). In order to minimise the incidence of abiotic factors, all three sites selected were geographically close (within a range of 40 km) and harboured similar habitats (humid dunes covered by psammophile vegetation (see Carretero et al., 2002, for a more detailed description). No other *Podarcis* species nor any other small lacertids were present in any of these localities (Sá-Sousa, 2000, unpubl. data); the members of *P. hispanica* complex rarely occupy such habitats in northeast Portugal (Douro Litoral and Minho provinces). The climate of all three sites is maritime Atlantic with warm midsummers and mild, rainy winters; annual temperature averages 12°C and total annual precipitation is 1000-1200 mm (Direcção Geral do Ambiente, 1995).

Males were considered adults if carrying active gonads in the reproductive season or, during the rest of the year, when they were larger than the smallest reproductively active male (Carretero and Llorente, 1993; Carretero et al., unpubl. data). Since adult males of both species were seen to be active even in winter (Carretero et al., unpubl. data) sampling was extended throughout the year. Based on the state of the gonads and on behavioural observations, the breeding season of both species lasted from February to July in the study sites (Carretero et al., unpubl. data).

A total of 203 adult males were collected in the three localities on a monthly basis, within a period of 1 week maximum. Lizards were immediately carried to the laboratory, humanely sacrificed and frozen. These specimens were used not only for this study but also for analysing the cycles of gonads and fat reserves (Carretero et al., unpubl. data) as well as morphometrics (Carretero et al., 2003; Kaliontzopoulou, 2004; Kaliontzopoulou et al., 2005) and trophic ecology. Snout-vent length (SVL) of each lizard was measured with a digital calliper to the nearest 0.01 mm. The degree of bilateral asymmetry was estimated counting the number of right and left femoral pores (Carretero, 2001; Crnobrnja-Isailovic et al., 2005). In order to simplify the analysis, lizards were only categorised as symmetric and asymmetric. The presence of intact vs. regenerated/broken tails was also recorded.

Seasonal variation of sexual cells was estimated by observation (optical microscope 400×) of right testis and epididymis extensions on microscope slides, coloured by the diff-quick method (Durfort, 1978; Bea, 1979). Three microscopic fields were selected at random and the number of distinct sexual cells was counted blindly, without individual assignation. All three fields were pooled for subsequent analysis for each male lizard (Roig et al., 2000). Identification of cell types followed Arrayago and Bea (1986).

Data analysis was based on AN(C)OVA, testing, in a first step, sympatry and month as factors determining the cell numbers for each species. In a second step, the analysis was restricted to spermatozoa during the breeding season and tail shedding and asymmetry were also tested. An $\alpha$ value of 0.05 was considered in all the analyses.

## RESULTS

### *Spermatogenic cycle*

Figure 1 shows the basic patterns of annual variation of all types of sexual cells in both species and the three localities. Table 1 shows the results of tests on the effects of sympatry and month. As expected, all the cell types displayed significant seasonal variation which showed similar general patterns in both species and localities (fig. 1), although the first appearance of each cell type was slightly displaced. Spermatogonia were abundant throughout the year except at the end of the breeding season (August). Spermatocytes gradually increased from October to the middle of the breeding season and then decreased abruptly. Spermatides, which were the most scarce cell type, appeared in November, peaked in April-May and then disappeared at the end of the breeding season. Spermatozoa (fig. 2) were already present in the testis in November-December but peaked in the middle of the breeding season and disappeared at the end. In contrast, spermatozoa were found in the epididymis only in the breeding season, with a peak in June-July. The number of spermatozoa was generally more variable in the epididymis than in the testes. Moreover, it is noteworthy that in the early breeding season (February), spermatozoa were scarce in testes but almost completely absent in the epididymis. The effect of sympatry was generally not significant per se but when interacting with the seasonal variation (table 1). In fact, the cycles of both species in sympatry appeared to be more concentrated in the second half of the reproductive season than in allopatry, especially in *P. carbonelli* (figs. 2, 3).

### *Relationships with male traits*

Snout-vent lengths of adult males were 49.68 ± 0.61 (40.44-58.07) for *P. carbonelli* in Torreira, 50.30 ± 0.66 (39.15-60.13) for *P. carbonelli* in Espinho, 57.01 ± 0.57 (47.79-63.95) for *P. bocagei* in Mindelo, and 57.39 ± 0.62 (46.93-64.35) for *P. bocagei* in Espinho. *Podarcis bocagei* was substantially bigger than *P. carbonelli* but no size differences between allopatric and sympatric populations were found (2-way ANOVA species $F_{1,199} = 0.67$, $P = 0.41$; sympatry $F_{1,199} = 134.36$, $P < 0.000001$; species * sympatry $F_{1,199} = 0.04$, $P = 0.84$).

The analyses were henceforth restricted to spermatozoa and to the reproductive period (February-July). The number of spermatozoa tended to be positively correlated with male size both in testes (*P. carbonelli*: allopatric $y = 51.28x - 1856.98$, $R^2 = 0.22$, $P < 0.01$, sympatric $y = 51.46x - 1677.93$, $R^2 = 0.21$, $P < 0.01$; *P. bocagei* allopatric $y = 8.77x - 297.03$, $R^2 = 0.003$, $P < 0.75$, sympatric $y = 6.82x - 807.57$, $R^2 = 0.04$, $P < 0.72$) and epididymis (*P. carbonelli*: allopatric $y = 99.73x - 3671.04$, $R^2 = 0.20$, $P < 0.01$, sympatric $y = 73.64x - 2113.17$, $R^2 = 0.06$, $P < 0.21$; *P. bocagei* allopatric $y = 159.54x - 7094.38$, $R^2 = 0.16$, $P < 0.02$, sympatric $y = 46.94x - 872.46$, $R^2 = 0.03$, $P < 0.36$). Although no variation in body size between either site or month was detected (2-way ANOVAs *P. carbonelli*, sympatry $F_{1,99} = 0.46$, $P = 0.50$, month $F_{5,99} = 0.46$, $P = 0.81$,

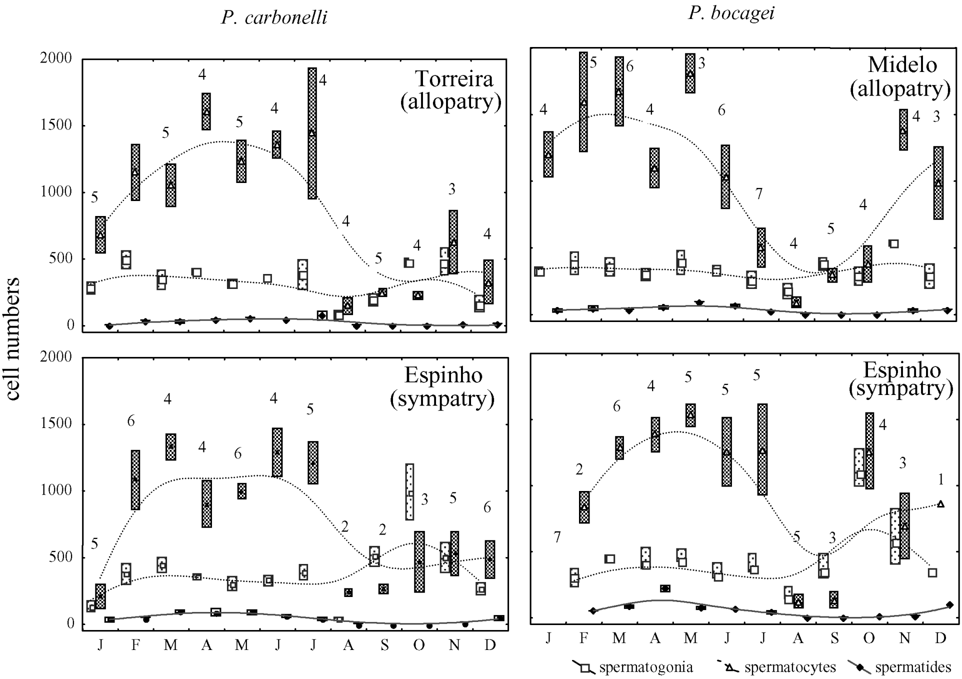

**Figure 1.** Annual patterns of the different cell types in both *Podarcis* species, considering the locality. Boxes: ±SE. Line is fitted by minimum squares. Numbers indicate sample sizes.

interaction $F_{5,99} = 0.44$, $P = 0.82$; *P. bocagei*, sympatry $F_{1,84} = 1.49$, $P = 0.23$, month $F_{5,84} = 0.48$, $P = 0.79$, interaction $F_{5,84} = 0.85$, $P = 0.52$) the seasonal analyses were repeated using SVL as a covariate with the same results (available from the authors on request).

Even though not all correlations were significant, they tended to be higher in the testes than in the epididymis. In a graphical analysis of the regression lines between spermatozoa in testis and body size (fig. 3), slopes were parallel between sympatric and allopatric populations within a species, but higher in *P. carbonelli* than in *P. bocagei*, whereas intercepts were higher in sympatry than in allopatry (parallelism tests $P < 0.01$ when significant). In fact, male *P. bocagei* carried more spermatozoa in testis when in sympatry independent of their size (ANCOVA, $F_{1,55} = 7.86$, $P = 0.007$); differences in *P. carbonelli* showed a similar but not significant tendency (ANCOVA, $F_{1,54} = 2.67$, $P = 0.10$). Spermatozoa in epididymis against body size showed steeper slopes in *P. bocagei* than in *P. carbonelli* and in allopatry than in sympatry for both species (fig. 3). No interspecific comparisons were carried out due to the lack of parallelism.

The effects of asymmetry and tail shedding on the density of spermatozoa in testis were simultaneously tested, with no significant results either for *P. carbonelli* (ANCOVA, sympatry $F_{1,48} = 1.41$, $P = 0.24$, asymmetry $F_{1,48} = 0.06$, $P = 0.80$; tail shedding $F_{1,48} = 0.76$, $P = 0.39$, all interactions $P > 0.29$) or *P. bocagei*

**Table 1.**
Results of the ANOVA comparisons for all cell types in both species, considering the effects of sympatry and month.

| Species/cell type | ANOVA effect | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|
| | sympatry | | | month | | | sympatry * month | | |
| | F | d.f. | P | F | d.f. | P | F | d.f. | P |
| *P. carbonelli* | | | | | | | | | |
| Spermatogonia | 5.69 | 1,80 | 0.02 | 9.10 | 11,80 | $2.59*10^{-10}$ | 3.16 | 11,80 | 0.001 |
| Spermatocytes | 1.38 | 1,80 | 0.24 | 11.32 | 11,80 | $2.35*10^{-12}$ | 1.23 | 11,80 | 0.28 |
| Spermatides | 16.37 | 1,80 | 0.0001 | 10.92 | 11,80 | $5.27*10^{-12}$ | 2.97 | 11,80 | 0.002 |
| Spermatozoa testis | 2.57 | 1,80 | 0.11 | 16.98 | 11,80 | $1.05*10^{-16}$ | 0.88 | 11,80 | 0.56 |
| Spermatozoa epididymis | 1.24 | 1,80 | 0.27 | 23.25 | 11,80 | $1.53*10^{-20}$ | 2.69 | 11,80 | 0.005 |
| *P. bocagei* | | | | | | | | | |
| Spermatogonia | 7.40 | 1,71 | 0.008 | 7.28 | 10,71 | $8.33*10^{-8}$ | 5.75 | 10,71 | $2.85*10^{-6}$ |
| Spermatocytes | 0.02 | 1,71 | 0.88 | 9.61 | 10,71 | $6.51*10^{-10}$ | 2.81 | 10,71 | 0.005 |
| Spermatides | 28.62 | 1,71 | 0.88 | 34.31 | 10,71 | $2.7*10^{-23}$ | 14.39 | 10,71 | $1.54*10^{-13}$ |
| Spermatozoa testis | 4.79 | 1,71 | 0.03 | 21.62 | 10,71 | $8.23*10^{-18}$ | 5.79 | 10,71 | $2.57*10^{-6}$ |
| Spermatozoa epididymis | 1.70 | 1,71 | 0.20 | 13.02 | 10,71 | $1.4*10^{-12}$ | 3.71 | 10,71 | 0.0005 |

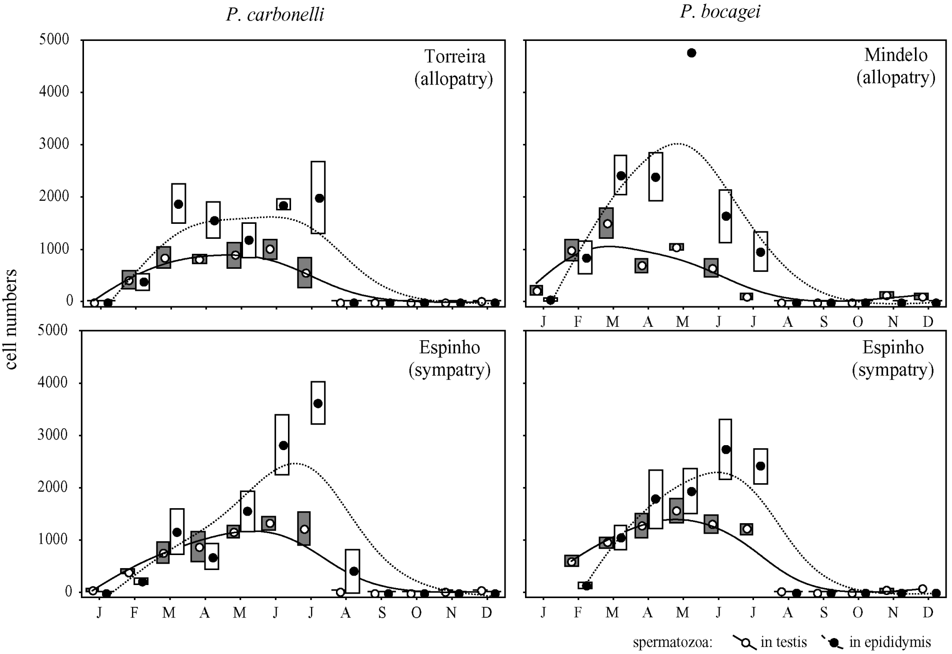

**Figure 2.** Annual variation of spermatozoa in testis and epididymis by species and locality. Boxes: ± SE. Line is fitted by minimum squares.

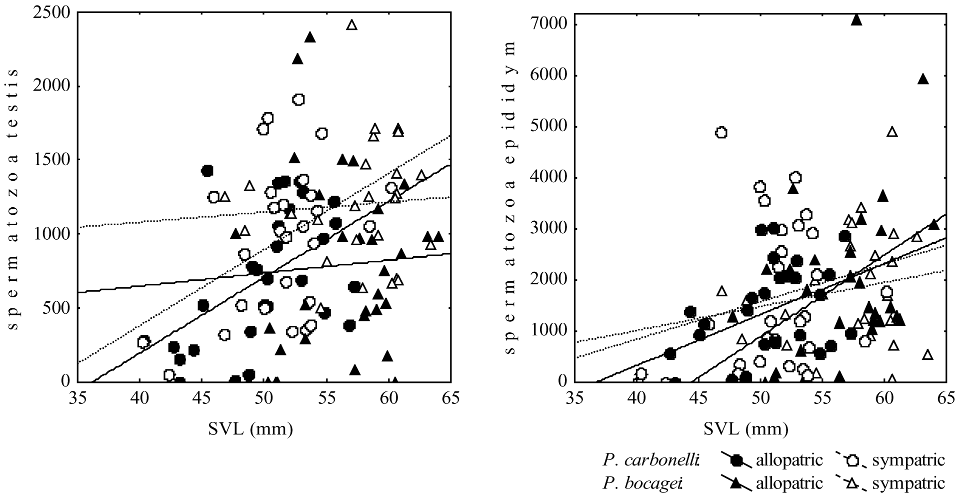

**Figure 3.** Correlation between body size and number of spermatozoa in testis and epididymis during breeding season (February-July) in both *Podarcis* species, considering the effect of sympatry.

(ANCOVA, sympatry $F_{1,49} = 4.87$, $P = 0.03$, asymmetry $F_{1,49} = 3.07$, $P = 0.09$; tail shedding $F_{1,49} = 0.08$, $P = 0.78$, all interactions $P > 0.37$).

## DISCUSSION

The maritime Atlantic climate of the three sites provides suitable temperature and humidity conditions for lizard activity, at least at midday, during most of the year. Thus, males of both species remain active in winter, start reproductive activities early and show a long reproductive season, from February to July (Carretero et al., unpubl. data). Galán (1996, 1997) reports a similar pattern for a coastal population of *P. bocagei* in northwest Spain. In contrast, available results for *P. carbonelli* in a mountain range of central Spain indicate a marked winter diapause and the beginning of activity and reproduction in late March (Pérez-Mellado, 1982).

Seasonal variation of the different cell types observed in both species is typical in lacertids of the temperate regions (Saint-Girons, 1984). The presence of spermatocytes, spermatides and even spermatozoa in autumn and early winter indicates mixed-type spermatogenesis (Saint-Girons, 1963, 1984), although this classification is probably simplistic for lacertids (Carretero, in press). Species with a short annual activity, such as the Eurosiberian *Lacerta vivipara* (Roig et al., 2000) and *L. agilis* (Amat et al., 2000), as well as the thermomediterranean *Acanthodactylus erythrurus* (Bons, 1969; Busack and Klosterman, 1987; Carretero and Llorente, 1995), all with a strongly synchronic phenology, show delayed patterns for every cell type. In contrast, both *Podarcis* just showed delaying in the first appearance of every cell type, but a mixing of types during the reproductive season. This result is attributable to an asynchrony in the timing of reproduction between individuals typically found in Mediterranean species, such as *Podarcis sicula* (Angelini et al., 1979), *Psammodromus hispanicus* (Carretero and Llorente, 1991) and *P. algirus* (Carretero and Llorente, 1997), characterised by long breeding periods. Since spermatogenesis has been demonstrated to be thermo-dependent in *Podarcis* (Joly and Saint-Girons, 1975 in *P. muralis*; Angelini et al., 1976 in *P. sicula*), populations of the same species living under more extreme climates are expected to delay the beginning of reproduction and to be more synchronic (Saint-Girons and Duguy, 1970; Hraoui-Bloquet and Bloquet, 1988; Braña et al., 1990). However, the testicular regression seems to be endogenous at least in *Podarcis* (Angelini et al., 1976) and, hence, similar between populations.

In all four populations, spermiogenesis tended to be vernal although some spermatozoa were already present in winter, especially in the few *P. bocagei* males found to be active (Galán, 1997). Those males were, in fact, functionally sterile (see Olsson and Madsen, 1996) since spermatozoa reached the epididymis only in February. Interestingly, since sharing similar thermal requirements to males, females remained inactive in December and January (Carretero et al., unpubl. data) suggesting an avoidance of mating with such males in a period of low trophic availability (unpubl. data), as reported for *Lacerta agilis* (Olsson and Madsen, 1996) and *L. vivipara* (Roig et al., 2000). Other constraints such as the environmental conditions required for oviposition (Galán, 1996) should also be taken into account.

The cycles of testicular and epididymal spermatozoa in both *Podarcis* match reasonably well with the size variation of both organs (Carretero et al., unpubl. data) corroborating the results of Roig et al. (2000) with *Lacerta vivipara*. In testis, this correspondence was, nevertheless, restricted to the reproductive period whereas, during the rest of the year, size variation in testis would be derived from the contribution of the other cell types.

For both species, the effect of sympatry consisted of a delayed phenology, especially in *P. carbonelli*. Although, this variation is higher than between other conspecific populations of lacertids and are not correlated with latitude (see Carretero and Llorente, 1997), this result cannot be unambiguously interpreted in terms of competitive interaction between both species since this could also be due to a non evident variation in local habitat or microclimate (although not, in general, site characteristics). The results of the analyses of gonads, fat reserves and clutch traits were also inconclusive in this aspect (Carretero et al., unpubl. data).

Amongst the lizard traits tested, only body size appeared to be important for explaining the abundance of spermatozoa in males. Several studies indicate that lacertid females usually select for bigger males as reproductive partners (López et al., 2002, 2003) but remain promiscuous (Olsson et al., 1994b, c; Moreira and Birkhead, 2004a, b). If these results are general to the present species, significant correlations should be interpreted as an evidence for sperm competition (Olsson et al., 1994a). Roig et al. (2000) indicated for *L. vivipara* an inverse but equivalent correlation, negative for testis and positive for epididymis, and deduced a high sperm release in large males during copulations in an extremely synchronic population with a short reproductive period. In the present case, both correlations were positive, suggesting that large males produce more sperm but do not necessarily release it at the same rate. A reasonable explanation for this would be that a prolonged reproductive season makes individual phenological differences more evident (due to body size and condition) whereas these remain masked when annual activity is short. This must be especially evident in females of these iteroparous lacertids (Braña, 1983; Galán, 1996, 1997); hence, male opportunities for fecundation extending throughout a long period. Therefore, a different mating system, shaped by long-term production of sperm with periodical releases instead of by short-term sperm release as found in *L. vivipara* (Roig et al., 2000), would be selected. Under this scenario, developmental instability and tail shedding may compromise survival and reproductive success in males (Martín and Salvador, 1993; Salvador et al., 1995; Martín and López, 2000) but not necessarily through differences in sperm production. If true, from the present results it can be deduced that sperm competition remains constant within species but is higher in *P. carbonelli* than in *P. bocagei*. Furthermore, sympatric males of both species produced more sperm for the same body size, which suggests that some kind of reproductive interaction between them is taking place. In fact, preliminary genetic analyses using both nuclear and mitochondrial markers have already demonstrated hybridisation between both species in Espinho (Pinho et al., 2003) although further studies are necessary to assess its nature and magnitude.

In conclusion, comparisons with other populations and species indicate that climate modifies the pattern of spermatogenesis in lacertids, mainly by restricting the beginning (but not the end) of the activity period. Moreover, present results corroborate previous studies reporting a general agreement between the variations of gonads observed at microscopic (cell numbers) and macroscopic (testis/epididymis measures) scales. Finally, competitive effects between both species cannot be directly concluded, although relationships between spermatozoa and size suggest sperm competition and reproductive interaction between both species.

## ACKNOWLEDGEMENTS

Funding was provided by the project POCTI/BSE/45664/2002 of Fundação para a Ciência e a Tecnologia, FCT (Portugal). M.A.C. and D.J.H were funded by post-doctoral grants (SFRH/BPD/3596/2000 and SFRH/BPD/5702/2001, respectively), and D.B. by a PhD grant (SFRH/BD/14084/2003), all also from FCT. R.R. was funded by a contract associated to the project POA – 1.1/00021 of Instituto de Conservação da Natureza, ICN (Portugal). Collecting permits were provided by ICN. B. Fráguas, R. Pereira, C. Soares and P. Sousa helped in the fieldwork.

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