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Reproductive ecology of the lacertid lizard *Podarcis bocagei*

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This paper presents data on aspects of the reproductive ecology of a population of *Podarcis bocagei* in northwestern Spain, as monitored over a two-year period (1990–1991). Data were obtained principally on the basis of mark-recapture experiments, but also from laboratory hatching studies. Mating took place between the end of March and July. During the laying period, from May to July, 8.5% of reproductive females produced three clutches, 52.1% two clutches and 39.4% one clutch. In general, single clutches were produced by small females. Only a small proportion of large females produced three clutches. Mean clutch size was 4.8 eggs (range 4–7) in May, 4.3 (2–6) in June and 3.9 (2–4) in July. There was significant variation in the mean snout-to-vent length (SVL) of females laying in each month of the season. Both clutch size and mean single-egg volume increased with mother's SVL. There was a significant partial correlation between egg volume and clutch size when both mother's SVL and month of laying were held constant. There was no significant between-year variation in clutch size, breeding females' SVL, egg weight or relative clutch mass. A delay in the timing of reproductive events in one year (1991) is attributable to adverse weather conditions during early spring. Hatching occurred between July and September. Hatch success (as estimated in 1989, 1990 and 1991 from natural nests at the study site) was high, ranging from 83% in 1991 to 91% in 1989. The mean SVL of female hatchlings was greater than that of male hatchlings. By contrast, adult females had lower mean SVL than adult males.

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The ecology of reproduction, as opposed to simply the anatomy and physiology of reproduction, is an especially critical aspect of an organism's life history (Gillis and Ballinger 1992, Dunham 1994). Reproductive ecology includes the mode and timing of reproductive events in natural populations, as well as the number and size of offspring produced under specific environmental conditions.

Studies of lizard reproductive ecology have become increasingly prominent in attempts to refine and test theories of life history evolution. Numerous thorough studies have documented variations in life-history traits among species (e.g. Tinkle 1969, Tinkle et al. 1970, Ballinger 1973, Vitt and Congdon 1978, Dunham 1981) as well as among populations of single species (e.g. Pianka 1970, Tinkle and Ballinger 1972, Dunham 1978, 1982, Ballinger 1979, 1983, Tinkle and Dunham 1983, 1986, Gillis and Ballinger 1992).

Similarly, studies of a number of lizard species have revealed considerable within-population temporal variation in reproductive characteristics (see for example Dunham 1981, Pilorge et al. 1983, Tinkle and Dunham 1986, Bauwens and Verheyen 1987, Jones et al. 1987, Tinkle et al. 1993, Parker 1994). Such temporal variation may be due to a) within-individual variation over the breeding season (e.g., a female may lay two or more clutches of different sizes), b) variation over the breeding season as a result of between-individual variation in time of breeding (e.g. older females and younger females may tend to breed at different times), and/or c) between-year variation.

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Of the lacertids, *Lacerta vivipara* has been extensively studied, however, data documenting temporal and geographic variation in the life histories of other species of the Lacertidae are still remarkably scarce.

Bocage's wall lizard, *Podarcis bocagei*, though widespread and abundant in northwestern Spain, has been relatively little studied from a reproductive point of view (though see Pérez-Mellado 1982, Braña 1983, Braña et al. 1991, 1992, Barbadillo et al. 1993, Galán 1994, 1995a).

Here, I report the results of a two-year study of the reproductive biology of a population of *Podarcis bocagei* in northwestern Spain. My aim was to describe the reproductive cycle of this species and identify possible relationships between female size and a series of reproductive characteristics including clutch size, egg size and offspring size. In addition, I examined between-year differences in the timing of reproduction, and attempted to identify environmental factors associated with this variation.

Material and methods

Bocage's wall lizard, *Podarcis bocagei* (Seoane 1884), is a species with a restricted distribution in the northwestern and western Iberian Peninsula. It is a small (adult snout-vent length 45–65 mm), diurnal, insectivorous lizard of the family Lacertidae.

Data were gathered in the course of a population study conducted between September 1989 and October 1991. Some additional data were gathered in July 1989 and in May–July 1992. Lizards were studied in a 45 × 60 m plot located in San Vicente de Vigo (municipio of Carral, 45°18'N, 8°20'W, UTM 29T NH5687, altitude 90 m, La Coruña Province, northwest Spain). The study population is here referred to as the Carral population.

The study area is included in the Wet Oceanic climatic type (Carballeira et al. 1983), characteristic of coastal areas of the northwest Iberian Peninsula. Average annual rainfall is 1200 mm and average annual number of hours of sunshine is ca 2000. Within-year temperature oscillation is very small: the mean temperature of the coldest month (January, mean temperature 8°C) is only ca 10°C lower than that of the hottest month (July, mean temperature 18°C). For more details of the study area, see Galán (1994).

The study site was visited 3–8 times per month between September 1989 and October 1991. At each visit, the number of lizards observed and the sex of each was recorded. I also recorded details of all reproductive events (i.e. courtships and matings) observed.

Whenever possible, lizards were captured by hand, marked individually by toe-clipping and released, noting identity, sex, reproductive condition, snout-vent length (SVL, to nearest 0.1 mm), tail length (including regenerated parts), weight (to nearest 0.1 g) and coloration of the occipital band. Each lizard was processed quickly (<5 min) at its capture site, and released immediately. In total, I captured and marked 611 lizards. The number of recaptures was 1150.

Three age classes could be distinguished, mainly on the basis of body length: juveniles (lizards born in the present year, SVL usually ≤40 mm), yearlings (subadult or young adults: lizards born in the preceding year, SVL 40–52 mm) and adults (two or more years old, SVL ≥ 52 mm).

Reproductive condition of live female lizards was evaluated by ventral palpation to detect enlarged ovarian follicles or oviductal eggs. Other reproductive signs (i.e. copulation marks or lateral skin folds) were also noted. In all cases of prompt recapture of females with a mating scar but not visibly pregnant, pregnancy was evident at the time of recapture. Sexually mature males were identified by their bright green dorsal coloration.

Between May and July of 1990, 1991 and 1992, a number of late-pregnant (i.e. highly distended) females were collected from the study area (50–1500 m from the border of study plot) and transported to the laboratory, where they were placed individually in plastic boxes (10 × 10 × 20 cm, filled to a depth of ca 15 cm with soil from the study site; note that natural nests of this species at the study site tend to be in the soil). These females were maintained in the laboratory for a maximum of three days, with daily determination of weight (±0.01 g). If during this period the female laid, I recorded number, size (length and width) and weight (to the nearest 0.001 g) of eggs. Egg volume was estimated as $V = 4/3\pi a^2 b$, where $a = 1/2$ shortest diameter and $b = 1/2$ largest diameter. Egg characteristics were in all cases determined within 8 h of laying.

After laying (or after 3 days), each female was measured (±0.1 cm), weighed, and then released at the capture site. In all cases each clutch could be unequivocally assigned to an individual female, allowing calculation of relative clutch mass as the weight of the clutch (immediately after laying) divided by the weight of the mother (excluding clutch weight).

Clutch and egg characteristics, and relationships between these and mother's body size, were investigated on the basis of data for clutches laid in 1990 and 1991. As a basis for characterization of hatchling characteristics, I also used data for clutches laid in 1992.

Each clutch was incubated in the same plastic box until hatching. To ensure near-natural conditions of humidity and temperature, the vivaria were half-filled with soil from the study site, sealed with an airtight lid and placed by an open south-facing window. Temperature was monitored daily with a maximum-minimum thermometer on each box. The absolute minimum recorded over the incubation period was 18°C, and the absolute maximum 33°C, these values are similar to those occurring at the study site over the same period. Relative humidity within the vivaria remained close to 100% throughout incubation. Eggs were measured (length and width ±0.01 mm) weekly until hatching.

After hatching I recorded the SVL, weight, colour and sex of hatchlings. Sex was determined as follows. The number of transverse rows of ventral scales differs between male and female *Podarcis bocagei* (see Pérez-Mellado 1981, Galán 1986). In a sample of 235 adult males and 311 adult females from the study site, all males had fewer than 28 rows and all females >28 rows (Galan 1994). This dimorphic character can be used to sex newborn lizards (see Bauwens and Thoen 1982). If an individual has exactly 28 rows, sex can be determined on the basis of the black dorsal pattern. After data recording, hatchlings were released at the study site.

In 1990 and 1991, a number of pregnant females were collected from the study area (again 50–1500 m from the border of study plot) for dissection. These lizards were first frozen and later thawed and measured for length and weight. Eggs were counted and oviductal eggs were measured (length and width) to the nearest 0.01 cm.

Mean clutch size and mean mother's SVL were estimated on the basis of both data for clutches laid in the laboratory and data for autopsied females (oviductal eggs). Other clutch and egg characteristics were estimated considering oviposited and oviductal eggs separately (see Results).

Hatch success in the field was estimated on the basis of the ratio of number of empty egg shells to number of dead eggs in natural nests at the study site. Nests were found by digging in different areas of the study site during the post-breeding season in 1989, 1990 and 1991. In total, I dug at 543 points in the study plot (ca one point every 5 m^2) and found 47 nests with hatching remains (empty egg shells and dead eggs). For details of this methodology, see House and Spellerberg (1980) and Strijbosch (1987, 1988).

The average body condition of adult females over the first two months of the activity season in 1990 and 1991 was evaluated by regressing log (body mass) on log (SVL), excluding data for gravid females. For each month of each season, an index of body condition was obtained as the residual deviation from the global regression.

Climatological information was obtained at the study site and from the meteorological stations of Mabegondo and Cañás, situated 2.5 and 2.3 km respectively from the study area and a similar altitude.

All statistical analyses were done with the aid of the Statview II statistical package (Feldman et al. 1987), except analysis of covariance, which was done with the aid of Systat (Wilkinson 1989). In the text, mean values are cited ± standard errors (SE). In some cases, standard deviation (SD) and coefficient of variation (CV) are also cited. When analysis of variance was used, normality was first confirmed. Multiple comparisons of means following analysis of variance were by Scheffé's test.

Results

Activity cycle

Active lizards were seen at the study site during all months of the year in 1990 and 1991. Nevertheless, between November and mid-/late-February, only a few individuals were seen, generally basking near winter refuges (mainly crevices in slopes) on sunny days. Full activity occurs between mid-February (1990) or the beginning of March (1991) and the end of October (both years). I did not detect any between-sex differences in activity cycle: males and females showed similar activity patterns during winter and early spring (sex ratio of lizards observed during January, February and March in 1990 and 1991 did not differ significantly from one-to-one, χ^2-test, $p > 0.05$ in all cases).

Sexual dimorphism

In the study population, mean SVL of males is slightly greater than that of females (males: mean ± SE = 55.2 ± 0.24 mm, range = 48.1–65.7 mm, n = 184, females: mean = 53.3 ± 0.17 mm, range = 45.3–63.2 mm, n = 314, Student's $t = 8.48$, $p < 0.0001$). Males also tend to be heavier than females (males: mean = 4.07 ± 0.06 g, range = 2.4–6.7 g, n = 184, females: mean = 2.90 ± 0.03 g, range = 1.9–5.9 g, n = 313, Student's $t = 19.57$, $p < 0.0001$).

Sexual dimorphism was also apparent in dorsal coloration. Adult males have a bright green dorsal coloration during the breeding season (March–July), whereas in females this area of the body is brown.

Female body condition at the beginning of the reproductive season

Residual deviations from the regression of log (body mass) on log (SVL) (data for non-gravid adult females) during March and April (pre-reproductive season and beginning of the reproductive season) of 1990 and 1991 are shown in Fig. 1.

Body condition index (i.e. residual deviation, see Methods) did not differ significantly between March 1990 and March 1991 ($F_{1,41} = 0.554$, $p = 0.461$), but did differ significantly between April 1990 and April 1991 ($F_{1,48} = 5.222$, $p = 0.027$). There was a significant difference between March and April in 1990 ($F_{1,40} = 2.827$, $p = 0.030$), but not in 1991 ($F_{1,49} = 1.295$, $p = 0.283$).

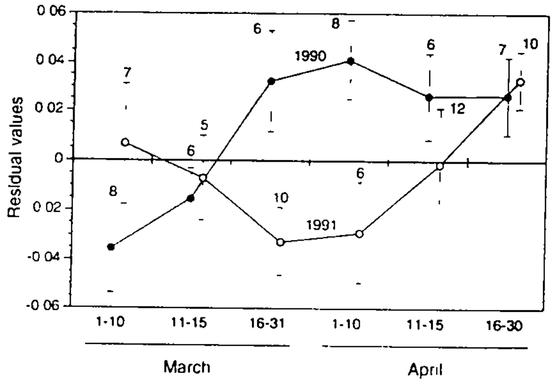

Fig 1 Mean residual deviations (±SE) and sample sizes from the regression of log (body mass) on log (SVL) for non-gravid adult females during each ten-day period of March and April of 1990 (black dots) and 1991 (circles) These months correspond to the pre-reproductive period and the beginning of the reproductive period The horizontal line at y = 0 indicates the average body condition of these lizards during March and April of 1990 and 1991

Mean body condition index at the beginning of March was worse in 1990 than in 1991, despite the fact that the winter of 1989/90 was warmer and drier than that of 1990/91 (see Table 1) However, body condition index worsened steadily between the end of March and mid-April 1990, but improved steadily over the same period in 1991 (Fig 1), this is in accordance with the fact that weather conditions were much more favourable during March 1990 than during March 1991 (see Table 1)

Reproductive cycles: field observations

Mating

The time of onset and duration of the mating season in the study area were determined in view of the presence of mating scars on females' bodies and by field observation of courtship and mating behaviour The first females with mating scars were observed in late March in 1990 and in mid-April in 1991 In both years, these first females to initiate reproduction were large individuals (SVL > 56 mm) Females with mating scars were most frequently observed during May and June The last observations of females with mating scars, and the last direct observations of mating behaviour, were in mid-July in both years In 1990, the first observation of copulation in the study site was on 8 April and the last on 5 July In 1991, I only observed copulation a few times, during May and June

Mating behaviour of *Podarcis bocagei* is similar to that of other *Podarcis* species Copulations last from 22 to 30 min After mating, both sexes remain in close proximity (showing behaviour similar to "male mate guarding") for a variable period of time (average 68 min, range 9–258 min, n = 7)

As noted above, seasonal changes in coloration were observed in adult specimens the dorsal region of males was bright green during the period March to July (when mating and aggressive behaviour take place), but brown or greenish brown in the other months of the year This bright coloration seems to be related to sexual and aggressive behaviour.

Female reproductive cycle

I was able to characterize the egg-laying cycle by ventral palpation of live females collected in the study area Enlarged follicles were detected from late March (1990) or the beginning of April (1991) to mid-July (both years) Ovulation occurs from mid-April to the second half of July, since in this period I observed females with oviductal eggs

Laying period, determined on the basis of the presence of deep skin folds in the flanks and empty oviducts as revealed by palpation, extended from late April

Table 1 Meteorological data obtained at the study site during the study period, and ten-year-average data from the meteorological stations of Mabegondo and Cañás (2 5 and 2 3 km respectively from the study area) Average temperatures are means of the maximum-minimum midpoint for each day of that month

	Average temperatures (°C)					Total rainfall (mm)				
	1989	1990	1991	Mabegondo	Cañas	1989	1990	1991	Mabegondo	Cañas
Jan	7 5	8 2	7 5	8 3	7 3	38	96	157	106	138
Feb	8 1	11 7	7 1	8 8	7 7	207	74	141	117	134
Mar	9 8	11 0	9 8	9.9	10 1	91	15	86	79	109
Apr	9 5	10 0	9 9	11 1	11 0	195	100	64	94	98
May	16 8	15 1	13.5	13 5	13 3	45	33	20	74	75
Jun	16 5	15 5	14 2	15 8	15 7	31	20	22	38	53
Jul	21 0	19 5	18 0	18 3	18 3	3	13	67	36	27
Aug	19 9	19 1	19 2	18 2	17 2	18	8	56	25	44
Sep	16 9	18 3	18 2	17 9	16 1	6	20	118	62	55
Oct	15 4	14 0	11 9	14.0	13 1	95	200	84	108	73
Nov	11 7	10 0	10 3	11.3	10 1	134	151	136	106	183
Dec	11 5	9 0	10 3	9 7	7 9	263	140	27	157	180
Average	13 7	13 5	12 5	13 1	12 3					
Total						1127	870	978	1002	1169

Table 2 Mother's snout-vent length (SVL) and clutch size (vivarium and dissection data for 1990 and 1991, see text)

Month	Mother's SVL (mean ± SE)	Range	Clutch size (mean ± SE)	Range	No of clutches
May	57.45 ± 0.56	52.0–63.2	4.83 ± 0.17	4–7	29
June	55.13 ± 0.72	48.3–63.2	4.28 ± 0.14	2–6	32
July	50.74 ± 0.92	41.7–62.1	3.21 ± 0.12	2–4	28
Total	54.50 ± 0.51	41.7–63.2	4.12 ± 0.11	2–7	89

(1990) or mid-May (1991) to the second half of July (both years). Most females collected after mid-July and all collected later were post-reproductive.

The fortuitous mark-recapture records for one particular female provide information on the period between two successive lays. This female was caught pregnant, released, and recaptured the following day without eggs, 32 days later she was recaptured, again pregnant, she was then released, and recaptured the following day, again without eggs. This indicated that 33 days had passed between successive lays.

Clutches

Clutch size

There were no statistically significant between-year differences in mean clutch size ($F_{1,87} = 0.19$, $p = 0.66$), mean mother's SVL ($F_{1,87} = 0.28$, $p = 0.60$), mean egg weight ($F_{1,62} = 2.33$, $p = 0.13$) or relative clutch mass ($F_{1,62} = 0.37$, $p = 0.55$). In what follows, I thus consider data for the two years together.

Mean clutch size was 4.12 eggs (4.30 in 1990 and 4.02 in 1991), with a range of 2–7 eggs (same range in both years). Clutch size varied significantly among the three months of the laying period (Table 2, $F_{2,88} = 29.78$, $p < 0.001$). Both average and maximum clutch size dropped between the first month of the laying period (May) and the third (July).

The difference in average clutch size between May and June was less marked than that between May and July and that between June and July, though Scheffé's test indicated that all three pairwise comparisons were statistically significant (May–June $F = 3.53$, $p < 0.05$, May–July $F = 28.82$, $p < 0.001$, June–July $F = 13.21$, $p < 0.001$). Analysis of covariance indicated that month has a significant effect on clutch size even when the effect of mother's SVL is accounted for ($F_{2,85} = 8.39$, $p < 0.001$).

Clutch size increased significantly with mother's SVL considering all clutches ($r^2 = 0.52$, $F_{1,88} = 94.66$, $p < 0.0001$; $y = 0.153x - 4.241$), and also considering separately clutches laid in each month of the laying season (May $F_{1,28} = 13.33$, $p = 0.001$; June $F_{1,31} = 25.95$, $p < 0.0001$, July: $F_{1,27} = 10.11$, $p = 0.004$) (Fig. 2). Both the average and the minimum SVL of mothers dropped significantly between May and July (Table 2 and Fig. 2, $F_{2,88} = 20.16$, $p < 0.001$). Significant between-month differences in mother's SVL were detected for May–July (Scheffe test, $F = 19.57$, $p < 0.001$) and June–July ($F = 8.77$, $p < 0.001$), but not for May–June ($F = 2.50$, $p > 0.05$).

Clutch frequency

Mark-recapture records for a number of females caught during the breeding season of 1990 and 1991 provided information on clutch frequency (Table 3). In both years, clutch frequency varied significantly among size-classes (1990 $F_{2,35} = 24.01$, $p < 0.001$, 1991 $F_{2,34} = 24.15$, $p < 0.001$, 1990–1991 $F_{2,70} = 52.60$, $p < 0.0001$).

Only large females (> 55 mm SVL) appear to be able to lay three clutches per year (5.6% and 11.4% of such females laid three clutches in 1990 and 1991 respectively, Table 3). These females were in at least their

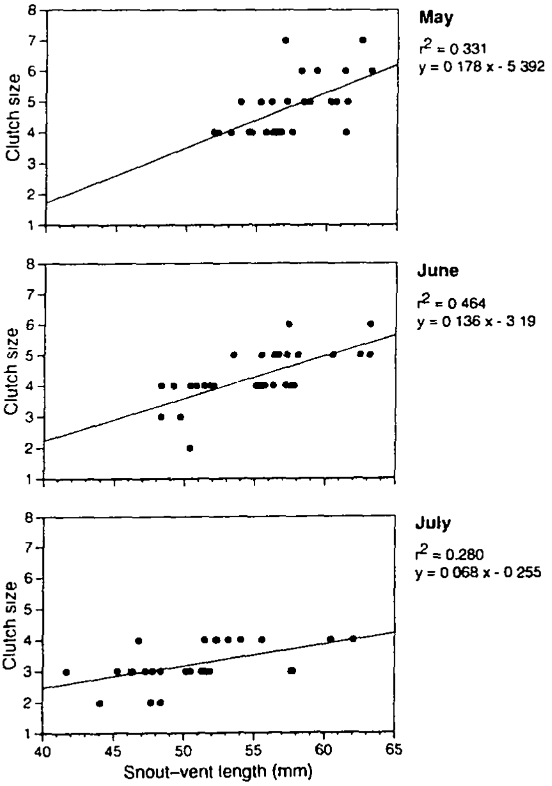

Fig 2 Relationships between mother's body size (snout-vent length, SVL) and clutch size in each month of the reproductive season

Table 3. Clutch frequency classified by year and mother's size class, as inferred from mark-recapture records. Most small (SVL 44–50 mm) females are in their second calendar year, and most medium (SVL 51–55 mm) females in their third calendar year. Large (SVL > 55 mm) females are in at least their third calendar year.

Year	Mother's SVL	Number of clutches per year 1	2	3
1990	44–50 mm	12	–	–
	51–55 mm	6	10	–
	>55 mm	–	6	2
1991	44–50 mm	7	–	–
	51–55 mm	3	12	–
	>55 mm	–	9	4
Total		28	37	6
% total		39.4	52.1	8.5

third activity season (two or more years old, age calculated on the basis of mark/recapture records). On the other hand, females that reach sexual maturity in their second activity season (one year old, with 44–50 mm SVL in June–July), appear to be able to lay only one clutch at the end of the laying season (late June or July).

Clutch characteristics

There was no significant difference between clutch size as determined by dissection of gravid females and as determined in vivaria ($F_{1,72} = 0.07$, $p = 0.79$). Likewise, there was no significant difference in mean SVL between dissected females and vivarium females ($F_{1,72} = 2.08$, $p = 0.15$). The characteristics of oviductal and vivarium-laid eggs are summarized in Table 4. Egg volume, egg mass, clutch mass and relative clutch mass were all lower in oviductal eggs that in vivarium-laid eggs. In most cases, the coefficients of variation for characteristics of vivarium-laid clutches and eggs were also lower. The higher variability of oviductal eggs probably reflects differences in developmental stage. An important consequence of this is that the relationships between clutch characteristics and mother's SVL differ depending on whether oviductal or vivarium-laid eggs are considered. For example, the relationship between average egg volume in each clutch and mother's SVL was not statistically significant for oviductal eggs ($r^2 = 0.001$, $F = 0.03$, $p = 0.86$) but was highly significant for vivarium-laid eggs ($r^2 = 0.306$, $F = 16.77$, $p < 0.001$, Fig. 3). In view of this, I considered only vivarium-laid eggs when defining clutch characteristics.

Average egg length in the sample of 43 vivarium-laid clutches was 11.22 ± 0.154 mm (range = 9.08–14.58 mm, SD = 1.01, CV = 9.013) and average egg width was 6.41 ± 0.054 mm (range = 5.10–7.10 mm, SD = 0.36, CV = 5.558). During incubation, eggs underwent a significant increase in size, particularly in width (length: Student's $t = 8.89$, $p < 0.001$; width: Student's $t = 32.87$, $p < 0.0001$). Immediately before hatching, average egg length was 13.01 ± 0.187 mm (range = 11.50–15.25 mm, SD = 0.989, CV = 7.599) and average egg width was 10.14 ± 0.084 mm (range = 8.85–10.85 mm, SD = 0.461, CV = 4.545). Mean egg volume increased significantly with mother's SVL (Fig. 3, see above).

Partial correlation analysis (with mother's SVL held constant) indicated a significant relationship between egg volume and clutch size ($r = -0.358$, $F = 5.441$, $p < 0.05$). With both mother's SVL and month of laying season held constant, there was a highly significant partial correlation between egg volume and clutch size ($r = -0.512$, $F = 14.183$, $p < 0.001$). Figure 4 shows the relationship between residuals from the regression of log (clutch size) on log (mother's SVL) and residuals from the regression of log (mean egg volume) on log (mother's SVL); the relationship between the two sets of residuals was again significant ($r^2 = 0.357$, $F_{1,41} = 22.72$, $p < 0.0001$). Considering clutches laid at about the same time by females of about the same size, the mean volume of the eggs in a clutch is thus negatively correlated with clutch size.

Relative clutch mass was not significantly related to mother's SVL ($r^2 = 0.032$, $F_{1,40} = 1.26$, $p = 0.27$).

Mean hatchling SVL increased significantly with mean egg volume (Fig. 5, $r^2 = 0.335$, $F_{1,37} = 17.60$, $p < 0.001$). In addition, mean hatchling SVL in each clutch increased significantly with mother's SVL (Fig. 6, $r^2 = 0.407$, $F_{1,37} = 24.76$, $p < 0.0001$). Hence, larger females laid larger eggs, and larger eggs produced larger hatchlings.

Incubation and hatching

In vivaria, average incubation time was 54 ± 0.53 days (range 48–59 days). Mean air temperature in the vivaria was 25.37 ± 0.48°C (range for daily means 22.7–28.3°C). The minimum temperature recorded in the laboratory during the incubation period was 18.5°C, and the maximum 32.9°C. Clutches hatched between June 27 and September 8 in 1990, between July 16 and September 9 in 1991 and between July 1 and September 14 in 1992. In all three years, the first clutches (laid in May) hatched in July (with two exceptions, which hatched in late June 1990). Clutches layed in June hatched mainly in August, while clutches laid in July hatched between late August and early September. This is in accordance with field observations (first clutches observed in early May, last in late July; first hatchlings observed in late June 1990 and mid-July 1991, last hatchlings in mid-September). In the field, hatchlings were defined as individuals with the navel scar open and SVL of <26 mm. Individuals of this size (but without open navel scars) were observed as late as October.

Mean hatch success in the laboratory, estimated from the pooled data for clutches laid in 1990, 1991 and 1992 was 90.24% (148 hatched eggs of 164 laid in 41 clutches). Estimated hatch success in the field was

Table 4 Mother's SVL and clutch/egg characteristics for vivarium-laid eggs and for oviductal eggs of dissected pregnant females

	Vivarium-laid eggs				Oviductal eggs			
	Mean ± SE	Range	Coefficient of variation	Sample size	Mean ± SE	Range	Coefficent of variation	Sample size
Mother's SVL (mm)	55 40 ± 0 66	46 8-63 2	7 59	43	56 99 ± 0 81	46 3-63 5	7 83	30
Clutch mass (g)	1 02 ± 0 04	0 55-1 90	28 95	43	0 87 ± 0 05	0 40-1 60	31 86	30
Egg mass (g)	0 26 ± 0 01	0 19-0 36	15 32	43	0 21 ± 0 01	0 15-0 27	16 29	30
Egg volume (mm^3)	236 3 ± 4 87	180 9-292 7	13 02	43	197 0 ± 7 09	128 8-304 8	19 72	30
Relative clutch mass	0 405 ± 0 01	0 266-0 613	19 60	43	0 311 ± 0 02	0 181-0 507	25 95	30
Clutch size	4 12 ± 0 16	2-7	24 38	43	4 23 ± 0 20	2-7	26 09	30

91 1% in 1989 (82 empty egg shells and 8 dead eggs in 22 natural nests found in the study site between October and December), 87 0% in 1990 (67 empty, 10 dead, 19 nests) and 82 6% in 1991 (19 empty, 4 dead, 6 nests)

Hatchlings

Body size and body mass of newborn hatchlings hatched in the laboratory, as measured within 24 h of emergence, are shown in Table 5. In all three years of study, both average SVL and average body mass were higher for female than for male hatchlings The between-sex differences in SVL were statistically significant (1990 $F_{1\,35} = 5\ 03$, $p < 0\ 05$, 1991 $F_{1\,60} = 22\ 08$, $p < 0\ 001$, 1992 $F_{1\,38} = 8\ 04$, $p < 0\ 01$) The between-sex differences in body mass were not significant (1991 $F_{1\,31} = 0\ 60$, $p = 0\ 44$, 1992 $F_{1\,38} = 0\ 33$, $p = 0\ 57$), indeed, analysis of covariance indicated that male hatchlings were significantly heavier than female hatchlings when the effect of SVL is accounted for (1991 $F_{1\,36} = 5\ 85$, $p = 0\ 02$, 1992 $F_{1,32} = 5\ 12$, $p = 0\ 03$, 1991/92 $F_{1\,68} = 8\ 96$, $p = 0\ 004$) (see Fig 7)

The dorsal coloration of hatchlings is dark brown, like that of subadults and most adult females The tail is green

The sex ratio of clutches hatched in the laboratory (considering only clutches in which all eggs hatched) was 1 0 94 (53 males to 50 females, 29 clutches) This ratio does not differ significantly from one-to-one ($\chi^2 = 0\ 09$, DF = 1, $p = 0\ 77$)

None of the hatchlings hatched in the laboratory was visibly malformed, although one egg which did not hatch contained an individual with mandibular prognathism

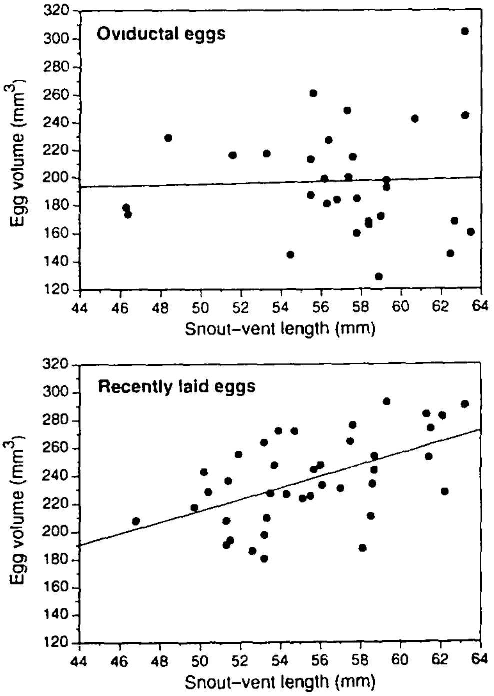

Fig 3 Relationships between mother's snout-vent length (SVL) and average single-egg volume in each clutch, for oviductal eggs (above) and for eggs laid in the laboratory (below) The latter were measured soon after oviposition

Discussion

Reproductive cycle

Reproductive phenology of *Podarcis bocagei* as evaluated in the present study is in accordance with my

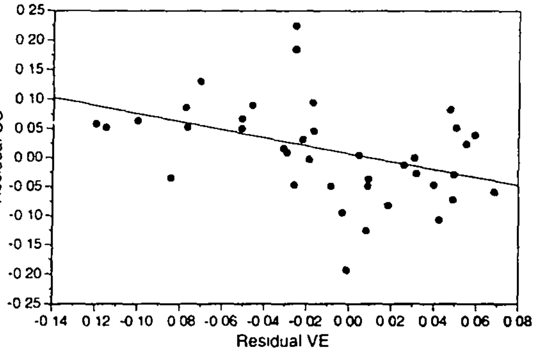

Fig 4 Relationships between residual deviations of clutch size [residual CS residual values of the regression of log (clutch size) on log (mother's SVL)] and residual deviations of average single-egg volume in these clutches [residual EV residual values of the regression of log (egg volume) on log (mother's SVL)]

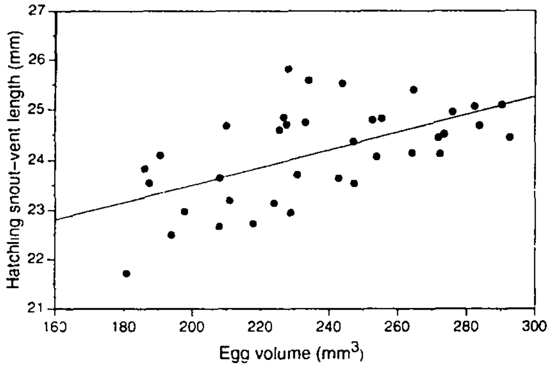

Fig 5 Relationships between average single-egg volume and average hatchling snout-vent length in each clutch

previous results on male and female gonadal cycles in the same population (Galán 1995a) The cycle is similar to that reported for other species of *Podarcis* in coastal and low-altitude inland regions of the northern Iberian Peninsula (see Braña 1983), and for lizards in general in temperate regions (see for example Fitch 1970, Saint Girons and Duguy 1970, James and Shine 1985, Hraoui-Bloquet 1987, Hraoui-Bloquet and Bloquet 1988)

As I have reported previously (Galán 1995b), the mild climate of the study area allows *P bocagei* to remain active throughout much of the year This is reflected in the long breeding season (ca 4 months, see Galán 1995a, and present results) In an all-year-active population of *Podarcis hispanica* on the Mediterranean coast of Spain, the length of the reproductive season was likewise found to be ca 4 months (Llorente 1988)

In areas of relatively harsh climate, lacertids tend to commence pairing almost as soon as females start to become active after the winter (see for example Nuland and Strijbosch 1981, Bauwens and Verheyen 1985, Marco et al 1994) In the Carral population, however, there is a pre-reproductive activity period lasting from mid- or late February to late March Males typically show increasingly aggressive behaviour during this period, and towards its end courtship behaviour is observed (Galán 1995c) It is worth noting that males and females in the Carral population emerge from hibernation at the same time, in many other species of lacertids, males typically emerge ca 3 weeks before females (Nuland and Strijbosch 1981, Bauwens et al 1989, Marco et al 1994) Indeed, in the Carral area, males of *Lacerta schreiberi* emerge ca 3 weeks before females (Galán 1989)

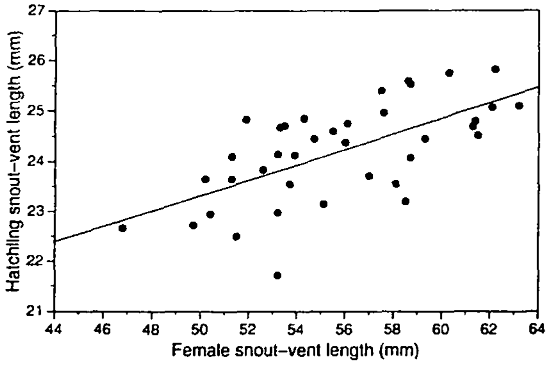

Fig 6 Relationships between mother's snout-vent length and average hatchling snout-vent length

In the present study, mating commenced later in 1991 than in 1990 This may be attributable to differences in weather between the two years March and April were warmer in 1990 than in 1991. Follicular development, and thus the onset of female receptivity, is accelerated at higher ambient temperatures (Duvall et al 1982, Castilla and Bauwens 1990) In addition, the amount of time available for feeding activity can be expected to have been greater during the warmer 1990 pre-reproductive period, favouring accumulation of energy reserves This interpretation is supported by the calculated values of female body condition index for the pre-reproductive periods of the two years (see Fig 1) Specifically, my data suggest that body condition during March is of critical importance In 1990, body condition index rose steadily throughout March, by contrast, body condition index dropped steadily during March 1991 Castilla et al (1992), in a study of the lacertid *Acanthodactylus erythrurus* in central Spain, found that the breeding season was shorter in years in which spring weather conditions were harsh

Females of the Carral population laid eggs between May and July, and laying period differed little between the two years of study, although it is possible that laying started somewhat earlier (late April) in 1990, the milder of the two years of this study (Galán 1995a) The first females to lay were large individuals Females which had attained reproductive maturity that year typically laid at the end of the population laying period (Galán 1994) That large females tend to breed earlier in the year than small females has been reported for *Lacerta vivipara* (Bauwens and Verheyen 1985) and other lizards (Van Loben Sels and Vitt 1984, Hraoui-Bloquet 1987)

Clutch characteristics

The eggs of *P bocagei* are retained in the oviduct for a relatively short time (Braña et al 1991) Despite this, I detected clear differences between oviductal eggs and recently laid eggs The observed variability in oviductal eggs may be attributable to differences in developmental stage, and/or to absorption of water as the egg passes along the duct (see Martin 1978, Congdon et al 1981, Cuellar 1984, Vitt et al. 1985).

Table 5 Snout-vent length (SVL) and weight of male and female hatchlings hatched in vivaria in 1990, 1991 and 1992 Weight data were not obtained in 1990 Measurements were in all cases taken within 24 h of hatching

	Hatchling sex	Year	Mean ± SE	Range	No of individuals
SVL (mm)	Male	1990	23 51 ± 0 25	22 5–24 9	10
		1991	23 55 ± 0 16	21 5–25 5	39
		1992	23 83 ± 0 25	21 3–25 5	31
	Female	1990	24 22 ± 0 17	22 9–26 1	26
		1991	24 93 ± 1 23	21 8–26 6	22
		1992	24 73 ± 0 19	23 3–26 1	25
Weight (g)	Male	1991	0 297 ± 0 01	0 221–0 363	16
		1992	0 312 ± 0 01	0 229–0 419	31
	Female	1991	0 311 ± 0 01	0 202–0 353	16
		1992	0 320 ± 0 01	0 245–0 392	25

Mean relative clutch mass (RCM), estimated on the basis of data for vivarium-laid eggs, was 0 405 This value is similar to that previously reported by Braña et al (1991) for *P muralis* populations in the Basque Country in northern Spain, but considerably higher than the value of 0 334 obtained by Braña et al (1991) for populations of *P bocagei* in Asturias (likewise in northern Spain) However, the maximum RCM recorded in the present study (0 613) was much higher than has been reported previously for any *Podarcis* species in the Iberian Peninsula

RCM can be considered to be a reflection of the maximum egg mass which a female is capable of carrying without incurring unacceptable costs in terms of reduced mobility (see Vitt and Congdon 1978, Vitt and Price 1982, Dunham et al 1988). The value of 0 405 obtained in the present study is relatively high, despite the fact that my behavioural observations indicate *P bocagei* to be a "widely foraging" (as opposed to "sit-and-wait") species sensu Vitt and Congdon (1978) These authors have suggested that the great majority of lacertids can be considered to belong to this group (see however Henle 1990, 1991, García-Fernández 1990)

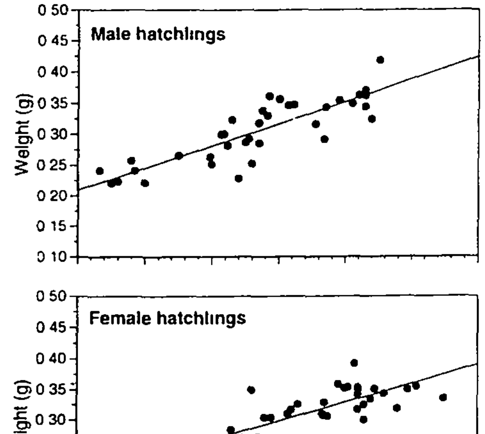

Fig 7 Relationships between body weight and snout-vent length for newborn male and female hatchlings

Both the mean and maximum clutch sizes recorded in the present study (4 12 and 7 eggs respectively) are higher than have been reported for *P bocagei bocagei* in Asturias (Braña et al 1991), despite the fact that females of the populations studied by Braña are of similar size to those of my study population However, maximum clutch sizes of up to 9 have been reported for populations of *P bocagei bocagei* in the same region as that of the present study (La Coruña Province, Barbadillo et al 1993) The mean and maximum clutch sizes reported for *P bocagei carbonelli* from central Spain (Pérez-Mellado 1982) and for *P bocagei berlengensis* from the Berlenga Isles off Portugal (Vicente 1989) are much lower than in the present study Mean single-egg weight in the present study was 0 26 g This is exactly the same as reported by Braña et al (1991) for Asturian populations of *P bocagei bocagei* (despite the differences in clutch size) Mean single-egg weight in populations of *P bocagei berlengensis* is much higher (Vicente 1989), as evolutionary theory predicts for a taxon restricted to an island

In lacertid lizards, it has been reported that reproductive variables (including clutch size, clutch mass, egg size, hatchling size and clutch frequency) are typically correlated with female size (Díaz-Uriarte 1993) In a comparative study of various lacertid species, Díaz-Uriarte (1993) and Bauwens and Díaz-Uriarte (1995) found that the relationship between total clutch mass and female size was isometric It was observed that number of eggs scaled positively with female size, whereas egg mass scaled negatively with female size The results of Frankenberg and Werner (1992) indicate that small oviparous lizards with small clutch size tend to increase egg size rather than clutch size, whereas large species with large clutch size (> 10 eggs) tend to increase clutch size This is presumably because the increase in reproductive effort required to produce one additional offspring is proportionally smaller in the latter species group (see also Marco et al 1994)

My data reveal highly significant positive correlations between mother's SVL and a number of reproductive variables (clutch size, clutch mass, mean single-egg volume and mean hatchling SVL) However, mother's SVL was not significantly correlated with relative clutch mass, nor was clutch size significantly correlated with mean hatchling SVL

In view of its small body size and small clutch size, *P bocagei* might be considered to fall into the first of the above-mentioned groups, however, my results suggest that females of the study population adopt an intermediate strategy, since mother's SVL was positively correlated with both egg size and clutch size On the basis of my data, a one-egg increase in the clutch size of a small female (SVL < 50 mm) will lead to an increase of 12–15% in relative clutch mass Smaller females can thus be expected to maximize egg size and lay only a single clutch per year Note, however, that single-egg volume is limited by the dimensions of the mother's pelvic girdle (Sinervo and Licht 1991) Larger females (SVL > 55 mm) likewise tend to maximize egg size, however, in such individuals, increasing clutch size by one will lead to an increase of only 6–8% in relative clutch mass Such females can therefore be expected to maximize clutch size and to lay more than one clutch per year These size-dependent differences imply a high degree of intrapopulational phenotypic plasticity, as has been reported for many species of lizard (see for example Tinkle and Ballinger 1972, Pilorge et al 1983, Bauwens et al 1986, Bauwens and Verheyen 1987, Frankenberg and Werner 1992).

However, despite the fact that I found significant positive correlations between mother's SVL and both single-egg volume and clutch size, two additional findings should be borne in mind First, the relationship between mother's SVL and single-egg volume is influenced by clutch size, since – when mother's SVL was held constant – single-egg volume was negatively correlated with clutch size That single-egg volume was negatively correlated with clutch size is in accordance with theoretical models of reproductive strategy (Smith and Fretwell 1974, Brockelman 1975, McGinley et al 1987) Second, the relationship between mother's SVL and clutch size is likely to be affected by the reduction in mean clutch size over the reproductive season, since second- or third-of-that-year clutches tend to be smaller than first-of-that-year clutches (see below)

When considering these relationships, it should also be borne in mind that egg size is adjusted after clutch size has been determined, depending on the energy available and the volume of the body cavity (Shine 1992), so that relative clutch mass tends to be conservative (DeMarco 1989, Ford and Siegel 1989, James and Whitford 1994)

Finally, my results indicate a significant positive correlation between egg volume and hatchling SVL This is of course as expected, and has been reported for a number of other lizards such as the iguanids *Uta stansburiana* (Ferguson et al 1990) and *Conolophus subcristatus* (Snell and Tracy 1985) (see however Werner 1986, 1989)

Clutch frequency

My results for the study population (notably the mark-recapture data) show that females are able to produce more than one clutch per year This is a common phenomenon among species of this genus (see for example Rollinat 1934, Saint Girons and Duguy 1970, Chondropoulos and Lykakis 1983, Barbault and Mou 1988), including *Podarcis bocagei* (Braña 1983, Galán 1987, Vicente 1989) Note, however, that females of *Podarcis bocagei carbonelli* from the western part of Spain's Sistema Central appear to lay only one clutch per season (Pérez-Mellado 1982)

The number of clutches per season is affected by both the mother's size and her age Small females in their first year of reproductive maturity (i e one or two years old, see Galán 1994) lay only a single clutch, towards the end of the reproductive season In subsequent years, females may lay two or three clutches Hraoui-Bloquet (1987), in a study of a population of *Lacerta laevis*, similarly found that young females (i e one-year-olds that had recently attained sexual maturity) laid only one or two clutches at the end of the season, whereas older females produced up to four clutches Barbault and Mou (1988), in a study of a French population of *Podarcis muralis*, found that females of three or more years old produced three clutches per year Likewise, Vicente (1989) found that older females of *Podarcis bocagei berlengensis* produce three clutches per year

It should be stressed that, in the Carral population, only a few females produce three clutches per year (ca 8 5%, considering data for both 1990 and 1991); most females – even very large individuals – produce only two Similar findings have been reported for other species which are capable of producing three clutches per year (Dunham 1981, 1982, Van Loben Sels and Vitt 1984). In the Carral population, it seems probable (in view of the relatively high values obtained for RCM) that most females have energy reserves sufficient for two but not three clutches (see also Braña et al 1992)

A decline in mean clutch size over the reproductive season has been observed previously in other lizards, such as *Lacerta laevis* (Hraoui-Bloquet 1987) and *Sceloporus undulatus* (Ferguson and Bohlem 1978, Ferguson and Snell 1986) The latter authors' findings were obtained in the laboratory, with strict control of light, temperature and diet Field observations in this regard should be interpreted with caution in another iguanid, *Uta stansburiana*, a decline over the season has been observed in the field (Nussbaum 1981), but when constant conditions are maintained in the laboratory there is no difference between the mean sizes of the first and second clutches (Ferguson et al 1990, James and Whitford 1994) Furthermore, the reduction in mean clutch size observed in the present study is partially attributable to the fact that young females (which produce small clutches, Galán 1994) lay towards the end of the season However, analysis of covariance indicated that clutch size declined significantly over the laying season even when the effect of mother's SVL was accounted for This may be attributable to the fact that large females which lay twice in the season tend to produce smaller clutches the second time

Hatching and hatchlings

Hatch success as estimated in the field was high (91% in 1989, 87% in 1990, 83% in 1991) Hatch success in vivaria was also high (up to 95% in 1990) All eggs laid in vivaria were in apparently perfect condition, unlike in previous vivarium studies of lacertids (for example, Barbadillo 1985), I did not observe eggshell malformations (decalcifications, wrinkling, etc)

Hatch success in the field is almost certainly influenced by the mother's behaviour, particularly as regards selection of the nest site Nest-site characteristics determine the physical environment for the eggs, and their degree of exposure to different predators (Overall 1994) In my study area, females of *Podarcis bocagei* tend to select nest sites on steeply sloping non-vegetated south-facing banks, at some distance above ground level, such sites receive high insolation and are much less prone to flooding than other parts of the study site (Galan 1994, 1996)

The mean SVL of female hatchlings was greater than that of male hatchlings By contrast, adult females have lower mean SVL, mean weight and maximum weight than adult males In addition, males reach sexual maturity at an SVL of 46–51 mm (vs 44–45 mm in females, Galán 1994) Higher SVL for female than for male hatchlings has also been reported for other lacertids, such as *Lacerta monticola* (Barbadillo 1985, Galán 1991), and appears to reflect the greater number of presacral vertebrae in females (Barbadillo 1985), as is the case in *Lacera viridis*, *L lepida* and *L. schreiberi* (Barbadillo and Sanz 1983) In *Lacerta monticola* and *L schreiberi*, however, females remain bigger than males in adulthood (Galán 1984, 1991) This suggests that the between-sex difference in adult size observed in *Podarcis bocagei* is attributable to some mechanism acting after birth In the study population of *P bocagei*, the growth rate of males is greater than that of females in all age classes (Galán 1994)

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