

Demography and population dynamics of the lacertid lizard *Podarcis bocagei* in north-west Spain

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Abstract

The demography and life-history traits of a population of the lacertid lizard *Podarcis bocagei* in north-west Spain were investigated. Most of the conclusions presented are based on mark–recapture studies carried out over a 2-year period. Reproductive characteristics are similar to those reported for other temperate-climate lacertids. Clutch size, egg size and hatchling size (snout–vent length, SVL) are all positively correlated with the mother's SVL. Only large females lay more than one clutch per year. Growth rate is highest in young animals and declines gradually with age. In both sexes, sexual maturity is reached between the ages of 1 and 2 years. Again in both sexes, the probability of survival was fairly constant over the lifespan. Considering the study period as a whole, there was no significant between-sex difference in survival probability. Among adults, the probability of survival was higher in winter than during other periods, but the differences were not statistically significant. The individuals of the study population are sedentary, making only short movements even when periods of up to 2 years are considered (the mean distance moved between marking and recapturing 18–24 months later was 15.7 m, maximum 45.6 m). On average, immature individuals move further than adults, and adult males move further than adult females. Estimated population density (all individuals) dropped from 1574 ha⁻¹ during the winter of 1989/90 to 1327 ha⁻¹ during the winter of 1990/91. The decline in population density over the study period was also reflected in the estimated net replacement rate for the population (0.85, i.e. considerably less than one), and is probably attributable to colonization of the study site by plants (reducing suitability as a habitat for *P. bocagei*). Estimated mean generation time was 2.09 years.

Key words: lizards, *Podarcis bocagei*, demography, population dynamics, Spain

INTRODUCTION

Studies on the demography and natural history of lizards have become increasingly frequent over the last 30 years, following the pioneer work of Blair (1960) and Tinkle (1967). Such studies have typically considered the population as the lowest level of complexity, and indeed population-level studies have uncovered a great deal of interesting information.

Much of the early work in this field was based on two-category reproductive strategy models (see Pianka, 1972; Stearns, 1976 for reviews). The principal models are the *r*-K model, which centres on resource availability and density dependence/independence (Dobzhansky, 1950; MacArthur & Wilson, 1967), and the b-d model, which centres on the demographic environment (Williams, 1966; Pianka, 1972; Schaffer, 1974; Hirshfield & Tinkle, 1975; Stearns, 1976).

More recently, interest has focused on behavioural strategy models, such as the 'active searching' versus

'sit-and-wait' classification of foraging strategies, or the 'flight' versus 'crypsis' classification of predator-evasion strategies (see for example Vitt & Congdon, 1978; Huey & Pianka, 1981; Vitt & Price, 1982; Vitt, 1983; Dunham, Miles & Reznick, 1988).

As was clearly stated by Williams (1966), organisms must 'decide', at each stage in their life, how much of their resources to devote to current fecundity, and how much to devote to survival and future fecundity; it is this trade-off that governs the evolution of life-history traits (see Tinkle, 1969; Hirshfield & Tinkle, 1975; Vitt & Congdon, 1978; Shine, 1980; Shine & Schwarzkopf, 1992). In the words of Miles & Dunham (1992), 'theoretical approaches to the evolution of life-history traits attempt to model the optimum life history in terms of age-specific survival and fecundity schedules that maximize fitness' (for reviews focusing on the order Squamata, see Dunham & Miles, 1985; Dunham *et al.*, 1988; Miles & Dunham, 1992).

Among-species and among-population variation in

reproductive characteristics and natural history can be attributed (a) to phylogenetic history and/or (b) to recent selective pressures (Dunham, 1994). Life-history traits have been extensively characterized in many lizard species, facilitating comparisons among species and populations (see Dunham *et al.*, 1988, and references therein). Nevertheless, the number of species that have been characterized is still too small to allow broad-based evaluations (Miles & Dunham, 1992, 1993; Dunham, 1994). Furthermore, most previous studies have considered Nearctic species, or species from tropical or subtropical regions; relatively few data are available on species of temperate zones of the Palearctic. More specifically, little information is available about species of the family Lacertidae, with the exception of *Lacerta vivipara* (e.g. see Bauwens & Thoen, 1981; Pilorge, 1982, 1987; Bauwens & Verheyen, 1985, 1987; Heulin, 1985; Bauwens, Heulin & Pilorge, 1986; Pilorge, Clobert & Massot, 1987; Clobert *et al.*, 1994).

Among the species of the lacertid genus *Podarcis* whose life-history traits have been best characterized is *P. muralis* (e.g. see Strijbosch, Bonnemayer & Dietvorst, 1980; Castanet & Roche, 1981; Mou, 1987; Barbault & Mou, 1988; Van Damme *et al.*, 1992; Bejakovic *et al.*, 1996). The life history of this species has been studied in the Iberian Peninsula (Braña, 1983; García-Fernández, 1990).

Here, I report data on the life-history traits of a population of Bocage's wall lizard *Podarcis bocagei* (Seoane 1884) (Lacertidae) in north-west Spain. This species is a small (adult snout-vent length 45–65 mm), diurnal, insectivorous lizard with a restricted distribution in the north-western and western Iberian Peninsula. Much less is known about the life-history traits of this species than those of *L. vivipara* (though see Galán, 1994a, 1996a, 1996b,c,d, 1997a). I studied aspects related to fecundity, survivorship, mobility and changes in population density over time.

STUDY AREA

The field work was carried out in an abandoned gravel pit in San Vicente de Vigo (*municipio* of Carral, A Coruña Province, north-west Spain; 45°18' N, 8°20' W, UTM 29T NH5687, altitude 90 m a.m.s.l.). Within the pit, a study plot of 60 × 45 m (2700 m²) was marked out with wooden posts at 5 m intervals.

This area is included in the Wet Oceanic climate type (Carballeira *et al.*, 1983), characteristic of coastal areas of the north-west Iberian Peninsula. Mean annual rainfall is 1200 mm, and the mean annual number of hours of sunshine is about 2000. Within-year temperature variation is small: the mean temperature of the coldest month (January, mean temperature 8 °C) is only 10 °C lower than that of the warmest month (July, mean temperature 18 °C). More details of the climate of the study area are given in Galán (1994a, 1997a).

The area around the study plot bears a vegetation mosaic, with patches of mixed woodland (*Quercus*

robur, *Pinus pinaster*, *Eucalyptus globulus*) interspersed with scrub (*Ulex europaeus*, *Cytisus striatus*, *Adenocarpus complicatus*) and mowed meadows. Within the gravel pit, vegetation is scarce, with patches of colonizing scrub. The study plot contained all major habitats and microhabitats present in the area, including woodland and meadow not directly affected by the gravel extraction operations (Galán, 1994a,b). Lizards are mainly present in areas with open scrub or scarce vegetation (Galán, 1994b).

MATERIAL AND METHODS

Data were collected in the course of a population study conducted between July 1989 and October 1991. Some additional data were gathered in May/July 1992. The study site was visited 3–8 times per month between July 1989 and October 1991. At each visit, the number of lizards observed and the sex of each was recorded. Also recorded were details of all the reproductive events (i.e. courtship and copulation) observed. Whenever possible, lizards were captured by hand, marked individually by toe-clipping and released, noting sex, reproductive condition, snout-vent length (SVL, to nearest 0.1 mm), tail length (including regenerated parts), weight (to nearest 0.1 g on a Pesola scale), coloration of the occipital band, and precise point of capture (on the 5 × 5 m grid into which the plot had been divided). Toe-clipping was considered the most appropriate method for identification of the lizards†. *Podarcis bocagei* hatchlings are too small (< 0.5 g at hatching) to allow scale clipping or the attachment of radio-transmitters, and because the skin is shed every 4–8 weeks marking with paint or dye is ineffective for a long-term study. Only the distal phalanx was removed and recapture results indicate that the long-term survival of the lizards was not affected. Each lizard was processed quickly (< 5 min) at the point of capture, and released immediately. In total, 611 lizards were captured and marked. The total number of recaptures was 1533.

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 (sub-adult or young adults; lizards born in the preceding year, SVL 40–52 mm); adults (2 or more years old; SVL > 52 mm).

Study periods

Mark-recapture visits were made weekly or fortnightly throughout the study. For analysis, however, the data for each year were grouped into 4 periods: (1) November–February inclusive (hibernation, or very short diurnal activity period); (2) March–April inclusive (onset-of-activity period, pre-reproductive period;

† Editor's note: The Ethical Committee of the Zoological Society of London considers that toe-clipping is no longer acceptable as a routine procedure for marking animals.

animals increasingly active); (3) May–July inclusive (reproductive period); (4) August–October inclusive (post-reproductive period for adults; hatching and neonatal period for juveniles).

Reproductive characteristics

Reproductive cycle

The time-course of the reproductive cycle was investigated on the basis of: (a) observations of reproductive behaviour (courtship and copulation episodes); (b) ventral palpation of live adult females (whenever captured; see above) to detect enlarged ovarian follicles or oviductal eggs. Other signs of reproduction (e.g. 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.

Clutch characteristics

Characteristics of clutches and neonatal juveniles were investigated on the basis of 44 clutches laid by captured pregnant females, and incubated and hatched in the laboratory. All 44 females were captured within 50–1500 m of the study plot in 1990, 1991 or 1992 (see Galán, 1997a). The number of clutches laid per season by females was estimated on the basis of examination of recaptured females within the study plot.

Growth and sexual maturation

Growth rates (mm/day) were estimated on the basis of measurements of recaptured animals. In all cases, only same-year recapture data were used (maximum interval 91 days); recaptures during the cold period (October–March inclusive) were not taken into account, since little or no growth occurs during these months (Galán, 1994a). The growth rates of juveniles in their year of birth were estimated on the basis of recaptures in August and September of 1989, 1990 and 1991 (interval 15–54 days), while growth rates of other age groups (1–3 years) were estimated on the basis of recaptures between April and September 1990 and between April and September 1991 (interval 15–91 days).

Age and size at attainment of sexual maturity were estimated on the basis of recaptures of animals marked in the year of their birth (1989 or 1990) and recaptured in subsequent years (1990 or 1991, respectively). An individual was considered to be sexually mature in view of external characteristics, namely the presence of oviductal eggs in females (as revealed by ventral palpation) or of an intense green dorsal coloration in males (see Galán, 1996b).

Population size and survivorship

The number of individuals in each age/sex group in each year of study was estimated on the basis of mark–recapture data, by the Jolly–Seber method (Jolly, 1965; Seber, 1965, 1982; see Krebs, 1989). This method additionally permits estimation of rates of loss (as a result of death or emigration) and rates of addition (as a result of birth or immigration) (Jolly, 1965; Krebs, 1989). The method requires mark–recapture data obtained on at least 3 occasions; the length of time between each occasion need not be constant, and sampling may extend over several years. In the present study, the 4 different periods of each year (as defined earlier) were each considered as a single sampling event.

Sometimes (e.g. juveniles during their first year), minimum survival rates were estimated simply on the basis of recapture rates; for example, if 25% of animals marked on day D1 are recaptured on day D50, then survival between D1 and D50 must be at least 25%.

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 during the post-breeding season in 1989, 1990 and 1991 (see Galán, 1996d, 1997a).

For construction of survivorship curves using loss rates for each age/sex group estimated by the Jolly–Seber method, emigration losses were assumed to be negligible. Possible causes of mortality were inferred from external signs including injuries, cutaneous infections (see Galán, 1996c) and missing or regenerated tails.

Movements

As already noted, the precise locations of all captures were marked on a 5 × 5 m grid map of the study plot. This allowed investigation of movements occurring during the major periods of the year and over longer periods (1 year or 2 years).

Population life table

A life table for the population was constructed on the basis of estimates of survivorship-at-age and fecundity-at-age for females. The table was constructed considering time intervals deliberately selected for their biological significance (see Table 9). Specifically, the first interval was 0–0.150 years (0.150 years being the mean incubation period); the second interval was 0.150–0.403 years (0.403 years being mean age of yearlings at the start of November, i.e. the start of the first winter); the third interval was 0.403–0.734 years (0.734 years being the mean age at the start of March of the following year, i.e. the start of the second activity period); and so on for subsequent periods (see Galán, 1994a). The probability of survival (loss rate) over each

Table 1. Reproductive characteristics of females of *Podarcis bocagei* captured while gravid in areas adjacent to the study plot and subsequently maintained in the laboratory. Animals were captured in 1990, 1991 and 1992. RCM = relative clutch mass. Offspring SVL and offspring weight were measured immediately after hatching. Values shown are means \pm SEM, with ranges in parentheses

Year	No. of females	Mean SVL (mm)	Mean clutch size	Mean single-egg weight (g)	Mean RCM	Mean offspring SVL (mm)	Mean offspring weight (g)	No. of juveniles
1990	10	55.2 \pm 1.49 (49.7–63.5)	4.40 \pm 0.48 (3–7)	0.273 \pm 0.01 (0.217–0.317)	0.430 \pm 0.02 (0.333–0.574)	24.1 \pm 0.26 (22.7–25.1)	0.330 \pm 0.01 (0.280–0.383)	36
1991	16	55.2 \pm 1.25 (46.8–62.1)	4.21 \pm 0.18 (2–6)	0.249 \pm 0.01 (0.201–0.325)	0.407 \pm 0.02 (0.267–0.613)	23.9 \pm 0.34 (21.7–25.7)	0.310 \pm 0.02 (0.217–0.361)	61
1992	18	54.9 \pm 0.81 (48.9–62.2)	3.92 \pm 0.27 (2–6)	0.267 \pm 0.01 (0.195–0.365)	0.391 \pm 0.02 (0.266–0.483)	24.6 \pm 0.18 (23.2–25.8)	0.332 \pm 0.01 (0.240–0.419)	56
Total/ average	44	55.1 \pm 0.64 (46.8–63.2)	4.13 \pm 0.17 (2–7)	0.262 \pm 0.01 (0.195–0.365)	0.405 \pm 0.01 (0.266–0.613)	24.3 \pm 0.16 (21.7–25.8)	0.328 \pm 0.01 (0.217–0.419)	153

interval was estimated by the Jolly–Seber method. The probability of survival between egg-laying (age 0 years) and hatching (age 0.150 years) was taken to be mean hatching success as estimated in the field (88.42%, $n = 47$ clutches, Galán, 1997a). Where probability-of-survival data for a given age were available for more than 1 cohort, mean values were used.

The mean number of female eggs laid by females of each age class was estimated in view of mean clutch sizes (in turn estimated on the basis of clutches laid in the laboratory by captured pregnant females; see Galán, 1994a, 1997a). Mean clutch size for pregnant 1-year-olds ($n = 18$) was 2.94 eggs (see Galán, 1996b); an estimated 45.71% of 1-year-old females are sexually mature (see Results); the mean number of female eggs produced by a 1-year-old female can thus be estimated as $[0.4571 \times 2.94 \times 0.5] = 0.672$. Of pregnant 2-year-olds ($n = 31$), 29.03% laid a single clutch (mean size 4.83 eggs) and the remaining 70.97% laid 2 clutches (mean sizes 4.28 and 3.21 eggs) (see Galán, 1997a); the mean number of female eggs produced by a 2-year-old female can thus be estimated as $[(0.2903 \times 4.83 \times 0.5) + (0.7097 \times (4.28 + 3.21) \times 0.5)] = 3.359$. Of pregnant females aged 3 years or more ($n = 21$), 71.43% laid 2 clutches (mean size 4.79 and 4.32 eggs) and the remaining 28.57% laid 3 clutches (mean sizes 4.81, 4.35 and 3.16 eggs); the mean number of female eggs produced by a female aged 3 years or more can thus be estimated as $[(0.7143 \times (4.79 + 4.32) \times 0.5) + (0.2857 \times (4.81 + 4.35 + 3.16) \times 0.5)] = 5.013$.

Mean generation time (MGT) was estimated from the life table as

$$\text{MGT} = \sum x l_{(x)} m_{(x)}$$

Statistics

All statistical analyses were performed with the aid of the STATVIEW II package (Feldman *et al.*, 1987), except analysis of covariance, which was done with the aid of SYSTAT (Wilkinson, 1989). In the text, and unless otherwise stated, mean values are cited \pm standard errors (SEM). When analysis of variance was used, normality was first confirmed; when the data were

not normally distributed, appropriate non-parametric tests were used. Multiple comparisons of means following analysis of variance were by Scheffé's test.

RESULTS

Reproductive characteristics

Reproductive cycle

Courting behaviour and copulation were observed from early April to early July, in both years of study. Females with oviductal eggs were observed from late April to mid-July, again in both years. Laying was observed between late April (1990) or mid-May (1991) and late July (both years).

Newborn juveniles were observed between late June (1990) or mid-July (1991) and mid-September (both years). From mid-September onwards, all juveniles observed showed a closed umbilical orifice.

Clutch characteristics

Clutch characteristics were investigated on the basis of clutches laid by pregnant females captured in areas adjoining the study plot in 1990, 1991 and 1992. The characteristics of these females, their clutches and the juveniles subsequently hatched are summarized in Table 1. None of the characteristics listed varied significantly among the 3 years of study (ANOVA, $P > 0.05$ in all cases). Clutch size was strongly correlated with mother's SVL in 1990 ($r = 0.86$, $P < 0.01$) and 1992 ($r = 0.74$, $P < 0.001$), but not in 1991 ($r = 0.46$, $P = 0.07$).

Mark-recapture data indicated that some females laid two clutches per season (44.4% in 1990, $n = 36$; 60.0% in 1991, $n = 35$) or three clutches per season (5.6% in 1990, $n = 36$; 11.4% in 1991, $n = 35$). No small female (SVL < 51 mm) laid more than one clutch per season, while only very large females (SVL > 55 mm) were able to lay three clutches per season.

Table 2. Estimated growth rates of *Podarcis bocagei* in the different age/sex groups considered

Age/sex	No. of recaptures	Mean no. of days between captures	Growth rate (mm/day) (mean \pm SEM)
Juveniles			
Males	7	20.3	0.186 \pm 0.028
Females	7	19.2	0.142 \pm 0.016
Yearlings			
Males	28	31.7	0.096 \pm 0.006
Females	42	25.4	0.091 \pm 0.005
2-year-olds			
Males	10	27.4	0.036 \pm 0.008
Females	31	35.4	0.032 \pm 0.005
3-year-olds			
Males	8	25.5	0.013 \pm 0.003
Females	16	29.2	0.008 \pm 0.002

Growth and sexual maturity

Mean growth rates (mm/day), estimated on the basis of mark–recapture data for the whole study period, are listed in Table 2. Growth rates were highest in first-year juveniles, and declined with age. In all age groups, growth rates were higher in males than in females (analysis of covariance with the factor *sex* and the covariate *SVL*, $F_{1,146} = 24.9$, $P < 0.0001$).

Mark–recapture of juveniles marked in the year of their birth likewise indicated that slightly less than half of all individuals reach sexual maturity within their first year (males: 50.0% of 10 individuals in 1990, 44.4% of 9 in 1991; females: 47.1% of 17 in 1990, 44.4% of 18 in 1991). The remaining individuals reach sexual maturity in the subsequent year. Mean SVL at maturity ranged from 48 to 51 mm in males and from 44 to 46 mm in females.

Survivorship

Hatch success

The data on clutch size and hatch success, as estimated in the field, are listed in Table 3. Hatch success, estimated by considering all clutches together (see table) was high (at least 82.6%) in all 3 years considered.

Survivorship of juveniles

The number of juveniles of each sex marked during the hatching period (July–September) and recaptured before the first winter (i.e. before December of the same year) is listed for each year of study in Table 4. The proportion of individuals recaptured did not differ significantly between males and females (Kolmogorov–Smirnov test, $Z = 0.408$, $n = 6$, $P = 0.68$). Application of the Jolly–Seber method to the cohort born in 1989 indicates that the probability of survival of first-year

Table 3. Clutch size and hatch success in natural *Podarcis bocagei* nests found in the study plot in 1989, 1990 and 1991

Year	Clutch size (mean \pm SEM)	SD	Range	<i>n</i>	Total no. of eggs	Hatch success (%)
1989	4.09 \pm 0.245	1.151	2–7	22	90	91.11
1990	4.05 \pm 0.235	1.026	2–6	19	77	87.01
1991	3.83 \pm 0.307	0.753	3–5	6	23	82.61
Total	4.04 \pm 0.152	1.042	2–7	47	190	88.42

Table 4. Percentage recapture rates (RR) for male and female juveniles marked during their first activity period (July–September) and recaptured in October–November of the same year; RR is thus a minimum estimate of survival rate over the first activity period. M = number of individuals marked; R = number of individuals recaptured

Sex	Cohort	M	R	RR (100 \times R/M)
Males	1989	11	5	45.45
	1990	10	4	40.00
	1991	9	3	33.33
Total		30	12	40.00
Females	1989	14	6	42.86
	1990	27	17	62.96
	1991	11	4	36.36
Total		52	27	51.92
Total		82	39	47.56

juveniles over the period August–October differs little between the two sexes (Table 5).

Yearling survivorship

For estimation of the survivorship of yearlings, only the 1989 cohort was considered, since this was the cohort in which the number of recaptures was highest and since the individuals of this cohort could be monitored until adulthood. Changes in survivorship with age were not statistically significant in either sex, even after exclusion of the hibernation periods (males: $r^2 = 0.029$, $P = 0.79$; females: $r^2 = 0.418$, $P = 0.24$). There was likewise no significant between-sex difference in yearling survivorship when all periods of the year are considered together (Kolmogorov–Smirnov test, $Z = 0.4$, $n = 6$, $P = 0.683$).

Adult survivorship

Changes in adult survivorship over the period September–October 1989 to March–April 1991 are shown in Fig. 1. The data suggest seasonal variation in the probability of survival: specifically, high survivorship over the winter inactivity period and low survivorship during the reproductive period, particularly among females. However, the wide overlap of the

Table 5. Probabilities of survival (PS) of individuals of both sexes from the 1989 cohort, for the different periods considered in the present study. Estimation was by the Jolly–Seber method. PS values are shown \pm standard errors, with 95% confidence limits (estimated by the method of Manly, 1984) below

Period	August–October 1989	November 1989–February 1990	March–April 1990	May–July 1990	August–October 1990	November 1990–February 1991	March–April 1991
Age (months)	0–3	2–7	6–9	8–12	11–15	14–19	18–21
Sex							
M	PS \pm SE CL	1.000 \pm 0.469 0.595–1.000	0.840 \pm 0.246 0.491–1.000	0.687 \pm 0.219 0.391–1.000	0.618 \pm 0.305 0.277–1.000	0.712 \pm 0.325 0.335–1.000	0.567 \pm 0.244 0.271–1.119
F	PS \pm SE CL	0.555 \pm 0.253 0.229–1.000	0.756 \pm 0.193 0.473–1.000	0.626 \pm 0.149 0.400–0.979	0.716 \pm 0.123 0.514–0.983	0.926 \pm 0.196 0.626–1.000	0.747 \pm 0.172 0.487–1.000

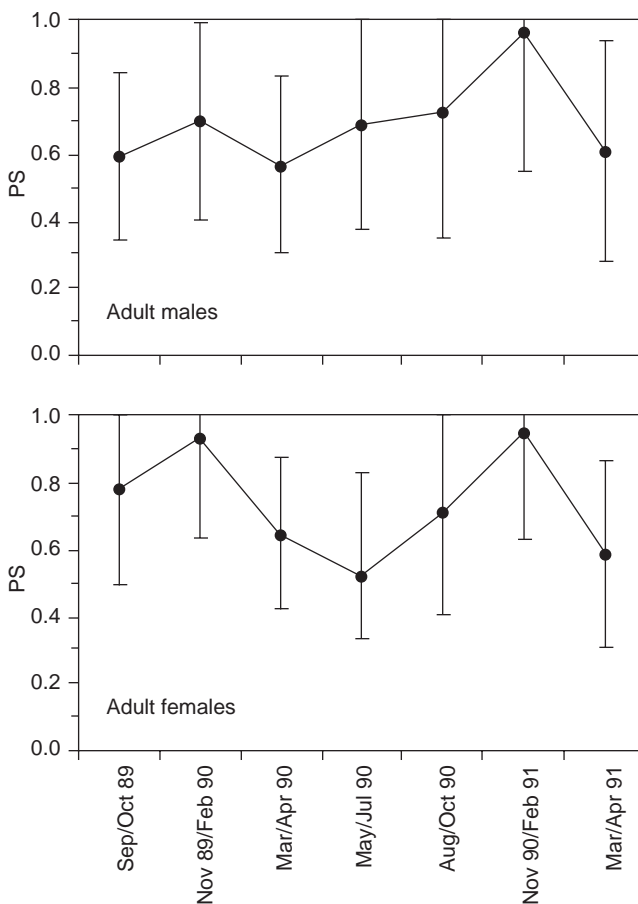


Fig. 1. Time-courses of survivorship in adult males and adult females (1988 and subsequent cohorts) over the study period. The probabilities of survival (PS) over each period considered were estimated by the Jolly–Seber method. Note that the different periods are not of the same length. Vertical bars show 95% confidence limits, estimated by the method of Manly (1984).

95% confidence intervals indicates that these differences cannot be considered statistically significant.

Likewise, and considering the study period as a whole, there was no significant between-sex difference

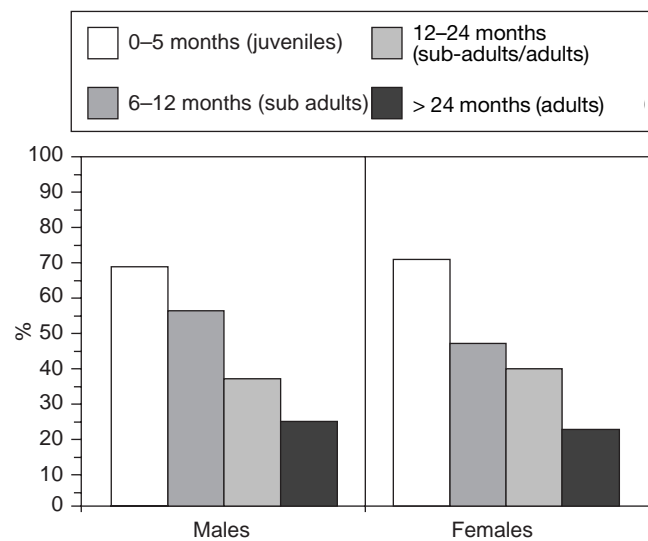


Fig. 2. Proportions of individuals with missing or regenerated tails, within the different age/sex groups considered.

in survival probability (Kruskal–Wallis test with these four groups: $H = 3.076$, $n = 26$, $P = 0.380$; Kolmogorov–Smirnov test for two groups, males vs females, $Z = 0.981$, $n = 26$, $P = 0.327$).

Causes of mortality

Predation

A number of potential predators of *P. bocagei* are present in the study area (two snakes, two birds of prey, two corvids, three Insectivora, two Carnivora). Direct evidence of predation by two species of snakes was obtained. The remains of four lizards and two tails were present in the stomachs of seven *Coronella austriaca* obliged to regurgitate their stomach contents, while the remains of three lizards were present in the stomachs of three *Vipera seoanei*. I have also observed a carabid beetle, *Hadrocarabus macrocephalus*, eating a juvenile of *P. bocagei*.

Tail loss

The proportion of individuals without a tail or with a regenerated tail can be used as a crude indicator of the intensity of predation. In the present study, 76.8% of all captured adults aged 2 years or more had lost their tail at least once in their life. The proportion of individuals who had at some stage lost their tail was significantly correlated with age in both sexes (males: $r = 0.985$, $P < 0.05$; females: $r = 0.964$, $P < 0.05$) (Fig. 2). The proportion of individuals who had at some stage lost their tail was not significantly affected by sex ($\chi^2 = 0.99$, $P = 0.319$).

Disease

A relatively large proportion of individuals from the study population (up to 57.6% of 33 individuals in January 1991) showed localized external infections on various parts of the body. Such infections were most frequent during the winter and early spring (the coldest and wettest parts of the year). These infections manifested as skin lesions, and often led to loss of toes when affecting the feet.

Of 65 individuals affected by disease of this type, 58.5% were recaptured the subsequent summer, with the lesions healed; of 62 unaffected individuals caught over the same period, 50.0% were recaptured. The proportion of individuals recaptured did not differ significantly between affected and unaffected individuals (χ^2 test, $P > 0.05$). There were likewise no significant differences when the sexes were considered separately. Infections of this type therefore do not appear to have an important effect on survival.

Symptoms of an internal infection (greenish coloration of ventral scales, indicating internal tissue necrosis) were observed in eight individuals (six juveniles and two adults) captured during December–February. All such individuals died within minutes or hours.

Other causes of mortality

Winter rainfall is high in the study area (567 mm between November 1989 and February 1990, and 589 mm between November 1990 and February 1991), and major rainfall events are frequent. Such events may be a significant catastrophic cause of mortality. One rainfall event in December 1989 totalled more than 150 mm in 24 h, and various embankments in the study area suffered localized landslides. Similarly, one rainfall event in the winter of 1990/91 led to the collapse of an area of stones and tunnels in which numerous individuals hibernated. Of the 34 individuals last captured in these areas, none was subsequently recaptured, supporting the view that extreme rainfall events are an important cause of mortality. Other climate-related effects seem to be less important, although as noted above, the reduced temperatures and increased humidity

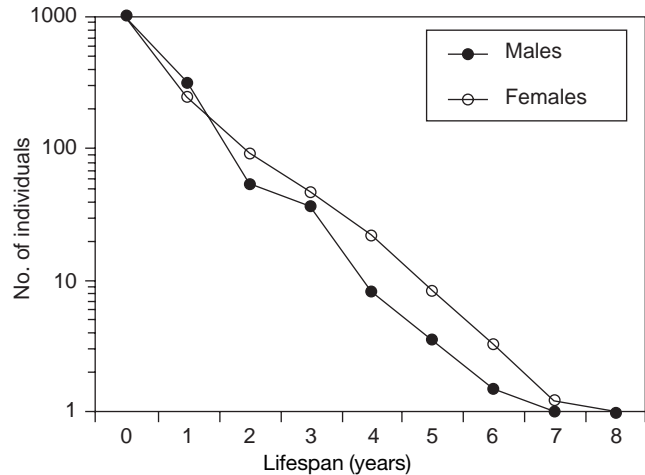


Fig. 3. Estimated survivorship curves for males and females of *Podarcis bocagei* in the study population.

in the winter may favour the development of skin infections.

Survivorship curves

Survivorship curves for males and females (as deduced from probabilities of survival estimated by the Jolly–Seber method) are shown in Fig. 3.

Movement

A total of 426 recaptures provided data on individual movements, ranging from 0 m (individual recaptured in the same grid square as the initial capture) to 46.5 m. The latter was the maximum movement detected, even though lizards were regularly captured in areas adjoining the study plot, at distances of up to 500 m from its border. Considering all three periods, and for all periods of the year except November–April, recapture rate was higher among females than among males.

Seasonal movements

The length of seasonal movements was significantly affected by both age and sex (Kruskal–Wallis test, $H = 8.749$, d.f. = 3, $P < 0.05$) (Table 6). Considering all seasonal movements together, the distances moved by adult females were significantly shorter than the distances moved by adult males, by sub-adults and by juveniles (Mann–Whitney test, $U = 4880$, 4311 and 3812, respectively; $P < 0.05$ in all cases). No significant differences were detected among adult males, sub-adults and juveniles.

There were significant differences among the periods of year only in the adult females (Kruskal–Wallis test,

Table 6. Distances moved by individuals of the different age/sex groups within the periods indicated. These results are based on mark–recapture data. Values shown are means \pm SEM, with ranges below

Period		Adult males	Adult females	Sub-adults	Juveniles
March–April	<i>x</i>	8.37 \pm 1.38 (0.9–32.4)	5.72 \pm 0.71 (0–14.1)	5.77 \pm 0.91 (0–15.3)	
	<i>n</i>	17	28	22	
May–July	<i>x</i>	6.33 \pm 0.85 (0–15.6)	3.72 \pm 0.69 (0–19.7)	7.72 \pm 1.48 (0–46.5)	
	<i>n</i>	22	32	33	
August–October	<i>x</i>	5.29 \pm 0.67 (0–10.0)	6.02 \pm 1.31 (0–33.2)	5.58 \pm 1.64 (0–10.3)	7.61 \pm 1.55 (0–35.9)
	<i>n</i>	18	30	6	22
November–February	<i>x</i>	4.73 \pm 0.81 (0–11.8)	4.82 \pm 0.89 (0–14.7)	9.48 \pm 3.99 (1.8–23.8)	6.88 \pm 1.13 (0–31.5)
	<i>n</i>	18	18	5	37
Total	<i>x</i>	6.16 \pm 0.56 (0–32.4)	5.06 \pm 0.48 (0–33.2)	7.01 \pm 0.86 (0–46.5)	7.15 \pm 0.91 (0–35.9)
	<i>n</i>	75	108	66	59

Table 7. Mean distances moved by individuals of the different age/sex groups within periods of 9–15 months, 18–24 months, and 9–24 months. These results are based on mark–recapture data. The results for ‘immature’ animals include those for animals that were immature at marking but adult on recapture. Values shown are means \pm SEM, with ranges and sample sizes below

Period	Adult males	Immature males	Adult females	Immature females
9–15 months	12.13 \pm 2.67 (5.0–35.9)	10.71 \pm 2.22 (1.5–29.4)	7.67 \pm 1.88 (0.1–34.7)	10.38 \pm 1.24 (0.1–36.5)
	11	13	17	51
18–24 months	24.13 \pm 8.93 (7.4–37.9)	26.77 \pm 12.02 (4.4–45.6)	9.30 \pm 2.78 (1.3–26.8)	11.08 \pm 2.45 (2.4–26.8)
	5	6	8	12
Total: 9–24 months	14.70 \pm 2.96 (5.0–37.9)	13.72 \pm 3.07 (1.5–45.6)	8.19 \pm 1.53 (0.1–34.7)	10.51 \pm 1.09 (0.1–36.5)
	16	19	25	63

$H = 7.414$, d.f. = 3, $P < 0.05$). Notably, adult females moved very little during the reproductive period.

Longer-term movements

As expected, mean distances moved by individuals recaptured > 9 months after initial capture were longer than mean distances moved within 9 months of initial capture (Table 7). Mean distance of movement (considering all data for the period 9–24 months) varied significantly among the four age/sex groups shown in this table (Kruskal–Wallis test: $H = 7.872$, d.f. = 3, $P < 0.05$). However, the only significant pairwise difference was that between adult males and adult females (Mann–Whitney test: $U = 303$, $P = 0.006$); specifically, and as in the shorter term, males are considerably more mobile than females.

Population size and population density

Population sizes in each study period were estimated by the Jolly–Seber method. Total population size and

population size in each age/sex group (except for juveniles born in 1991, the last year of study) were estimated independently. The results (expressed as number of individuals per hectare) are listed in Table 8.

The totals obtained by summing the subtotals for each age/sex group differ slightly from the estimate of total population size. However, this difference is not statistically significant ($t = 0.755$, $P = 0.479$). Estimated density was highest at the start of the study period, and subsequently declined: for example, estimated density in March–April 1991 was only 80% of that recorded in March–April 1990.

Surprisingly, there was only a small increase in estimated total population size between May–July 1990 and August–October 1990, despite the incorporation of newborn juveniles into the population over this period. However, examination of the data for the different age/sex groups during this period (see Table 8 & Fig. 4) indicates that the total adult population (1988 and pre-1988 cohorts) suffered a marked decline over this period. The increase in population size during this period due to incorporation of newborn juveniles was thus counteracted by a decrease due to loss of older animals.

Nevertheless, the total number of adults in the

Table 8. Population densities (individuals per ha) estimated by the Jolly–Seber method for each age/sex group and each period considered. Total 1 is the sum of ‘All adults’ and ‘All immatures’; Total 2 is the population density estimated considering all mark–recapture data together. 95% confidence limits for Total 2 are also shown

Period	Adult males	Adult females	All adults (A)	Immature males	Immature females	All immatures (B)	Total 1 (A + B)	Total 2	95% CL for Total 2
November 1989–February 1990	172	307	479	580	496	1076	1555	1574	979–2049
March–April 1990	172	317	489	244	522	766	1255	1276	817–1434
May–July 1990	168	325	493	289	340	629	1122	1389	1026–1533
August–October 1990	92	196	288	382	854	1236	1524	1407	965–1517
November 1990–February 1991	133	170	303	192	742	934	1237	1327	826–1455
March–April 1991	289	405	694	83	202	285	979	1022	744–1087
May–July 1991	156	311	467	319	157	476	943	868	644–952

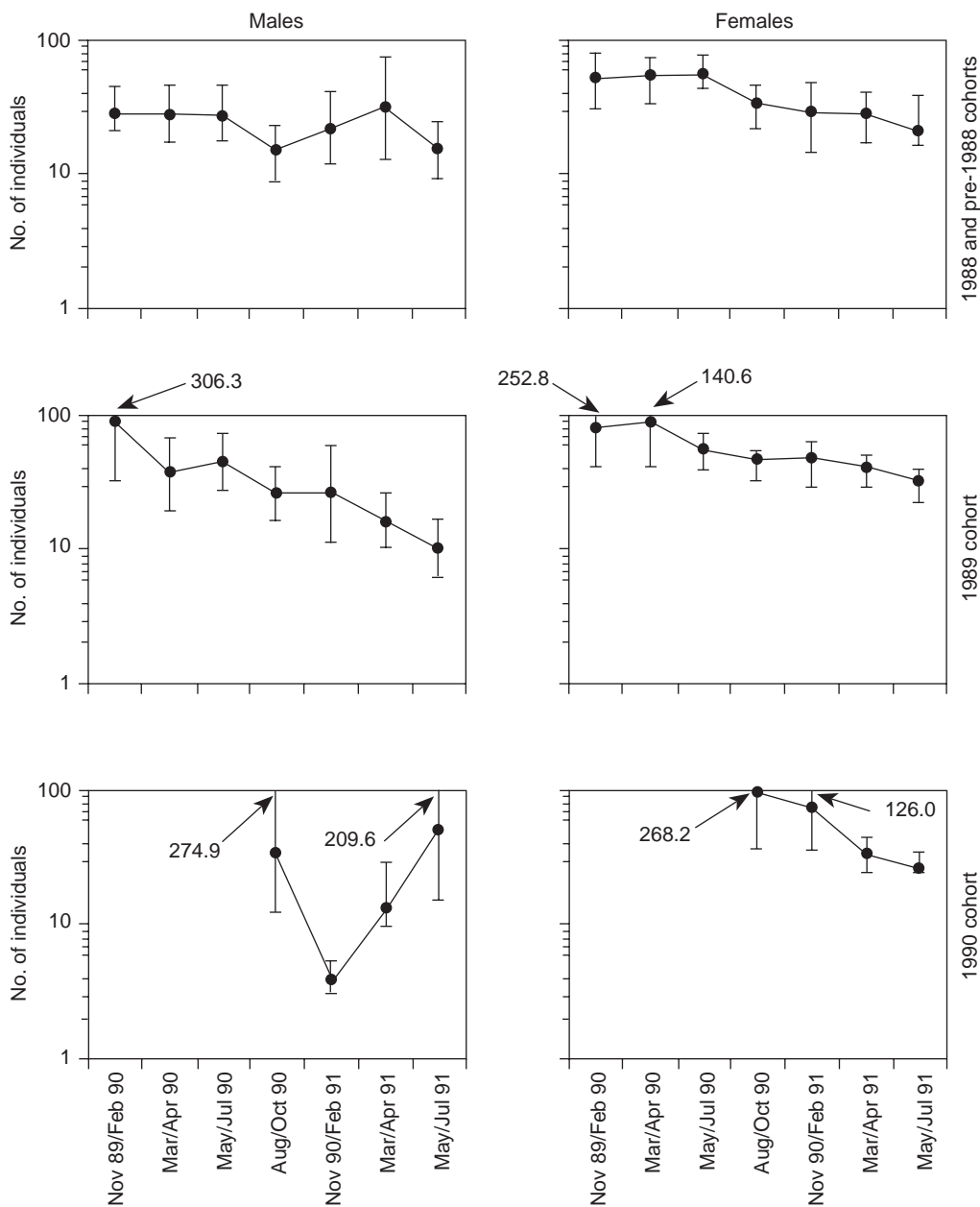


Fig. 4. Time-courses over the study period of number of individuals of males and females of the different cohorts. Values shown are means estimated by the Jolly–Seber method; vertical bars show 95% confidence limits estimated by the method of Manly (1984).

Table 9. Life table for the study population of *Podarcis bocagei*, constructed on the basis of estimates of survivorship-at-age (as estimated by the Jolly-Seber method) and of fecundity-at-age (see Material and Methods). x is age in years; $P(x)$ is the probability of survival from age x to the start of the next age class; $l(x)$ is the probability of surviving from laying to age x ; $m(x)$ is the expected number of daughters produced by a female between age x and the next age class. Net reproductive rate is thus given by $\sum l(x)m(x)$

x	$P(x)$	$l(x)$	$m(x)$	$l(x)m(x)$
0.000	0.8842	1.00000	0.000	0.000000
0.151	0.7775	0.88420	0.000	0.000000
0.403	0.6275	0.68747	0.000	0.000000
0.734	0.5665	0.43138	0.000	0.000000
0.901	0.7160	0.24438	0.672	0.164223
1.151	0.9260	0.17498	0.000	0.000000
1.405	0.7470	0.16202	0.000	0.000000
1.737	0.7240	0.12103	0.000	0.000000
1.901	0.5170	0.08763	3.359	0.294346
2.901	0.4582	0.04530	5.013	0.227110
3.901	0.3794	0.02076	5.013	0.104062
4.901	0.3794	0.00788	5.013	0.039481
5.901	0.3794	0.00299	5.013	0.014979
6.901	0.3794	0.00113	5.013	0.005683

$$R_0 = 0.849884$$

population (considering all cohorts) showed little change over the study period. The density of adult males (1988 and pre-1988 cohorts) was 172 ha⁻¹ in the winter of 1989/90, and 156 ha⁻¹ in the summer of 1991 (by which time this group includes the 1989 cohort). The difference was even less marked in the females: the density of adult females was 307 ha⁻¹ in the winter of 1989/90, and 311 ha⁻¹ in the summer of 1991 (Table 8).

Life table

The life table for the study population, constructed on the basis of estimates of fecundity-at-age and survival-at-age, is shown in Table 9. The estimated net replacement rate (R_0) is less than one, indicating that the population is in decline. Estimated mean generation time is 2.09 years.

DISCUSSION

Reproductive characteristics

The reproductive characteristics of *P. bocagei* have been considered in previous studies (Galán, 1994a, 1996a,b, 1997a). The cycle is broadly coincident with that of other species of this genus in low-altitude coastal areas of the north-west Iberian Peninsula (see Braña, 1983), and in general similar to that of many temperate-zone lizards (e.g. see Fitch, 1970; Saint Girons & Duguy, 1970; James & Shine, 1985; Hraoui-Bloquet, 1987; Hraoui-Bloquet & Bloquet, 1988).

In the population considered in the present study, there was a positive correlation between mothers' SVL and both egg size and clutch size (Galán, 1997a). In view of its small body size and small clutch size, *P. bocagei* would be expected to follow the standard strategy for small lizards (i.e. to increase reproductive investment with increasing size by augmenting individual egg size as opposed to clutch size; see Frankenberg & Werner, 1992). In fact, however, *P. bocagei* appears to adopt an intermediate strategy, probably because of body-size-related limitations on egg size (see Galán, 1994a, 1997a; Bauwens & Díaz-Urriarte, 1997). This is a clear example of the marked within-population phenotypic plasticity observed in many species of lizard (see for example Tinkle & Ballinger, 1972; Pilorge, Xavier & Barbault, 1983; Bauwens *et al.*, 1986; Bauwens & Verheyen, 1987; Frankenberg & Werner, 1992).

Growth and sexual maturity

The mathematical model that best fits the growth-rate estimates obtained on the basis of mark-recapture data is that of Von Bertalanffy (Galán, 1994a). The smallest individuals (i.e. first-year juveniles) show the highest growth rates. The decline in growth rate with age is gradual, and 2- and 3-year-old adults continue to grow, though very slowly.

The growth rate of males was markedly higher than that of females. This is consistent with the finding that mean SVL, maximum SVL and SVL-at-maturity were all higher for males than for females (Galán, 1996b, 1997a).

Seasonal variation in growth rate is very pronounced. SVL increased rapidly during the summer but remained constant over the winter (Galán, 1994a).

The principal factors affecting growth rate in the study population, apart from size and age, are reproduction (particularly in females), disease (Galán, 1996c), injuries and tail regeneration (Galán, 1994a).

Sexual maturity is attained on reaching a certain minimum size, not a minimum age (Galán, 1996b). This is typical of small lacertids. However, there is marked interindividual and seasonal variation in SVL-at-maturation. Minimum SVL-at-maturation declines over the reproductive period. The smallest females do not reproduce until the end of the reproductive period, and lay only a single clutch. The smallest males, who have only recently acquired sexual maturity, are generally displaced by larger males and do not reproduce (Galán, 1995c, 1996b). Age-at-maturation ranges from 1 to 2 years, and is largely dependent on whether the individual was born early or late in the season: individuals hatched from the first clutches of the year (May, early June) usually reach maturity within a year, while individuals hatched from later clutches (late June, July) usually reach maturity within 2 years (Galán, 1996b).

This high degree of phenotypic plasticity as regards reproductive characteristics, growth and age-at-

maturation has a direct effect on population demography.

Survival and causes of mortality

A good understanding of the factors affecting population dynamics requires estimation of hatching rates (hatch success) in natural nests (Overall, 1994). In the study population, the hatch success was higher (between 83% and 91%) than is typical among lizards (Andrews, 1989). Previous reports of high hatch success appear to be due to absence of predators (e.g. the island-dwelling species *Eumeces okadae*, hatch success 91.5%, Hasegawa, 1990) or to maternal care (see Hasegawa, 1985). However, females of *P. bocagei* do not look after their eggs in any way, and there are a number of potential egg predators in the study area (Galán, 1994a). It is possible that the high hatch success observed in the present study reflects the frequency of favourable microsites in the study area. Such sites are typically located in steep south-facing banks with no vegetation (so that insolation is maximized) and with a sandy clay substrate that is easily excavated by the lizards, and that drains well and has high thermal conductivity (see Galán, 1996d). It should be stressed that the method used for evaluation of hatch success probably led to over-estimation, since clutches that had been totally destroyed (by a predator or by a catastrophic event such as burrow collapse) were not detected; nevertheless, such events are probably relatively infrequent, so that the degree of over-estimation was rather small.

Survival rates of juveniles, sub-adults and adults were estimated on the basis of mark-recapture data (see Methods). Note that this approach does not discriminate between individuals who die and individuals who move out of the study area; nevertheless, and as discussed in the next section, movements out of the study area can be assumed to have been relatively infrequent, so that loss rates can be considered good indicators of mortality rates.

The survival curves (Fig. 3) suggest that probability of survival was fairly constant over the lifespan in both sexes. Similar results have been obtained in studies of other lizards (see for example Schoener & Schoener, 1980; Dunham, 1981; Andrews & Nichols, 1990), though in some species there is clear variation with age (see for example Turner, 1977; Dunham, 1982; Selcer, 1986). The apparent between-sex differences in probability of survival were not statistically significant. Between-sex differences in adult probability of survival have however been detected in another Iberian lizard, *Psammodromus algirus* (Díaz, 1993).

In lizards that live in areas of seasonal climate and that undergo a period of hibernation, survival over the winter is typically higher than over the summer (see for example Bauwens, 1981; Ruby & Dunham, 1984). However, seasonal-climate lizards that are active during the winter typically show high mortality during this period (Tinkle,

1967; Ruby, 1977). The lizards of the Carral population show significant winter activity (Galán, 1995b); however, winter survival rates were high. This may be attributable to the relatively mild winters of the study area. Note, however, that the 95% confidence intervals for the survival rate estimates show considerable overlap (Fig. 1), so that the differences cannot be considered statistically significant. In other words, survival rate probably remains more or less constant over the year. In some species of lizard, gravid females are rather slow-moving and thus relatively easy for predators to catch (see Shine, 1980; Bauwens & Thoen, 1981; Garland & Else, 1987). In many lacertids, females switch from the characteristic 'flight' predator-evasion strategy to a more crypsis-dependent strategy when they are gravid (see Bauwens & Thoen, 1981; Braña, 1993), and indeed in these two studies mortality among adult females was no higher during the reproductive period than during other periods. It is possible that gravid females of *P. bocagei* show a similar switch of predator-evasion strategy, and thus maintain a high probability of survival.

Predators can be expected to have a significant effect on mortality in the study population: there are various potential predators in the study area and, as noted in Results, direct evidence was obtained of predation by two snake species. Some authors have used the frequency of missing or regenerated tails as an index of the intensity of predation suffered by different lizard populations (see for example Pianka, 1970; Tinkle & Ballinger, 1972; Parker & Pianka, 1975; Dunham, 1981; Turner *et al.*, 1982; Cooper & Vitt, 1985), although other authors have questioned the validity of this technique (Schoener, 1979; Schoener & Schoener, 1980). In the Carral population, individuals with a missing or regenerated tail were very frequent (about 30% of juveniles aged < 5 months, about 77% of adults). These frequencies are higher than have been reported for species of other lizard families (see for example Jaksic & Fuentes, 1980; Vitt, 1983), though similar to or lower than frequencies reported for other *Podarcis* species (Castilla & Bauwens, 1991; Gil, 1992). Some authors have suggested that a high frequency of missing or regenerated tails may reflect the use of 'tail exhibiting' as a predator-evasion technique (Ballinger, 1973; Vitt, 1983). *Podarcis bocagei* may use a strategy of this type, since juveniles have a conspicuous green or greenish tail, and individuals of all ages make undulatory movements of the tail in the presence of predators. I did not detect significant between-sex differences in the proportion of individuals with missing or regenerated tails in any of the age groups considered.

A large proportion of individuals showed skin infections, particularly during the winter. Considering the different age/sex groups separately, I did not detect any relationship between proportion of individuals with skin infections and probability of survival. However, skin infections do appear to affect fertility (impeding reproduction by some of the affected females) and growth rates (which were significantly lower in affected juveniles and sub-adults) (see Galán, 1996c).

The longevity estimates for the study population (maximum 6–7 years, see Fig. 3; estimated from survival curves) are intermediate within the range of values reported for lacertid lizards of other genera. Some species appear to live for no more than 12 months (for example, *Psammodromus hispanicus* in the Iberian Peninsula: Pascual-González & Pérez-Mellado, 1989; Pollo & Pérez-Mellado, 1990), while others – typically large species – may live for >10 years (e.g. *Lacerta lepida*, Castilla, 1989).

The only previously published estimate for *P. bocagei* refers to an island population, that of the subspecies *berlengensis* on Berlenga Island off northern Portugal, for which maximum longevity was estimated by skeletochronological methods as 6 years (Vicente, 1989).

Movements

The data on the distances moved by marked–recaptured animals indicate that *P. bocagei* is a highly sedentary species. Indeed, the distances moved are considerably less than in species classified by other authors as ‘sedentary’ (e.g. see Stebbins & Robinson, 1946; Fitch, 1955), though not as short as in certain extremely sedentary species of geconid and xantusid (Zweifel & Lowe, 1966; Bustard, 1968; Fellers & Drost, 1991).

The relatively long distances moved by a relatively small number of animals can be considered as ‘dispersion’ movements. Previous studies of other sedentary lizard species have likewise found that a subset of the population moves relatively long distances (Moritz, 1987; Massot, 1992; Clobert *et al.*, 1994; Lecomte & Clobert, 1996). The present results indicate that the rate of emigration from the study plot (60 × 45 m) is probably very low (the mean distance moved between marking and recapturing 18–24 months later was 15.7 m, maximum 45.6 m; see Table 7). Longer-distance movements were more frequent among males (both adults and juveniles). Adult females were more sedentary than adult males over all time intervals considered, though particularly within the reproductive season. Many lizard studies have documented significant differences between males and females as regards mobility (e.g. see Blair, 1960; Bostic, 1965; Tinkle, 1967; Tinkle & Woodward, 1967; Berry, 1974; Clobert *et al.*, 1994); however, in some species no such difference is observed (Fellers & Drost, 1991; James, 1991; Massot, 1992).

The sedentary behaviour of females during the reproductive season presumably reflects the fact that females remain in the courtship areas, and particularly in the area in which they lay. Indeed, a large proportion of sightings of females during this period were on banks and slopes (i.e. typical nesting sites) (Galán, 1996*d*). Studies of other lizard species have likewise found females to be particularly sedentary during the reproductive period (e.g. see Bauwens & Thoen, 1981; Russell, 1985; Zucker, 1987; Brodie, 1989; Deslippe *et al.*, 1990; Braña, 1993), and this is typically

interpreted as an adaptation favouring predator evasion and energy conservation during the critical egg-laying period (Rose, 1981).

Mean distances moved by juveniles were somewhat greater than mean distances moved by adults, though the difference was only statistically significant in the females. Considering both sexes together, no significant differences were detected between mean distance moved by juveniles in their first activity period and mean distance moved by sub-adults (second activity period). This result contrasts with that obtained by Massot (1992) and Clobert *et al.* (1994) in *Lacerta vivipara*, who found that dispersion movements occurred principally during the first activity period.

The fact that mean distances moved by juveniles were greater than those moved by adults suggests that juveniles may be more prone to disperse than adults (as found in *L. vivipara* by Heulin, 1985 and Clobert *et al.*, 1994). However, we also recaptured many adults in the places in which they had been first captured as juveniles, 1 or 2 years previously. Thus some but not all juveniles appear to disperse.

Within the study area, immature and adult animals differ in their distribution with respect to microhabitats (Galán, 1994*b*), as has been reported for other lacertids (Mellado, 1980; Carrascal, Díaz & Cano, 1990; Pollo & Pérez-Mellado, 1991; Gil, 1992). Specifically, juveniles and sub-adults typically occur on sites with less vegetation cover and gentler slope (i.e. with fewer refuges; see Stamps, 1983) than adults. This suggests that immature individuals occupy less favourable sites than adults, as has been reported for other lizards (Bradshaw, 1971; Schall, 1974). This is consistent with the greater tendency of immature individuals to disperse.

Population density

The population density estimates, considering all individuals captured (adults and immature animals), ranged from a maximum of 1574 ha⁻¹ in the winter of 1989/90 to a minimum of 868 ha⁻¹ in May/July 1991. Mean population density, considering all periods, was 1266 ha⁻¹. The only previous estimate of population density for a mainland population of *P. bocagei* is that of Delibes & Salvador (1986), in heathland of the Cantabrian Range in north-west Spain; using transect methods, these authors estimated population density to be in the 46–250 ha⁻¹ range. Much higher estimates (in some areas over 5000 ha⁻¹) were obtained for populations on Berlenga Island off the coast of Portugal (Vicente, 1989). This pattern (much higher densities on islands than in mainland environments) is common among lizards (see Turner, 1977 for review). Other species of the genus *Podarcis* likewise show very high population densities on islands in the Mediterranean (Salvador, 1986; Henle, 1988; Pérez-Mellado, 1989).

Reported densities of mainland populations of

Podarcis species show considerable variation, both between species and between populations of the same species (Delibes & Salvador, 1986; Barbault & Mou, 1988; Henle, 1988; Martín-Vallejo, 1990).

The high densities obtained in the present study are not representative of the study area in general: outside the gravel pit, densities of *P. bocagei* are much lower. This pattern (i.e. high densities in limited areas only) is common among lizards (Turner, 1977; Ouboter, 1981; Henle, 1988). The gravel pit considered in the present study clearly presents particularly favourable conditions for *P. bocagei*: over recent years, population densities have risen rapidly (see Galán, 1994a), though they have subsequently declined somewhat, as noted in the present study. The gravel pit has large areas without vegetation and a complex microtopography (banks and slopes). Partial colonization by various scrub plants has given rise to a habitat mosaic that is highly favourable to *P. bocagei* (Galán, 1994b). I have likewise observed rapid colonization by *P. bocagei* of other sites affected by mining activities, where similar microhabitats develop (Galán, 1997b). Nevertheless, the continuing colonization of sites of this type by plants means that the soil surface is soon completely covered and shaded (Galán, 1995a), making the environment much less favourable for *P. bocagei* (see below).

Variation in population size

Total population size appears to have declined throughout the study period: the estimate for winter 1990/91 was 84% of that for winter 1989/90, while the estimate for March/April 1991 was 80% of that for March/April 1990. Note that the decline between March/April 1990 and March/April 1991 was associated with a marked increase in the estimated size of the adult population and a marked decline in the estimated size of the immature population, suggesting that the observed overall decline is largely due to reduction in the size of the immature population.

A previous study of *L. vivipara* found that high population densities were associated with an increase in juvenile mortality and decreases in the proportion of females reproducing, in clutch size and in hatch success (Massot *et al.*, 1992). These reductions in birth rate would thus reduce the number of juveniles in the next generation. Interestingly, in the present study mean clutch size declined between 1990 and 1991, considering both clutches laid by captured gravid females (Table 1) and clutches found in natural nests (Table 3), although in neither case was the decline statistically significant. Mean hatch success likewise declined between 1989 and 1991, though again the decline was not statistically significant.

The apparent changes in population size and in age distribution observed in the present study may thus be at least partially attributable to density-dependent factors (see Massot *et al.*, 1992).

Life table

The life table for the study population (Table 9) likewise indicates that the population is in decline, with net replacement rate being less than one. Note, however, that the data are insufficient to rule out the possibility that (a) the apparent decline is simply due to sampling error, or (b) although a decline took place over the study period, this decline is not representative of the longer-term trend. Nevertheless, my results taken together support the view that the population was in long-term decline during the study period, and in what follows I will assume this to be the case.

A decline in population size may be attributable to increased mortality, reduced natality, or a combination of both. The only previously reported data related to natality in *P. bocagei* are estimated mean clutch sizes for populations of this species in Asturias (north-west Spain): 3.59 eggs (Braña, 1983) and 3.30 eggs (Braña, Bea & Arrayago, 1991). Both estimates are markedly lower than that obtained in the present study (4.13 eggs), arguing against the possibility that natality is low in the Carral population. By contrast, there are good reasons for suspecting that mortality rates increased over the study period. Within the study plot, *P. bocagei* typically occupies areas with sparse vegetation, not areas of dense *Ulex* scrub. As a result, it is increasingly relegated to marginal areas as colonization proceeds (Galán, 1994b, 1997b). Furthermore, predators such as *Coronella austriaca* become more abundant as the vegetation develops. Nevertheless, the present data are insufficient to determine whether increased mortality, reduced natality or both are the causes of the declining size of the Carral population.

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