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Structure of a population of the lizard *Podarcis bocagei* in northwest Spain: variations in age distribution, size distribution and sex ratio

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Abstract—Mark-recapture techniques were used to investigate population size, age distribution, size distribution and sex ratio in a population of the lacertid lizard *Podarcis bocagei* in an abandoned gravel pit in northwest Spain. The study was carried out over a 2-year period. Despite relatively high maximum longevity, the population age distribution was characteristic of small, short-lived lizard species (i.e., there was a relatively high proportion of immature individuals). Population size declined over the study period, largely because of a drop in the number of immature animals: this may be partially attributable to density-dependent factors, but was probably due largely to a decline in habitat favourability as a result of colonisation of the study site by vegetation. The sex ratio was significantly female-biased in all cohorts studied, not only among adults but also among juveniles and sub-adults. However, sex ratio at hatching (as investigated by laboratory hatching of clutches laid by captured pregnant females) did not differ significantly from one-to-one. There was no difference found in survival probabilities between males and females. The observed bias in sex ratio must therefore be attributed to between-sex differences in net emigration.

Keywords: Lacertidae; life history; *Podarcis bocagei*; population structure, reptiles; sex-ratio.

INTRODUCTION

The stability of animal populations over time is a central problem in ecology (Connell and Sousa, 1983). Most natural populations undergo numerical fluctuations, both within years (reflecting seasonal variation in recruitment) and among years (Barbault, 1991). Beyond general observations of this type, however, little is currently known about the real stability of natural populations, or of the extent to which

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stability varies among taxonomic groups and environments (Connell and Sousa, 1983).

It has been suggested that lizard populations are typically rather stable, with population size fluctuating little over time (Schoener, 1985; Abts, 1987; Jones and Ballinger, 1987; Strijbosch and Creemers, 1988). However, other studies have indicated that lizard populations may undergo fluctuations (Andrews and Wright, 1994). For example, some tropical species show pronounced fluctuations in density, both from one year to the next and between decades; these fluctuations are correlated with variation in the amount and timing of rainfall (Andrews, 1991). In other tropical species, predation as well as rainfall may also play an important role in such fluctuations (Barbault, 1991). Another factor affecting the stability of lizard populations is the abundance of habitat space, and the spatial arrangement of habitat patches (Case, 1994; Smith et al., 1996; Díaz et al., 2000). However, little is known about factors affecting the density of lizards of temperate climates, such as the European lacertids (Heulin, 1985; Bauwens et al., 1987; Pilorge, 1987; Castilla and Bauwens, 1991; Massot et al., 1992).

Clearly, the fundamental properties of a population include not only its size but also its age distribution and sex ratio. Pilorge et al. (1987) have demonstrated that, in a population of *Lacerta vivipara*, males, females and immature individuals may be subject to different selective pressures. It is thus important to understand the structure of a population in order to analyse its dynamics.

The structure of reptile populations is often analysed in terms of size classes. Size is typically a reliable indicator of age among younger animals, but not among older animals (Barbault, 1974; Avery, 1975; Barbault et al., 1980). In the present study, I therefore estimated age, taking into account both size and previous capture dates, and eliminated from the analyses individuals whose age could not be estimated accurately.

The sex ratio of animal populations is usually one-to-one (Fisher, 1930); however, significant deviations from this ratio have been reported in several groups including lizards. A number of hypotheses have been put forward to explain such deviations from one-to-one in lizards, including higher mortality or higher rates of emigration among one sex, or temperature-dependent sex-determination (Stamps, 1983; Pérez-Mellado et al., 1988; Crews et al., 1994; M'Closkey et al., 1998).

In general, little is known about the population structure of European lizards (Pilorge and Castanet, 1981; Busack and Jaksic, 1982; Pilorge, 1982, 1987; Barbault and Mou, 1988; Salvador, 1988; Cavin, 1993; Roytberg and Smirina, 1995). In the case of the lacertid *Podarcis bocagei*, there have been no previous reports of population structure (although see Galán, 1994a, 1999).

This paper outlines a study of the structure of a population of *P. bocagei* in northwest Spain. Specifically, size, age and sex structure were monitored over a 27-month period.

MATERIALS AND METHODS

The study was carried out in a disused gravel pit in San Vicente de Vigo (municipality of Carral, A Coruña Province, northwest Spain; 45°18′N, 8°20′W, UTM 29T NH5687, altitude 90 m a.s.l.). The gravel pit had been abandoned 4 years before the start of the study and it was overgrown by colonising vegetation (mainly *Ulex europaeus* scrub). The study area is included in the 'wet oceanic' climate type (Carballeira et al., 1983), characteristic of coastal areas of the northwest Iberian Peninsula. Annual rainfall was 1127 mm in 1989, 870 mm in 1990, and 978 mm in 1991. Mean temperature (i.e. grand mean of monthly means of daily maximum-minimum midpoints) was 13.7°C in 1989 (difference between January mean and July mean 13.5°C), 13.5°C in 1990 (difference between January mean and July mean 11.3°C), and 12.5°C in 1991 (difference between January mean and July mean 12.1°C). Further information on the study area is given in Galán (1994c, 1997a, 1999).

A study plot of 1100 m^2 was visited 3-8 times per month between July 1989 and October 1991. At each visit, lizards were captured by hand whenever possible, 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) and age (see below). Each lizard was processed quickly (less than 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 (captures + recaptures = 2144). All measurements were taken by a single person. Since SVL is difficult to measure accurately in live animals, this variable was determined as the mean of at least three consecutive determinations.

The age of marked-recaptured individuals was inferred from the date(s) of previous capture(s), while the age of unmarked-captured individuals was inferred from size; however, since in previous studies of this population it has been found that there is considerable size overlap between age classes (Galán, 1994a), 43 unmarked-captured individuals falling into one of the overlap ranges were excluded from the analysis.

In all cases three age classes were distinguished, namely juveniles (individuals in their 1st calendar year), sub-adults (including young adults, all in their 2nd calendar year) and adults (3 or more calendar years).

Population size was estimated on the basis of the mark-recapture data using the Jolly-Seber method (Jolly, 1965; Seber, 1965, 1982; Krebs 1989), considering the three age classes separately. For this analysis, and for each year of the study, only mark-recapture data for four periods (each being considered as a single sampling event) were used; namely i) November-February, ii) May, iii) July and iv) September.

The first visits to the plot (July-Sept 1989) were for marking only, and the first recaptures were not obtained until winter 1989/90.

The calculations were done with the JOLLY program (Krebs, 1989), which additionally provides estimates of the 95% confidence interval of population size, survival probabilities and capture probabilities.

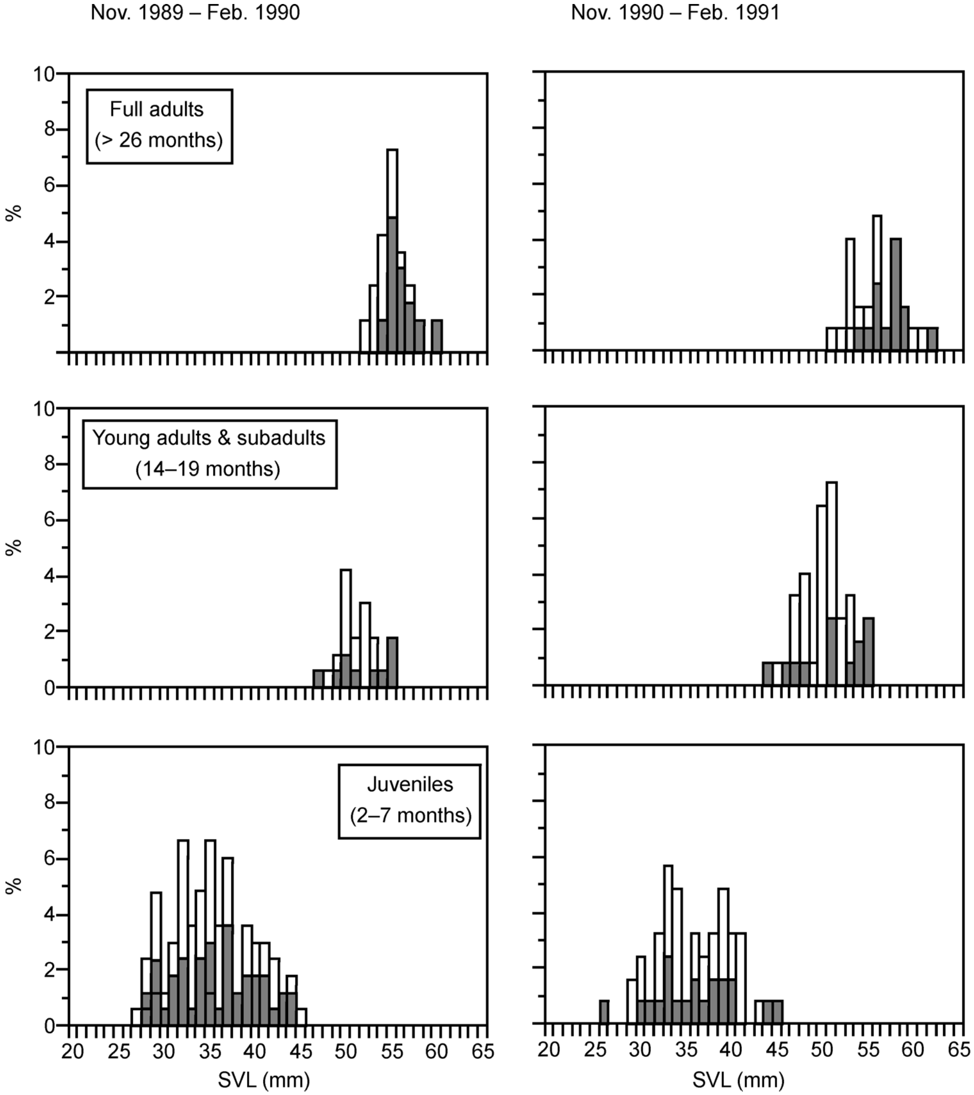

Figure 1. Size (SVL) distributions of animals captured in Nov-Feb 1989/90 ($n = 165$) and Nov-Feb 1990/91 ($n = 123$). Within each year, the vertical axes show numbers of individuals expressed as percentages with respect to the total for all age groups. SVL classes are 1 mm intervals. White bars indicate females, and shaded bars males.

For each age class, histograms of size distribution (figs 1-4) were constructed directly from the raw data, considering 1 mm SVL intervals.

Note also that the age classes used for the construction of these histograms were different from those used in the rest of the study: juveniles (aged 0-7 months), sub-adults (aged 8-10 months), sub-adults and young adults (aged 10-22 months; note that, over this age range, some individuals attain sexual maturity while others remain immature, Galán 1996a), and full adults (aged more than 22 months). For the

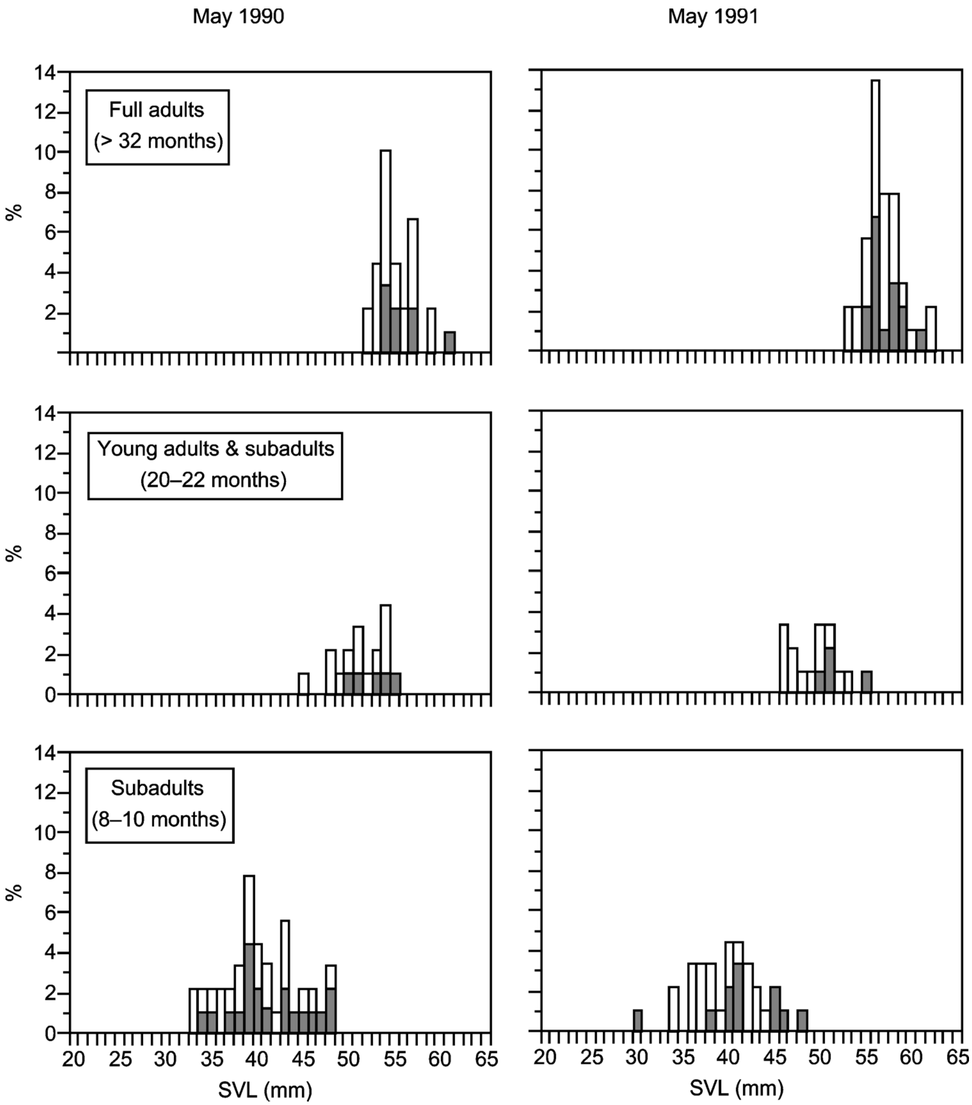

Figure 2. Size (SVL) distributions of animals captured in May 1990 ($n = 87$) and May 1991 ($n = 89$). Within each year, the vertical axes show numbers of individuals expressed as percentages with respect to the total for all age groups. SVL classes are 1 mm intervals. White bars indicate females, and shaded bars males.

July data, I distinguished between full adults aged 2 years (22-24 months), and full adults aged 3 years or more (more than 34 months). The size (SVL) distributions shown in figures 1-4 are based on real capture data, while the values shown in table 1 are estimates of the number of individuals obtained by the Jolly-Seber method.

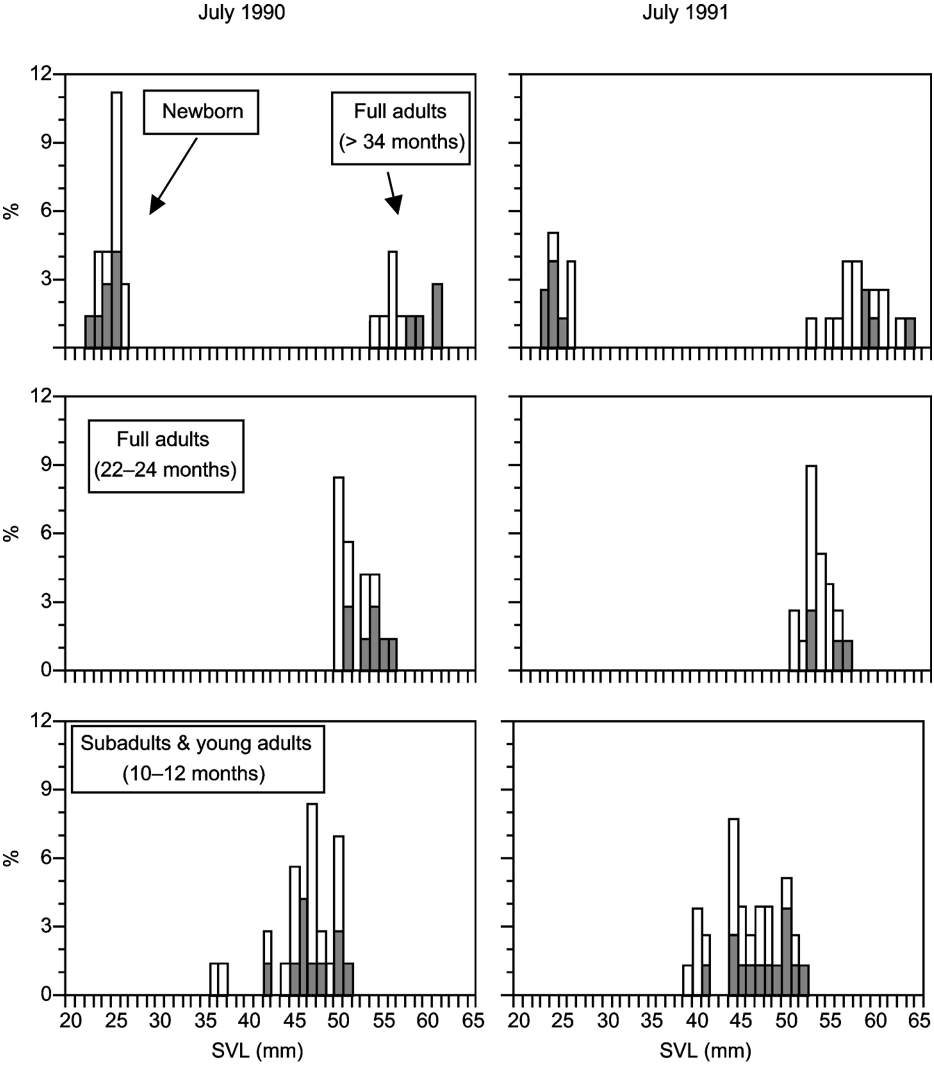

Figure 3. Size (SVL) distributions of animals captured in July 1990 ($n = 69$) and July 1991 ($n = 75$). Within each year, the vertical axes show numbers of individuals expressed as percentages with respect to the total for all age groups (e.g. 69 for 1990). SVL classes are 1 mm intervals. White bars indicate females, and shaded bars males.

Sex ratio

All captured animals were sexed. Sexual dimorphism is evident in adults of *P. bocagei:* males have larger heads and a green dorsal coloration, while females are brown with a different dorsal pattern, etc. For sexing of juveniles, I used the relationship between sex and the number of rows of transverse scales (less than 28 in males, more than 28 in females; see Bauwens and Thoen, 1982; Galán, 1986).

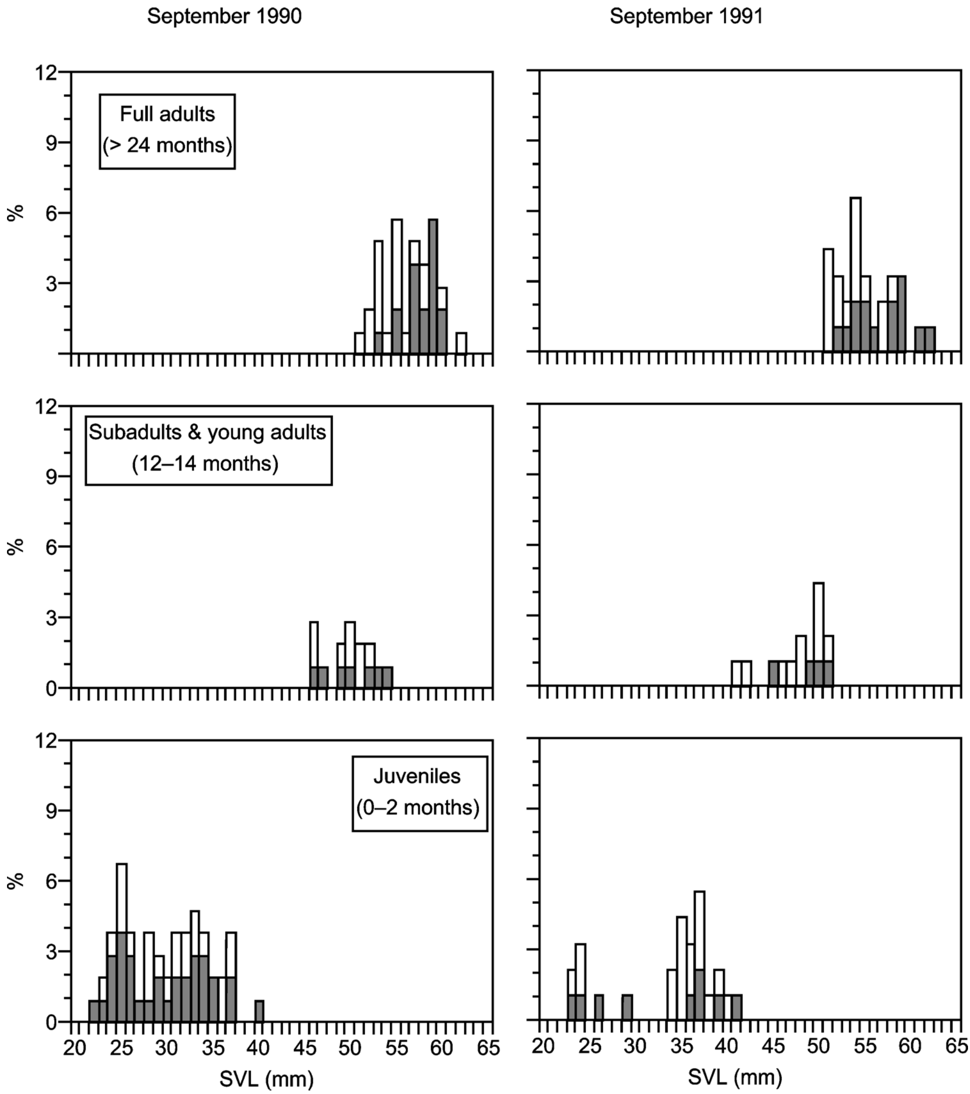

Figure 4. Size (SVL) distributions of animals captured in September 1990 ($n = 66$) and September 1991 ($n = 104$). Within each year, the vertical axes show numbers of individuals expressed as percentages with respect to the total for all age groups. SVL classes are 1 mm intervals. White bars indicate females, and shaded bars males.

Juveniles with exactly 28 rows of transverse scales were sexed on the basis of dorsal pattern.

Sex ratio at hatching was estimated on the basis of laboratory hatching, as follows. Gravid females were collected from areas adjoining the study plot (maximum distance from the plot 2 km), and brought to the laboratory to lay eggs. Only those clutches (29 in total) with 100% hatch success and with all hatchlings readily sexed (on the basis of number of rows of transverse scales) were considered. In addition, data was used for another 18 laboratory-hatched 100% success clutches, laid by gravid females collected in other parts of the study region, giving a total of 47 clutches.

Incubation temperature in natural nests in the study plot ranges from 15 to 39°C, with mean clutch incubation temperature over the incubation period ranging from 26.5 to 29.1°C (Galán, unpubl.). It was attempted to reproduce these conditions in the laboratory, using a 100 W bulb placed near the incubation boxes, switched on between 0900 and 2100 h (maximum temperature inside the box 35-37°C), and switched off at night (minimum temperature 16-17°C). Overall mean incubation temperature, considering all clutches, was 28.2°C. The incubation substrate (a mixture of clay and sand) was the same as in natural nests in the study plot (Galán, 1997a).

RESULTS

Population size and age distribution

Total population size underwent a clear decline between the 1st and 2nd year of the study: the decline ranged from 12% (considering the May estimates) to 32% (considering the September estimates) (table 1). The short-term increase in total population size between July and September (due to hatching) was likewise smaller in 1991 than in 1990 (table 1). Furthermore, as can be inferred from the estimated number of juveniles in November-February 1989/90, the July to September increase in total population size must have been smaller in 1990 than in 1989.

Hatching period (July-September). The estimated number of full adults (age >22 months) was 78 in July 1990, vs 75 in July 1991. However, these individuals accounted for 60% of the total population (excluding newborn juveniles) in July 1991, vs only 44% in July 1990. The hatching period finishes in September, by which time newborn juveniles make up more than half of the population (52% in 1990, 51% in 1991): as a consequence, the proportion of adults was lower during this period than during any other period (19% in 1990, 29% in 1991) (table 1).

Resting period (November-February). The proportion of subadults was much lower in November-February 1989/90 (12%) than in November-February 1990/91 (37%). The number of adults was similar in both periods, but the proportion of adults was higher in November-February 1990/91 (25%, vs 18% in November-February 1989/90).

Pre-hatching period (March-June). The proportion of subadults dropped sharply from 61% in May 1990 to 37% in May 1991.

Size distribution

Size distributions for each age class and each year/period considered are shown in figures 1-4. Throughout the resting period (November-February; fig. 1), the

Table 1.
Numbers of individuals (as estimated by the Jolly-Seber method) in each age-group/period combination considered. Sub = subadults, Juv = juveniles; A/I is the ratio of adults to immature (i.e. Juv + Sub) individuals. The abbreviation 'ap' indicates 'and previous (cohorts)'. Values in brackets are 95% confidence limits. The two values shown for adults in 1991 are for the 1988 and previous cohorts (first value) and for the 1989 and previous cohorts (second value).

Period	Adults	Cohort	Sub	Cohort	Juv	Cohort	Total	A/I
Nov 89-Feb 90	46 (30-99)	1988 ap	31 (16-62)	1988	172 (93-329)	1989	249	0.23
May 1990	78 (48-115)	1988 ap	122 (80-189)	1989			200	0.64
July 1990	78 (58-117)	1988 ap	101 (65-142)	1989			179	0.77
Sept 1990	46 (29-64)	1988 ap	71 (47-92)	1989	127 (88-181)	1990	244	0.23
Nov 90-Feb 91	49 (24-84)	1988 ap	73 (45-108)	1989	86 (55-143)	1990	208	0.31
May 1991	111: 55 (28-99) + 56 (38-74)	1988/89	66 (52-85)	1990			177	1.68
July 1991	75: 34 (24-58) + 41 (28-53)	1988/89	50 (38-69)	1990			125	1.50
Sept 1991	48: 20 (16-26) + 28 (20-44)	1988/89	33 (23-53)	1990	85 (44-125)	1991	166	0.41

population fell into one of two major size classes, the first corresponding almost entirely of juveniles aged 2-7 months, the second corresponding of individuals from a series of cohorts with overlapping size ranges. In May, by contrast, there is much more overlap between juveniles and the rest of the population (fig. 2).

Sex ratio

The total numbers of individuals of each sex captured throughout the study period in the study plot (excluding 58 individuals that could not be sexed) are listed in the lower part of table 2. The data are subdivided by cohort. For all cohorts except 1991, and considering all cohorts together, the sex ratio is significantly different from one-to-one (χ^2 tests, $P < 0.05$).

The upper part of table 2 shows sex ratios estimated on the basis of Jolly-Seber population estimates for juveniles, sub-adults and adults during the different sampling periods. Also shown are 95% confidence limits and survival probabilities. Sex ratio differed significantly from one-to-one in 12 of the 23 age-group/period combinations considered, and in two of the three age groups (juveniles and adults): in all these cases the ratio was female-biased.

There were no differences between sexes either in probability of survival or probability of capture. Specifically, in none of the age classes shown in table 2 were there statistically significant differences between the sexes (Kolmogorov-Smirnov tests; juveniles, $z = 0.408$, $n = 6$; subadults and young adults, $z = 0.577$, $n = 12$; adults, $z = 0.535$, $n = 14$; $P > 0.05$ in all cases). Likewise, in view of the

Table 2.
Sex ratios (male-to-female ratios) in the different age- group/period combinations considered, as estimated on the basis of Jolly-Seber estimates of numbers of male and female individuals. Also shown are 95% confidence limits and, for some periods, survival probabilities. The lower part of the table shows the total number of individuals of each sex captured in each cohort, together with the sex ratio. The abbreviation 'ap' indicates 'and previous cohorts'. The statistical significance of the difference from one-to-one is also shown (χ^2 tests; NS, $P \geqslant 0.05$; *, $P < 0.05$; **, $P < 0.01$; ***, $P < 0.001$).

Age group	Cohort	Period	Males			Females			Sex ratio	*P*
			Total number	95% confidence limits	Probability of survival	Total number	95% confidence limits	Probability of survival		
Juveniles	1989	11/89-02/90	93	53-176	1.000	79	40-153	0.756	1.18	NS
	1990	09-90	35	12-55	0.521	92	76-126	0.786	0.38	***
	1990	11/90-02/91	14	11-27	0.799	72	44-116	0.896	0.19	***
	1991	09-91	39	16-65		46	28-60		0.85	NS
Mean			45.2			72.2			0.63	*
Subadults and young adults	1988	11/89-02/90	11	7-20	0.734	20	10-42	0.789	0.55	NS
	1989	05-90	39	30-58	0.840	83	50-131	0.626	0.47	***
	1989	07-90	46	27-73	0.687	54	38-69	0.716	0.85	NS
	1989	09-90	26	16-40	0.618	44	31-52	0.926	0.59	*
	1989	11/90-02/91	27	18-48	0.712	47	27-60	0.747	0.57	*
	1990	05-91	23	19-31	0.853	42	33-54	0.779	0.55	*
	1990	07-91	25	15-36		25	23-33		1.00	NS
	1990	09-91	15	12-26		18	11-27		0.83	NS
Mean			26.5			41.6			0.64	NS
Adults	1988 ap	11/89-02/90	17	11-44	0.696	29	19-55	0.924	0.59	NS
	1988 ap	05-90	28	17-46	0.561	51	32-69	0.639	0.55	**
	1988 ap	07-90	27	18-45	0.681	52	40-72	0.517	0.52	**
	1988 ap	09-90	15	9-22	0.723	31	20-42	0.707	0.48	*
	1988 ap	11/90-02/91	21	11-41	0.957	27	13-43	0.935	0.78	NS
	1988 ap	05-91	30	12-62	0.600	25	16-37	0.574	1.20	NS

Table 2.
(Continued).

Age group	Cohort	Period	Males			Females			Sex ratio	*P*
			Total number	95% confidence limits	Probability of survival	Total number	95% confidence limits	Probability of survival		
	1988 ap	07-91	15	9-23	0.567	19	15-35	0.724	0.79	NS
	1988 ap	09-91	6	4-9		14	12-17		0.43	NS
	1989	05-91	16	10-26		39	28-48		0.41	**
	1989	07-91	10	6-16		30	22-37		0.33	**
	1989	09-91	8	4-13		20	16-31		0.40	*
Mean			17.5			30.6			0.57	*
No of individuals captured	1988 ap		80			107			0.75	*
	1989		76			115			0.66	**
	1990		49			75			0.65	*
	1991		24			27			0.89	NS
Total			229			324			0.71	***

Table 3.
Sex ratios in laboratory-hatched clutches. None of the ratios shown differs significantly from one-to-one (χ^2 tests, all $P > 0.05$).

Sites where females collected	No. of clutches	Males	Females	Sex ratio
Gravel pit (50-200 m from study plot)	10	17	22	0.77
Adjacent areas (500-2000 m from study plot)	19	36	28	1.29
Other sites in the study region (A Coruña Province)	18	36	35	1.03

data for all recaptures of males and females by the Jolly-Seber method, probability of capture did not differ significantly between the sexes ($\chi^2 = 0.23$; df $= 7$, $P > 0.05$).

In view of this finding (i.e., a female-biased sex ratio not only among adults but also among juveniles and subadults), it was investigated whether sex ratio at hatching is female-biased. The 29 clutches laid by females collected from the study area produced a total of 53 males and 50 females (male-to-female ratio 1.06, not significantly different from one-to-one); similarly, the data for the 18 clutches laid by females collected from other sites in the study region show no evidence of a biased sex ratio (table 3). These results suggest that sex ratio at hatching is one-to-one.

Regardless of the area considered, within-clutch sex ratio shows marked variation: of the 47 clutches considered, 23 (49%) showed a male-biased ratio, 18 (38%) showed a female-biased sex ratio, while only six (13%) produced the same number of males and females. Nine (19%) of the clutches produced either all males (six clutches) or all females (three clutches).

DISCUSSION

Age and size distribution

Most mark-recapture studies of reptiles have used size as an indicator of age (for review see Dunham et al., 1988). Such methods require the construction of a model of growth, based on determination of the sizes of animals of known age (Dunham, 1978; Schoener and Schoener, 1978; Andrews, 1982). In the study population, growth rate decreases with age and with SVL. Two- and 3-year-olds show slow but non-zero growth rates (Galán, 1999).

Interindividual variation in size may be attributable to variations at birth and/or variations in subsequent growth rate, whether this be due to genetic or environmental effects. In my study population, SVL-at-hatching ranges from 21 to 26 mm (Galán, 1997a), and growth rates vary greatly, both among individuals and within years (summer growth rate high, winter growth rate negligible) (Galán, 1994a, 1999). Factors that appear to be associated with reduced growth include disease (Galán, 1996d), the reaching of sexual maturity (Galán, 1996a), reproduction (principally among females; Galán, 1994a), and loss and regeneration of the tail (Galán, 1994a). In addition, the size of a given individual is strongly influenced by month of hatching (Galán, 1996c, 1997a, 1999). This leads to very considerable overlap in SVL among animals of different ages.

The age distribution of the study population is similar to that of other short-lived lizards in which immature individuals make up a large proportion of the population (see for example Crenshaw, 1955; Hirth, 1963; Tinkle, 1967), though the maximum longevity in the wild of *P. bocagei* (at least 3-4 years; Galán, 1994a, 1999) is considerably greater than that reported for the species studied by these authors (in all cases less than 2 years).

My data suggest that the proportion of juvenile individuals dropped considerably over the 2 years of the study period (by 56% in view of the estimates for November-February 89/90 and Nov-Feb 90/91, or by 33% in view of the estimates for Sep 90 and Sep 91). The number of adults did not show parallel declines (see table 1).

The difference in age distribution between the 2 years of study, and the parallel decline in total population size, might be attributable to the high population density observed at the start of the study period (more than 1500 individuals per hectare). In an experimental study of another lacertid species (*Lacerta vivipara*), high population densities led to a) an increase in juvenile mortality, b) a reduction in the proportion of young reproductive females, and c) a decline in clutch size and hatch success (Massot et al., 1992). In the present study, this explanation is supported i) by the decline between 1990 and 1992 in mean clutch size (Galán, 1996b, 1999; note, however, that the decline was not statistically significant at the 5% level), ii) by the decline between 1989 and 1991 in mean hatch success in natural nests (Galán, 1996b, 1997a, 1999; decline again not statistically significant), iii) by the declines between 1990 and 1991 in the proportions of individuals of both sexes reaching sexual maturity before one year of age (Galán, 1996a), and iv) by the net replacement rate, as estimated from the life table for the study population, of less than one ($r = 0.85$; Galán, 1999).

The second possible explanation relates to changes in the environmental characteristics of the study plot. At the start of the study period, the habitats created by initial colonization of the gravel pit by vegetation appear to have been near optimal for *P. bocagei* (Galán, 1999); however habitat favourability rapidly declined as colonization of the site by vegetation proceeded, and within a few years the area was largely covered by scrub (mainly *Ulex europaeus*). Dense vegetation cover prevents insolation of the soil surface, making the environment much less favourable for *P. bocagei* (Galán, 1995a). Ballinger and Watts (1995) showed that an increasing vegetation cover can lead to the local extinction of the lizard *Holbrookia maculata* and reduce the population size of the lizard *Sceloporus undulatus.* Also, Jäggi and Baur (1999) suggest that overgrowing vegetation (bushes and trees) may degrade the habitat quality for *Vipera aspis*, which may lead to the local extinction of this snake and probably other reptiles as well. It has recently been suggested that habitat favourability for reptile species is often strongly dependent on favourability for the egg stage (Andrews and Wright, 1994; Overall, 1994). In the study area, an analysis of the location of 47 nests showed that 41 (87%) were in sites with little or no vegetation cover, and none in sites with dense vegetation cover (Galán, 1996b). This strongly supports the view that the gradual coverage of the study site by vegetation reduces habitat favourability not only for adults and immature animals, but also for eggs, by reducing the availability of optimal nesting sites. Data indicate a decline over the study period in hatching success in natural nests (91% in 1989, 87% in 1990, 83% in 1991; Galán, 1996b, 1997a, 1999), though note that this is consistent both with a decline in nesting site favourability and with density-dependent effects of the type discussed above.

In the strongly Atlantic conditions of the study area, shrubs such as *Ulex europaeus* can reduce reptile habitat quality very quickly, especially for species that deposit their clutches in open, sunny spots, and this is a very likely explanation for the observed drop in population size. Furthermore, the possibility that habitat change may have reduced natality is supported by the dramatic decline in juvenile population size observed over the period of the study. Relationships between nest-site availability and population size have been demonstrated in a number of previous studies (e.g., of *Lacerta agilis* in the UK; Corbet and Tamarind, 1979; House and Spellerberg, 1980).

Sex ratio

Results indicate a female-biased sex ratio in all cohorts and the majority of age-group/period combinations considered. Clearly, results of this type may simply indicate between-sex differences in probability of capture (Ream and Ream, 1966; Gibbons, 1970; Hurly, 1987). In the present case, however, this appears unlikely, since probability of capture did not differ significantly between the sexes. Furthermore, males are markedly more conspicuous (in both appearance and behaviour) than females, while activity rates of the two sexes are similar (Galán, 1995b). Interestingly, results consistently indicate that sex ratio is female-biased not only among adults but also among juveniles and subadults.

As pointed out by Gibbons (1970, 1990), a biased sex ratio may be attributable i) to a biased primary sex ratio (i.e. at conception or hatching); ii) to environmental sex determination; iii) to a between-sex difference in mortality rates; and/or iv) to a between-sex difference in net emigration.

The fact that a female-biased sex ratio was observed not only among adults but also among immature animals is consistent with the possibility that the bias is due to an unequal sex ratio at hatching; however, data on sex ratio in laboratory-hatched clutches do not support this possibility. Furthermore, within-clutch sex ratio showed considerable variation, as has been reported for other lacertids from the Iberian Peninsula (for example *Lacerta monticola*; Barbadillo, 1985; Galán, 1991).

There is likewise no evidence to suggest that environmental sex determination occurs in *P. bocagei.* Temperature-dependent sex determination has not been observed previously in *Podarcis bocagei* (Galán, 1997a, 1999, unpubl.) or in any other species of the genus *Podarcis*, despite the fact that incubation experiments have been performed over a wide temperature range (Van Damme et al., 1992). Indeed, temperature-dependent sex determination has not been observed previously in any lacertid (Deeming and Ferguson, 1988; Janzen and Paukstis, 1991). Thus explanations (i) and (ii) can probably be ruled out, leaving (iii) and (iv).

Strongly female-biased sex ratios have been detected in other mark-recapture studies of lacertids (Heulin, 1985; Pérez-Mellado et al., 1988); indeed, it has been suggested that such a bias is characteristic of polygynous, territorial, insectivorous species (Schoener and Schoener, 1980; Stamps, 1983). Stamps (1983) hypothesised that this might be attributable to high mortality of males during territorial combat and/or to the emigration of males unable to win a territory. Nevertheless, such an explanation cannot fully explain the results of the present study, in which sex ratios were biased even when immature animals were considered. Pérez-Mellado et al. (1988), in a study of *Lacerta monticola*, found a male-to-female ratio of 0.66 (considering all age classes together), and suggested that this might be attributable to higher mobility of adult males, leading to increased exposure to predators and thus higher mortality (also see Schoener and Schoener, 1982). In the present study, it was found that survival rates did not differ significantly between the two sexes, suggesting that one of the causes of the female-biased sex ratio may be the different behaviour or mobility of males and females, as in other lizard species (M'Closkey et al., 1998). Previous studies have shown that the mean distances moved by adult males over 1-24 month periods are significantly greater than those moved by adult females: females were much more sedentary, particularly within the reproductive season, but also when 1- or 2-year periods are considered (Galán, 1994a, 1999).

Another possibility is that females migrated into (or remained in) the study area, which would be consistent with the abundance of favourable nesting sites (Galán, 1996b). Indeed, it has previously been observed that females concentrate around favourable nesting sites (Galán, 1994b, 1996b). A hypothesis of this type was put forward by Heulin (1985) to explain a female-biased sex ratio in a population of *Lacerta vivipara.*

Despite the fact that a female-biased sex ratio was observed in all cohorts and the majority of age-group/period combinations considered, in a number of periods (some including the period of reproduction) sex ratio was not significantly different from one-to-one (table 2). This might reflect seasonal concentration of males around females for breeding, but there are insufficient data to confirm this hypothesis.

In view of the fact that no between-sex difference in mortality rates were found, the biased sex ratio is probably attributable to differences in migratory behaviour. However, this cannot be confirmed with certainty, and the factors responsible may include others not considered here.

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