

DENSITY DEPENDENCE OF SURVIVAL IN THE IBERIAN WALL LIZARD (*PODARCIS HISPANICA*)

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Abstract: In this work we studied the effect of an experimental increment of density on survival of the Iberian wall lizard, *Podarcis hispanica*. The manipulation of density took place through introduction of adult males at the experimental plot located in the western zone of the Sistema Central (Iberian Peninsula). In our study area, *P. hispanica* shows one of the highest densities reported for *Podarcis* genus in the mainland. Densities not experimentally altered varied between 530 ha⁻¹ and 920 ha⁻¹, excluding hatchlings (Jolly-Seber model estimates). A departure from 1:1 sex-ratio was observed in the population under study, adult females being more numerous than adult males. Survival probability of adult males, residents and introduced, greatly decreased after the introduction of adult males at the experimental plot, but survivorship of adult females and subadult individuals of both sexes was not affected. Reduction in survival probability of resident and introduced males was directly related to density of introduced males. However, we did not detect any relation between their survival probability and density of resident adult males. Density could influence survival through competition. Thus, increment of density had a significant effect on frequency of aggressive encounters among adult males, but not on other age and sex categories. In spite of the fact that

subadult individuals were not affected by the introduction of adult males at the experimental plot, their survival probability was significantly reduced when density of resident adult males increased, perhaps because of an asymmetric competition or interference from older individuals. In conclusion, our experimental increment of adult males density has evidenced a balanced demographic structure in relation to environmental resources, and that density does not have the same effect with respect to age and sex.

Key words: density dependent, *Podarcis*, population density, population dynamics, survival.

Resumen: Supervivencia dependiente de la densidad en la lagartija ibérica (*Podarcis hispanica*). Estudiamos el efecto de un incremento experimental de la densidad sobre la supervivencia de la lagartija Ibérica, *Podarcis hispanica*. La manipulación de la densidad se efectuó liberando machos adultos en una parcela experimental situada en el oeste del Sistema Central (Península Ibérica). En nuestra área de estudio, *P. hispanica* presenta una de las densidades más altas descritas para el género *Podarcis* en áreas continentales. En condiciones no afectadas por nuestra manipulación, presenta densidades que oscilan entre los 530 ha⁻¹ y los 920 ha⁻¹, excluyendo los ejemplares juveniles (modelo

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de Jolly-Seber). La probabilidad de supervivencia de los machos adultos, residentes e introducidos, disminuyó notablemente después de la introducción de los machos adultos en la parcela experimental, pero la supervivencia de las hembras adultas y de los individuos subadultos de ambos sexos no experimentó variación alguna. La disminución en la probabilidad de supervivencia de los machos residentes e introducidos estuvo directamente relacionada con la densidad de los machos introducidos. Sin embargo, no detectamos relación alguna entre su probabilidad de supervivencia y la densidad de los machos adultos residentes. La manipulación de la densidad afecta a la supervivencia de los animales generando una situación de competencia entre ellos, aumentando la frecuencia de interacciones sociales, especialmente agresiones entre machos adultos. A pesar de que los individuos subadultos no se vieron afectados por la introducción de los machos en la parcela, su probabilidad de supervivencia disminuyó significativamente al aumentar la densidad de machos adultos residentes, quizás como consecuencia de su desventaja en la competencia con los ejemplares adultos. En conclusión, nuestro incremento experimental de la densidad ha puesto de manifiesto una estructura demográfica equilibrada en relación a los recursos del medio, no teniendo la densidad el mismo efecto sobre las distintas clases de edad y sexo.

Palabras clave: densidad dependiente, *Podarcis*, densidad de población, dinámica de población, supervivencia.

Resum: Supervivència depenent de la densitat de la sargantana ibèrica (*Podarcis hispanica*). Vam estudiar l'efecte d'un increment experimental de la densitat sobre la supervivència de la Sargantana Ibèrica, *Podarcis hispanica*. La manipulació de la densitat es va efectuar alliberant mascles

adults en una parcel·la experimental situada a l'Oest del Sistema Central (Península Ibèrica). A la nostra àrea d'estudi, *P. hispanica* presenta una de les densitats més altes descrites pel gènere *Podarcis* en àrees continentals. En condicions no afectades per la nostra manipulació, presenta densitats que oscil·len entre els 530 ha⁻¹ i els 920 ha⁻¹, excloent els exemplars juvenils (model de Jolly-Seber). La probabilitat de supervivència dels mascles adults, residents i introduïts, va disminuir notablement després de la introducció dels mascles adults en la parcel·la experimental, però la supervivència de les femelles adultes i dels individus subadults d'ambdós sexes no experimentà cap variació. La disminució en la probabilitat de supervivència dels mascles residents i introduïts va estar directament relacionada amb la densitat dels mascles introduïts. No obstant això, no vam detectar cap relació entre la seva probabilitat de supervivència i la densitat dels mascles adults residents. La manipulació de la densitat afecta a la supervivència dels animals generant una situació de competència entre ells, augmentant la freqüència d'interaccions socials, especialment agressions entre mascles adults. Malgrat que els individus subadults no es van veure afectats per la introducció dels mascles dins la parcel·la, la seva probabilitat de supervivència va disminuir significativament en augmentar la densitat de mascles adults residents, potser com a conseqüència del seu desavantatge en la competència amb exemplars adults. En conclusió, el nostre increment experimental de la densitat ha posat de manifest una estructura demogràfica equilibrada en relació als recursos del medi, mentre que la densitat no té el mateix efecte sobre les diferents classes d'edat i sexe.

Paraules clau: dependència de la densitat, *Podarcis*, densitat de població, dinàmica de poblacions, supervivència.

INTRODUCTION

Constancy in time is a measure of density stability (PIMM & REDFEARN, 1988). Lizard populations in which density fluctuates only moderately have been described (TURNER *et al.*, 1970; BRADSHAW, 1971; BARBAULT, 1975; BARBAULT & MOU, 1988), but populations in which density usually differs between years have been described, too (LAURIE, 1989a; LAURIE & BROWN, 1990a; ANDREWS, 1991; GALÁN, 1994). So, it is certainly interesting to analyse the role that density dependence plays in the demographic strategies of reptile populations (LEBRETON *et al.*, 1992). Diverse extrinsic factors may regulate the density of species, such as food availability (GUYER, 1988; LAURIE, 1989a; BOUTIN, 1990; STAMPS & TANAKA, 1981), habitat (LEE, 1974; TURNER, 1977), predation (TURNER *et al.*, 1974), parasitism (DOBSON & HUDSON, 1986), and other environmental fluctuations (TURNER *et al.*, 1974; LAURIE, 1989a, 1989b; LAURIE & BROWN, 1990a).

The probability of survival may vary with individual characteristics such as age, sex, mass, genotype, or phenotype, and as a function of biotic and abiotic environmental variables (BEGON, 1984; LAURIE, 1990; LAURIE & BROWN, 1990b; LEBRETON *et al.*, 1992). Intra- and interspecific competition and predation can also affect the probability of survival. Testing hypotheses concerning the survival process and estimating survival rates are therefore critical to understanding animal population dynamics (TURNER *et al.*, 1974; LOREY & NICHOLS, 1985; LEBRETON *et al.*, 1992).

The particular ways in which mortality differs according to sex, age, size, condition and reproductive history have important consequences for population structure and stability (LOMNICKI, 1980; LAURIE, 1990). Hence, when densities exceed environmental capacities (food, space, shelter,...), mortality or emigration acts to balance numbers and resources (TURNER, 1977).

By manipulating population density we use one of the most powerful tools for investigating demography (KREBS, 1988). Density manipulations have rarely been carried out on lacertids (PILORGE, 1988; MASSOT *et al.*, 1992). In this work we studied the effect of an experimental increment of density on survival of the Iberian wall lizard, *Podarcis hispanica*.

MATERIAL AND METHODS

The species

P. hispanica (Squamata, Lacertidae) is a small (adult snout-vent length 37-70 mm) wall lizard whose distributional range is limited to the Iberian Peninsula, southern France and North Africa. A complete description of this species and its geographical distribution can be found in PÉREZ-MELLADO (1997, 1998).

Field description and experimental protocol

The study area is situated in the western zone of the Sistema Central of the Iberian Peninsula, at the Sierra de la Peña de Francia (elevation 1074 m a. s. l.),

Salamanca, Spain (40° 31' 44" N, 06° 07' 10" W). This area comprised a granite outcrop within an open mixed deciduous woodland dominated by oak *Quercus pyrenaica*. A more detailed description of the study area can be found in DIEGO-RASILLA & PÉREZ-MELLADO (2000a, 2003).

We carried out a selective manipulation of density on a *P. hispanica* population. The manipulation of density took place through introduction of adult males at the experimental plot of 1500 m² defined on the study area. The individuals were captured from neighbouring areas approximately 6-7 kilometres from the study plot (DIEGO-RASILLA, 1999).

The study was conducted from 1991 to 1993. The field site was monitored each year during May, June, July and September. In each period, the site was visited during five to ten consecutive days. We experimentally increased the density at the beginning of the summer in 1991 and 1993. In 1991, the introduction of 29 adult males in the experimental plot increased the density of adult males by 0.94 times. In 1993 we introduced 63 adult males which increased the density of adult males by 3.5 times (DIEGO-RASILLA, 1999).

Demographic analyses require the capture and recapture of individuals. Lizards were permanently marked using a system of clipping off the distal phalanx of one or more toes (DUNHAM *et al.*, 1988). Removal of toes has been considered to have little or no effect of the fitness or survival of the specimen (WOODBURY, 1956; FERNER, 1979;

DUNHAM *et al.*, 1988; HUDSON, 1996). In addition, we applied unique paint marks to individuals. These marks were colour-coded dots applied to the dorsum that allowed visual identification of individuals (DUNHAM *et al.*, 1988). Two studies suggest that paint marking does not increase the mortality rate of marked individuals (JONES & FERGUSON, 1980; SIMON & BISSINGER, 1983). We captured 293 resident animals in the experimental plot throughout three years study. During each census, we attempted to register all of the individuals in the population. Three age-classes of lizards were distinguished: hatchlings (born during August and September); subadults (born during the preceding year, nonreproductive); and adults (reproductive lizards).

Climatic data

The National Institute of Meteorology (Territorial Meteorological Center of Castilla y León) provided climatic data from four weather stations up to 10 kilometres from the study site. These data revealed quite similar climatological characteristics throughout the study (see Results).

Data and statistical methods

Age, sex, body length (SVL in millimetres, accuracy: ± 1 mm) and mass (accuracy: ± 0.01 g), and other morphological and behavioural characteristics were recorded at each capture. Every time an animal was captured or recaptured, we recorded its

behaviour. Three mutually exclusive behavioural categories were recognized:

1-Agonistic behaviour among males.

2-Courtship and mating.

3-Other behaviours.

Agonistic behaviour among females was not included due to its low frequency. We only recorded eight cases during the study. Aggressions by females to adult males were not recorded due to their low frequency; there were only five cases.

Within each sampling period, captures and recaptures provided data for studying the evolution of demographic parameters through time considering an open population model. The basic open population model suitable for this situation is the Jolly-Seber model (JOLLY, 1965; SEBER, 1965, 1982). This model allows the estimation of population size at each sampling time as well as survival rates and birth numbers between sampling times. However, migration cannot be separated from the birth and death processes without additional information (POLLOCK *et al.*, 1990).

The Jolly-Seber method is described fully by POLLOCK (1981) and POLLOCK *et al.* (1990), so only brief details are given here. The following notation is used: M_i = the number of marked animals in the population at the time the i th sample is taken ($i = 1, \dots, k$; $M_0 = 0$); N_i = the total number of animals in the population at the time the i th sample is taken ($i = 1, \dots, k$); B_i = the total number of new animals entering the population between the i th

and $(i + 1)$ th sample and still in the population at the time $(i + 1)$ th sample is taken ($i = 1, \dots, k-1$); N_i = the survival probability for all animals between the i th and $(i + 1)$ th sample ($i = 1, \dots, k - 1$); p_i = the capture probability for all animals in the i th sample ($i = 1, \dots, k$); m_i = the number of previously marked animals captured in the i th sample ($i = 1, \dots, k$); R_i = the number of marked animals known to be in the population at the end of the i th sample ($i = 1, \dots, k-1$), R_c is thus m_i plus the number of additional marked animals in i th sample less the number of previously marked animals found dead; r_i = the number of the R_i animals released at i that are captured again ($i = 1, \dots, k-1$); z_i = the number of animals captured before i , not captured at i , and captured again later ($i = 2, \dots, k-1$). POLLOCK *et al.* (1990) give an intuitive discussion of parameter estimation and of variances and covariances for the estimators.

This model makes a critical assumption: equal catchability for marked and unmarked individuals (POLLOCK *et al.*, 1990). In order to guarantee that all model assumptions had been met by the data we applied the goodness-of-fit test of the Jolly-Seber model (POLLOCK *et al.*, 1985). This test has been implemented in the program JOLLY (© James E. Hines, 1990).

The values of m_i , R_i , r_i and z_i for each group in each period of the study are shown in appendix 1. We estimated population density (No. of animals/1500 m²) for each sampling period, excluding hatchlings.

We used standard statistical methods (Spearman rank correlation

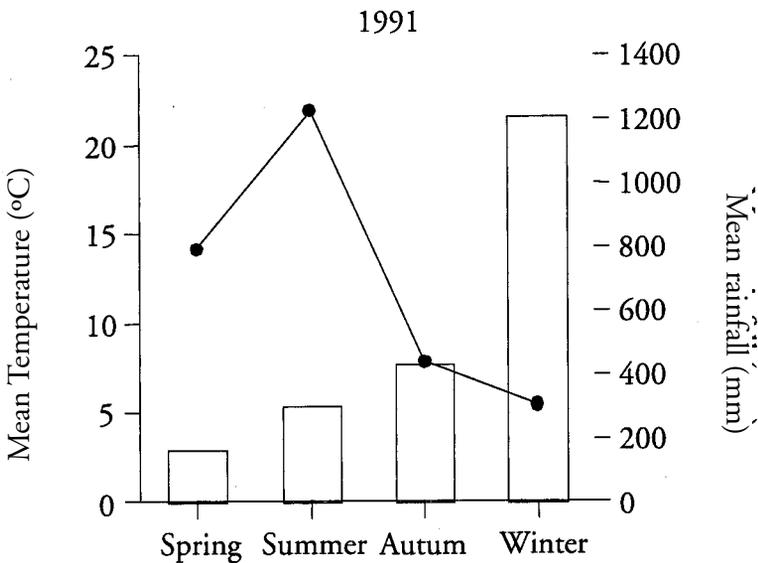
test, *t*-test, ANOVA, Scheffé *a posteriori* test, Kruskal-Wallis test, Dunn *a posteriori* test, and chi-square test) to evaluate relationships or differences among variables. The standard criterion of statistical significance was $p < 0.05$.

RESULTS

Climatic conditions

Weather conditions were quite stable during the study (Figure 1), which is important for comparative purposes. There were no significant differences between years in mean temperature during the spring (One-way ANOVA; $F_{[2, 17]} = 0.209$, $p = 0.814$), summer

(Kruskal-Wallis test; $\chi^2 = 4.013$, $df = 2$, $p = 0.134$), autumn (One-way ANOVA; $F_{[2, 17]} = 0.401$, $p = 0.677$) or winter (One-way ANOVA; $F_{[2, 17]} = 0.067$, $p = 0.935$). There were no significant differences between years in summer (Kruskal-Wallis test; $\chi^2 = 1.132$, $df = 2$, $p = 0.568$), or autumn (Kruskal-Wallis test; $\chi^2 = 2.653$, $df = 2$, $p = 0.265$) rainfall. Mean rainfall was higher during the spring of 1993 than during the spring of 1991 (Kruskal-Wallis test; $\chi^2 = 13.534$, $df = 2$, $p = 0.001$) (Dunn *a posteriori* test; $p < 0.05$), and it was higher during the winter of 1991 than during the winter of 1992 and 1993 (Kruskal-Wallis test; $\chi^2 = 13.629$, $df = 2$, $p = 0.001$) (Dunn *a posteriori* test; $p < 0.05$).



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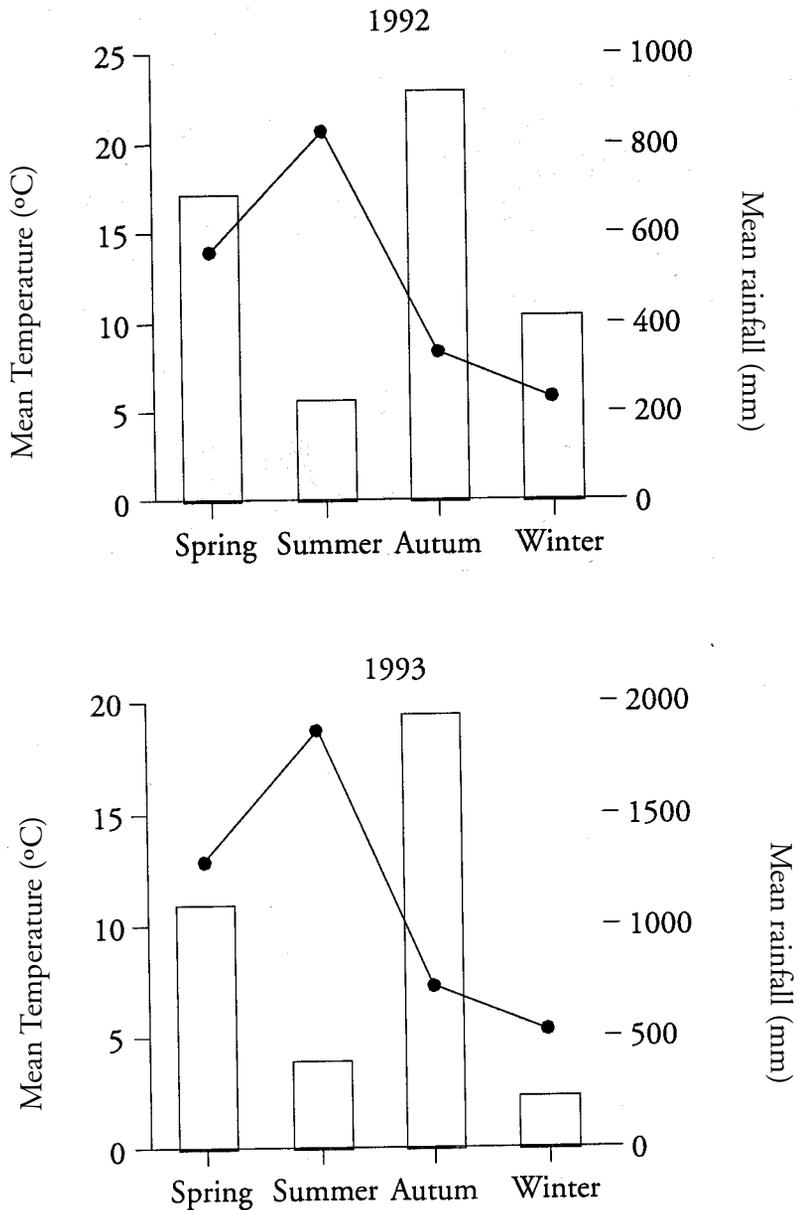


Figure 1. Mean temperature (lines) and mean rainfall (bars) during 1991, 1992 and 1993. The National Institute of Meteorology provided climatic data from four weather stations up to 10 km from the study site

Density and sex-ratio

Mean estimated population density, when the introduced adult males were excluded from the analyses, varies between 66.45/1500 m² (standard error = 17.05) and 137.99/1500 m² (standard error = 26.88) (Figure 2). It is important

to point out the marked reduction in density in sampling periods following the introduction of adult males at the experimental plot (July 1991: 95.39/1500 m², September 1991: 83.72/1500 m², June-July 1993: 78.20/1500 m², and July 1993: 66.45/1500 m²).

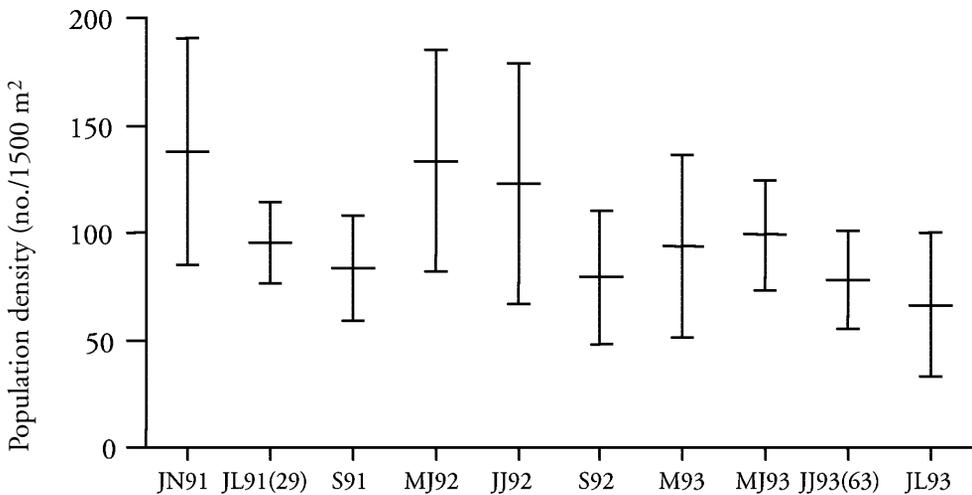


Figure 2. Estimates of total population density of *Podarcis hispanica* at the experimental plot, where density manipulation was performed. Introduced adult males were excluded from these estimations. Density was estimated using Jolly-Seber model. On the time axis, (29 and 63): where adult male numbers were increased through introduction of 29 and 63 adult males at the experimental plot; sessions of capture: JN91 = June 1991, JL91 = July 1991, S91 = September 1991, MJ92 = May-June 1992, JJ92 = June-July 1992, S92 = September 1992, M93 = May 1993, MJ93 = May-June 1993, JJ93 = June-July 1993, JL93 = July 1993. Vertical lines = 95% confidence intervals

Operational sex ratio (adult males/adult females) was estimated for resident animals (Table 1). In all sampling periods, except periods number 7 and 9, operational sex ratio differed significantly from 1:1 ratio (Chi-square test, $p < 0.05$), the number of adult females being greater than the number of resident adult males. If we group sampling periods belonging to summer of 1992 (sampling periods

number 6 and 7), the number of adult females was significantly greater than the number of adult males (Chi-square test; $\chi^2 = 8.58$, $p = 0.003$). Similarly, grouping sampling periods in spring of 1993 (sampling periods number 8 and 9), operational sex ratio differed significantly from unity (Chi-square test; $\chi^2 = 5.26$, $p = 0.02$), more adult females inhabiting the plot than adult males.

Study period	Date	Operative sex-ratio (♂/♀)	χ^2	P
2	June 1991	0.57(31.28/55.04)	6.54	0.01
3	July 1991	0.49(27.8/56.67)	9.87	0.002
4	September 1991	0.34(17.9/52.02)	16.7	<0.0001
5	May-June 1992	0.44(15.38/35.10)	7.7	0.006
6	June-July 1992	0.51(21.25/41.87)	6.74	0.009
7	September 1992	0.67(24.85/36.98)	2.38	0.12
8	May 1993	0.44(9.67/22.10)	4.86	0.03
9	May-June 1993	0.72(21.30/29.75)	1.4	0.24
10	June-July 1993	0.55(18.35/33.46)	4.41	0.036
11	July 1993	0.27(9.33/34.83)	14.7	0.0001

Table 1. Operative sex-ratio of the Iberian wall lizard, *Podarcis hispanica*, at the experimental plot, where density manipulation was performed. Only resident lizards were included

We estimated operational sex ratio including introduced adult males too. Our results indicated that the introduction of adult males in July of 1991 balanced the number of adult individuals of both sexes [operational sex ratio = 0.72 (40.8/56.67)] (Chi-square test; $\chi^2 = 2.58$, $p = 0.11$). The second introduction (June-July 1993) unbalanced the operational sex ratio [operational sex ratio = 2.46 (82.35/33.46)] (Chi-square test; $\chi^2 = 20.64$, $p < 0.0001$). However, in the next sampling period (July 1993), the reduced survival probability of adult males, resident and introduced, led to an operational sex ratio of 1:1 [operational sex ratio = 0.64 (22.33/34.83)] (Chi-square test; $\chi^2 = 2.73$, $p = 0.10$).

Survival rate

Basic data used to estimate survival rates of different sex and age classes are presented in appendix 1. The number of resident adult males in the population kept fairly stable and their survival probability was high during the study period, excepting sampling periods that followed the experimental introductions of adult males in the plot. Thus, survival of resident males greatly decreased in July and September of 1991, just after we carried out the introduction of adult males, that took place in late June (Table 2, Figure 3). The sampling period of June 1991 was immediately before the introduction, and the survival probability of adult males was higher in

Study Period	Date	RESIDENT ADULT MALES				INTRODUCED ADULT MALES			
		Φ_i	SE(Φ_i)	B_i	SE(B_i)	Φ_i	SE(Φ_i)	B_i	SE(B_i)
1	May 91	0.5958	0.1518						
2	June 91	0.8205	0.1217	2.13	7.36	0.4483	0.1091		
3	July 91	0.5839	0.1402	1.67	1.35	0.6818	0.4668	0.14	0.09
4	September 91	0.3419	0.1245	9.26	1.78	0.2917	0.2663	0.87	0.41
5	May-June 92	1.0000	0.2562	4.01	4.15	0.7500	?	0.37	?
6	June-July 92	0.7172	0.2743	9.61	8.87	?	?	?	?
7	September 92	0.8056	0.3114	4.15	12.04	1.0000	?	0.00	?
8	May 93	0.8192	0.2444	1.50	8.83	?	?	?	?
10	June-July 93	0.2844	0.1237	4.11	2.21	0.2031	0.0997	0.00	0.00
11	July 93								
12	September 93								
Mean		0.7028	0.0338	3.87	1.11	0.6250	?	10.73	?

Table 2. Estimates and approximate standard errors of survival rates and total number of new animals entering the population using the Jolly-Seber model. ? denotes estimates which cannot be computed due to poor data. Means do not include these study periods

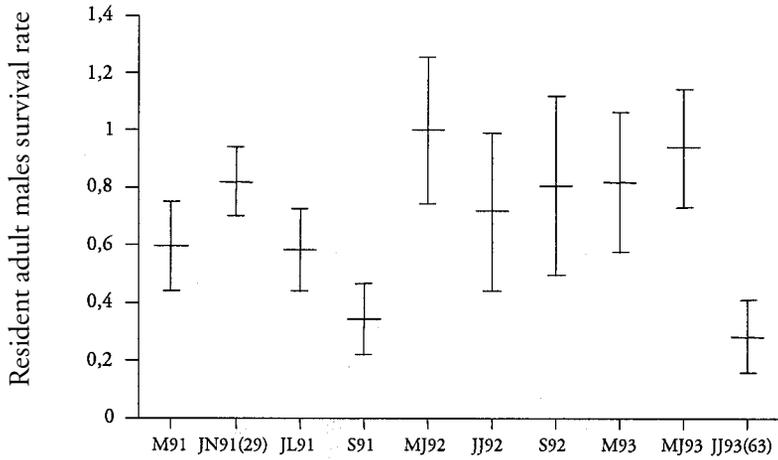


Figure 3. Survival rates (mean \pm 1 SE) of *Podarcis hispanica* at the experimental plot, where density manipulation was performed. On the time axis, (29 and 63) : where adult male numbers were increased through introduction of 29 and 63 adult males at the experimental plot; sessions of capture: JN91 = June 1991, JL91 = July 1991, S91 = September 1991, MJ92 = May-June 1992, JJ92 = June-July 1992, S92 = September 1992, M93 = May 1993, MJ93 = May-June 1993, JJ93 = June-July 1993, JL93 = July 1993

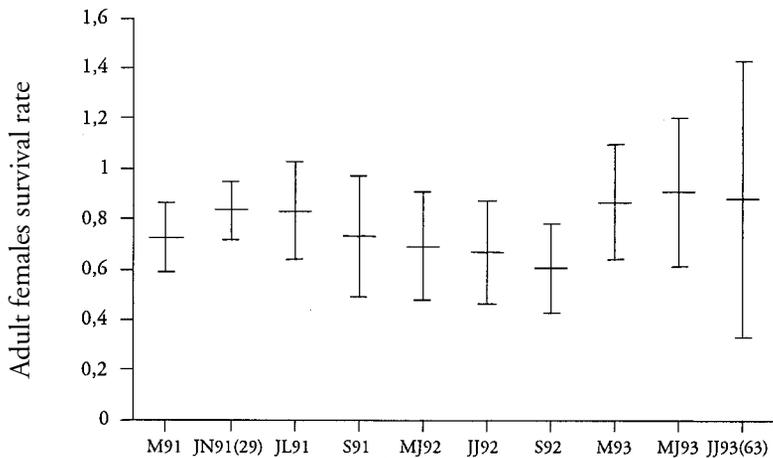


Figure 4. Survival rates (mean \pm 1 SE) of adult females at the experimental plot, where density manipulation was performed. On the time axis, (29 and 63) : where adult male numbers were increased through introduction of 29 and 63 adult males at the experimental plot; session of capture: JN91 = June 1991, JL91 = July, S91 = September 1991, MJ92 = May-June, 1992, JJ92 = June-July 1992, S92 = September 1992, M93 = May 1993, MJ03 = May-June 1993, JJ93 = June-July 1993, JL93 = July 1993

this period ($\phi_i = 0.8205$). Similarly, this happened during the spring of 1993 ($\phi_i = 0.9382$), just before we performed the second introduction. This second manipulation (see Table 2 and Figure 3) was more extreme and with a clear influence on the survival probability of resident adult males ($\phi_i = 0.2844$), fairly lower than in the summer of 1991 ($\phi_{i[\text{July}]} = 0.5839$, $\phi_{i[\text{September}]} = 0.3419$).

Survival probability of adult females is notably high throughout the study ($\phi_{i(\text{mean})} = 0.7731$, standard error = 0.0564) and we did not detect any variations in response to the introduction of adult males, unlike what happened with resident adult males (Table 3, Figure 4).

Survival rate of introduced adult males was certainly low during sampling periods following their release in the plot (June, July and September of 1991, and June-July of 1993). However, the survival probability of those males that became settled at the plot was really high (Table 2, Figure 5).

Survival probability of subadult individuals of both sexes was high throughout the study, except in summer of 1992. Their survival rate was high after the introductions of adult males (Table 3, Figure 6). The survival probability for hatchlings between September of 1991 and May of 1992 was 0.7600 ± 0.2771 , and between

Period	Date	ADULT FEMALES				SUBADULT INDIVIDUALS			
		ϕ_i	SE(ϕ_i)	B_i	SE(B_i)	ϕ_i	SE(ϕ_i)	B_i	SE(B_i)
1	May 91	0.7242	0.1379			1.0000	0.3578		
2	June 91	0.8327	0.1185	10.84	11.62	0.5887	0.1922	0.00	10.83
3	July 91	0.8320	0.1932	4.88	6.68	0.7879	0.1600	3.67	1.45
4	September 91	0.7286	0.2400	59.24	32.71	0.8697	0.2193	18.69	7.48
5	May-June 92	0.6899	0.2142	0.00	22.15	1.0000	0.7334	3.86	12.26
6	June-July 92	0.6658	0.2034	9.10	5.70	0.3210	0.2309	0.00	3.16
7	September 92	0.6042	0.1767	0.00	4.02	0.4178	0.2240	27.99	16.06
8	May 93	0.8658	0.2299	10.62	4.81	1.0000	0.1448	4.30	26.78
9	May-June 93	0.9085	0.2970	6.43	6.77	0.6209	0.1268	0.00	3.83
10	June-July 93	0.8796	0.5519	5.40	8.12	1.0000	0.5368	0.00	1.62
11	July 93								
12	September 93								
Mean		0.7731	0.0564	8.69	2.59	0.8047	0.0832	5.39	2.88

Table 3. Estimates and approximate standard errors of survival rates and total number of new animals entering the population using the Jolly-Seber model

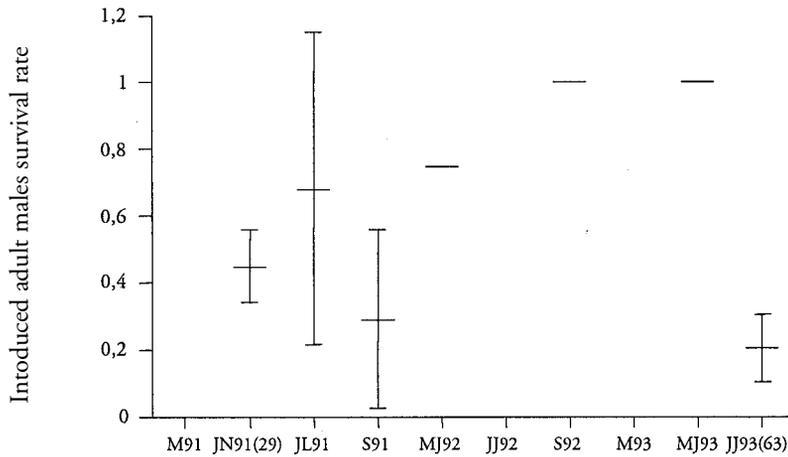


Figure 5. Survival rates (mean \pm 1 SE) of introduced adult males at the experimental plot. On the time axis, (29 and 63): where adult male numbers were increased through introduction of 29 and 63 adult males at the experimental plot; sessions of capture: JN91 = June 1991, JL91 = July 1991, S91 = September 1991, MJ92 = May-June 1992, JJ92 = June-July 1992, S92 = September 1992, M93 = May 1993, MJ93 = May-June, JJ93 = June-July 1993, JL93 = July 1993

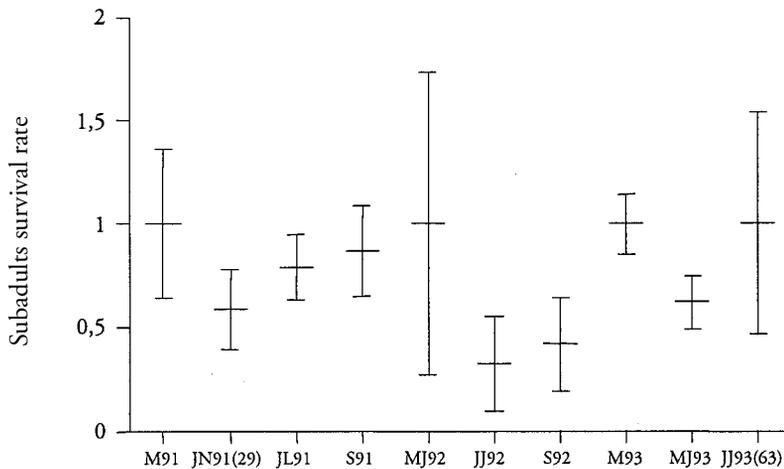


Figure 6. Survival rates (mean \pm 1 SE) of subadult individuals at the experimental plot, where density manipulation was performed. On the time axis, (29 and 63): where adult male numbers were increased through introduction of 29 and 63 adult males at the experimental plot; sessions of capture: JN91 = June 1991, JL91 = July 1991, S91 = September 1991, MJ92 = May-June 1992, JJ92 = June-July 1992, S92 = September 1992, M93 = May 1993, MJ93 = May-June, JJ93 = June-July 1993, JL93 = July 1993

September of 1992 and May of 1993 was 0.4118 ± 0.1184 .

A two-way ANOVA revealed a significant effect of higher density ($F_{[1, 21]} = 13.550$, $p = 0.001$), but not of animal categories (resident adult males, introduced adult males, and adult females) on survival rates ($F_{[2, 21]} = 3.233$, $p = 0.060$). However, density and categories interacted significantly ($F_{[2, 21]} = 5.307$, $p = 0.014$). The increment of density led to a significant reduction of survival probability in adult males, both resident and introduced males, but it did not affect survival by adult females. The survival rates of subadult individuals were not affected by the increment of density (t-test; $t = -1.415$, $df = 7.994$, $p = 0.195$) (Figures 3, 4, 5 and 6).

Survival probability of subadult animals was inversely related to the density of resident adult males in the experimental plot (Spearman rank

correlation test; $r_s = -0.695$, $p = 0.038$). Apart from this, the only effect of density on survival rate was found in adult males, both resident and introduced. Density of introduced males was inversely related to survival probability of resident (Spearman rank correlation test; $r_s = -0.708$, $p = 0.050$) and introduced males (Spearman rank correlation test; $r_s = -0.941$, $p = 0.005$), whereas density of resident males was not related to survival rate of resident (Spearman rank correlation test; $r_s = -0.017$, $p = 0.966$), and introduced males (Spearman rank correlation test; $r_s = 0.126$, $p = 0.788$).

Effect of density on behaviour

Table 4 shows frequencies and percentages of recorded behavioural categories during the study. We did not find significant differences in frequencies of behavioural categories

	Agonistic behaviour among adult males		Courtship and mating		Other behaviours	
	Frequency	Percentage	Frequency	Percentage	Frequency	Percentage
Spring 1991	0	0	10	4.03	238	95.97
Summer 1991	14	1.32	8	0.76	1035	97.92
Spring 1992	3	1.72	5	2.87	166	95.40
Summer 1992	1	0.40	3	1.21	244	98.39
Spring 1993	4	1.05	8	2.11	368	96.84
Summer 1993	32	4.92	16	2.46	602	92.62

Table 4. Frequency and percentages of behavioural categories during the spring and summer of 1991, 1992 and 1993

during the springs of 1991, 1992, and 1993 (Chi-square test; $\chi^2 = 4.26$, $p > 0.05$). However, frequency of behavioural categories showed significant differences between years, when we considered the summer months (Chi-square test; $\chi^2 = 36.24$, $p < 0.001$).

As we pointed out above, after the second release of adult males (i.e., summer of 1993) we obtained the greatest increment of density, which apparently produced higher effects on lizard behaviour. The frequency of agonistic behaviours among adult males significantly increased, as well as frequency of courtships and mating (Table 4). Courtship behaviour and mating usually take place during spring, but some courtship behaviour and mating were observed during early summer. The frequency of these behaviours increased during the summer of 1993, being even higher than during the spring of the same year (Table 4).

DISCUSSION

Density

TURNER (1977) compiled density values for several lizard populations. He found that the lowest reported densities ($< 10/\text{ha}$) are those of species occupying relatively unproductive environments, whereas the highest densities ($\sim 1000/\text{ha}$) are from lizards inhabiting particularly productive areas, or species with adaptations permitting the exploitation of an unusually rich food source (e.g., *Amblyrhynchus cristatus*, CARPENTER, 1966).

The population we studied showed intermediate densities, if comparing with these values. The lowest and highest densities, not experimentally altered, were 530/ha (September of 1992) and 920/ha (June of 1991). MARCOS-LEÓN (1992), studied *P. hispanica* densities in an area close to our study site, obtaining lower densities, ranging from 312-563 animals/ha over four years. In other areas of the Iberian Peninsula even lower densities have been described for this species. Thus, DELIBES & SALVADOR (1986) obtained a mean density of 45/ha, and a highest density of 112.5/ha. Consequently, *P. hispanica*, in our study area, shows one of the highest densities reported for *Podarcis* in the mainland. Our estimates are even slightly higher than those reported by PÉREZ-MELLADO *et al.* (1994) in *P. hispanica* from Benidorm Island (southeastern Spain, 400-500/ha). However, a closely related species, *Podarcis bocagei*, may reach densities of up to 2049/ha in northwestern Iberian Peninsula, including hatchlings (GALÁN, 1994). Hatchlings were not included in the estimates cited above.

High densities of island populations of lacertids of the genus *Podarcis* have been reported (OUBOTER, 1981; CASTILLA & BAUWENS, 1991; BROWN *et al.*, 1992; BROWN & PÉREZ-MELLADO, 1994). In these populations the density is usually explained in terms of release from interspecific competition and lack or relaxation of predation. Inversely, our study site, is characterized by a strong predation pressure on lizard populations (CASTILLA *et al.*, 1999).

Current models of habitat selection assume that higher quality resource habitats will be occupied at higher densities than poor habitats (FRETWELL, 1972). This factor can explain the high density observed. Our experimental plot is situated on a granite outcrop and *P. hispanica* is a saxicolous species that employs rocks as perching sites for thermoregulation, foraging, and refuge (DIEGO-RASILLA & PÉREZ-MELLADO, 2000b, 2003).

Effect of density on sex ratio

Sex ratios of lizard populations are usually close to 1:1 (TURNER, 1977). In *P. hispanica*, PÉREZ-MELLADO *et al.* (1991) and MARCOS-LEÓN (1992), found a 1:1 sex ratio, as did CASTILLA & BAUWENS (1991) in a population of *P. atrata*, the phylogenetically closest species (CASTILLA *et al.*, 1998). However, a departure from a 1:1 sex ratio was observed in the population under study, adult females being more numerous than adult males. This result agrees with those of STRIJBOSCH & CREEMERS (1988) for *Lacerta vivipara* and *Lacerta agilis*. Our skewed sex-ratio can be interpreted as the result of different survival rates for males and females, as it has been shown for some lizard species, where females enjoy better survivorship than males throughout life (BLAIR, 1960; TINKLE, 1967a; STRIJBOSCH & CREEMERS, 1988). In this sense, increased density is responsible for a reduction in survival probability of adult males, both resident and introduced males, in the experimental plot. The apparently high mortality of

adult males, reduced density in the months following introduction, and immigration contributed to later density readjustment. Disappearance of adult males from the study area, during the summer of 1991, produced an important immigration of individuals from the surroundings, from late summer of 1991 to early summer of 1992. Thus, floaters quickly moved into vacated home ranges. These variations in immigration appear to have modified the sex-ratio to 1:1 by late summer of 1992. However, a readjustment of sex ratio to the prior increment of density levels (i.e., adult females being more numerous than adult males) was achieved in the spring of 1993.

Survival rate

Considering the strong fidelity to home ranges (DIEGO-RASILLA & PÉREZ-MELLADO, 2003), losses owing to emigration are small compared to the number of animals dying, which may be roughly offset by gains due to immigration (TINKLE, 1967b). Some studies have indicated that effects of emigration and immigration on population size and structure are negligible (BALLINGER, 1973) or influence the population structure only slightly (COGGER, 1969). Thus, it is reasonable to consider losses of individuals as essentially due to mortality (TURNER, 1977).

Reduction in survival probability of resident and introduced males was directly related to density of introduced males. However, we did not detect any relation between the survival probability and density of resident adult males. Our

experiment confirmed the key role of density in affecting survival rates of adult males. Adult male survivorship responded to changes in density and contributed most to density readjustment. Thus, survival probability of adult males, both resident and introduced males, greatly decreased after the introduction of adult males at the experimental plot, but survivorship of adult females and subadult individuals of both sexes was not affected.

We found that survival probability of each class of individuals was affected in a different way. Density can influence animal survival through competition (LEBRETON *et al.*, 1992). Increment of density had a significant effect on frequency of aggressive encounters among adult males, but not on other age and sex categories. This led adult males to modify their normal activity patterns, increasing significantly the time devoted to basking (DIEGO-RASILLA & PÉREZ-MELLADO, 2000a). Hence, thermoregulation is influenced by the presence of competitors, which increases thermoregulatory costs. Temperature exerts a profound effect on virtually everything a reptile does, and the rates of many physiological processes reach optima within a species activity temperature range (HUEY, 1982; POUGH *et al.*, 1998). Thus, if adult males could not maintain body temperatures within the activity range, their capacity for performance declined (BENNETT, 1980; WALDSCHMIDT & TRACY, 1983; VAN BERKUM, 1986). In addition, high levels of social interaction might allow introduced adult males and juveniles to track resources by assessing the

behaviour of neighbouring lizards (KIESTER & SLATKIN, 1974; STAMPS, 1987, 1988).

In lizards, a positive effect of ownership on fighting success has been demonstrated experimentally (COOPER & VITT, 1987). Thus, the effect of residency on competitive ability could be very important. Resident animals exhibited remarkable fidelity to their home range (DIEGO-RASILLA & PÉREZ-MELLADO, 2003), which conferred an advantage in relation to intruders (LEIMAR & ENQUIST, 1984; COOPER & VITT, 1987; EDSMAN, 1990). Hence, adult males released at the experimental plot were at a disadvantage in this sense. In addition, introduced adult males modified their normal activity patterns, which might have contributed to their decrease in survival.

Studies carried out in this population showed an association between the habitat choice of lizards and the presence of refuges. This suggests that habitat-specific predation rates may be a major selective force in habitat selection (DIEGO-RASILLA & PÉREZ-MELLADO, 2000b, 2003). Being familiar with the habitat, a lizard has a precise knowledge of safe hiding places to avoid predation (KREKORIAN, 1977; CHRISTIAN & TRACY, 1981; SNELL *et al.*, 1988). Lizards released in the experimental plot were not, obviously, familiar with their new habitat. These animals would not have the benefit of memorized escape routes from predators as they would within their home ranges. Thus, the high rate of disappearance of introduced males during the first weeks after release may have been due to

predation. Lizards released within the plot would be forced to wander in search of favourable sites, thus increasing their exposure to predators, or to occupy poor quality habitats with similar results (DIEGO-RASILLA & PÉREZ-MELLADO, 2000b, 2003). WEINTRAUB (1970) found the same result working with *Sceloporus orcutti*. He displaced animals from their home range and observed a high rate of disappearance of displaced *S. orcutti* during the first 20 days after release. This can explain why released animals finally settled in our experimental plot achieved a survival probability higher than 0.7500.

In spite of the fact that subadult individuals were not affected by introduction of adult males at the experimental plot, their survival probability was significantly reduced when density of resident adult males increased. The existence of asymmetric competition or interference from older individuals can explain this result. It is likely that there may be competition for shelter or basking sites, as well as for food, between both categories when density of adult males increases, and this can result in density dependent effects on growth and survival of subadult animals. Density dependence of juvenile survival rates has been described in other studies (LAURIE & BROWN, 1990b; MASSOT *et al.*, 1992). In this sense, TUBBS & FERGUSON (1976) demonstrated that juveniles of *S. undulatus* showed a growth rate strongly affected by density (see also a similar result in *L. vivipara*, MASSOT *et al.*, 1992).

We can conclude that our experimental increment of adult males density has evidenced that density does not have the same effect with respect to age and sex (BEGON, 1984; LAURIE & BROWN, 1990a; MASSOT *et al.*, 1992). Our observations emphasize the importance of social behaviour as a part of the regulatory mechanism of the population.

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Appendix 1. Basic data used to estimate survival rates in animals of different sexes and age classes. m_i = the number of previously marked animals captured in the i th sample ($i = 1, \dots, k$); R_i = the number of marked animals known to be in the population at the end of the i th sample ($i = 1, \dots, k-1$); R_i is thus m_i plus the number of additional

marked animals in i th sample less the number of previously marked animals found dead; r_i = the number of the R_i animals released at i that are captured again ($i = 1, \dots, k-1$); z_i = the number of animals captured before i , not captured at i , and captured again later ($i = 2, \dots, k-1$).

a) Resident adult males

Period	Date	m_i	R_i	r_i	z_i
1	May 91	0	15	8	0
2	June 91	5	20	15	3
3	July 91	16	23	12	2
4	September 91	13	15	5	1
5	May-June 92	5	14	12	1
6	June-July 92	7	9	5	6
7	September 92	3	6	4	8
8	May 93	2	4	3	10
9	May-June 93	7	11	9	6
10	June-July 93	14	15	14	1
11	July 93	3	6	5	2
12	September 93	7	15	0	0

b) Adults females

Period	Date	m_i	R_i	r_i	z_i
1	May 91	0	19	12	0
2	June 91	8	35	24	4
3	July 91	20	34	19	8
4	September 91	16	21	9	11
5	May-June 92	6	19	9	14
6	June-July 92	11	14	7	12
7	September 92	12	18	9	7
8	May 93	6	7	5	10
9	May-June 93	10	17	10	5
10	June-July 93	8	12	5	7
11	July 93	7	10	2	5
12	September 93	7	10	0	0

c) Introduced adult males

Period	Date	m_i	R_i	r_i	z_i
1	May 91				
2	June 91	0	29	12	0
3	July 91	11	11	5	1
4	September 91	4	4	1	2
5	May-June 92	2	2	1	1
6	June-July 92	1	1	0	1
7	September 92	1	1	1	0
8	May 93	0	0	0	1
9	May-June 93	1	1	1	0
10	June-July 93	1	64	9	0
11	July 93	6	6	2	3
12	September 93	5	5	0	0

d) Subadults individuals

Period	Date	m_i	R_i	r_i	z_i
1	May 91	0	13	9	0
2	June 91	2	7	4	7
3	July 91	10	11	8	1
4	September 91	7	10	7	2
5	May-June 92	6	18	10	3
6	June-July 92	6	9	2	7
7	September 92	5	5	2	4
8	May 93	2	15	14	4
9	May-June 93	13	26	14	5
10	June-July 93	15	18	10	4
11	July 93	8	8	2	6
12	September 93	8	8	0	0