

REPRODUCTIVE STRATEGY IN A MONTANE POPULATION OF THE LIZARD *LACERTA SCHREIBERI* (SAURIA: LACERTIDAE)

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The mountain population of *Lacerta schreiberi* studied at the Sistema Central (Spain) showed a narrow and highly synchronized reproductive period, adjusted to short periods of annual activity, that are characteristic of these Iberian areas. Adult females reached sexual maturity at a minimum age of four years. Only one clutch of eggs is laid per year. The average clutch size of 14 eggs was positively correlated with female body size. Clutch weight was high (25 to 56% of net female weight), and incubation time was long (65 to 110 days). During incubation eggs reached three times their initial weight. We found a noticeable variability in some reproductive characteristics during the three years under study and among individual females. The greatest phenotypic plasticity was in the size of the eggs, incubation time, and the size of hatchlings, while clutch size showed a higher stability in its average values.

INTRODUCTION

Reproductive traits of several species of lizards can be considered unstable characteristics with important variation between populations (Ballinger, 1979, 1983; Braña & Bea, 1987; Dunham, 1978; Pianka, 1970; Tinkle & Ballinger, 1972), as well as within populations (Bauwens & Verheyen, 1987; Ferguson, Snell & Landwer, 1990; Pilorge, Xavier & Barbault, 1983). Such variability is due to annual variation of climatic factors and/or individual differences (fat reserves, body size, annual frequency of clutches), and suggest that some selective pressures are involved in producing adaptive phenotypes (Ferguson, Brown & Demarco, 1982).

The best strategy to study reproductive traits seems to be the long term tracking of marked individuals in populations of the temperate area. Such populations are subject to unpredictable annual variations of climate that promote differential selection of individual phenotypes (Braña, Bea & Arrayago, 1991; Frankenberg & Werner, 1992; Pilorge *et al.*, 1983; Shine, 1983).

In this work we present basic information about the reproductive characteristics of *Lacerta schreiberi*, an endemic lacertid lizard that inhabits humid areas of mountainous regions of the Iberian Peninsula (Salvador, 1984).

We studied clutch size variation, laying period, and appearance of hatchlings in natural conditions during three consecutive years in a mountain area where annual activity is reduced. We compare our data with those of two previous studies made in different areas of the northern Iberian Peninsula (Braña, 1983; Galán, 1986), as well as with scarce information which appeared in other works (Salvador, 1974, 1984; Barbadillo, 1987; Marco & Pérez-Mellado, 1989).

MATERIAL AND METHODS

The low probability of finding clutches of lacertid lizards in the field, especially in stony areas, precluded their study in fully natural conditions. For this reason we studied oviposition and incubation phenology under semi-natural conditions.

Hence, throughout the years 1990, 1991, and 1992 twenty-six gravid females were captured from a population of *Lacerta schreiberi* inhabiting an Holm oak forest of *Quercus pyrenaica*, at an altitude of 1250 m in the area of Dehesa de Candelario, Sistema Central (province of Salamanca, Spain, U.T.M. co-ordinates: 30TTK653691). Individuals were then housed in open-air terraria with open tops of 120 x 60 x 60 cm, situated at a distance of 3 km from the collecting site. Terrarium floors were covered with a 20 cm depth of natural soil from the collecting site and maintained under natural conditions of temperature, humidity and photoperiod. Each lizard was housed individually. We fed lizards with a mixed diet of *Tenebrio molitor* larvae and *Gryllus campestris*, providing water *ad libitum*.

Every three days we recorded the snout-vent length (SVL) (± 0.1 mm) and weight (± 0.02 g) of each female. The reproductive state of each female and its corresponding behaviour was observed at least twice daily from its capture to the first day of oviposition. After laying the last egg, each female was measured, weighed, and then released at the capture site. In all cases each clutch could be unequivocally assigned to an individual female so, the relative clutch mass (RCM) was estimated as the quotient between the weight of the clutch, taken immediately after laying, and female mass (excluding the clutch mass). We consider adjusted clutch sizes as the residual values of the regression analysis of clutch sizes on SVL of corresponding females.

Each clutch was placed in a plastic container (20 cm in diameter, 15 cm height) and covered with 5 cm of wet sand. The incubation was done in the same conditions as mentioned above for terraria (natural temperature and constant humidity). Eggs were measured (± 0.01 mm), weighed with an electronic balance (± 0.02 g) and their volume estimated as an ellipsoid. These measurements were repeated for each egg twice weekly until hatching. Embryonic growth rate was therefore estimated as the quotient between egg measurements (weight, volume, length and width) before hatching and after laying. Newborn lizards were marked, measured and weighed within 24 hr of hatching.

In addition, the reproductive phenology was observed in a study plot of approximately 2 Ha situated at the site of collection previously described, during 1989-1992. Seventy-one females were captured and marked by toe-clipping. For each female we recorded reproductive state (oviductal eggs, copulation marks and lateral skin folds), SVL, and weight. The age at maturity was known from the lizards marked in their first or second calendar years (Marco & Pérez-Mellado, 1990). Natural phenology observed during this study was similar to dates recorded from clutches developed under semi-natural conditions.

Climatological information was obtained from La Angostura Weather Station (National Meteorological Service), situated 1 km from the capture site, 3 km from the incubation site, and at a similar altitude to both localities.

Average annual rainfall in the period 1988-1991 was 1.015 litres/m². Average temperature for the same period was 10.96°C, with a minimum value of 4.30°C and a maximum of 18.02°C. Highest temperature recorded was 34°C, and lowest -3.2°C. Diel variation of temperatures ranged from 5.76°C to 21.14°C, with an annual average of 13.38°C.

Descriptive statistics included arithmetic mean (\bar{x}), standard deviation (SD) and 95 % confidence intervals (Sokal & Rohlf, 1969). Comparisons between years were made with ANOVA analyses of data previously checked for homoscedasticity (F_{\max} test) and normality (David test, Martín-Andrés & Luna del Castillo, 1990). Comparisons between individuals were made with Pearson correlations, analyses of partial correlation and linear regression (Sokal & Rohlf, 1969; Martín-Andrés & Luna del Castillo, 1990).

RESULTS

REPRODUCTIVE PHENOLOGY

Reproductive behaviour of females begins a few days after the onset of annual activity, that is, around the second week of April. Matings were observed during May and the first clutches of eggs were laid from the last week of May to the first half of June. First hatchlings appeared in the third week of August at 1990, in the second half of August at 1991 and in the

first half of September at 1992, just before the end of the annual activity period.

It is interesting to point out the striking synchronization of matings as well as of the development of eggs. This observation was consistent, even in the course of years with cold and rainy springs (1990 and 1991). In fact, a great amount of phenological variability was due to annual differences (Table 1). The mating period was always less than 25 days, and every year, the first oviposition was made after the last mating of all females.

REPRODUCTIVE FEMALES, CLUTCHES AND HATCHLINGS

Minimum reproductive body size recorded for females in the population under study was 91 mm SVL (Table 2) with an estimated age of four or five calendar years (males were mature at three or four calendar years). All observed females above this body size showed reproductive behaviour.

Only one annual clutch with a high egg number (mean=13.7; 7-24 eggs) is confirmed for *Lacerta schreiberi* in the study. Also we observed a long incubation time between 65 and 110 days (average= 84 days). The average RCM was 37%, with a highly variable egg survival rate (62.5%, Table 2). All the non-viable eggs were fertilized and the largest part of those embryos died at the end of the incubation period.

One day before the laying of the first egg, the female starts intense digging activity using the forelegs. She constructs a narrow, deep and long gallery, only limited by terrarium size, that ends in a circular cavity of 4 to 7 cm in diameter. Eggs are deposited in a crowded mass, sometimes strongly stuck together. The cavity is closed with natural ground after laying.

Egg sizes at laying and a few days before hatching are shown in Table 3. We can see an important growth in weight and volume during the incubation period, attaining as much as three times the initial values (volume ratio, \bar{x} =2.78, SD=0.518; weight ratio \bar{x} =2.84, SD=0.342). The difference between the two growth ratios was not significant (t =0.517, P =0.61). Egg width (ratio: \bar{x} =1.42, SD=0.094) grows slightly more than its length (ratio: \bar{x} =1.36, SD=0.103), but this growth rate does not influence the final weight of hatchlings (Pearson correlation coefficient, weight ratio vs hatchling weight: r =0.140, P =0.514; volume ratio vs hatchling SVL: r =0.05, P =0.81).

Two hundred and sixteen out of 320 eggs hatched. The elastic shell of the egg is broken and only after some hours could the emergence of the head be observed. Morphometrics of newborn lizards are summarized in Table 4. Hatchlings are fully active on hatching. 32.5% of eggs stopped their development before hatching for unknown reasons. We did not find any statistical correlation between egg survival rate and recorded reproductive parameters (vs female SVL: r =0.095, P =0.65; vs RCM: r =0.15, P =0.47; vs egg mass: r =0.13, P =0.54; vs egg volume: r =0.16, P =0.46).

	YEARS			ANOVA TESTS		
	1990	1991	1992	<i>F</i>	d.f.	<i>p</i>
Female SVL	107.7	110.37	116.58	0.638	6,44	0.699
Clutch size	11.6	14.12	12.93	1.407	6,45	0.233
RCM	28.69	38.8	39.81	4.579	2,23	0.0212
Incub. days	68.75	74.00	96.21	35.745	2,21	<0.0001
Juv. no.	7.0	10.375	7.0	1.799	2,23	0.1880
Egg surv.	0.688	0.735	0.543	1.782	2,23	0.1908
Egg mass	0.658	0.677	0.763	7.158	2,23	0.0038
Egg volume	0.589	0.636	0.852	34.039	2,21	<0.0001
Hatch. SVL	30.96	31.54	32.06	8.598	2,213	0.0003
Hatch. weight	0.723	0.751	0.797	6.521	2,213	0.0018

TABLE 1. Annual variation of reproductive characteristics of *Lacerta schreiberi*. (Incub.=incubation; Juv.= juvenile; Surv.= survival; Hatch.= Hatchlings).

	<i>n</i>	\bar{x}	95% C.I.	SD	Min.	Max.
Female SVL (mm)	51	108.49	2.082	7.403	91	124
Female weight (g)	26	25.665	3.143	7.780	13.75	41.0
Clutch weight (g)	26	9.3708	1.1264	2.788	4.25	14.97
Clutch vol. (cm ³)	25	10.068	1.309	3.171	5.76	16.75
RCM (%)	26	37.361	3.284	8.129	25.85	56.06
Clutch size	52	13.7	0.95	3.41	7	24
Number offsprings	26	8.3	1.68	4.17	0	17
SR (%)	26	62.5	8.31	25.05	0	100
Incubation time	24	84.23	5.94	14.07	65	109.4

TABLE 2. Sizes of adult reproductive females of *Lacerta schreiberi* and general characteristics of clutches. *n*: sample size, \bar{x} : arithmetic mean; 95% C.I.: 95% confidence interval; SD: standard deviation; Min: minimum; Max: maximum; RCM: relative clutch mass; SR: survival rate of eggs (see text for more details).

	<i>n</i>	\bar{x}	95% C.I.	SD	Min.	Max.
I						
Weight (g)	320	0.716	0.010	0.0955	0.05	1.02
Length (mm)	320	13.80	0.129	1.172	11.5	17.3
Width (mm)	320	10.05	0.073	0.668	8.5	11.7
Volume (cm ³)	320	0.744	0.016	0.1474	0.44	1.13
II						
Weight (g)	293	1.977	0.040	0.3595	0.95	3.00
Length (mm)	293	18.51	0.20	1.740	13.7	26.5
Width (mm)	293	14.16	0.11	0.952	11.2	16.0
Volume (cm ³)	293	1.965	0.043	0.370	1.00	2.84

TABLE 3. Sizes of eggs from 26 clutches of *Lacerta schreiberi*. I: After laying; II: Before hatching. *n*: sample size; \bar{x} : arithmetic mean; 95% C.I.: 95% confidence interval; SD: standard deviation; Min: minimum; Max: maximum.

	<i>n</i>	\bar{x}	95% C.I.	SD	Min.	Max.
SVL(mm)	216	31.6	0.1959	1.46	27	35
Tail(mm)	216	45.7	0.601	4.48	14.0	55.5
Weight (g)	216	0.767	0.016	0.12	0.37	1.0

TABLE 4. Size of hatchlings of *Lacerta schreiberi*. *n*: sample size; \bar{x} : arithmetic mean; 95% C.I.: 95% confidence interval; SD: standard deviation; Min.: minimum, Max.: maximum.

Average weight of hatchlings was 38.8 % of egg weight nearest the time of hatching.

ANNUAL VARIATION

We did not detect statistical differences between years in the size of adult females, clutch size, survival rate of the eggs or reproductive success (Table 1). However, we found significant variability in the size of the eggs, incubation time, and hatchling characteristics (Table 1). It is interesting to point out that in years with longer incubation time we found higher weights and volumes of the eggs and, consequently, bigger newborn lizards.

Recorded temperatures during the incubation period were significantly different among years (Table 5). In 1992 temperatures were lower than in the remaining years of study and hence the longest incubation period was longer.

VARIATION BETWEEN INDIVIDUALS

There were strong correlations between clutch size, number of hatchlings, clutch weight and female body size (Fig. 1). However, egg and hatchling sizes were not related to female size (clutch size and RCM) (Table 6). RCM was independent of female weight (before laying,

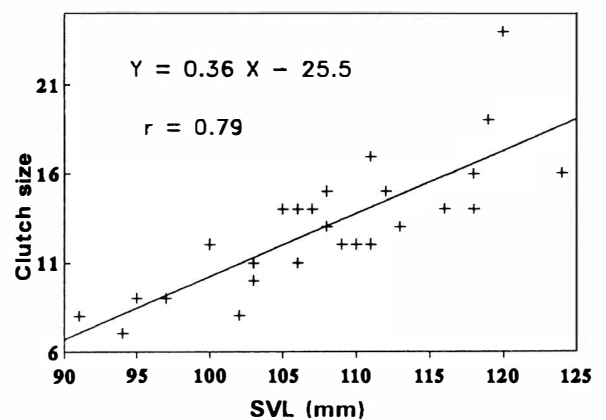


FIG. 1. Relationship between clutch size (egg numbers) and maternal SVL (mm) for *Lacerta schreiberi*.

Year	<i>n</i>	Incubation	T	Min.	Max.
1990	4	68.75 (1.31)	22.06 (0.20)	32.11 (0.20)	11.85 (0.14)
1991	8	74.00 (0.89)	19.59 (0.14)	27.54 (0.14)	12.25 (0.10)
1992	12	96.21 (2.71)	17.43 (0.21)	24.47 (0.26)	10.67 (0.16)
Total	24	84.23 (1.43)	18.92 (0.12)	26.77 (0.15)	11.40 (0.09)
$F_{2,21}$		35.745	100.80	179.50	33.979
P		<0.001	<0.001	<0.001	<0.001

TABLE 5. Annual variation of incubation time in *L. schreiberi* and ambient temperatures during these periods. Average and standard error. (*n*= sample size, T= average temperature, Max.=Maximum temperature, Min.= Minimum temperature, d.f.= degrees of freedom).

$r=-0.217$, $P=0.287$) and showed a partial negative correlation with female SVL (Table 6). Also, there was a positive correlation between average egg weight of each clutch just before laying and hatchlings SVL (stepwise model: coefficient=1.793, $F=6.829$, $P<0.01$).

DISCUSSION

The reproductive patterns found each year in an experimental plot accorded with the phenology of clutches kept in semi-natural conditions. Hence, we can discard strong artificial influences on laying dates and incubation times (Braña *et al.*, 1991; Cuéllar, 1984; Stamps, 1976) due to stress and subsequent inhibitory response of oviductal contractions (Jones & Guillette, 1982).

In natural conditions, all females are reproductively active throughout their adult life, with only one clutch per year. Reproductive periods are synchronized between females and strongly adjusted to the annual activity period. Hence, reproduction starts during an unfavourable period and newborn lizards appear a few days before the first frosts (Marco & Pérez-Mellado, 1989). Consequently, body size and weight of hatchlings can be regarded as adaptive factors (Nussbaum, 1981) influencing the survival of juveniles (Ferguson & Böhlen, 1978), that have only a short period to obtain fat reserves for wintering (Shine, 1983).

Relatively long incubation times found in *L. schreiberi* are similar to those of other green lizards, such as *Lacerta viridis* and *L. trilineata* (Nettmann &

	Fem. SVL	Clutch size	RCM	Egg mass	Hat. SVL
Clutch size	0.862 (***)	1.000			
RCM	-0.58 (**)	0.608 (**)	1.000		
Egg mass	0.202 (NS)	-0.201 (NS)	0.347 (NS)	1.000	
Hatchling SVL	0.085 (NS)	-0.204 (NS)	0.054 (NS)	0.399 (NS)	1.000

TABLE 6. Coefficients of partial correlations between females lizards (*Lacerta schreiberi*) size and reproductive characteristics. At each correlation another three variables were controlled. Significance levels indicated thus: n.s.= $P>0.05$; **= $P<0.01$; ***= $P<0.0001$. (Fem.= female; Hat.= hatchling).

Rykena, 1984) or *L. agilis* (Bischoff, 1984). This long incubation precludes the development of a second clutch and suggests a synchronous pattern of annual reproduction. The main influence of temperature seems to be on the length of incubation.

The reproductive characteristics of the population under study showed some differences from data gathered by Braña (1983) and Galán (1986). In the coastal region of Galicia (north western Iberian Peninsula), females reach sexual maturity at a similar body size, likewise have only one clutch per year, but of larger size (average: 15.9) and smaller eggs (13.1 x 9.3 mm). Newborn lizards are also smaller (26.5 to 29.3 mm and 0.5 to 0.8 g) (Galán, 1986).

Hence, climatological constraints imposed by mountains and the shorter activity period (Marco & Pérez-Mellado, in prep.) compared to the coastal areas of Galicia, could be considered selective pressures for a higher investment in egg size (Nussbaum, 1981) at the expense of clutch size, maximizing the probability of hatchling survival (Shine, 1983). In the Asturias region, more favourable climatological conditions allow two clutches per year (Braña, 1983) each with fewer eggs (12.5) than in areas where only single clutches are produced.

The reproductive strategy of the lizards under study demands a concentration of reproductive effort during a short period of time. To maximize reproductive success, *L. schreiberi* possess a high relative clutch mass (average RCM: 37%), linked with a partial sit-and-wait foraging strategy and a cryptic antipredator escape tactic of the females (Marco & Pérez-Mellado, in prep.; Vitt & Price, 1982). Huey & Pianka (1981) proposed

that RCM is a consequence of foraging mode. In mountain zones, with a shorter activity period, an increase in survival of larger hatchlings (Ferguson & Bohlen, 1978) and a high mortality rate of the eggs, is probably related to an unstable environment (Ratterman & Ackerman, 1989). This may select for the evolution of higher RCM, and in some species, a sit-and-wait foraging strategy.

Furthermore, the synchronized oviposition precludes an inverse correlation between ovulation time and female size (Bauwens & Verheyen, 1985), promoting a delayed acquisition of sexual maturity (fourth or fifth calendar year) in comparison to males, and a very high relative clutch mass (maximum: 56%) in smaller females. Hence, during their lifetime, females tend to raise egg number (RCM dependent) instead of egg size (see Frankenberg & Werner, 1992). Egg size, is in fact, independent of female SVL and already maximized (see above).

The situation is different in the smaller lacertid lizard *Podarcis bocagei* (Galán, 1992), which inhabits unstable environments similar to those occupied by Schreiber's lizard. In such small oviparous species, to increase the small clutch size (4-5 eggs) by only one egg involves an increase of 15 to 20% in RCM, so it opts for a maximization of egg size (but see Frankenberg & Werner, 1992). However, in species with more than 10 eggs per clutch, as *Lacerta schreiberi*, the increase in reproductive effort to add one offspring is proportionally smaller. The relationship between the number of annual clutches (*L. schreiberi*-one; *P. bocagei*-two, at least) and incubation period and body size (at the same climate) could be important to understand these differences between egg mass and clutch size.

We detected a noticeable increase in egg volume during the incubation, as was also found in other reptile species (Andrews & Sexton, 1981; Tracy, 1980; Deeming, 1989). This increase of egg volume is due to water input from external sources (Cagle, 1950; Legler, 1954; Whitaker, 1968), and allows eggs to be laid with a lower water content, lower volume and, consequently, higher clutch size. On the contrary, such hydric exchange could be unfeasible in arid regions, where the lack of soil water can be a direct mortality factor for embryos (Packard, Packard & Boardman, 1980). Perhaps, this could be an important constraint in the geographical distribution of *Lacerta schreiberi* (Marco & Pollo, 1989) and other species with a similar strategy.

Finally, our comparisons between years show clear differences in egg size, incubation period, egg survival rate and hatchling size. Hence, reproductive fitness can vary between years, with important effects on population dynamics and natural history of the species. This is, again, evidence for the phenotypic plasticity referred to by other workers (Ballinger, 1977; Dunham, 1981), and that must be studied to discover the physiological

mechanisms and environmental variables involved (Marco & Pérez-Mellado, in prep.).

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