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Reproductive characteristics of a lowland population of an alpine lizard: *Lacerta monticola* (Squamata, Lacertidae) in north-west Spain

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Abstract—We studied the reproductive ecology of a population of the lacertid lizard *Lacerta monticola* at a lowland location in A Coruña (NW Spain) from 1997 to 2002. The timing of the reproductive cycle was examined based on mark-recapture records of individual lizards in the field. The characteristics of the eggs and hatchlings were obtained from clutches laid in the laboratory by pregnant females that were temporarily removed from the study area. Our results indicate that mating took place between late March and July. The smallest female with signs of sexual maturity had a snout-vent length (SVL) of 52.4 mm and the smallest male was 50.7 mm. Sexual maturity was attained at the age of 2 years by 41% of the individuals, while the remaining 59% of the lizards matured at the age of 3 years. The laying period occurred between June and the beginning of August considering all years. About 61% of the reproductive females produced a single clutch annually, while 39% of the females produced two clutches per year. Females that produced two clutches were generally larger (average SVL = 70.9 mm) than those that laid a single annual clutch (average SVL = 62.6 mm). The mean clutch size was 6.4 eggs (range 4-9). Both clutch size and clutch mass increased significantly with female SVL. The mean egg mass in a clutch decreased significantly with clutch size. Hatching occurred between August and September. Hatching success in the laboratory was 71.7%. The mean SVL was higher in female hatchlings than in males.

Keywords: clutches; *Lacerta monticola*; Lacertidae; life history; NW Spain; reproduction; reptiles; sexual maturity.

INTRODUCTION

The ecology of reproduction explores the patterns of covariation among life history characteristics such as the mode and timing of reproductive events, age and

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size at maturity, frequency of reproduction, clutch size, size and mass of eggs and hatchlings, etc. (Dunham, 1981, 1994; Gillis and Ballinger, 1992; Bauwens, 1999). Rigorous data are needed to undertake a study of the general patterns of the reproductive ecology and life history of lizards. These data must include, for instance, clutch characteristics from eggs laid recently under controlled conditions, clutch frequency from marked females in populations being monitored, characteristics of the hatchlings, the success rate of hatching, etc. Also of utmost importance is the ability to relate all of these characteristics to those of the female progenitors. These kinds of studies are scarce in lacertid lizards (Pilorge et al., 1983; Barbault and Mou, 1988; Bauwens and Díaz-Uriarte, 1997; Galán, 1997; Bauwens, 1999; Castilla and Bauwens, 2000a, b).

Recently, the Iberian rock lizard, *Lacerta monticola*, became a model organism for studies of behaviour (Martín and López, 1999, 2000, 2001), the effect of caudal autotomy (Martín and Salvador, 1995, 1997), and chemical communication (López et al., 1998; Aragón et al., 2000). However, these studies address populations inhabiting the high mountain areas of central Spain (Sierra de Guadarrama) and that belong to the clearly differentiated taxon *L. m. cyreni* (see below). The northwesternmost part of the Iberian Peninsula is known to have populations of this species, which are unique in that they live in the lowlands (Galán, 1982), traditionally assigned to the subspecies *L. m. cantabrica*. At present, very little is known about the ecological characteristics and demography of these animals (Braña et al., 1990; Galán, 1991).

The first studies dealing with the reproduction of *L. monticola* were conducted on the subspecies living in high mountain areas in central Spain, *L. m. cyreni* (Palacios and Salvador, 1974; Melendro and Gisbert, 1976; Barbadillo, 1985; Elvira and Vigal 1985). This taxon is considered by some authors to be a different species, which they denominated *L. cyreni* (Arribas, 1996, 1999; Mayer and Arribas, 1996; Odierna et al., 1996). More recent studies have been published on the nominal subspecies, *L. m. monticola*, which is endemic in the Serra da Estrela, the central mountain range of Portugal (Matos, 1988; Moreira et al., 1999). With regard to the form inhabiting the north west area of the Iberian Peninsula, *L. m. cantabrica*, a certain amount of information has been compiled on both the mountain-dwelling populations and those living on the Cantabrian coast which live in areas with very different altitudes (Braña, 1983; Braña et al., 1990), as well as the populations inhabiting the low altitude zones of Galicia (Galán, 1991). Lastly, diverse data on the reproductive characteristics of this species have been published in more general studies on the reproduction of Iberian or Palearctic lacertid lizards (Braña et al., 1991, 1992; Bauwens and Díaz-Uriarte, 1997; Bosch and Bout, 1998).

Our aim was to describe the reproductive cycle and reproductive characteristics of a lowland population from north-western Spain, belonging to the well-differentiated subspecies *Lacerta monticola cantabrica*. It is of utmost importance to compile information on the ecological characteristics and demographic tendencies of these populations, since, owing to their isolation, their small area of distribution and the scarcity of individuals, they are considered to be threatened (Galán, 1999a).

MATERIAL AND METHODS

Study species

The Iberian rock lizard, *Lacerta monticola* Boulenger, 1905, is a diurnal lacertid lizard found mainly in the rocky habitats of high altitudes in several mountain ranges of the Iberian Peninsula: the Sistema Central mountains, in central Spain (subspecies or species *cyreni*), the Serra da Estrela mountains in Portugal (subspecies *monticola*), and the Cantabrian mountains in northern Spain (subspecies *cantabrica*). In contrast with its affinity for mountains, it is also found at sea level, from altitudes of 0 to 400-500 m on the damp, north-facing slopes and deep river valleys in the north of Galicia and west of Asturias, north-west Spain (Elvira and Vigal, 1982; Galán, 1982; Pérez-Mellado, 1997, 1998, 2002). Recent studies found an unexpectedly close genetic similarity between the populations of Galicia and the Serra da Estrela, as well as a considerable genetic differentiation between the Galician and Cantabrian populations, both included in the same subspecies, *L. monticola cantabrica* (Almeida et al., 2001).

Study area

The study area is located at the end of the geographic ensemble composed of the lower basin of the Mandeo River (Betanzos, Coirós and Paderne municipalities, A Coruña province, NW Spain, 8°8′W and 43°15′N; UTM: 29T NJ 79), which forms a steep valley of fluvial erosion. The altitude of the area inhabited by the population of *L. monticola* ranges from 20 m above sea level (Chelo) to up to 150 m (Zarzo). This area is included in the Wet Oceanic climatic type, characteristic of coastal areas of the north-west Iberian Peninsula. The annual rainfall and temperature data from two meteorological stations near the study area are shown in table 1.

Table 1.
Meteorological data from the meteorological stations of Irixoa and Betanzos, 6 and 5 km respectively from the study area. Data from Martínez-Cortizas et al. (1999).

Meteorological station	Longitude	Latitude	Altitude	Average annual temperature (°C)	Average annual rainfall	Temperature of the coldest month	Temperature of the hottest month
Irixoa	8°6′W	43°17′N	398 m	11.9°	1107 mm	6.7°C	17.6°C
Betanzos	8°12′W	43°16′N	38 m	12.1°	909 mm	7.0°C	16.6°C

Data collection in the field

Data on the annual activity cycle of this population were gathered between July 1997 and October 1998 and between March and September in 1999, 2000, 2001 and 2002. These times coincide with the activity period of this species. During this period, the study site was visited one to four times every month, on days with favourable weather conditions, conducive to lizard activity. On each visit, we set out to collect, by hand or by noosing, the greatest possible number of specimens. For each lizard caught we recorded sex, age class, snout-vent length (SVL, to the nearest 0.1 mm using steel callipers), tail length (including regenerated parts), mass (to the nearest 0.1 g with a Pesola dynamometer), dorsal and ventral coloration, number of blue spots on the ventral scales and flanks, as well as the arrangement of the cephalic plates. For each lizard observed in the field we also recorded details of all reproductive events detected, such as courtships and matings. Each lizard was marked individually by toe clipping and was processed quickly (<5 min) at the capture site, and released immediately.

Three age classes could be distinguished, mainly on the basis of body length (SVL) and other external signs (see below): juveniles (lizards born in the present year), sub-adults (lizards born in the preceding year or 2 years old until they reached sexual maturity) and adults (after the onset of sexual maturity).

All the results reported in this study, including the timing of annual activity and of reproductive events, were obtained from live specimens, by observing their behaviour in the field and by the successive marking and recapturing of the animals. The time of onset and duration of the mating season was determined by the presence of recent mating scars (copulation marks) on the bodies of the females and by the mating behaviour observed in the field. The gravidity period of the females was evaluated by ventral palpation to detect enlarged ovarian follicles or oviductal eggs. The egg-laying period was evaluated from the first to the last clutch oviposited in the laboratory and by females observed in the field with lateral skin folds, which is indicative of a recent egg-laying event. The hatching period was determined by the juvenile hatchlings in the laboratory and by the juveniles, observed in the study area, showing an open navel scar, and having the hatchling size recorded in the laboratory (SVL < 32 mm). The hatching period lasted until all hatchlings exhibited a closed navel scar.

The attainment of sexual maturity was identified in females by reproductive signs such as the presence of mating scars on their bodies, enlarged ovarian follicles or oviductal eggs determined by ventral palpation. Sexually mature males were identified by a developed hemipenes, determined by the enlarged basal portion of the tail. Another sign of sexual maturity in males is the bright green ventral coloration that is present only in mature individuals. Field observations of courtship and mating behaviour were also recorded to determine sexual maturity. Age at maturity was investigated by reference to records of juveniles born and marked during their first year of life in 1997, 1998 and 1999, and recaptured during 2000, 2001 and 2002. Although a large number of hatchlings were marked, only 39 were recaptured during the following 3 years. The reason for this low recapture rate is probably the high mortality rate and the fact that the young age classes travel longer distances.

Mark-recapture records for a number of females caught during the breeding season of 1998, 1999, 2000, 2001 and 2002 provided information on clutch frequency. In a small portion of reproductive females, it was possible to ascertain successive clutches of the same female, as well as to find out if it laid only a single clutch per season.

Data collection in the laboratory

Between May and July of 1998, 2000, 2001 and 2002, a number of pregnant females were collected from the study area and temporarily transported to the laboratory. In the laboratory the females were housed in terraria with direct exposure to an artificial light that created a thermal gradient for 12 hours a day (roughly from sunrise to sunset). Food consisting of a variety of insects and water were provided ad libitum. The rest of the time, gravid females were placed individually in plastic boxes (25 × 13 × 6 cm) filled with 4 cm of soil from the study site. Theses boxes were provided for oviposition. The airtight seal of the plastic boxes allowed the natural humidity of the soil to be maintained, thus preventing dehydration of the eggs. These boxes were kept in the laboratory at room temperature (20-25°C). We inspected the boxes with the gravid females every morning. All clutches were laid in these plastic boxes containing soil. Following oviposition, females were measured (SVL), weighed and then released at the capture site. The eggs were dug up and carefully removed, weighed (to the nearest 0.001 g) and measured (maximum length and width, to the nearest 0.01 mm), and their viability judged by the external characteristics of the eggshell. Clutch mass was calculated as the sum of the masses of the eggs. Egg volume was estimated as $V = 4/3\pi a^2 b$, where $a = 1/2$ of the shortest diameter and $b = 1/2$ of the largest diameter. Egg characteristics were in all cases determined within 8 h of laying. In all cases each clutch was able to be unequivocally assigned to an individual female, resulting in the calculation of relative clutch mass (RCM) as the ratio of the clutch mass (immediately after laying) to the mass of the female after laying. Each clutch was incubated individually in the same plastic box until hatching. The eggs were incubated at room temperature, but an additional heat source was provided for 5 h a day by a 100 W light bulb placed 15 cm above the boxes, which gave a temperature range of 20-29°C, just like the one observed in the study area (unpubl. data). To ensure near-natural conditions of humidity, the clutches were checked daily so that any excess humidity in the form of water that had condensed on the cover of the boxes could be removed, and thus prevent mould from forming.

Immediately after hatching, hatchlings were weighed (±0.001 g) and measured (SVL and tail length; ±0.1 mm). The sex of hatchlings was determined by morphological characteristics, such as the dorsal pattern and the number of transverse rows of ventral scales (Galán, 1991, 1997). Female hatchlings have uniformly dark flanks and the number of transverse rows is greater than 27. Males have a slightly lighter spotted pattern in the flanks which gives them a more reticulated appearance, and the number of transverse rows is fewer than 27 (Galán, 1991). After recording the data, hatchlings were marked individually and released at the study site. Hatch success in the laboratory was estimated on the basis of the ratio of the number of eggs normally hatched to the total number of eggs in each clutch.

Statistical analysis

All statistical analyses were done with the Statview III, SPSS (version 11.0), and Statistica (version 5.97) statistical packages. In the text, we report mean values ± 1 standard error (SE). When analysis of variance (ANOVA) and other parametric statistical tests were used, we first confirmed normality, independence and homoscedasticity of the data. Multiple comparisons of the means following the variance analyses were carried out by Scheffé's test. We used correlation and simple regression analyses to examine the relation between two variables. When a third variable correlated with both, we used residual analysis, checking statistically for the effect of the third variable (all variables were log-transformed prior to the analyses). All statistical tests were used with a significance level of $p < 0.05$.

RESULTS

Annual activity cycle and reproductive season

Between November and the beginning of February no individuals were seen at the study site. This time coincides with the winter inactivity period during all the study years (1997-2002). The activity season lasted from late February to October. Between February and late March, lizards were seen to be active, but without any signs of reproductive behaviour. The sex ratio of the lizards observed during February and March in 1998, 2000, 2001 and 2002 did not differ significantly from one-to-one (χ^2 test, $p > 0.05$ in all cases).

The mating season lasted from late March to the beginning of August. The first females with mating scars were observed in late March in 1998 or early April in 1999, 2000, 2001 and 2002, and the last one in mid-July (all the study years). The gestation period (females with oviductal eggs, determined by palpation) lasted from early May to mid-July (all the study years). In the laboratory the clutches were laid between 17 June and 7 August in 1998 and between 25 June and 19 July in 2002. The incubation period lasted from late June to mid-September and hatching occurred between August and September. At the end of September, all hatchlings exhibited a closed navel scar. The activity season of the hatchlings lasted from August, when hatching starts, until the end of October.

Sexual dimorphism

Although some females attained a larger SVL than males, there were no differences between the sexes in mean SVL (males: 65.90 ± 0.71 mm, range = 50.7-76.5 mm, $n = 59$; females: 64.47 ± 0.56 mm, range = 52.4-79.0 mm, $n = 118$; $t = 1.522$, $p > 0.10$).

Dorsal coloration showed a marked sexual dimorphism. Adult males have a bright green dorsal coloration whereas females are brown. Ventral coloration is also bright green in adult males, while females are pale green. Older males also have some blue spots on the edges of the external ventral scales.

Sexual maturity

The smallest female showing signs of sexual activity (oviductal eggs and mating scars) had a SVL of 52.4 mm, but we observed a female measuring 56.0 mm that was still immature. Therefore the size at which females attain sexual maturity ranges between 52.4 and 56.0 mm.

The smallest male with an enlarged basal portion of the tail (sign of a developed hemipenes) and bright green ventral coloration had a SVL of 50.7 mm, but we collected an immature male measuring 51.8 mm. Thus, the size at which males attain sexual maturity varies between 50.7 mm and 51.8 mm.

Recapture data of lizards marked during their first year of life allowed us to ascertain the age at which the minimum maturity size is attained. Overall, 41% ($n = 39$) of the individuals attained sexual maturity at 2-years old (3rd calendar year) and the remaining 59% do so at 3-years old (4th calendar year). The proportions of individuals maturing at 2-years old or later do not differ significantly between the sexes ($\chi^2 = 0.61$, $p = 0.43$).

Clutch frequency

Of the 33 reproductive females with a sufficient number of recaptures from May to July/August to provide information on clutch frequency, 20 females (61%) laid only one clutch, whereas 13 females (39%) produced two clutches per year. Females that laid only one clutch were on average smaller (SVL: 62.56 ± 0.81 mm, range: 55.5-69.7 mm) than those producing two clutches per year (SVL: 70.88 ± 1.11 mm, range: 65.0-79.0 mm; $t = 6.18$, $p < 0.0001$). Only the largest females (SVL > 65.0 mm), that were at least in their 4th calendar year (3 or more years old) appear to be able to lay two clutches per year. Recapture records made it possible for us to determine. The first clutch was produced in June and the second clutch in July, after an interval of 20-30 days. On the other hand, females that attain sexual maturity in their third activity season lay only one clutch at the end of the laying season.

Clutch size

There were no statistically significant among-year differences in mean female SVL, mean clutch size, mean egg mass, mean clutch mass or relative clutch mass

Table 2.
Reproductive characteristics of *Lacerta monticola* from the Mandeo basin (A Coruña). Shown are the mean ± 1SE, D.S.: the standard deviation, range and sample size (N).

	Mean ± S.E.	D.S.	Range	N
Female SVL (mm)	67.28 ± 0.53	3.92	59.70-78.0	54
Female mass (g)	4.92 ± 0.09	0.73	3.50-6.90	54
Clutch size	6.41 ± 0.18	1.34	4-9	54
Clutch mass (g)	2.631 ± 0.08	0.57	1.493-3.880	54
Relative clutch mass	0.539 ± 0.01	0.11	0.325-0.818	54
Egg mass (g)	0.417 ± 0.01	0.06	0.291-0.554	54
Egg length (mm)	12.62 ± 0.09	0.68	11.10-14.13	54
Egg width (mm)	7.83 ± 0.06	0.41	6.88-8.80	54
Egg volume (mm^3)	407.62 ± 7.36	54.13	293.64-535.23	54
Hatchling SVL (mm)				
Males	25.46 ± 0.08	1.01	23.00-28.10	134
Females	26.21 ± 0.11	1.26	22.90-29.50	114
Hatchling mass (g)				
Males	0.410 ± 0.004	0.05	0.288-0.625	134
Females	0.406 ± 0.006	0.06	0.245-0.611	114

(ANOVA: $p > 0.05$ in all cases). Therefore, we lumped data for the 4 years (1998, 2000, 2001, 2002) for further analyses. Considering all the clutches, the mean clutch size was 6.4 eggs, with a range of four to nine eggs (table 2). Clutch size increased significantly with the mother's SVL, considering all clutches ($r = 0.61$, $p < 0.0001$) (fig. 1).

In a small sample of reproductive females, we were able to identify successive clutches from the same female (first and/or second clutch), as well as to determine whether it laid only a single annual clutch (table 3). There were significant differences in clutch size among the three classes of clutches (ANOVA, $F_{2,23} = 17.07$, $p < 0.0001$). The first clutch was larger than the second annual clutch (Scheffé's a posteriori test: $F = 16.56$, $p < 0.001$), and than the single annual clutch ($F = 4.14$, $p < 0.05$).

Clutch characteristics

Female reproductive characteristics and clutch/egg characteristics, taking into consideration all the clutches studied, are summarised in table 2. Mean egg mass in a clutch was not related to female SVL ($r = -0.14$, $F_{1,53} = 1.09$, $p = 0.301$) but decreased significantly with clutch size ($r = -0.36$, $F_{1,53} = 7.84$, $p = 0.0072$) (fig. 2). An analysis of the relationships between residuals from the regression of log (clutch size) on log (female SVL) and residuals from the regression of log (mean egg mass) on log (female SVL) revealed a negative relation between the two sets of residuals ($r = -0.36$, $F_{1,53} = 7.86$, $p = 0.007$) (fig. 3). Hence, larger clutches were composed of smaller eggs and this relation is independent of female SVL. There were no significant differences in egg mass between the single annual

Table 3.
Mother size and mass, clutch and egg size and mass and RCM in different clutches from the same breeding season of females that laid a single clutch in the laboratory and those laying two clutches, differentiating between the first and second clutch in the latter. Note that we obtained only a small sample of females that laid a second clutch, because all lizards were released after each birth and the recapture rates were low.

	One single clutch per season			Two clutches per season					
				First clutch			Second clutch		
	Mean ± 1SE	Range	N	Mean ± 1SE	Range	N	Mean ± 1SE	Range	N
Female SVL (mm)	65.88 ± 1.01	61.40-68.40	6	71.01 ± 0.82	68.50-79.00	12	69.65 ± 1.46	65.00-73.30	6
Female mass (g), after birth	4.20 ± 0.25	3.50-5.05	6	5.09 ± 0.25	3.60-6.90	12	4.91 ± 0.15	4.60-5.50	6
Clutch size	6.17 ± 0.40	5-7	6	7.67 ± 0.31	5-9	12	4.67 ± 0.42	4-6	6
Clutch mass (g)	2.650 ± 0.25	1.779-3.540	6	3.010 ± 0.17	1.940-3.762	12	2.151 ± 0.27	1.493-3.334	6
Relative clutch mass	0.629 ± 0.05	0.473-0.755	6	0.598 ± 0.03	0.406-0.784	12	0.404 ± 0.03	0.324-0.502	6
Egg mass (g)	0.443 ± 0.03	0.347-0.520	6	0.393 ± 0.02	0.291-0.537	12	0.430 ± 0.02	0.373-0.506	6
Egg length (mm)	12.73 ± 0.27	11.80-13.54	6	12.48 ± 0.22	11.10-14.13	12	12.83 ± 0.31	12.20-14.06	6
Egg width (mm)	7.78 ± 0.15	7.35-8.29	6	7.93 ± 0.12	7.17-8.80	12	7.73 ± 0.08	7.55-8.05	6

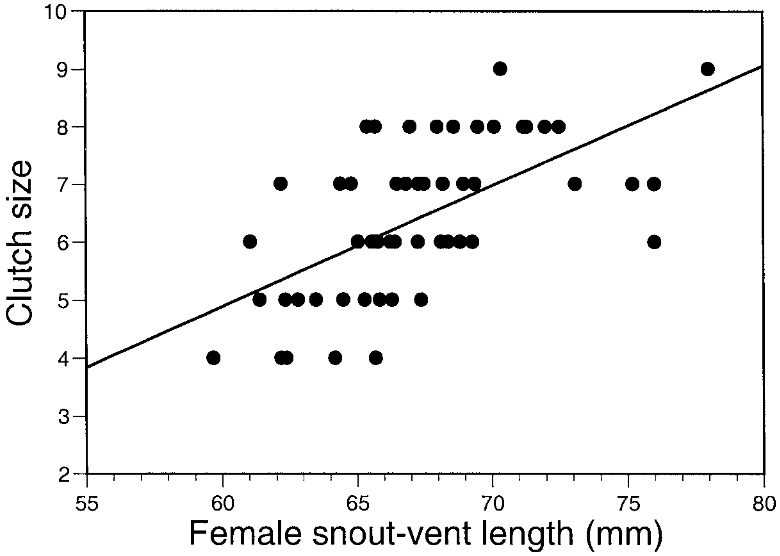

Figure 1. Relationship between mother's body size (snout-vent length, SVL) and clutch size considering all clutches from 1998, 2000, 2001 and 2002.

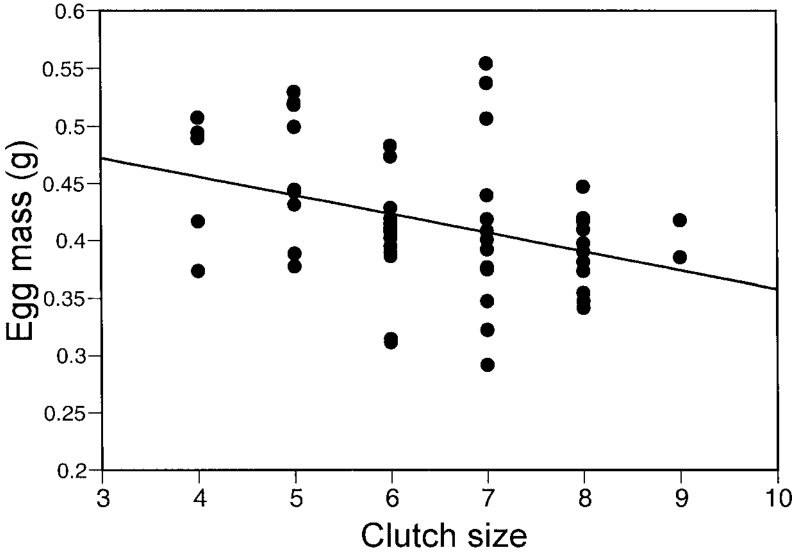

Figure 2. Relationship between clutch size and mean egg mass.

clutch and the first and second subsequent clutch from the same reproductive female (ANOVA: $p > 0.05$; table 3).

Clutch mass increased significantly with female SVL ($r = 0.53$, $F_{1,53} = 20.42$, $p < 0.0001$), but relative clutch mass was not related to the length of the female ($r = 0.12$, $F_{1,53} = 0.774$, $p = 0.383$). There were significant differences in clutch mass (ANOVA: $F_{2,23} = 3.99$, $p = 0.03$) among the single annual clutch and the first

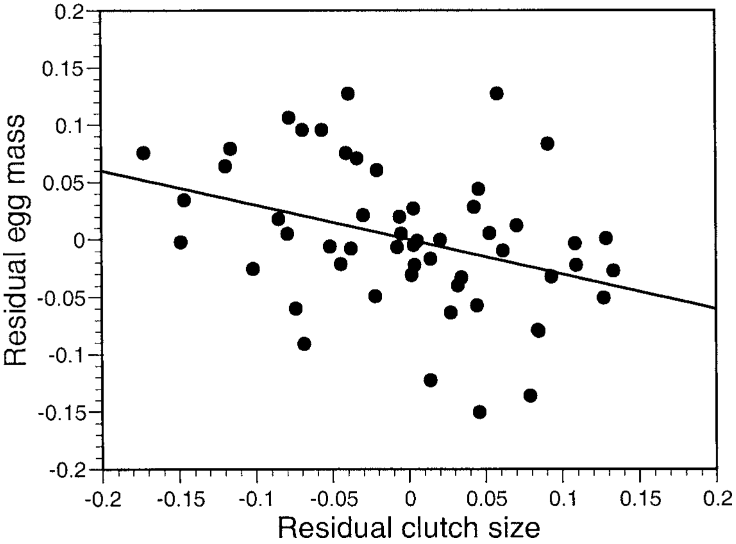

Figure 3. Relationship between residual deviations of clutch size (residual values of the regression of log-clutch size on log-mother's SVL) and residual deviations of mean egg mass (residual values of the regression of log-egg mass on log-mother's SVL).

and second clutches of the same reproductive female. An a posteriori Scheffé test revealed significant differences between the first and second clutches ($F = 3.96$, $p < 0.05$; table 3). Likewise there was a significant difference in relative clutch mass among the three categories of clutches (ANOVA: $F_{2,23} = 8.32$, $p = 0.002$). An a posteriori Scheffé test revealed significant differences in RCM between one single clutch per season and the second clutch ($F = 6.59$, $p < 0.01$) and between the first and second clutches ($F = 6.53$, $p < 0.01$; table 3).

Hatchlings and hatching success

Hatchling SVL and mass, measured within 24 h of hatching, are shown in table 2. Female hatchlings had a larger SVL than males ($t = 5.09$, $p < 0.0001$), but there were no between-sex differences in body mass ($t = 0.47$, $p = 0.64$). The sex ratio of hatchlings born in the laboratory was 1:0.85 (134 males to 114 females) and does not differ significantly from one-to-one ($\chi^2 = 1.62$, $df = 1$, $p = 0.20$).

The mean SVL of hatchlings in a clutch was positively related to the mean mass of the eggs ($r = 0.59$, $F_{1,45} = 24.35$, $p < 0.0001$).

Of the 346 eggs pertaining to 54 clutches that were incubated in the laboratory, 248 eggs hatched successfully, corresponding to a hatching success of 71.7%. In eight out of 54 clutches all eggs failed to hatch.

DISCUSSION

Activity cycle

The mild, temperate climate in the study area allows *L. monticola* to remain active from late February to October. A consequence of this long period of annual activity is a long breeding season (ca 4 months), which enables some individual females to produce two clutches during the same reproductive season. In this study, mating commenced in late March and the last eggs were laid at the beginning of August. In other studies on *L. monticola* from NW Spain, the breeding season started later (Braña et al., 1990; Galán, 1991). In populations living in areas with harsh climatic conditions, such as the mountain populations of *L. monticola* and of other lacertid lizards, the breeding season starts much later than in coastal populations and males tend to commence mating as soon as females become active after the winter (Saint-Girons and Duguy, 1970; Goldberg, 1974; Mellado and Olmedo, 1987; Hraoui-Bloquet and Bloquet, 1988; Braña et al., 1990). Females of this population laid eggs between mid-June and the beginning of August. In the mountain populations of central Spain the laying period starts later and is shorter, taking place between July and August (Pérez-Mellado, 1982; Barbadillo, 1985).

During their winter activity, both males and females are equally active. Also, the beginning of full activity, at the end of winter, occurs at the same time in both sexes. In other lacertid lizard species from temperate areas, different authors have reported that the onset of annual activity in males begins 2-3 weeks before it occurs in females (Nuland and Strijbosch, 1981; Bauwens et al., 1989; Galán, 1989; Nicholson and Spellerberg, 1989; Marco et al., 1994).

Sexual maturity

Mark-recapture data provide precise knowledge on the minimum body size and age at which *L. monticola* from A Coruña reached sexual maturity. In this population, individuals become sexually mature upon attaining a minimum body size, rather than a minimum age, as in other lacertid lizard species (Spellerberg, 1982; Heulin, 1985; Bauwens and Verheyen, 1987; Galán, 1996a; Bauwens, 1999). Females mature at a minimum body length (SVL) of 52.4 mm and males at 50.7 mm. In another coastal lowland population of *L. monticola*, Galán (1991) reported a minimum body size at maturity that was slightly larger in females (SVL: 53.5 mm). Bauwens and Díaz-Uriarte (1997) reported a minimum length at maturity of 56 mm for the *L. m. cantabrica* subspecies. There are important differences among coastal populations of *L. monticola* and the populations of the Sistema Central (*L. monticola cyreni*). The minimum body size in adults of the latter populations is 65.8 mm SVL in females and 61.2 mm in males (Elvira and Vigal, 1985), or 60 mm in females (Bauwens and Díaz-Uriarte, 1997). Unpublished data would point to the presence of copulation marks at a minimum SVL of 57-59 mm in females in the Sierra de Gredos and 58.5 mm in the Sierra de Guadarrama (Oscar Arribas, pers.

comm.). Hence, lowland populations attain sexual maturity at a smaller body size, and possibly at a younger age than in the mountain populations.

Both sexes of the *L. monticola* population studied here reached sexual maturity at 2 or 3 years old (3rd or 4th calendar year). Recapture records allowed us to observe that the earliest born hatchlings (hatched in early August until early September) attained sexual maturity before the end of the mating season of their 3rd calendar year (mid-June or July) and participated in reproduction. Hatchlings that were born after mid-September reach the sexually mature size near the end of their third activity season, so that they delay reproduction to the following spring (4th calendar year).

Despite differences in age at maturity due to the timing of hatching, differences in age at maturity between individuals of the same cohort may also be attributed to particular events, such as diseases and injury, that would delay growth (Galán, 1996b), and may also cause differences in age at maturity (Galán, 1996a).

Clutch frequency

A considerable fraction (39%) of the females in our study population produced two clutches within the same breeding season. The production of two clutches per season was also documented in other lowland populations of *L. monticola cantabrica* (Braña, 1983; Braña et al., 1990; Galán, 1991), whereas mountain populations of the same species (or subspecies), with a shorter activity period, produced a single annual clutch (Braña et al., 1990, in *L. monticola cantabrica*; Moreira et al., 1999, in *L. monticola monticola*; Pérez-Mellado, 1982; Barbadillo, 1985; Elvira and Vigal, 1985, in *L. monticola cyreni*). The production of multiple clutches per year has been described for many other lacertid lizards, mainly in species living in areas with a Mediterranean climate (Saint-Girons and Duguy, 1970; Braña, 1983; Chondropoulos and Lykakis, 1983; Barbault and Mou, 1988; Castilla et al., 1992; James and Whitford, 1994). The production of single or multiple clutches within the same season is primarily related to female body size (Bauwens and Verheyen, 1987; Galán, 1997) and to the timing of oviposition (Braña, 1983; Braña et al., 1990; Galán, 1991, 1997). Large females, which initiate reproductive activities early in the season, produce two or more clutches annually (Hraoui-Bloquet, 1987; Barbault and Mou, 1988; Braña et al., 1990; Galán, 1997), whereas the smallest individuals, which postpone reproduction until the season is well advanced, lay only a single clutch (Braña, 1983; Hraoui-Bloquet, 1987; Galán, 1996a, 1997). Hence, female size is a major determinant of reproductive investment: larger females lay more clutches per year and they also produce bigger clutches, such that they have a larger total egg number (annual fecundity).

Clutch size and clutch characteristics

Our results show a mean clutch size of 6.41 eggs and a maximum clutch size of nine eggs. These data are similar to what was reported by Galán (1991) and Braña

(1983) for the same subspecies. Nevertheless, other *Lacerta monticola* populations from the mountain areas of Galicia (NW Spain) may attain a maximum clutch size of 12 eggs (unpubl. data). Mountain populations of *L. monticola cyreni* present greater mean clutch sizes (Pérez-Mellado, 1982; Elvira and Vigal, 1985). This trend is evident in lizards which produce only one annual clutch each year and invest the reproductive effort in the single clutch (Bauwens, 1999). James and Withford (1994) suggest the existence of phenotypic plasticity in clutch size influenced by weather conditions. In the population studied here, the production of two clutches in the same year is possibly an adaptation to the favourable weather conditions which permit a long breeding season.

Similarly to the pattern reported for other multiple-clutched lizards (Guillette and Bearce, 1986; Anderson and Karasow, 1988; Barbault and Mou, 1988; Heulin et al., 1994; Galán, 1997; Olsson and Shine, 1997b; Castilla and Bauwens, 2000a; Ji and Braña, 2000), the initial clutch of *L. monticola* is larger than the subsequent clutch. So clutch size declines as the reproductive season progresses. Another effect is that smaller-sized females, which produce fewer eggs, start to breed later in the season (Barbault and Mou, 1988; Heulin et al., 1994; Galán, 1996a, 1997; Olsson and Shine, 1997a). This seasonal variation seems to be induced by differences in the proximate source of energy allocated to different annual clutches. Material for yolk production for the first clutch is mainly derived from fat reserves stored before hibernation, whereas energy shunted to subsequent clutches is mainly derived from recent food intake (Braña et al., 1992; Castilla and Bauwens, 2000a). It is noteworthy that *L. monticola* from A Coruña did not lay bigger eggs in the later clutch.

Another phenomenon reported from this study is that clutch size increases with female size. Several studies have described this pattern for other species like *Lacerta vivipara* (Pilorge et al., 1983; Heulin, 1985; Bauwens and Verheyen, 1987), *Podarcis muralis* (Barbault and Mou, 1988), *Lacerta lepida* (Castilla and Bauwens, 1989), *Podarcis lilfordi* (Castilla and Bauwens, 2000a) and others (Reiss, 1989; Bauwens and Díaz-Uriarte, 1997; In Den Bosch and Bout, 1998). Elvira and Vigal (1985), Barbadillo (1985) and Galán (1991) suggest this relation for *L. monticola*. Several studies have suggested that clutch size is limited by the volume of the maternal body cavity or by energy availability, while the egg mass is optimised by natural selection (Berrigan, 1991; Godfray et al., 1991; Roff, 1992; Shine, 1992; Olsson and Shine, 1997b). Under the assumption that the amount of energy available is limited and egg size is variable, clutch size should be inversely correlated with egg size in each particular clutch because of energy and space constraints (Smith and Fretwell, 1974; Roff, 1992; Doughty and Shine, 1997; Ji and Braña, 2000). Our results show that among-clutch differences in egg mass are negatively correlated with clutch size, and that this relationship is independent of female size. Overall, clutch size is more variable by far than egg size, both among females and between successive clutches of the same female. This pattern is demonstrated by lacertid lizards exhibiting steep slopes in the regression of clutch size on female size (Castilla et al., 1992; Ji and Braña, 2000).

Relative clutch mass

The RCM value obtained for *L. monticola* (average = 0.54) is higher than in most other lacertid lizards such as *Podarcis muralis*, 0.24-0.47 (Braña et al., 1991; Braña, 1993; Bejakovic et al., 1996a, 1996b; Ji and Braña, 2000), *P. bocagei*, 0.33-0.40 (Braña *et al.*, 1991; Galán, 1997), *P. lilfordi*, 0.25 (Castilla and Bauwens, 2000a), *P. melisellensis*, 0.25 (Bejakovic et al., 1995b), *Lacerta oxycephala*, 0.22 (Bejakovic et al., 1995a), *Algyroides nigropunctatus*, 0.29 (Bejakovic et al., 1996a); with the exception of *Lacerta vivipara*, which may reach up to 0.81 (Bauwens and Thoen, 1981; Bauwens et al.,1986) or even 1.02 (Pilorge et al., 1983). A similarly high RCM value (0.56) was found by Braña et al. (1991) in another population of *Lacerta monticola* from NW Spain (Asturias). According to the roles of foraging tactics and predator escape developed by Vitt and Congdon (1978), Huey and Pianka (1981) and Brodie (1989), behavioural observations indicate *L. monticola* to be a ‘widely foraging’ lizard, like the great majority of lacertids (Henle, 1990, 1991; Bauwens, 1999). In theses species, the primary escape behaviour involves wariness and rapid running (Vitt and Congdon, 1978; Vitt, 1981; Vitt and Price, 1982). Species utilising this strategy exhibited a lower RCM than species using the ‘sit-and-wait’ strategy. This is why it is surprising that *L. monticola* has such a high RCM value. A similar observation was made by Bauwens and Thoen (1981) in *Lacerta vivipara* and by Braña (1993) in *Podarcis muralis*; in these species, changes occur in the predator-avoidance tactics from flight to cripsis, which would explain this apparent paradox. As in other lizard species, our data indicate that RCM is not correlated with female size.

Hatching and hatchlings

The mean SVL of female hatchlings was greater than that of male hatchlings. In *L. monticola*, females continue to be bigger than males in adulthood (Galán, 1991). In this study, we observed that females attain a larger body size than males, although there were no differences in mean body size. In *L. schreiberi*, females also have a greater body size than males (Galán, 1984). A higher SVL in female as compared to male hatchlings has also been reported for other populations of *Lacerta monticola* (Barbadillo, 1985; Galán, 1991; Pérez-Mellado, 1998), and other lacertid lizards, such as *Lacerta schreiberi* (Galán, 1989; Braña, 1996), *Podarcis muralis* (Ji and Braña, 2000) and *Podarcis bocagei* (Galán, 1997). In lacertid lizards the larger size of female juveniles could be a general phenomenon that could be induced by the higher number of presacral vertebrae in females (Barbadillo and Sanz, 1983; Barbadillo, 1985).

Hatchling SVL is positively correlated with the egg mass, suggesting that the latter may be a good estimator of the energy content of an egg (Sinervo, 1990;

Van Damme et al., 1992; Marco and Pérez-Mellado, 1998). Hatchling SVL does not correlate with the mother's SVL or weight. Such relationships were not found in *Lacerta vivipara* (Bauwens and Verheyen, 1987), *Lacerta agilis* (Olsson and Shine, 1997b) or *Lacerta schreiberi* (Marco and Pérez-Mellado, 1998) either. Nevertheless, others authors reported that the mean egg or hatchling mass of a clutch increases with female length in, for instance, *Podarcis muralis* (Van Damme et al., 1992), *Podarcis melisellensis* (Bejakovic et al., 1995b), *Podarcis bocagei* (Galán, 1997) and *Acanthodactylus erythrurus* (Castilla et al., 1992). Small-sized oviparous lizards that have a small clutch size tend to increase the egg size rather than the clutch size, resulting in significant, positive correlations between egg size and female SVL, whereas large-sized lizards tend to increase the clutch size instead of the egg size (Frankenberg and Werner, 1992; Marco et al., 1994). In some species both characteristics (egg size and clutch size) correlated significantly with the mother's SVL (Galán, 1997, 1999b). In this case, *Lacerta monticola* would appear to adopt a strategy that is similar to the one used by bigger lizards with large clutch sizes (>10 eggs), tending to increase the clutch size and not the egg size, despite the fact their body size is small and their clutch consists of less than ten eggs. This and other life history characteristics of the population of *Lacerta monticola* studied, such as the delay and the variability at age (2-3 years) and size at the onset of sexual maturity, a higher RCM than in other lacertid lizards or the negligible increase in the egg mass in the second clutches with respect to the first (even though the clutch size is low in the second clutches), give a high degree of singularity to this population, which in itself is unique because, while primarily an alpine species, here it is found to inhabit the lowlands.

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