

Reproductive characteristics of the Pyrenean high-mountain lizards: *Iberolacerta aranica* (Arribas, 1993), *I. aurelioi* (Arribas, 1994) and *I. bonnali* (Lantz, 1927)

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Abstract—The three lacertid lizards species of the *Iberolacerta* genus, which have recently been described or recognised as different species, are reptiles that live strictly at the highest altitudes in Europe, from elevations of near 1900 up to more than 3000 m a.s.l. in the Pyrenees (Spain, Andorra, France). In this paper, the reproductive cycle and reproductive characteristics of these species are described for the first time. Data were obtained from field studies carried out in different high-mountain Pyrenean locations from 1989-2002. In addition we also conducted hatching studies in laboratory. Due to the harsh climatic conditions in the high mountains the activity cycle of these species is very short, just over 4 months, from mid-May to late September or beginning of October. This affects their reproductive cycle (i.e., only one annual egg-clutch is produced), as well as other reproductive characteristics, as the existence of a very advanced embryonic development at oviposition, which is interpreted as an advanced stage in the tendency towards viviparity, and diverse life history characteristics as a very little annual growth which greatly delays sexual maturity to 4 years in males and 4-5 years in females. Clutch size correlates significantly with female snout-vent length (SVL) in all three species. The average clutch size is 2.53 eggs in *I. aurelioi* (the smallest species), 3.03 in *I. bonnali* and 3.44 in *I. aranica* (the biggest species). Notwithstanding the differences in egg number the three species have a similar egg volume. The incubation period in the laboratory is very short with an average of 30-36 days among the species. The low reproductive potential observed in these three species and revealed in this paper is a strongly threatening factor which, together with their extremely reduced distribution area, endangers these endemic, rare and very threatened species.

Keywords: alpine; *Iberolacerta bonnali*; *I. aranica*; *I. aurelioi*; Lacertidae; life-history; lizards; oviparity; reproduction; reptiles; sex-ratio; viviparity.

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INTRODUCTION

The genus *Iberolacerta* Arribas, 1997, is a monophyletic and deeply rooted group of seven species from the Iberian Peninsula, the Alps and northern Dinaric chains, characterised by morphological and osteological traits as well as by karyotypes composed of only 36 or less macrochromosomes, instead of the usual karyotypes of 38 chromosomes (36 macro and 2 microchromosomes) that are very widespread among the eurasian radiation clade of Lacertids (sensu Mayer and Benyr, 1994) (Arribas, 1997a, 1999c; Odierna et al., 1996; Mayer and Arribas, 2003).

The Pyrenees are inhabited by three closely related and allopatric species: *Iberolacerta aranica* (Arribas, 1993), *I. aurelioi* (Arribas, 1994) and *I. bonnali* (Lantz, 1927) (fig. 1a, b, c, respectively), recently described or elevated to species rank and almost unknown in terms of their biological aspects (Arribas, 1993a, b, 1994, 1997a, b, c, 1999a, c, 2000, 2001; Arribas and Martínez-Rica, 1997).

Iberolacerta bonnali (Lantz, 1927), is classified as 'vulnerable' by Spanish authorities and included in Anexes II and III of the Habitats Directive (European Union). It is also the most widespread of the three species, inhabiting the Ossau massif in the west to the mountains of San Mauricio-Aigüestortes National Park in the east. It was described in 1927 as *Lacerta (Podarcis) monticola bonnali* and elevated to species level rank in 1993 (Arribas, 1993a; Perez-Mellado et al., 1993). Hardly known for nearly a century, it was described for the first time in Spanish territory in 1976 by Martínez-Rica. In the last few years it has been found in 26 10×10 UTM (Universal Transverse Mercator) grids, at elevations of 1600 m-3062 m (Arribas, 2002c).

Iberolacerta aranica (Arribas, 1993), classified as 'critically endangered' in Spain (Arribas, 2002a) and pending EU classification, is endemic to the Mauberge Massif and its spurs. It was first described in 1993 and is one of the most restricted and threatened European vertebrates. It has been found in four 10×10 UTM grid squares, in locations at elevations of 1940 m-2540 m (Arribas, 2001, 2002a).

Iberolacerta aurelioi (Arribas, 1994), is classified as 'endangered' in Spain (Arribas, 2002) and is also pending EU classification. It is endemic to the three massifs of Mont-Roig, Pica d'Estats and Coma Pedrosa. Described in 1994, this species inhabits six 10×10 UTM grids, at elevations of 2200-2940 m (Arribas, 1999a, 2002).

All three species have an insular-like distribution pattern due to their geographical isolation and inhabit the supraforestal alpine belt areas.

They are characterised by a very short annual activity period (from mid-May to mid-October, at most) conditioned by duration of snow cover and photoperiod. Alpine zones are subjected to strong circadian contrasts in temperature, moisture, wind, insolation, etc., and the ground is snow covered for almost 6 months. All these characteristics make supraforestal areas very harsh, extreme environments for ectotherms, such as these high mountain (alpine) lizards. The Pyrenean lizards constitute an excellent model to study the mechanisms of speciation in continental



Figure 1. A: *Iberolacerta aranica* (Arribas, 1993); male from Tuc de Mauborme (2500 m a.s.l., Lérida Province, Spain). B: *Iberolacerta aurelioi* (Arribas, 1994); male from Pica de Estats Massif (2300 m a.s.l., Lérida Province, Spain). C: *Iberolacerta bonnali* (Lantz, 1927); male from Aigüestortes and Estany de Sant Maurici National Park (2200 m a.s.l., Lérida Province, Spain).

areas, as well as the survival in climatically extreme localities for ectothermic animals (Arribas, 1997a, b, c, 1999c; Arribas and Martínez-Rica, 1997).

Data on the reproductive biology from Pyrenean *Iberolacerta* species are very scarce. Only Lantz (1927) provides data regarding the date of one *I. bonnali* clutch, measurements of eggs and one newly hatched specimen. Arribas (1993a) also adds data on the incubation period of '*I. bonnali*' (in fact, mixed data regarding *I. bonnali* and *I. aranica*). Meanwhile, the reproductive biology of *I. aranica* and *I. aurelioi* remains unknown.

Harsh and hostile environmental conditions in the high mountain impose strong restrictions and constraints upon the reproductive characteristics and life history of these reptiles. Most other lizard species that live at comparable elevations are viviparous (e.g., Hernández-Gallegos et al., 2002; Shine, 2002). *Iberolacerta* species, however, are oviparous, as are the Pyrenean populations of *Zootoca vivipara*, the other lacertid lizard species that lives from nearly sea level up to similar high altitudes in the same localities inhabited by *Iberolacerta* spp. (Bea et al., 1990; Braña et al., 1991; Heulin et al., 1991; Guillaume et al., 2000).

Oviparous saurians can be submitted to clutch depredation or parasitism during incubation (Chalcraft and Andrews, 1999; Andrews, 2000), but, up to now, this aspect has received little attention in studies about the reproductive ecology of lizards. However, egg depredation or parasitism can represent an important mortality factor which conditions egg-clutch site selection and other relevant aspects of their life histories (Andrews, 2000).

Here, we present the first comparative study on the reproductive cycle and reproductive characteristics of the three Pyrenean *Iberolacerta* species. We studied nest site selection, egg and clutch size, and other reproductive aspects of utmost importance to know their life history and necessary for the effective protection of these isolated, poorly known and threatened species.

MATERIALS AND METHODS

Localities and sampling

Data from different localities were mixed for each species in order to achieve a larger sample size and give an overall description of the taxon characteristics. For *I. bonnali*, data from the Bigorre, Monte-Perdido, Maladeta and Aigües-Tortes areas were used. For *I. aranica*, we took data from different points of the Mauberge Massif, and for *I. aurelioi*, data from the Mont-Roig, Pica d'Estats and Coma Pedrosa Massifs were used.

Habitat characteristics

All these localities are situated in the Pyrenean alpine belt, and are largely similar in characteristics over the whole Pyrenean range. For this reason, we give a general

account of their climatic and physiognomic characteristics without particularising at any specific point.

All three species have an insular-like distribution pattern and inhabit the supraforestral (alpine) areas usually above 2000 m up to higher than 3000 m a.s.l., on rocky substrates and very sheltered areas, characterised by a very short annual activity period (from mid-May to mid-October, at most) conditioned by the photoperiod and the permanence of snow cover. Sun radiation (especially ultraviolet rays), precipitation (mainly in the form of snow) and wind effect increase with altitude, whereas temperature and atmospheric pressure decrease. Mean annual temperatures range between -2 and 5°C (usually $<3^{\circ}\text{C}$). Mean temperatures from the coldest month are -10°C or less, whereas maximum summer temperatures oscillate from 20 - 25°C . The pluviometric regime is hyperhumid (>1400 mm) and the vegetative period ranges from 1-3 months. Snow covers the ground continuously over a period lasting from 6-9 months. There are 7 months of continuous night frosts, which also occur frequently for another 2 or 3 months. Occasional snowfall may occur during any month of the year.

These zones are also subjected to strong circadian contrasts in temperature, moisture, wind, insolation and, especially, dramatic differences between ground and air temperatures. Even in summer, temperatures drop to almost 0°C during the night due to intense nocturnal radiation (Vigo, 1976; Dupias, 1985; Ozenda, 1985; Rivas-Martinez, 1987; Arribas, 1997a, 1998 (2000)).

Field and laboratory study

The localities under study were surveyed carefully from 1989-2003 in the framework of a complete study on the ecology and life story of these species.

Gravid females were located when active or under stones and transported to the laboratory (sited at 1020 m a.s.l.) to monitor the oviposition and incubation processes. Freshly caught females (captured within a week of their oviposition) were placed in 30×20 cm glass or plastic aquaria with peat and a flat stone. Small arthropods and water were supplied *ad libitum*. Gravid females near oviposition did not feed at all. Lizards were maintained under natural light and photoperiod conditions (direct sunlight for several hours from sunrise to almost 12 hours GMT, and shade from this time until sunset).

Females were checked almost every hour during the day and twice at night, throughout the study of the oviposition process. We recorded the number, length, width and mass (to the nearest 0.1 g) of the eggs. The characteristics of the eggs were, in all cases, determined within 8 h of laying. After laying, each female was measured (± 0.1 mm), weighed, and then released at the capture site. Recently laid eggs were deposited in empty slide cases for incubation under natural temperature conditions (from 24 - 30°C) in the laboratory conditions described above. The slide cases were filled with 4 cm of soil from the study sites and a piece of moss to cover the eggs and provide moisture retention and darkness and to facilitate periodic

inspection. Four perforations in the case ensured limited air circulation for the eggs and prevented the growth of mould.

Clutch and newborn data

Egg data (length, width and mass) were taken each week, and clutches controlled daily. Egg volume was calculated as an ellipsoid: $V = 4/3\pi a^2 b$, with a and b being half of the width and length of the egg, respectively. Total clutch volume is the sum of all egg volumes. In all cases each clutch was unequivocally assigned to an individual female, allowing us to calculate the relative clutch mass as the mass of the clutch (immediately after laying) divided by the mass of the mother (excluding clutch mass).

Measurements were taken with a Mitutoyo digital caliper (to 0.1 mm) and egg and female masses were recorded with a portable Tanita 1479-model digital scale (accuracy 0.1 g).

When hatchlings broke the egg envelopes, the time and total duration of egg emergence were recorded, as well as the time of egg-tooth persistence. The following data were also recorded for each newborn lizard; snout-vent length (SVL), mass and number of ventral scales (to determine sex). Hatchlings were assigned to either sex by comparison with adult counts of ventral scales (see Arribas, 1997a, 1999b, 2000, 2001): *Iberolacerta aurelioi*: males up to 28 ventral scales, females 29 or more; *I. aranica*: males up to 26, females 27 or more; *I. bonnali*: males up to 27, females 28 or more. After morphological description and sex determination, newborn specimens were fed with aphids until they were released in their origin localities, usually within a week of birth.

Embryonal stages at egg-laying

A reduced number of eggs belonging to different clutches (8 eggs from *I. aurelioi*, 16 from *I. aranica*, and 1 from *I. bonnali*), were dissected within 8 hours following oviposition, to ascertain the degree of embryonic development at egg-laying. Embryonic states were determined by comparison with Dufaure and Hubert (1961) tables.

Sexual maturity

The attainment of sexual maturity was determined in males by the presence of developed hemipenes, identified by the enlarged basal portion of the tail. Also, sexual maturity in some small males used for osteologic work was confirmed by testicle development. In females, maturity was identified by reproductive signs such as the presence of enlarged ovarian follicles or oviductal eggs determined by ventral palpation.

Age at maturity was investigated by skeleto-chronology, i.e., by counting the number of growth rings in the femur of the two smallest adult individuals of both

sexes (four in each species). Age at maturity was also studied using records of juveniles marked during their first year of life and recaptured as adults some years later.

Clutch site selection

Nest site selection of the three species was investigated by checking for eggs under stones, both fresh (from the current year) and old ones (eggshells from previous years' clutches). The number of fresh eggs and/or empty eggshells found under stones was counted, and the eggs' largest and smallest diagonals for surface (size) assessment were recorded. Also, eggs found in the field were examined to determine possible clutch aggregation and the degree of predation by maggots of the dipter *Sarcophaga protuberans* Pandellé, 1896 (Pape and Arribas, 1999).

Statistical procedures

Statistical calculations were performed with NCSS-2002[®] (Hintze, 2001). Inter-specific differences in each sex were tested with the two tail ANOVA and Tukey-Kramer tests ($p < 0.05$) for multiple comparisons for all pairwise differences between the group means. In pairwise comparisons taxa names appear abbreviated (ara: *I. aranica*; aur: *I. aurelioi*; and bon: *I. bonnali*). Differences between males and females from the same species were compared by t-tests. If normality conditions were not met, non-parametric Kruskal-Wallis tests were used. All values are presented as means \pm standard error of means (S.E.).

RESULTS

Annual activity cycle

All three species are opportunistic in terms of their time of emergence, appearing when the snow melts (triggering event for emergence of specimens), usually in the second half of May (preliminary observations by the authors: 19 May 1992 (Monte Perdido) in *I. bonnali*, 5 June 1994 (Andorra) in *I. aurelioi*; and 16 June 2001 (Mauberge) in *I. aranica*, but localities of the latter species are not accessible until mid-June owing to snow avalanches). They are, however, very conservative as regards the moment they decide to retreat to hibernate, during the second half of September in adults, and first half of October for juveniles (all study years). The total length of the annual activity cycle is very short in comparison with other temperate-zone reptiles and quite similar in the three species. It lasts for nearly 4 months in adult males and females, from mid-May-September, and slightly under 5 months (or 4.5 months) in subadults (mid May-early October).

Reproductive cycle

Iberolacerta aurelioi. In this species, if the snow melts early, as was the case in Andorra during 1994 and 1995, at the beginning of June (6 June) females showed mating scars and bore eggs in development (small to medium vitellogenic follicles or oviductal eggs). However, in 1996 and 1997 in mid-June they bore mating scars but oviductal eggs were still not discernable. In 1993 in mid-June, Mont-Roig females exhibited all mating scars and eggs in formation, but in 1995 the cycle was slightly delayed and at the beginning of July (7 July) mating scars and eggs near oviposition were present in all the adult females observed. Finally in Pica d'Estats Massif, females were developing eggs in mid-June (12 June 1993) and near or during the clutch period at the beginning of July (1-4 July) in 1991, 1992 and 1993. In Capifonts, eggs were in formation in the first half of June (7 June) in 1995. The main oviposition period over the years was near mid-July in 1991, 1992 and 1993; at the end of June to the beginning of July in 1994; in the second half of June (Andorra) to the first half of July (Mont-Roig) in 1995; the second half of June in 1996 and 1997 and the last days of June and first days of July in 2002.

Iberolacerta aranica. The phenology of this species is largely parallel to *I. aurelioi*. Oviposition occurred mainly during the first week of July in 1989, first half of July in 1991 and 1992; more extensive from the second week to almost 25 July in 1993; the last week of June and first week of July in 1994 and 2003; mainly the last week of June in 1995; around the second week of July in 1996; the last third of June (Barradós) to almost the end of July (the last observed, Orlà) depending on the site (orientation, winter snow accumulation) in 1997; the second half of June in 1998; the first half of July in 1999 and 2000; mainly towards the end of June in 2001 and from the first to third week of July in 2002.

Iberolacerta bonnali. The same pattern is true for *I. bonnali*. Oviposition took place during the second half of June (Monte Perdido) to the first week of July (Bigorre) in 1989; the second half of June (Monte Perdido) in 1991; the first half of July in 1992; the last week of June and first half of July in 1994; mainly the last week of June and first week of July in 1995; from 10 June (earliest data for all three Pyrenean species) but mainly in the second half of June in 1996; second half of June in 1997; the last week of June and first week of July in 1998 and 1999; the last week of June and first week of July 2002 and around mid-June in 2003.

In conclusion, reproduction in the three *Iberolacerta* species begins with matings soon after emergence (second half of May or first half of June). Eggs develop in June and clutches are laid from mid-June to mid-July (exceptionally until the end of July), depending upon the snow-melt of the year and locality in question.

The first hatchlings of the three species appeared in the field in the second half of August during all the years studied, and are commonly seen in September and October, until activity ends.

Table 1.

Biometric characteristics, sex dimorphism and interspecific differences among the three *Iberolacerta* species.

	Males mean SVL \pm SE min-max (n)	Females mean SVL \pm SE min-max (n)	Differences among sexes t-test p
<i>I. bonnali</i> (1)	52.23 \pm 0.24 45.03-58.73 (n = 166)	56.27 \pm 0.26 49.53-65.36 (n = 147)	t = 7.02 p < 0.0001
<i>I. aranica</i> (2)	53.98 \pm 0.38 45.4-61.8 (n = 81)	56.97 \pm 0.31 48.04-66.88 (n = 138)	t = 4.32 p < 0.0001
<i>I. aurelioi</i> (3)	52.41 \pm 0.24 45.1-65.25 (n = 123)	55.31 \pm 0.31 48.43-62.21 (n = 99)	t = 6.31 p < 0.0001
ANOVA: F, p df	F = 8.09; p < 0.001; 2, 236	F = 6.88; p < 0.01; 2, 338	
Species difference (Tukey MCT)	2-1; 2-3	2-1; 2-3	

Table 2.

Gravid female size (SVL, in mm) and clutch size of the three *Iberolacerta* species studied.

	<i>I. bonnali</i>	<i>I. aranica</i>	<i>I. aurelioi</i>
Gravid female size, mean \pm SE SVL (mm)	56.82 \pm 0.52	57.56 \pm 0.64	55.84 \pm 0.65
Range	51.4-64.2	50.3-66.5	48.9-60.5
n	25	40	23
Clutch size, mean \pm SE	3.03 \pm 0.13	3.44 \pm 0.11	2.53 \pm 0.10
Range	2-4	2-5	1-3
n	29	54	32

Adult size. Mature males and females of the three species differ in SVL, with males being significantly smaller than females (t-test; all species p < 0.0001; table 1).

Both male and female adults of *I. aranica* are slightly larger than their counterparts of *I. bonnali* and *I. aurelioi* (p < 0.01). The size (SVL) of studied gravid females in the three species is given in table 2. This size does not differ statistically among the three species (ANOVA: $F_{2,85} = 1.8$; p = 0.17).

Sexual maturity. The smallest adult male in *Iberolacerta bonnali* was 45.0 mm SVL, in *I. aranica* 45.4 mm and in *I. aurelioi* 45.1 mm. This size is reached when the animal is almost 4 years old, i.e., in its 5th Calendar Year (CY), confirmed by

the skeletochronology of two individuals of this size in each sex and species, and by recapture records of individuals marked in the year of their birth.

The attainment of sexual maturity was identified in females by reproductive signs such as the presence of enlarged ovarian follicles or oviductal eggs determined by ventral palpation. The three smallest females found carrying oviductal eggs were recorded as follows: in *I. bonnali*, 51.4, 52.3 and 54.3 mm SVL from a total of 25 gravid females measured; in *I. aranica*, 50.3, 51.0 and 52.1 mm SVL from 40 gravid females measured and in *I. aurelioi*, 48.9, 49.1 and 50.7 mm from 23 gravid females measured, all slightly larger than the minimum size of the 5CY females, confirmed by skeletochronology (*I. bonnali*: 49.5 mm; *I. aranica*: 48.0 mm; and *I. aurelioi*: 48.4 mm). Thus, sexual maturity in females is attained when they are five years old (6CY). Also, it cannot be ruled out that some females reach maturity in 5CY while others do so in 6CY.

Reproductive characteristics

Clutch size. Clutch size differs in the three species (table 2). In *I. bonnali* the usual number of eggs is three; in *I. aranica*, numbers of three and four eggs are almost equally common; and lastly, in *I. aurelioi*, clutches of two and three eggs occur with practically the same frequency. The three species differ from each other in clutch size (ANOVA: $F_{2,112} = 15.17$; $p < 0.0001$; Tukey-Kramer MCT). If means are adjusted for female SVL, only *I. aranica* differs from the other two species, showing a higher clutch size (ANCOVA for SVL as the covariate: $F = 13.86$; $df = 87$; $p < 0.0001$; Tukey-Kramer MCT: ara-aur, ara-bon). Adjusted means for SVL are: *I. bonnali* = 2.93 eggs; *I. aranica* = 3.46 eggs; *I. aurelioi* = 2.65 eggs.

Clutch characteristics. Egg characteristics are presented in table 3. *Iberolacerta aranica* lays eggs that are shorter in length than *I. bonnali* and *I. aurelioi*. In terms of egg width, *I. bonnali* exhibits the widest and *I. aurelioi* the narrowest eggs (table 3).

Notwithstanding the differences in egg number and size, the three species have a relatively similar egg volume, without reaching (but close to) the threshold of significant differences among them. Egg mass does not show differences among the three species (table 3).

Clutch and egg relationships. Clutch size is significantly correlated with female SVL in all three species (fig. 2). Nevertheless, egg length does not correlate with female length (table 4). Several characteristics, such as egg width, egg volume and total volume of the clutch, are correlated with female length in *I. aranica* but they are not correlated in the other two species, probably due to the small sample size (table 4).

If we consider the cubic root of the total clutch volume (to linearise or reduce to only one dimension the three-dimensionality of volume) and compare it to female SVL as one approach to calculate Reproductive Investment, this ratio is very similar

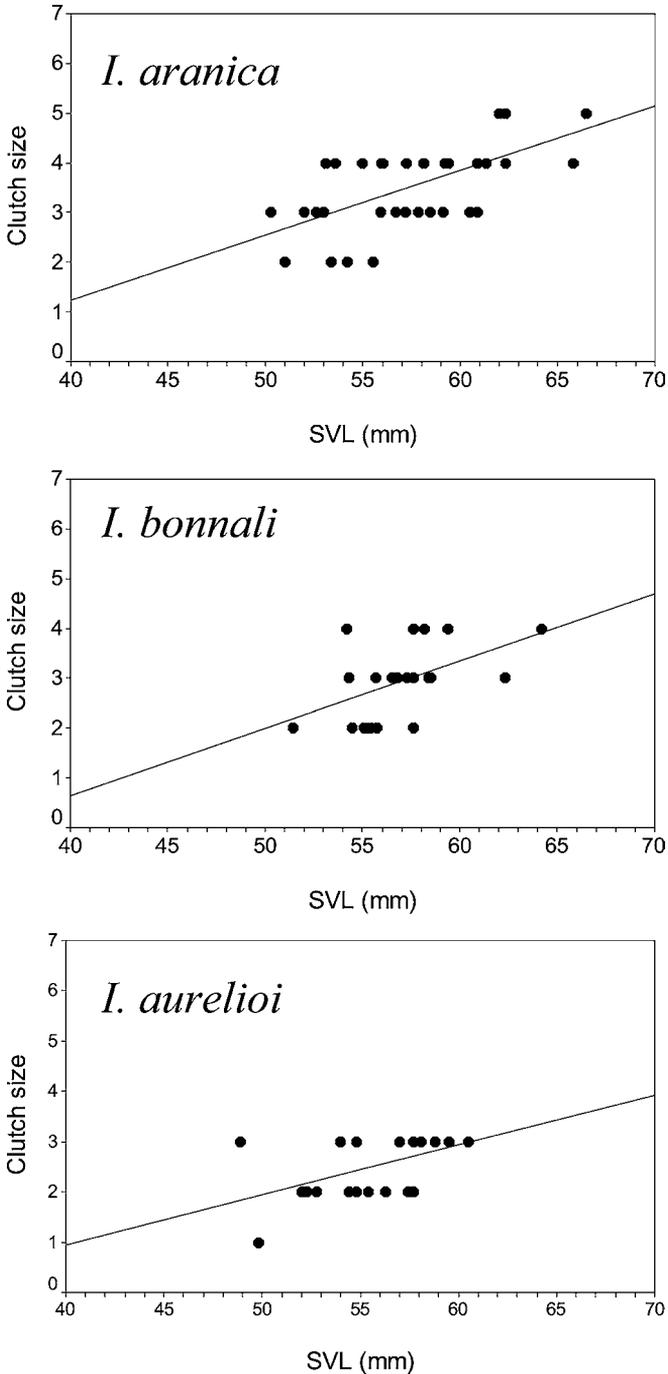


Figure 2. Relationships between female body size (snout-vent length, SVL) and clutch size in each Pyrenean *Iberolacerta* species. From top to bottom *I. aranica*: $y = 0.131x - 3.99$; $r^2 = 0.393$; *I. bonnali*: $y = 0.135x - 4.76$; $r^2 = 0.254$; *I. aurelioii*: $y = 0.099x - 3.01$; $r^2 = 0.254$.

Table 3.Egg and clutch characteristics of the three *Iberolacerta* species studied (NS: not significant).

	<i>I. bonnali</i>	<i>I. aranica</i>	<i>I. aurelioi</i>	ANOVA
Egg length (mm)				
Mean ± SE	13.37 ± 0.18	12.59 ± 0.10	13.81 ± 0.18	F = 17.45
Range	11.8-14.9	10.09-15.3	11.6-15.35	df = 2, 138
n	20	95	26	p < 0.0001
Egg width (mm)				
Mean ± SE	7.99 ± 0.22	7.65 ± 0.01	7.28 ± 0.10	F = 4.54
Range	6.18-9.9	6.8-11.1	6.2-8.2	df = 2, 138
n	20	95	26	p < 0.05
Egg volume (mm ³)				
Mean ± SE	485.33 ± 29.43	393 ± 12.1	386 ± 13.43	F = 2.99
Range	252.36-692.79	276.58-954.78	289.17-517.54	df = 2, 138
n	20	95	26	p = 0.053 (NS)
Total clutch volume (mm ³)				
Mean ± SE	1074.55 ± 140.26	1338.27 ± 80.37	1208.58 ± 114.40	F = 1.01
Range	820.27-1304.30	847.86-2332.67	935.15-1474.5	df = 2, 22
n	3	18	4	p = 0.38 (NS)
Egg mass (g)				
Mean ± SE	0.46 ± 0.008	0.46 ± 0.03	0.430 ± 0.09	F = 0.16
Range	0.46-0.475	0.3-1.1	0.30-0.60	df = 2, 53
n	7	36	13	p = 0.85 (NS)
Total clutch mass (g)				
Mean ± SE	1.30 ± 0.10	1.46 ± 0.16	–	–
Range	1.20-1.40	0.90-2.40	–	–
n	2	8	–	–
Relative clutch mass (RCM)				
Mean ± SE	0.457 ± 0.01	0.557 ± 0.04	–	–
Range	0.452-0.462	0.360-0.750	–	–
n	2	8	–	–

in all three species, without any statistical differences (ANOVA: $F_{2,22} = 1.2$; $p = 0.32$); *Iberolacerta bonnali*: mean = 18.18 ± 0.85 (range: 16.48-19.07; $n = 3$); *I. aranica*: mean = 19.22 ± 0.28 (range: 17.04-21.28; $n = 18$); *I. aurelioi*: mean = 18.65 ± 0.46 (range: 17.65-19.85; $n = 4$).

The relationships between residuals from the regression of log (clutch size) on log (SVL of mother) and residuals from the regression of log (egg mass) on log (SVL of mother) were significant for the three species: *Iberolacerta bonnali*: $r^2 = 0.72$ ($F_{1,8} = 17.21$; $p < 0.01$); *I. aranica*: $r^2 = 0.77$ ($F_{1,65} = 213.74$; $p < 0.0001$); *I. aurelioi*: $r^2 = 0.61$ ($F_{1,10} = 14.67$; $p < 0.01$).

Clutch size (number of eggs) is positively correlated with the total clutch volume in the three species, but only significant in *I. aranica* ($r = 0.80$; $F_{1,17} = 28.86$; $p < 0.0001$). Low sample size does not permit the extraction of conclusive data for the other two species.

Table 4.

Relationships between female size (SVL) and clutch and egg characteristics in the Pyrenean *Iberolacerta* (NS: not significant).

		<i>I. bonnali</i>	<i>I. aranica</i>	<i>I. aurelioi</i>
Clutch size	r	0.50	0.64	0.52
	F	7.82	27.17	8.05
	n	25	40	23
	p	p < 0.01	p < 0.0001	p < 0.01
Egg length	r	-0.03	-0.05	-0.08
	F	0.03	0.16	0.06
	n	9	66	11
	p	p = 0.85 (NS)	p = 0.68 (NS)	p = 0.80 (NS)
Egg width	r	0.05	0.43	0.35
	F	0.01	15.08	1.28
	n	9	66	11
	p	p = 0.89 (NS)	p < 0.001	p = 0.28 (NS)
Egg volume	r	0.05	0.29	0.33
	F	0.02	6.19	1.12
	n	9	66	11
	p	p = 0.88 (NS)	p < 0.05	p = 0.31 (NS)
Total clutch volume	r	0.06	0.64	0.67
	F	0.004	11.20	1.71
	n	3	18	4
	p	p = 0.95 (NS)	p < 0.01	p = 0.32 (NS)

Stages of embryonic development at oviposition. Eggs are laid in an advanced stage of embryonic development in the three species (determined from the tables of Dufaure and Hubert, 1961): in *I. aurelioi* from stages 30 (n = 2), 31 (n = 4), and 32 (n = 2); in *I. aranica* from stages 30 (n = 5), 31 (n = 7), 32 (n = 3) and 33 (n = 1); in *I. bonnali* the only recently laid egg examined was in stage 31. All eggs studied belong to different clutches.

Nesting places. The three Pyrenean *Iberolacerta* lizards seek out medium-sized stones under which to lay their eggs. The number of fresh eggs (from the year) found together under a single stone varied among species (As numbers of eggs found have very biased distributions medians are also given). In *I. bonnali* the mean is 5.11 ± 1.53 eggs (median = 4; range: 2-16 eggs; n = 9 clutch sites). In *I. aranica* the mean is 6.22 ± 1.02 eggs (median = 3; range: 2-29; n = 27 clutch sites). In *I. aurelioi* the mean is 4.21 ± 0.72 eggs (median = 3; range: 2-12; n = 14 clutch sites). There are no significant differences in the accumulation of fresh eggs among the three species (Kruskal-Wallis test: H = 3.50; df = 2; p = 0.17). Our results suggest that the most common situation is that only one female lays under a given

stone. Communal clutches can be found (see ranges), but as can be seen, they are not very frequent.

The total number of old eggshells accumulated under the same stone gives an idea of the use of a specific site for egg-laying in previous years. Also, the concurrence of fresh and old clutches would suggest the reiterative use of the same sites year after year. In *I. bonnali* the average number of old eggshells found in these places is 11.76 (median = 5; SE = 2.48; range: 1-67 eggs, but probably more than a hundred, some very fragmented, shells, were found in one specific place; n = 39 clutch sites studied). In *I. aranica* the average number of eggshells is 9.87 (median = 6; SE = 2.01; range: 1-58 eggs; n = 31 clutch sites studied). Finally, in *I. aurelioi* the average is 9.75 (median = 6; SE = 4.13; range: 1-70 eggs; n = 16 clutch sites studied). There are no differences among the three species in the number of old eggshells accumulated at the clutch sites (Kruskal-Wallis test: $H = 0.47$; $df = 2$; $p = 0.78$).

There is no significant relationship between the number of recently laid eggs and the stone size (surface), both if we use the pooled data from the three Pyrenean *Iberolacerta* ($r = 0.22$; $F_{1,40} = 2.02$) or the different species data (*I. bonnali*: $r = 0.24$; $F_{1,37} = 0.01$; *I. aranica*: $r = 0.24$; $F_{1,40} = 2.61$; and *I. aurelioi*: $r = 0.14$; $F_{1,24} = 0.53$; $p > 0.05$ in all cases). Notwithstanding, if we consider the number of old eggshells, a relationship does exist for the pooled data of the three-species (old eggs-stone size: $r = 0.47$; $F_{1,105} = 31.16$, $p < 0.0001$) as well as for the separate species (except the old eggs of *I. aranica* which are also close to the significance threshold): *I. bonnali* ($r = 0.50$; $F_{1,37} = 12.80$, $p = 0.001$); *I. aranica* ($r = 0.28$; $F_{1,40} = 3.55$, $p > 0.05$); *I. aurelioi* ($r = 0.57$; $F_{1,24} = 12.00$, $p < 0.01$). Our hypothesis is that this relationship is an artifact produced because bigger stones maintain old eggshells in better condition for a longer period of time against deterioration by external agents, facilitating their accumulation.

Egg predation. The number of clutches parasitised (preyed on by the dipter *Sarcophaga protuberans*) amounted to 5% of the clutches in *I. bonnali* (total sample n = 39 clutches), 21% in *I. aranica* (n = 51 clutches) and 25% in *I. aurelioi* (n = 24 clutches). Of the number of eggs (from Pape and Arribas, 1999) examined in *I. bonnali*, out of 479 eggs (both fresh and old ones), 10 were parasitised (2.1%); in *I. aranica*, out of 384 eggs, 26 were parasitised (6.7%), and in *I. aurelioi*, out of 196 eggs, 17 were parasitised (8.6%), relatively high values for these low productive lizards.

Differences among the three species in the number of clutches parasitised do not reach the significance threshold (Kruskal-Wallis test: $H = 5.76$; $df = 2$; $p = 0.055$).

Incubation period. *Iberolacerta aranica* has the shortest incubation period (nearly 4 weeks) in the laboratory. Incubation length in *I. aranica* differs statistically from *I. bonnali* and *I. aurelioi* which are more similar to each other, usually with incubations of nearly 5 weeks under the same conditions (Kruskal-Wallis test: $H = 21.78$, $df = 2$, $p < 0.0001$, Bonferroni test; table 5).

Table 5.Days of incubation and newborn characteristics of Pyrenean *Iberolacerta* species.

		<i>I. bonnali</i>	<i>I. aranica</i>	<i>I. aurelioi</i>
Incubation (days)	Mean \pm SE	34.15 \pm 0.61	30.45 \pm 0.32	35.60 \pm 1.60
	range	31-36	23-34	31-44
	n (eggs)	13	64	10
Hatchling SVL (mm)	Mean \pm SE	25.82 \pm 0.81	26.15 \pm 0.18	27.57 \pm 0.30
	range	23.6-27.0	22.1-28.7	26.4-29.9
	n	3	68	19
Hatchling mass (g)	Mean \pm SE	0.40 \pm 0.057	0.41 \pm 0.007	0.49 \pm 0.017
	range	0.3-0.5	0.2-0.5	0.4-0.6
	n	3	79	19

Table 6.Sex-ratio of the hatchlings of the three Pyrenean *Iberolacerta* (NS: not significant).

	<i>I. bonnali</i>	<i>I. aranica</i>	<i>I. aurelioi</i>
Sex ratio	3:1	1.8:1	0.78:1
No. Males-No. females	3-1	68-36	15-19
χ^2	1	9.84	0.47
df	1	1	1
p	0.317 (NS)	<0.01	0.493 (NS)

Hatchling characteristics. Body size (SVL) and body mass of newborn lizards hatched in the laboratory are shown in table 5. *Iberolacerta aurelioi* has the longest hatchlings (in SVL) and differs statistically from *I. aranica* with the smallest (in our calculations, however, the small sample of *I. bonnali* – not representative – appears as the smallest) (ANOVA: $F_{2,87} = 7.81$; $p < 0.001$).

Also, *I. aurelioi* hatchlings have a greater mass than *I. aranica* and *I. bonnali* (Kruskal-Wallis test: $H = 14.68$, $df = 2$, $p < 0.001$).

Newborn lizards from the three species have coloration and patterns similar to adults, especially to adult females. In *I. aurelioi* hatchlings are always brown-backed with striking green tails. In *I. aranica* and *I. bonnali* the back is greyish and tails are usually also of the same colour, but on rare occasions blueish tails can be found (morphological description of newborn lizards and ontogenic changes in their morphology are described for each species in Arribas, 1999a, 2000, 2001).

SVL females-SVL hatchlings. For the most representative sample from which the two parameters are available, *I. aranica*, there is no relationship between females and their offspring size ($r = -0.20$, $F = 0.61$, $p = 0.45$, $n = 16$).

Hatchling sex ratio. For all the sex-identified hatchlings raised under laboratory conditions, the proportions between males and females are shown in table 6. Hatchlings of *I. aurelioi* do not differ significantly from 1:1. Interestingly, the important newborn *I. aranica* sample differs clearly from 1:1 (1.8:1) clearly favouring males (nearly twice as many). Moreover, the sex-ratio in adult *I. aranica* is also different from 1:1 (0.55:1) but in the opposite way, clearly favouring females ($\chi^2 = 18.44$; $df = 1$; $p < 0.0001$; $n = 229$ adult specimens sexed). In *I. bonnali* the sex-ratio in adults is balanced (0.98:1; $\chi^2 = 0.01$; $df = 1$; $p = 0.91$; $n = 334$ adult specimens sexed), as in *I. aurelioi* (1.21:1; $\chi^2 = 2.14$; $df = 1$; $p = 0.14$; $n = 226$ sexed specimens).

DISCUSSION

Analysis of patterns of life-history covariation within lacertid lizards show that species can be arranged along a single, multivariate axis. At one end of this continuum are small-sized species that 1) mature early; 2) have small clutches of relatively large eggs (and offspring); 3) may have multiple broods per year; and 4) have short adult lives. At the other extreme are the larger lacertids with the opposite set of traits (Bauwens and Díaz-Uriarte, 1997).

The three Pyrenean *Iberolacerta* species are small sized lacertids, but only meet two of the four above-mentioned characteristics that, theoretically, should correspond to them due to their small size (small clutches of relatively large eggs and offspring). The negative correlation of clutch size and offspring size is a universal phenomenon among lacertid lizards and is associated with a size-related change in the partitioning of reproductive investment: all the small lacertids (like these three *Iberolacerta*) produce few, relatively large eggs and offspring (Bauwens and Díaz-Uriarte, 1997). Clutch and egg size in the three Pyrenean *Iberolacerta* species are similar to other similarly sized lacertids (i.e., *Podarcis hispanica* from Central Spain, with an average SVL of 56-57 mm, average clutch sizes of 3.0-3.6 eggs and mean egg mass of 0.33 g; García-Fernández, 1990; Castilla and Bauwens, 2000b). Selective pressures responsible for the egg size determination in a lizard species of a given SVL, which limit their egg size both above or below these optimal values, are generally well-known for reptiles (Congdon and Gibbons, 1987; Sinervo, 1990; Sinervo and Licht, 1991), including lacertids lizards (Bauwens and Díaz-Uriarte, 1997; Bauwens, 1999).

However, other life history characteristics of the three Pyrenean *Iberolacerta* are in contrast with those that we would expect to find due to their small size, following the model of Bauwens and Díaz-Uriarte (1997). In these high mountain lizards, sexual maturity is very delayed (≥ 4 years); they probably have a relatively long lifespan and only produce a single clutch yearly. We attribute these shifts in their life history as linked to the abiotic (mainly climatic) characteristics of the high mountain areas inhabited by these lizards, as has been pointed out in other high

mountain lizard populations (Saint-Girons and Duguy, 1970; Heulin, 1985; Braña et al., 1990; Marco et al., 1994; Olsson and Shine, 1999).

Reproductive cycle

One of the most outstanding characteristics in the life history of these alpine species is the shortness of their annual activity cycle, due to harsh weather conditions in the alpine environment. Parallel to the short activity period, the reproductive cycle is also very short, starting very late. The lizards mate during the end of May or June and lay eggs generally from mid-June to mid-July. Short, delayed reproductive cycles are characteristic of populations of lacertid lizards (as of other reptiles) living in areas with harsh climatic conditions, such as the high latitude populations of *Zootoca vivipara* (Nuland and Strijbosch, 1981; Bauwens et al., 1986; Bauwens and Verheyen, 1987; Pilorge, 1987), or mountain populations of *Podarcis muralis* (Saint Girons and Duguy, 1970), *Iberolacerta cyreni* from the Sierra de Guadarrama (Barbadillo, 1985) and *I. monticola* from the Serra da Estrela (Moreira et al., 1999) and Cantabrian Mountains (Braña et al., 1990).

Apart from the short duration of the reproductive period, an outstanding inter-annual variability in activity onset and egg laying data related to the specific year climatic characteristics was observed, with shifts of nearly a month in the reproductive process during cold springs due to the prolonged presence of snow on the ground. A similar phenomenon has been observed in *I. monticola* from the Serra da Estrela (Portugal), where populations inhabiting altitudes above 1700 m are submitted to strong interannual variability in their phenology, conditioned by the specific climatic characteristics of the year in question in the highest localities and by the end of the snow-melting period (Moreira et al., 1999).

Number of clutches

One of the main consequences of the short annual-cycle and the interannual variability of the reproductive period in these species is the impossibility of laying more than a single clutch in the same reproductive season. The three Pyrenean *Iberolacerta* species produce only a single annual clutch, regardless of the female size. Within lacertid lizards, the production of a single annual clutch is the rule in most of the populations of large-sized species (e.g., *Lacerta agilis*, *L. schreiberi* or *L. lepida*, see revision of literature in Bauwens, 1999). In small-sized species like the three Pyrenean *Iberolacerta*, a single annual clutch is only described in a few populations or taxa, such as the viviparous populations of *Zootoca vivipara* (Heulin et al., 1997), the high altitude populations of *Podarcis muralis* (Saint Girons and Duguy, 1970), or the northernmost population of this same species (Strijbosch et al., 1980). In the first case, the single clutch is conditioned by the viviparous modality of reproduction and the need to carry the eggs until fully developed inside the female body. In the case of the northernmost or high altitude populations of *Podarcis muralis*, it is affected by the short duration of the activity and reproductive

period in these areas (*P. muralis* is nearly sympatric with *I. bonnali* in the Pyrenean area of the Neouvielle Massif studied by Saint Girons and Duguy, 1970). Thus, in populations or species of small sized oviparous lizards (mainly polyestrous, at least the largest sized females from each population), climatic factors limit the duration of the reproductive period and would seem to be responsible for the absence of second or multiple clutches in the same season, as occurs in these specific populations on their northern boundaries of distribution (Strijbosch et al., 1980) or in the high mountain *Podarcis* (Saint Girons and Duguy, 1970) and *Iberolacerta* populations (Braña et al., 1990; Moreira et al., 1999; this paper).

Adult size and sexual maturity

Another important issue imposed by the short annual cycle in these three species is their limited annual growth rate. Due to the reduction in the number of days available for food intake and fat reserve accumulation between the beginning and the end of the vegetative season in the high mountains, it takes immature animals several years to reach minimum sizes for reproduction, despite the fact that they are small sized lacertids.

Sexual maturity is not achieved until after the fourth hibernation (5CY) when subadults reach the smallest adult (reproductive) size. Females probably take even longer to reach their first reproduction (probably 6CY). In *I. aurelioi* the largest (and presumably oldest) male (SVL 57.18) from Pica d'Estats Massif (Spain) apparently exhibited 18 growth rings in its femur which corresponds to approximately 17 years, and the largest female (SVL 62.21 mm) from Coma Pedrosa Massif (Andorra) had 11 narrow (full adult) growth rings and probably (uncertain because of bone reabsorption) four wider rings, which means nearly 14 years (Arribas, unpubl.).

The maximum longevity is still unknown (see below), but they must be among the longest-lived of the European small sized lizards, on the basis of their low reproductive potential and delayed sex maturity, both probably linked to the short yearly activity period.

The mean SVL of adult females from the three species was greater than that of males. In addition, females reach sexual maturity at an SVL of 48.9-51.4 mm (vs. 45.0-45.4 in males). A higher SVL in females versus males has also been reported for other lacertids such as *Iberolacerta monticola* (Galán, 1991), *Lacerta schreiberi* (Galán, 1984) or *Zootoca vivipara* (Braña, 1996), and appears to reflect the greater number of presacral vertebrae in female lacertids (Barbadillo and Sanz, 1983; Barbadillo, 1985).

The RCM value obtained for *Iberolacerta* species (an average of 0.54-0.56 in *I. monticola*; Braña et al., 1991; Rúa and Galán, 2003; average RCM 0.55 in *I. aranica*, present paper) is higher than in most other lacertid lizards, with the exception of *Zootoca vivipara*, which may reach up to 0.81 (Bauwens and Thoen, 1981; Bauwens et al., 1986) or even 1.02 (Pilorge et al., 1983). Other lacertid lizards have a RCM of less than 0.48, such as *Podarcis muralis*, 0.24-0.47 (Braña et al.,

1991; Braña, 1993; Bejakovic et al., 1996a, b; 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., 1995), *Lacerta (i. s.) oxycephala*, 0.22 (Bejakovic et al., 1996b, c), *Algyroides nigropunctatus*, 0.29 (Bejakovic et al., 1996c).

We lack a sufficient sample size to compare RCM among the three species. However, the ratio that relates clutch volume (cubic root) with female SVL does not show significant differences among species.

Clutch size

Despite the small clutch size of the three species, both inter- and intraspecific significant differences in the number of eggs per clutch were detected. In both cases, a positive correlation between clutch size and female-SVL was found. The species with the greatest mean female SVL (*aranica*, 57.0 mm) also shows the highest average and maximum clutch size (3.4 and 5 eggs, respectively), and the lowest one (*aurelioi*, 55.3 mm SVL) has the smallest average and maximum clutch size (2.5 and 3 eggs, respectively). *I. bonnali*, which is intermediate in size between the above-mentioned species (average 56.3 mm SVL), also shows an intermediate average and maximum clutch sizes (3.0 and 4 eggs, respectively). Nevertheless, differences in body size are quite small among species, and do not explain, in themselves, the high differences in clutch size, if not due to slightly different reproductive strategies in the three species. On the other hand, in each separate species a positive correlation was found among female SVL and clutch size, and the females with the largest body size lay more eggs. This increase in egg number with female size is a general phenomenon in lizards with variable clutch size, including lacertid lizards (see revision of data in Bauwens and Díaz-Uriarte, 1997; den Bosch and Bout, 1998; Bauwens, 1999). However, this relationship is absent in some populations of small body sized species, such as *Podarcis hispanica* from Asturias and Cantabria, in northern Spain (Braña et al., 1991; Braña, 1996). Nevertheless, these populations have females with a slightly smaller body size and clutch size than the three Pyrenean *Iberolacerta* species (47.6-51.8 mm SVL on average and 2.2-2.3 clutch size, respectively).

Based on 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 due to energy and volume 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. This pattern is characteristic of lacertid lizards, exhibiting steep slopes in the regression of clutch size on female size (Castilla, Barbadillo and Bauwens, 1992; De Luca, 1992; Ji and Braña, 2000).

Nesting places

The frequent low values of total eggs found together (both fresh and old eggshells) also suggest that a large part of the specific egg laying sites are used very few times or only from time to time. For the overall data of the Pyrenean *Iberolacerta* ($n = 119$ clutch sites in the wild), 58% of the sites contained fresh eggs when detected but not old ones (i.e. new clutch sites or at least not used during the previous years), 27.7% contained old eggs but not recent ones (sites not reutilised in that year) and only 13.4% contained both new eggs and old eggshells (sites reutilised in the given year).

As can be seen, although a few females (usually around two) may lay in the same site, the most frequent situation is a single female laying alone in a new clutch site. There is a strong renewal of clutch sites from year to year. Inhabiting rocky areas and stony slopes, these lizards have a great number of suitably sized rocks for egg laying, and the choice of a given site for oviposition does not seem to pose any major problems for the animals. Continuous solifluction (ground movement) and rock disgregation by weathering lead to slow, but gradual, changes in the surface characteristics of these high mountain slopes and contribute to the creation of suitable new clutch sites each year, while others are destroyed.

The three Pyrenean *Iberolacerta* seek out moderate sized stones under which to lay eggs. Although communal clutches are present in these species (up to 29 newly laid eggs found together from *I. aranica*), this is not the most common situation. The mean values of 'fresh' eggs found in the field correspond frequently to only one or two clutches from different females laying in the same place, at most. The large accumulations of old eggs found in certain favoured places might correspond to year after year egg remains of the same few long-lived females or several of them with occasional contributions from young newcomer females, but more possibly to other factors that favour the persistence of the eggshell under the stone for a long period of time. The frequent low values of coincidence among fresh and old clutches also suggest that a large number of the egg laying sites are used very rarely or only occasionally, helping to decrease the risk of egg predation.

Despite the fact that, theoretically, the larger stones provide a more stable environment, protecting against wide fluctuations in temperature and loss of moisture (Huey et al., 1989; Kearney, 2002), our results show that they are not used by a greater number of females. The differences between number of fresh eggs found together and the accumulated old eggshells are a consequence of the permanence of the old eggshells in the clutch sites and would be due to the combined effect of their longer endurance under the bigger versus the smaller stones, and their possible greater (more frequent) use over the years. One can hypothesise that, although larger stones are not used by a greater number of females in a given year, they are used more frequently over the years (larger stones are more visible reference landmarks in the area for the lizards, as well as less prone to weathering by external agents). Other eventual factors such as snow accumulation and differential patchy snowmelt in spring may influence the greater or lesser availability of egg laying sites during

some years, although the snow has usually already disappeared when the clutch is laid.

It seems to be a fact that lizards in extreme environments tend to aggregate their clutches in specific places. This is due to the great limitation in the availability of favourable sites for the most sensitive of their vital phases, the egg, which apart from being ectothermal and ectohydric, is an immobile and a very vulnerable phase (Packard and Packard, 1988; Overall, 1994; Galán, 1996). However, in the high mountains, suitable sites for egg laying (stones on the ground) are plentiful, and soil moisture during the egg laying season is widespread due to the recent snowmelt. However, this does not seem to be a critical factor, as adults also actively choose moister areas during the summer drought (Arribas and Martínez-Rica, 1997; Arribas 2002b, c).

Incubation

Arribas (1993a) points out that the incubation time in '*I. bonnali*' is very short, only 28-35 days, a fact related to the long oviductal egg retention as an adaptation to the high mountain conditions. In *I. horvathi*, another mountain *Iberolacerta* species, incubation lasted 37-41 days at 27-29°C (Bischoff, 1984), in *I. cyreni* about 46 days (Barbadillo, 1985) and in *I. monticola* (from the Galician coast, at a low altitude), 45-54 days (Galán, 1991). In this study, the short incubation time observed in the three *Iberolacerta* species studied (an average of 30, 34 and 36 days for *aranica*, *bonnali* and *aurelioi*, respectively) and the degree of embryonic development from eggs in the clutch period (stages 30-33 according to Dufaure and Hubert, 1961), indicate a lengthened oviductal retention period before oviposition. A similar degree of retention (the maximum described in lacertids) is found in Cantabrian-Pyrenean oviparous populations of *Zootoca vivipara* (Braña et al., 1991; Heulin et al., 2000), some of which share the distribution area at higher elevations with the Pyrenean *Iberolacerta*. Recently, other oviparous populations of *Z. vivipara* have been discovered in Slovenia, Austria (Heulin et al., 2000; Mayer et al., 2000) and northeastern Italy (Ghielmi et al., 2001). All of them have a prolonged oviductal retention of the eggs, which are laid with embryos in stages 30 to 32 from Dufaure and Hubert (1961), and thus are similar to the Cantabrian-Pyrenean oviparous populations of the same species. For this reason, the three Pyrenean oviparous *Iberolacerta* species are the only known lacertids to have an oviductal retention period nearly as prolonged as the one seen in the oviparous *Zootoca vivipara* populations and, thus, the only lacertid species to reach an evolutionary stage towards viviparity as advanced as the oviparous populations of *Z. vivipara*. Interestingly, this occurs in the same geographical areas, the mountain slopes of the Southern European Peninsulas, which were near the northern limit of the glacier refuges and presumably have harsher conditions than other southernmost areas. Although exaptation (or 'pre-adaptation') to viviparity through egg retention cannot be excluded by the fact that several of the concerned species inhabit a wide altitude interval, the fact of the unrelatedness among *Iberolacerta* and *Zootoca*, and the

distinctly advanced retention degree in *Iberolacerta* in accordance with the currently occupied habitat conditions (progressively harsher in relation to altitude) point more towards an adaptative explanation for this phenomenon.

Shine (2002) has demonstrated, by means of field and laboratory studies, that the selective advantage of uterine egg retention (accelerated hatching, enhanced hatchling success, and increased locomotor speed of hatchlings) was greater at higher elevations and increased with longer egg retentions, in the so-called 'cold-climate model'. This seems to be in accordance with our data on Pyrenean *Iberolacerta*, in which the selective forces promoting the uterine retention of eggs would also seem to operate; hence, the evolution of viviparity, as in other high altitude reptiles (Shine, 1983, 1999, 2002).

Egg predation

Andrews (2000) proposes an alternative hypothesis to the 'cold-climate model' to explain the evolution of viviparity, pointing out that selective forces tending to avoid egg predation could also be in operation. In keeping with this, it is interesting to note that the number of clutches preyed on by the dipter *Sarcophaga protuberans* in the three Pyrenean *Iberolacerta* species is relatively high (Pape and Arribas, 1999; this paper). However, there are no data on the incidence of predation on Lacertid clutches which would enable us to make comparisons among species or populations subjected to different environmental conditions.

The above-mentioned tendency of females to lay alone, and particularly, to change clutch sites from year to year, allows them to escape from fly predation, not a negligible threat for such low productive lizards. In Pyrenees, this fly would seem to have a univoltine cycle and overwinters as diapausing pupae, emerging after the snowmelt, synchronised with the lizard's reproductive cycle (Pape and Arribas, 1999). If clutch sites were used year after year or communal clutches were common, adult flies emerging from pupae of a previous year's destroyed clutches would find females laying immediately in the same site, and again destroy the clutches of the year. This would lead to the disappearance of a large number of the eggs of these species.

Hatchling sex-ratio

In the sample of *Iberolacerta aranica* studied, the hatchling sex ratio differs from the 1:1 proportion. It is not easy to explain what the reason might be for both the unbalanced sex ratio and the clear difference between hatchlings and adults. As laboratory conditions for the eggs were the same for all species, some intrinsic cause related to *I. aranica* must be involved in these differences. In regard to this, it should be pointed out that *I. aranica* is the only one of the three Pyrenean species without discernible sex chromosomes (assumed to be homomorphic and euchromatic; Odierna et al., 1996). This could be related to this biased sex ratio, perhaps with some degree of temperature induced sex determination, which is well

known in crocodylians, turtles, and even agamids, but not in lacertids up to now. In this case, higher temperatures (or more stable ones along their circadian oscillation) in the laboratory versus the wild would be linked to this male-biased sex-ratio. However, the advanced embryonic stage of development at clutch seems to suggest that the sex of the embryo must be defined before this time and, in this case, the temperature characteristics to which the female is subjected prior to the clutch could be a determining factor. This would be an important subject to examine in future research, although the scarcity of the species would make it difficult to study.

Another quite different question is the fully inverted adult sex-ratio in *I. aranica*. Either there is a very different mortality rate between sexes, which changes their proportions from hatchlings to adults, (Galán, 1999) or, with the lower temperatures under high mountain conditions, the true hatchling sex-ratio is the one known for wild adults. All these aspects will be investigated in greater depth in future studies.

The three Pyrenean *Iberolacerta* species are threatened, especially *I. aranica* (CR) and *I. aurelioi* (EN), in addition to *I. bonnali* (VU). In all cases, the principal factors causing them to be threatened are their reduced (*I. bonnali*) or extremely small (*I. aranica* and *I. aurelioi*) distribution areas, their population fragmentation in continuous decline due to increasing human activities in the high mountain areas, as well as heating due to global climatic change, which will probably restrict their distribution area even more in the future (Arribas, 2002a, b, c).

To these threatening factors we must add the results of this paper regarding the reproductive and demographic characteristics of these populations.

Their small body size would make them similar in morphology to other small lacertids, such as the *Podarcis* species. But the latter species, which are opportunistic in their life history characteristics, usually possess demographic strategies that facilitate a rapid increase in the population size (Bauwens, 1999; Galán, 1999) and this does not occur in these Pyrenean *Iberolacerta*.

According to the data obtained, the three Pyrenean *Iberolacerta* species show a very low fertility and delayed sexual maturation. Owing to these characteristics, the viability of these populations will be based on adult survival, due to the scarce and late incorporation of immature animals to the adult (reproductive) population, which makes them very vulnerable to any kind of anthropic alteration or cause of the disappearance of adult specimens.

Therefore, it will be necessary in future to take into account these peculiar characteristics related to reproductive and population dynamics to plan an appropriate conservation of these endangered endemic Pyrenean species.

ACKNOWLEDGEMENTS

The Generalitat de Catalunya (DARP) gave permits n° 2017 (1989 to 1992), 1152 (1993), 563 (1994), 516 (1995), 5787 (1996), 106 (1997), 51 (1998), 195 (1999), 239 (2000), 006 (2001) and 214 (2002), the Diputación General de Aragón (DGA) gave permits n° 26203 (1992), 12458 (1993), 16023 (1996), 12600 (1997); Conselh

Generau d'Aran gave permit n° 458 (2002) and, finally, Aigüestortes National Park also gave special permission (in 1995) for the study or collection of specimens.

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