Characteristics of the reproductive biology
of *Iberolacerta aurelioi* (Arribas, 1994)
(Squamata: Sauria: Lacertidae)

Kenndaten zur Fortpflanzungsbiologie von *Iberolacerta aurelioi* (Arribas, 1994)
(Squamata: Sauria: Lacertidae)

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KURZFASSUNG

Iberolacerta aurelioi (Arribas, 1994) ist eine in ihrem Bestand gefährdete Eidechsenart mit einer sehr kleinräumigen Verbreitung. Wesentliche Merkmale ihrer Fortpflanzungsbiologie wie etwa die hohe Lebenserwartung (von bis zu 17 Jahren), die verzögerte Geschlechtsreife (nicht vor dem 5. Kalenderjahr bzw. 4 Überwinterungen) und sehr geringe Vermehrungsrate (ein Gelege aus 2 oder 3 Eiern pro Jahr) stehen in Zusammenhang mit der kurzen Jahresaktivitätsdauer in großen Höhen. Das Datum des Erscheinens nach der Winterruhe hing von den tatsächlichen Wetterverhältnissen im jeweiligen Jahr ab und war dann für alle Altersstufen und beide Geschlechter dasselbe. Die Paarung begann bald nach dem Verlassen der Winterquartiere (zweite Maihälfte bis erste Junihälfte). Für die Paarungsstellung war der Flankenbiß des Männchens charakteristisch. Die Eientwicklung erfolgte im Verlauf des Juni und die Eiablage fand zwischen Mitte Juni und Mitte Juli statt.

Es erfolgte nur eine Eiablage pro Jahr, wobei (1) 2 oder 3 Eier gelegt wurden, welche Embryonen in fortgeschrittenen Reifestadien enthielten (Stadium 30 bis 32 nach Dufaure et al. 1961). Bevorzugt wurden Ablageorte unter mittelgroßen bis großen flachen Steinen in leicht geneigtem Gelände. Unter solchen Steinen fanden sich zwei bis 12 frisch gelegte Eier, die von mehreren (im Durchschnitt zwei) Weibchen gemeinsam am selben Platz abgelegt worden sein mußten. Allerdings wurden solche Ablageorte häufig von Jahr zu Jahr gewechselt, sodaß nur wenige von ihnen in aufeinanderfolgenden Jahren benutzt waren. Die Veränderungen in den Abmessungen der Eier während der Inkubation werden beschrieben. Die Eizeitigung dauerte im Labor zwischen 31 bis 44 (im Mittel 35) Tage. Im Freiland traten die ersten Schlüpflinge zwischen Mitte August und Mitte September auf. Im Freiland zerstörte Fraß durch die Larve der Fliege *Sarcophaga protuberans* 25% der Gelege. 64% der im Labor erbrüteten Eier schlüpften. Der Schlupfvorgang und das frisch geschlüpfte Jungtier werden beschrieben.

ABSTRACT

Iberolacerta aurelioi (Arribas, 1994) is an endangered lizard species of very restricted geographic distribution. Key features of its reproductive biology such as its long lifespan (up to 17 years), delayed maturation (not before 5th calendar year, i.e. after 4 hibernations) and very low fecundity (one clutch of 2 or 3 eggs per year) are linked to the short annual activity-period in high altitudes. The date of first emergence after overwintering depended on the actual weather regime of the year, irrespective of sex or age. Mating began soon after emergence from the hibernacula (second half of May to first half of June). The copulatory posture was characterized by a male grasp to the females flank. Eggs developed during June and clutches were laid from middle of June to middle of July.

A single clutch was laid per year consisting of (1) 2 or 3 eggs which contained embryos in advanced developmental stages (stages 30 to 32 according to Dufaure et al. 1961). Clutches were laid preferentially under medium to big slabs in stony gently sloped grassland areas. Two to 12 fresh eggs deposited collectively by several females (two on the average) were found under the stones. However, there was considerable rotation of the oviposition sites utilized each year, very few being used in successive years. The variation of the egg measurements during incubation are described. Incubation took 31 to 44 days (average 35) under laboratory conditions. In the field the first hatchlings appeared from middle of August to middle of September. Predation by larvae of the fly *Sarcophaga protuberans* destroyed 25% of the clutches in the wild. In the lab 64% of the eggs hatched. The hatching process and the new-born lizard are described.

KEY WORDS

Reptilia: Squamata: Sauria: Lacertidae; *Iberolacerta aurelioi*; phenology, reproduction, reproductive biology, high altitude environment, Alpine environment, Pyrenees, Spain

INTRODUCTION

The Pyrenean Mountains are inhabited by three closely related allopatric *Iberolacerta* species: *Iberolacerta aranica* (Arribas, 1993), *I. aurelioi* (Arribas, 1994), and *I. bonnali* (Lantz, 1927), described or elevated to species rank within the last decade, however still almost unknown in their biology (Arribas 1993a, 1993b, 1994, 1997a, 1997b,

1997c, 1999c, 2000, 2001a, 2002a, 2002b, 2002c; ARRIBAS & MARTINEZ-RICA 1997).

These three species have insular distribution patterns, inhabit rocky substrates in sheltered areas of the supraforestal alpine belt above 2,000 m. This zone is characterized by a very short annual vegetative period (from middle of May to middle of October, but frequently shorter) and is submitted to strong circadian contrasts in temperature, moisture, wind, and insolation; the ground being continuously snow-covered almost six months per year. All these characteristics configure these areas as very harsh and extreme environments for these ectotherms, the only truly exclusive high-mountain lizards of Europe. They constitute first-order models for studies to understand the mechanisms of speciation in ectothermic animals of the mountains, as well as survival strategies in climatically extreme regions (ARRIBAS 1997a, 1997b, 1997c, 1999c, 2000, 2001a; ARRIBAS & MARTINEZ-RICA 1997).

Iberolacerta aurelioi is an "endangered" (ARRIBAS 2002b), endemic to three Pyrenean massifs: Mont-Roig, Pica d'Estats and Coma Pedrosa where it inhabits alpine (supraforestal) altitudes from 2,200 to 2,940 m. It occurs in six U.T.M. grid squares only, each 100 km^2 in size but inhabits only small parts of them (ARRIBAS 1999a, 2002). Here I report on the hitherto unknown reproductive biology of this lizard.

STUDY AREA, MATERIALS AND METHODS

Study sites

All localities known to be inhabited by the species (ARRIBAS 1999a, 2002b) were surveyed carefully from 1991 to 2002 in the framework of a complete study on the biology and chorology of the three Pyrenean *Iberolacerta* species. *Iberolacerta aurelioi* is strictly protected. Administration (Agriculture and Environment Departments from Generalitat de Catalunya) gave permissions number 2017 (1992), 1152 (1993), 563 (1994), 516 (1995), 5787 (1996), 106 (1997), 51 (1998), 195 (1999), SF239/00 (2000), SF/006 (2001) and SF/214 (2002) for capture and manipulation of the specimens. Data from various localities covering all of the species' range (Mont-Roig, Pica d'Estats and Coma Pedrosa Massifs) were pooled in order to achieve reasonable sample size.

Intensity of sun light (mainly ultraviolet radiation), precipitation (especially the proportion of snow) and wind effects increase with altitude, whereas temperature and atmospheric pressure decrease. Air temperature annual means oscillate between -2 and +5°C (usually < 3°C). Temperature means of the coldest month are -10°C or less, whereas maximum summer temperatures oscillate between 20°C and 25°C. Pluviometric regime is hyperhumid (>1400 mm), length of vegetative period is from one to three months. Snow persists continuously on the ground between 6 and 9 months. There are seven months of continuous night frosts and two to three more months in which they occur frequently. Occasional snow fall can occur at any time during the activity period of the lizard.

These zones are submitted to strong circadian contrasts in temperature, moisture, wind, insolation, and there are also dramatic differences between ground and air temperatures during the activity hours. Even in summer, temperatures descend to near 0°C during night due to intense nocturnal infrared radiation to the atmosphere, and during sunny days rock temperature increases frequently above 40-50°C (VIGO 1976, DUPIAS 1985, OZENDA 1985, RIVAS-MARTINEZ 1987, ARRIBAS 1997a).

Gravid females

Data on females were collected concerning the following aspects:

i) Activity: Inactive (cold or warm), active (basking or moving).

ii) Reproductive state: copulated (mating scars present), highly gravid (oviductal eggs palpable), or short after oviposition (lateral folds present).

iii) Habitat: Estimation of percentage covers of rocks, stones, bare ground, grass or shrubs in a 2-meter radius around the first localization of the animal. These percent-

age covers (%) were estimated by sight and comparison with graphic surface-calculation scales (EMBERGER 1983). Inclination of the site was recorded as well.

Clutches in laboratory

Gravid females were transported to the laboratory (located at 1,020 m a.s.l.) for monitoring of the oviposition and incubation processes. Females were placed in glass or plastic terraria (base: 30 cm x 20 cm) with peat substratum and a flat stone for digging underneath. Food (small arthropods from the laboratory area) was supplied ad libitum, although gravid females near oviposition do not feed at all. Lizards were maintained under natural illumination and photoperiod conditions (direct sun from sunrise to near 12:00 GMT, and shadow until sunset).

Females were controlled about hourly during the day, and twice per night, during the entire study of the oviposition process. Eggs laid were marked, measured and placed in plastic boxes for incubation under natural temperature conditions (24°C - 30°C) in the open air. These plastic boxes were furnished with peat substrate and a piece of moss to cover the eggs in order to provide a humid environment and facilitate easy periodic inspection. Four perforations in the boxes ensured air circulation and prevented from mold development.

Clutches were controlled daily and egg metrics (length, width, mass) were taken each week. Egg volume (V) was calculated based on an ellipsoid approximation ($V = 4/3 \pi a^2 b$) a and b being the width and length of the egg, respectively.

Length measurements were taken with digital calipers (Mitutoyo®, accuracy 0.1 mm), egg-weights with a portable digital scale (Tanita®, 1479, accuracy 0.1g).

When hatchlings perforated their egg-shells, hour (GTM) and total duration of hatching process were recorded, as well as duration of egg-tooth persistence. From each new-born lizard, snout-vent length (SVL), weigth and number of transversal seies of ventrals (for sex determination) were noted as well as the extent (relative to ventral scale rows) of the umbilical scar. New-born lizards were sexed by ventral scale count (males up to 28, females 29 or more, see ARRIBAS 1997a, 1999a). New-born specimens were fed with aphids until release in the site of their mother's origin.

Clutches in the field

When clutches were found in the field, the following data were recorded:

i) Number of freshly laid eggs.

ii) Number of old eggs (egg-shells from previous years).

iii) Presence of destroyed or parasitized eggs (both from current year and previous years, revealed by the presence of fly-puparia inside the empty egg-shells).

iv) Size (greatest and smallest diameters) as well as thickness of the stone that covers the clutch. The approximate surface area of these stones was defined by the product of greatest diameter x smallest diameter.

v) Habitat parameters for clutches were taken as in gravid females (see above).

Statistical calculations were performed with NCSS-2002© (HINTZE 2001). Interespecific differences in each sex were tested with One-Way ANOVA, and Tukey-Kramer post-hoc tests with Bonferroni correction for pairwise comparisons among the group means, difference between males and females by *t*-tests. If normal distribution was not met, non-parametric tests (Kruskal-Wallis or Chi-square [χ^2] tests) were used.

Table 1: Difference (*t*-test) in snout-vent-length (mm) between males and females of *I. aurelioi*. SE – Standard error of the mean.

Tab. 1: Die Unterschiede (*t*-Test) in der Kopf-Rumpf-Länge (mm) zwischen Männchen und Weibchen von *I. aurelioi*. SE – Standardfehler des Mittelwertes.

Males / Männchen mean±SE, min-max (n) Mittel±SE, min-max (n)	Females / Weibchen mean ±SE, min-max (n) Mittel±SE, min-max (n)	Difference / Unterschied *t* value, *p* value *t*-Wert, *p*-Wert
52.41±0.24, 45.1-65.25 (123)	55.31±0.31, 48.43-62.21 (99)	$t = 6.31$, $p = 0.000000$

RESULTS AND DISCUSSION

Age classes

Due to the short annual activity period, age classes are clear-cut in the population. Before the hatching of the young of the year, the population is composed of adults and four non-adult cohorts (ARRIBAS unpublished). Sexual maturity is achieved at least after the fourth hibernation (fifth calendar year; 5CY hereinafter) when animals reach the minimum size for reproduction (see section on adult size and sexual maturity). Achievement of female reproductive maturity takes longer (first reproduction probably 6CY, see below). In captivity, the closely related *I. bonnali* reaches sexual maturity at the age of two years (3CY), however, under an extended activity period due to unnatural favorable conditions (near sea-level, in Holland) (IN DEN BOSCH, pers. comm). Theorically, in *I. aurelioi* maximum longevity should be among the longest of the European small-sized lizards, because of low reproductive potential and delayed sexual maturity, probably linked to its short annual activity period. The biggest (and presumably oldest) male (SVL 57.18 mm) from Estany de Sotllo (Pica d'Estats Massif) (depicted in ARRIBAS 1999a: plate 1, nº 15 & fig 8) apparently shows 18 growth rings in its femur which correspond to approximately 17 years of age, and the longest female (SVL 62.21 mm) from Coma del Forat (depicted in ARRIBAS 1999a: plate 2, nº 15) shows 11 narrow (full adult) growth rings and probably (uncertain because of bone resorption) 4 wider growth rings, wich means an age of about 14 years. These are clearly very old specimens also from their external morphology (heavily sculptured head scales, very intensive pigmentation, etc.) and represent individuals of extreme ages. The usual lifespan of *I. aurelioi* should be expected to be shorter than the abovementioned ones, however longer than in lowland or low-mountain lizards (6-7 years in several *Darevskia* species and up to 11 years in *I. monticola* (BOULENGER, 1905) which, however, reaches sexual maturity earlier than *I. aurelioi*, in their 3CY in the case of *Darevskia armeniaca* (MÉHELY,

1909), *D. lindholmi* (LANTZ & CYRÉN, 1936) and *D. valentini* (BOETTGER, 1892) or 4CY (rarely 3CY) in *I. monticola* females, in contrast to 5CY in the three Pyrenean *Iberolacerta* species including *I. aurelioi*) (DAREVSKY 1967; MOREIRA et al. 1999; ARAKELYAN 2002). Both in their sexual maturity achievement and longevity, the Pyrenean *Iberolacerta* species behave rather like the bigger *Lacerta* and *Timon* lizards, than other similar small-sized representatives of the genera *Iberolacerta*, *Podarcis* or *Zootoca*. The ultimate causes of these peculiarities in life-history seem to be the shortness of their activity and growth periods.

Adult size
and sexual maturity

Males and females of *I. aurelioi* differed in their SVL, in that males were significantly smaller than females (table 1).

Minimum size for sexual maturity in males was determined by the presence of clear sexual secondary characteristics (i.e. swollen tail-base due to the presence of developed hemipenes, which however in this species is smaller and, thus, not as easily discerned from that of females as in other *Iberolacerta* species; see ARRIBAS 2001b). The smallest apparently adult male in *I. aurelioi* measured 45.1 mm SVL. This size was reached in the 5CY. A young male from Andorra captured in 6 June 1994 (SVL 45.63 mm) showed besides reabsortion of the first growth ring (1CY), three wide growth rings (2CY, 3CY, 4CY) and a very narrow one from the year of capture (5CY) which fits well with the previous observations.

In females, determination of the sexual maturity age was more problematic. The attainment of sexual maturity was identified by reproductive signs such as the presence of large oviductal eggs determined by ventral palpation. Females of the age of the above mentioned males (5CY) frequently showed scars in the flanks presumably produced by encounters with males. However, they were of subadult appearance and it is not clear whether these females were ready

to reproduce since it usually takes one more year to reach sexual maturity (6CY). From 23 gravid females measured, SVL of the three smallest females which contained ova was 48.9 mm, 49.08 mm and 50.68 mm; this is slightly longer than the minimum size of 5CY females (48.43 mm). It cannot be ruled out that some females reach sexual maturity even in the 5CY. However, if this occurred after the end of the reproductive season, it would not take effect before the following year (6CY). There are no satisfactory skeletochronological findings available to enlighten this issue.

Mean snout-vent length of the gravid females studied was 55.84±0.65 (arithmetic mean ± Standard Error of the mean, SE) mm (range: 48.9-60.5; n = 23).

Phenology, mating and egg-laying period

Like the other Pyrenean *Iberolacerta* species, these lizards appeared from their hibernacula when the snow melted, usually in the second half of May. and retreated for overwintering during the second half of September (adults) or the first half of October (juveniles).

Annual activity period was quite short (four and a half to five months). Adults appeared around mid May or later when snowfall still covered the ground. Rocks were among the first spots to become free of snow and lizards utilized them for basking upon emerging from hibernation as observed on 5 June 1994 and 1995 in Andorra. Animals began to disappear towards the end of September or early in October (last adult observation: 20 September) depending on the specific weather of the year. Differences in emergence time between sexes or age classes were not observed. The sequence of several cold snaps before the definitive installation of cold marked the moment of the adult retreat to their winter quarters.

Copulation posture was characterized by a male grasp to the females flank, as is usual in European lacertids (ARRIBAS 1997a, 1999b). Males shed their hemipenis skin almost daily (IN DEN BOSCH 2001).

In years when the snow melt started early, as was the case in Andorra in 1994 and 1995, females showed mating scars and eggs in formation already at the beginning of June (6 June), while in 1996 and 1997 they bore mating scars in the middle of June, however oviductal eggs were still not discernable. In Capifonts, eggs were in formation in the first half of June (7 June) in 1995, which means oviposition towards the end of June.

In 1993 all Mont-Roig females had mating scars and eggs in formation in the middle of June, but in 1995 the cycle was delayed when compared with the Andorran population and mating scars and eggs close to oviposition were present only at the beginning of July (7 July).

Finally, in the Pica d'Estats Massif, females were developing eggs in the middle of June (12-VI-1993) and near to, or almost ready for oviposition at the beginning of July (1 - 4 July) in 1991, 1992 and 1993.

In conclusion, reproduction in *I. aurelioi* began with matings soon after emergence from overwintering (second half of May to first half of June), eggs were developing during June and clutches were deposited from middle of June to middle of July depending on the time of the snow melt of the year in question. Main egglaying period was from beginning to mid July in 1991, 1992 and 1993; end of June or beginning of July in 1994; second half of June (Andorra) to first half of July (Mont-Roig) in 1995; second half of June in 1996 and 1997; and last days of June and first ones of July in 2002.

Egg-laying behaviour

Females dug a small gallery under a stone scratching with their forelegs and using the head as a wedge if the ground was sufficiently loose. The hindlegs were used only occasionally for moving the soil. When this small and narrow hole was dug, the female turned around in the bottom of the short tunnel and - facing towards the entrance - laid the eggs. Females usually kept their bodies bent in "S-shape" during the oviposition process. Eggs became usually coiled, as in the other Pyrenean *Iberolacerta* and in the sympatric oviparous populations

of *Zootoca vivipara* (JACQUIN, 1787) (ARRIBAS unpublished). After egg-laying, females had very flat and shrunk bellies, with lateral folds between the temporal and infratemporal (= lateral inferior) dark bands.

Clutch size, number of clutches per year

Iberolacerta aurelioi is monoestrous, i. e. it lays one clutch per year and does this every year since all mature females were gravid at the beginning of summer.

There was little variation in clutch size (number of eggs) in *I. aurelioi*. Usually two or three eggs (numbers nearly equally frequent) were laid (mean±SE = 2.53±0.1; range = 1-3 eggs; n = 32 clutches) (fig. 5). When clutch size was adjusted for female SVL, the mean clutch size was 2.65 eggs.

Exceptionally, one case of a female developing a single egg is known (a relatively small and presumably young female with 49.8 mm SVL from Estany de Calberante). Also a clutch of four eggs coiled together was found in the field (Port de Rat, Andorra; 9-8-98), however, one egg was very small (abnormal) and without embryo, one was dried and the remaining two normal. These four eggs probably belong to two females, as several females can lay their eggs jointly in the same site (see PAPE & ARRIBAS 1999 and below).

Clutch size was significantly correlated with female SVL ($r = 0.52$; $F_{1,22} = 8.05$; $p = 0.0098$) (fig. 6A), i.e. larger females tend to lay three eggs and smaller (younger) ones, two.

Metric egg characteristics

Table 2 shows the metrics of 26 recently laid eggs and their relation to female SVL. Egg length, width and volume (fig. 6B) were not correlated with female SVL (n = 11 females).

The relationships between the residuals from the regression of log (clutch size) on log (mother's SVL) and the residuals from the regression of log (egg mass) on log (mother's SVL) also showed the relation between the variations in the individual eggs mass and the total number of eggs. This relationship was significant in *I. aurelioi* (n = 11): $r = 0.78$; $F_{1,10} = 14.67$; $p = 0.004$).

Two conflictive strategies acting in females and determining clutch and egg size are involved at a time to enlarge their reproductive success: investment in the increase of the egg-volume would enhance the fitness and survival possibilities of the new born lizards, while investment in the increase of the egg number would produce more descendants. Decrease in egg-volume with increasing clutch size (or vice versa) is a general phenomenon, and also true in the Pyrenean

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Figs. 1 - 4 (opposite page): *Iberolacerta aurelioi* (ARRIBAS, 1994)

Fig. 1: Embryos from recently laid eggs. Eggs are laid in an advanced stage of embryonic development [from stage 30 (n = 2) and 31 (n = 4) to stage 32 (n = 2) (determined from tables of DUFAURE & HUBERT 1961)]. Frequently, a dark dot can be observed in early candled eggs, which corresponds to the embryo's eye.

Abb. 1: Embryos aus frisch gelegten Eiern. Bei der Eiablage befinden sich die Embryonen in fortgeschrittenen Reifestadien [von Stadium 30 bis Stadium 32] (nach Bestimmungstabellen von DUFAURE & HUBERT 1961). Häufig ist beim Durchleuchten der Eier das Auge des Embryos als dunkler Fleck zu erkennen.

Fig. 2: Eggs found in the field (Port de Rat, Andorra, 18-VIII-1997). Note the big size of the eggs.

Abb. 2: Eier aus dem Freiland (Port de Rat, Andorra, 18-VIII-1997). Man beachte deren Größe .

Fig. 3: Clutch destroyed by larvae of the fly *Sarcophaga protuberans*. Estany de Sotllo (Pica d'Estats Massif) (4-VII-1996).

Abb. 3: Gelege von Larven der Fliege *Sarcophaga protuberans* zerstört. Estany de Sotllo (Pica d'Estats Massiv) (4-VII-1996).

Fig. 4: Hatchling from Port de Rat (Andorra). Note the vividly coloured greenish tail.

Abb. 4: Schlüpfling von Port de Rat (Andorra). Man beachte die lebhafte Grünfärbung des Schwanzes.
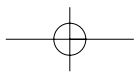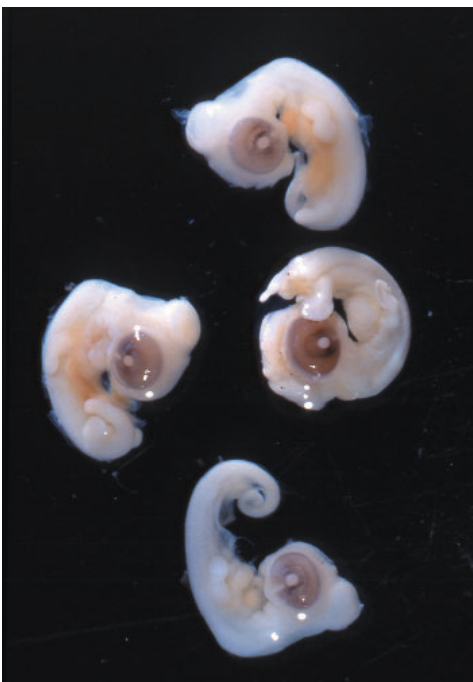
1 2

3 4

Table 2: Measurements (length, width, volume, mass) taken from 26 freshly laid eggs of *I. aurelioi* and their relationship with female (n = 11) snout-vent-length (SVL). SE – Standard error of ther mean; NS – not significant.

Tab. 2: Maße (Länge, Breite, Volumen, Masse) von 26 frisch gelegten Eiern von *I. aurelioi* und deren Beziehung zur Kopf-Rumpf-Länge (SVL) der Mutter (n = 11). SE – Standardfehler des Mittelwertes, NS – nicht signifikant.

	Length / Länge (mm)	Width / Breite (mm)	Volume / Volumen (mm^3)	Mass / Masse (g)
Mean±SE / Mittel±SE	13.8±0.2	7.3±0.1	386±13.4	0.43±0.1
Min-max	11.6 - 15.3	6.2 - 8.2	289.2 - 517.5	0.3 - 0.6
Correlation with SVL	$r = -0.08$; $F_{1,10} = 0.06$	$r = 0.35$; $F_{1,10} = 1.28$	$r = 0.33$; $F_{1,10} = 1.12$	--
Beziehung zu SVL	$p = 0.80$, NS	$p = 0.28$; NS	$p = 0.31$; NS	--

Iberolacerta (ANCOVA, with female SVL as a covariate: $F_{3,81} = 4.95$, $p = 0.0033$). As can be seen in fig. 6A there was a considerable overlap in size (snout-vent length) among females laying two and three eggs in this species. Within the range of overlap, egg volume in three-eggs-laying females was only slightly smaller (mean± SE = 381.84±24.6 mm^3; n = 8 eggs) than the egg volume in two-eggs laying females (mean ± SE = 389.01±16.4 mm^3; n = 18 eggs) without reaching the significance threshold (ANOVA: $F_{1,24} = 0.06$, $p = 0.81$). The mechanism which controls the trade-off between more and smaller versus fewer and bigger eggs is not yet understood. It is undoubtedly influenced by the female's fat reserves but is also largely overridden by the fact that small egg size is necessary for passing through the female's pelvic canal which seems to be an important limiting factor for the egg growth at a given clutch size.

The total clutch-volume (sum of egg volumes) was (mean±SE) 1208.6±114.4 mm^3 (range: 935.1-1474.5; n = 4 clutches). Based on this small sample the total clutch-volume was not correlated with female SVL ($r = 0.67$; $F_{1,3} = 1.71$, $p = 0.3207$, NS).

Exceptionally, abnormal eggs were found that exceeded or did not reach the usual dimensions. A very small egg (not measured) without visible embryo was found in Port de Rat (Andorra; 9-8-1998) whereas at the same site and date a very big one measured 20.2 x 11.2 mm (1.5 g) well above the usual values of eggs in this species (see table 3).

Embryonic developmental stages at oviposition

In *I. aurelioi* eggs were laid in an advanced stage of embryonic development (determined from tables of Dufaure & Hubert 1961) (fig. 1). Recently-laid eggs contained embryos of stages 30 (n = 2), 31 (n = 4) and 32 (n = 2). Similarly, eggs containing advanced developmental stages were found in oviparous *Z. vivipara* populations (Braña et al 1991; Heulin et al. 2000). The phenomenon appears to be linked with the extremely short annual activity period in the high mountains inhabited by these species and arrived at its final point by transition to viviparity. Full viviparity in these lizards could be constrained by their short annual activity cycle. If females spent more than a month under conditions of limited food intake due to the developing eggs in their body, they would probably not be able to accumulate sufficient reserves for annual reproduction. The benefit to reproduce yearly would then surpass the advantage of carrying and protecting the eggs until the end of incubation.

It should be noted that eggs from this and the other Pyrenean *Iberolacerta* species seemed to be fairly resistant against accidental changes of position e.g. rotation during transport, which can be related to the advanced embryonic stage at oviposition.

Egg-laying sites

All 26 clutches found in the field were deposited under stones lying on the soil. This seemed to be the usual oviposition site as it provides warmth from the ground and some protection against desiccation, cold, rainwater and predators.

Mean maximum diameter of the stones was 40.19±3.03 cm (mean±SE) (range: 20-70 cm), mean minimum diameter 25.73±1.77 cm (range: 10-50 cm), mean maximum thickness 10.87±0.86 cm (range: 4 to 20 cm). The mean surface area of the
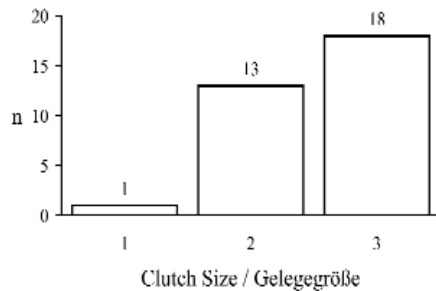
Fig. 5: Frequency distribution of clutch size (= number of eggs) in 32 clutches of *I. aurelioi*.
Abb. 5: Häufigkeitsverteilung der Gelegegröße (= Eizahl) bei 32 Gelegen von *I. aurelioi*.

stones (in a simplified approach represented by a parallelogram) was 1132.11 ± 154.2 cm^2 (range: 250 - 3500 cm^2).

Although very small stones were chosen occasionally, usually medium to big relatively flat slabs were the most frequently used places under which clutches were deposited.

Biotope characteristics of the oviposition sites

In most cases the biotopes used for oviposition were grassy areas covered wih the above mentioned medium to big sized flat stones (fig. 8). In 24 sites where egg clutches were found rocks covered 34.37 ± 13.29 % (mean$\pm$SE) (range: 10-80 %) of the biotope surface, grass 28.54 ± 2.97 % (range: 0-60 %), small fragments of stones 18.95 ± 3.57 % (range:0-80%) and bare ground 17.5 ± 2.35 % (range: 0-50%). On the average, shrubs (mainly *Juniperus communis* var. *nana*, *Rhododendron ferrugineum* and *Erica* spp.) constituted less than 1 % (0.41 ± 0.41 %; range: 0-10%) of the ground cover.

The majority of these sites were situated in gently sloped areas (mean inclination: $33\pm2.68°$; range: 10-70º).

Aggregation of clutches found in the field

The number of recently laid eggs found together in one spot varied from 2 to 12 (mean = 4.21; SE = 0.72), suggesting that the most common situation is two (from one to a maximum of six) females laying their eggs together in one place. There was no significant correlation between the number of females laying in one place (in a given year) and the surface area of the stone used ($r = 0.14$; $F_{1,24} = 0.53$, $p = 0.47$).

Frequently, aggregations of numerous pieces of old egg-shells of *I. aurelioi* were found under stones. In places where fresh clutches were observed, the median value of the number of old eggs was 2 (arithmetic mean value: 6.0; range: 1-70). Contrary to the situation in fresh eggs, the number of old eggs was positively correlated with the size of the stone ($r = 0.57$; $F_{1,24} = 12$, $p = 0.002$). This could be explained by the increased persistence of these remains under great stones, probably because of better protection against adverse weather effects that destroy egg remains.

However, not all oviposition sites were used every year. From 27 oviposition sites found in the field, 10 contained fresh eggs but not old ones (i.e. 37% of oviposition sites used were new, not used in previous years), 13 contained old egg shells but not fresh clutches (i.e. 48.1% of oviposition sites were used in previous years but not in the year of study) and only 4 of them contained both fresh eggs and old egg shells (i.e. 14.8% of oviposition sites were in more or less continuous use).

The great number of rocks suited for egg laying along with the wide spectrum of rock sizes accepted for this purpose provides a great variety of egg laying sites for these lizards. Continuous solifluction and rock meteorization slowly but continuously change the surface characteristics of these high mountain slopes and contribute to the creation of new suitable egg laying sites each year, while destroying others.

Incubation period

Mean incubation period of *I. aurelioi* eggs (n = 13) was (mean$\pm$SE) 35.6 ± 1.6 days (range: 31-44), about five weeks under laboratory conditions (mean temperature: 27.8ºC, range: 24-30ºC).

Number of eggs /
Eizahl

6 A

♀ SVL (mm)

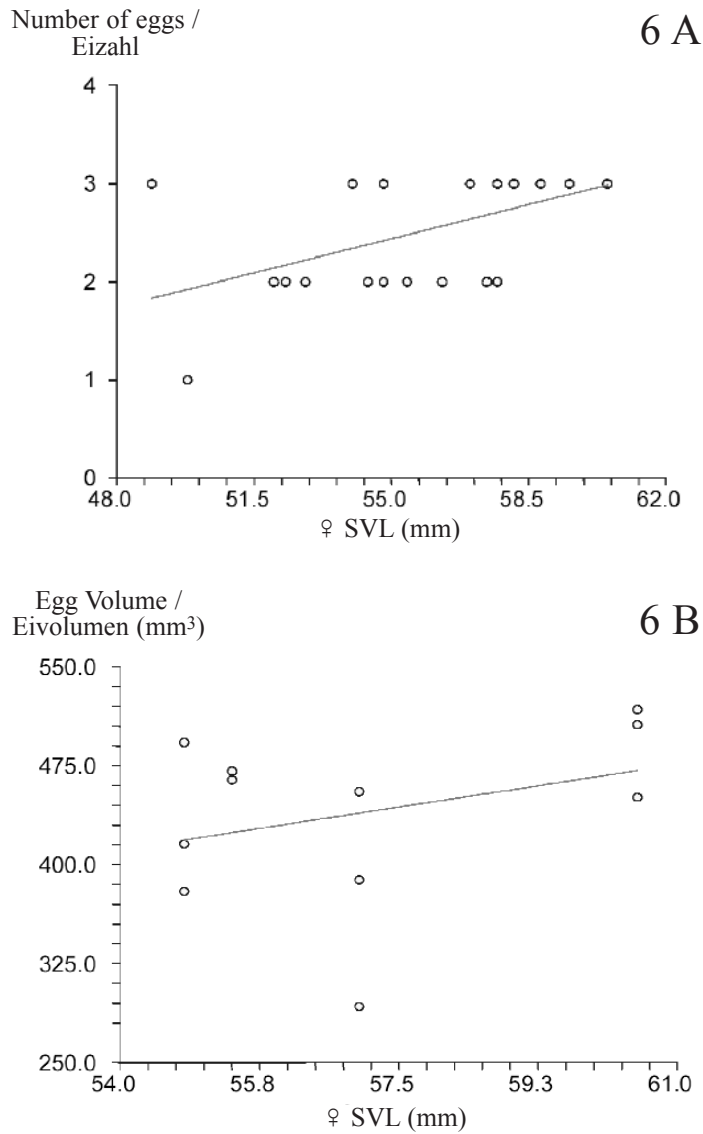Egg Volume /
Eivolumen (mm³)

6 B

♀ SVL (mm)

Fig. 6: Relationship between egg/clutch parameters and female SVL.
A - Relationship between number of eggs (clutch size) and female SVL. Both parameters show significant positive correlation ($r = 0.52$; $F_{1,22} = 8.05$; $p = 0.0098$); larger females tend to lay three eggs while smaller (younger) ones tend to lay two. B - Relationship between egg volume and female SVL. This relationship is not significant ($r = 0.33$, $F_{1,10} = 1.12$; $p = 0.31$). (see text for interpretation).

Abb. 6: Beziehung zwischen Ei/Gelege – Parametern und Kopf-Rumpf-Länge (SVL) des Muttertieres.
A – Beziehung zwischen Eizahl und Kopf-Rumpf-Länge (SVL) des Muttertieres. Beide Parameter korrelieren signifikant positiv ($r = 0.52$; $F_{1,22} = 8.05$; $p = 0.0098$); größere Weibchen tendieren demnach zu Gelegen aus drei Eiern, kleinere (jüngere) Tiere zu solchen aus zwei Eiern. B – Der Zusammenhang zwischen Eivolumen und Kopf-Rumpf-Länge (SVL) des Weibchens ist nicht signifikant ($r = 0.33$, $F_{1,10} = 1.12$; $p = 0.31$).

Table 3: Length, width, mass and volume [mean±SE (min-max)] taken from eggs of *I. aurelioi* during incubation. SE – Standard error of the mean.
Tab. 3: Länge, Breite, Masse und Volumen [Mittelwert±SE (min-max)] von *I. aurelioi* – Eiern im Verlauf der Inkubation. Mean – Mittelwert, SE – Standardfehler des Mittelwertes.

Time / Zeitpunkt	Length / Länge (mm)	Width / Breite (mm)	Mass / Masse (g)	Volume / Volumen (mm^3)
Oviposition (n = 18)	13.81±0.18	7.28±0.10	0.43±0.02	386.81±13.43
Eiablage (n = 18)	(11.6-15.35)	(6.2-8.2)	(0.3-0.6)	(289.17-517.54)
First-Week (n = 18)	14.3±0.23	8.9±0.20	0.64±0.07	600.70±31.95
1. Woche (n = 18)	(12.8-15.9)	(6.9-10.5)	(0.6-0.8)	(329.05-917.85)
Second-Week (n = 18)	14.75±0.29	9.3±0.23	0.71±0.09	678.53±41.18
2. Woche (n = 18)	(13-16.7)	(7.3-10.8)	(0.4-1.1)	(379.47-1019.91)
Third-Week (n = 18)	15.93±0.29	10.83±0.35	1.22±0.07	1012.25±76.04
3. Woche (n = 18)	(13.7-18.22)	(7.6-12.95)	(0.7-1.7)	(414.33-1599.88)
Fourth-Week (n = 12)	16.72±0.34	11.01±0.25	1.22±0.07	1077±68.10
4. Woche (n = 12)	(14.97-19.04)	(9.54-12.47)	(0.8-1.6)	(713.37-1550.24)
Fifth-Week (n = 8)	16.95±0.34	10.92±0.13	1.26±0.06	1061±39.98
5. Woche (n = 8)	(15.84-18.37)	(10.42-11.31)	(1.1-1.4)	(927.23-1211.61)

The earliest hatching occurred on July 29 in the laboratory (a date too early for the conditions in nature), and the last ones were registered on September 8 from eggs found in the wild (probably more in accordance to the lizard's cycle in nature). In nature, hatchlings emerged from middle of August to middle of September.

Egg-growth during incubation

Recently laid eggs had a pinkish tinge, were slightly translucent and became whiter and more opaque in the subsequent days. Recently laid eggs are not fully turgid and easily deformed under the finger's pressure. This is probably because the volume of the relatively big eggs of *I. aurelioi* has to be adapted to the size of the female's cloacal diameter during oviposition.

After oviposition, eggs increased notably in size due to water absorption by the egg which became fully turgid and resistant to the finger's slight pressure (fig. 2). During the first week the increase of the egg volume was remarkable (plus 35.6 %). During the second week the growth was less marked but continuous (plus 11.47 % increase in volume) and again became remarkable during the third week (plus 32.9 % of increase), and less again during the fourth week (plus 6.01 %) before hatching. Finally, during the fifth incubation week, eggs lost volume (minus 1.5 %). This phenomenon is not well understood but almost universal in the three Pyrenean *Iberolacerta* and probably widespread in other species. In fact, one to two days before hatching, eggs lost volume but, more strikingly, their turgescence and resistance to the fingers' pressure; they became "softer", announcing the imminence of hatching. See table 3 and fig. 7 for details on egg-growth during incubation.

Hatching success

64 % of the eggs studied in the laboratory and in the field (n = 53) hatched successfully. If only fully controlled clutches from the laboratory were considered (n = 37 eggs), this number decreased to 59 %. The presence of apparently unfertilized eggs in a clutch was not uncommon, and additional loss was mainly due to excessive moisture. After all, the eggs were relatively resistant to small mould attacks although they destroyed the external calcareous layer, caused transparency of the shell and gave view to the young lizard. When the attack was more severe, serious deformities appeared in the hatchling or led to failures in egg development even shortly before hatching.

In nature the larvae of the fly *Sarcophaga protuberans* PANDELLÉ (Diptera: Sarcophagidae) frequently preyed on fresh clutches of *I. aurelioi* (6 out of 24 clutches in the field) (fig. 3). Clutches affected by this fly were found in all massifs studied (Mont-Roig, Pica d'Estats and Coma Pedrosa in Andorra). From 196 eggs found in the wild (both fresh and old) only 17 were parasitized (8.6%). Once they are in
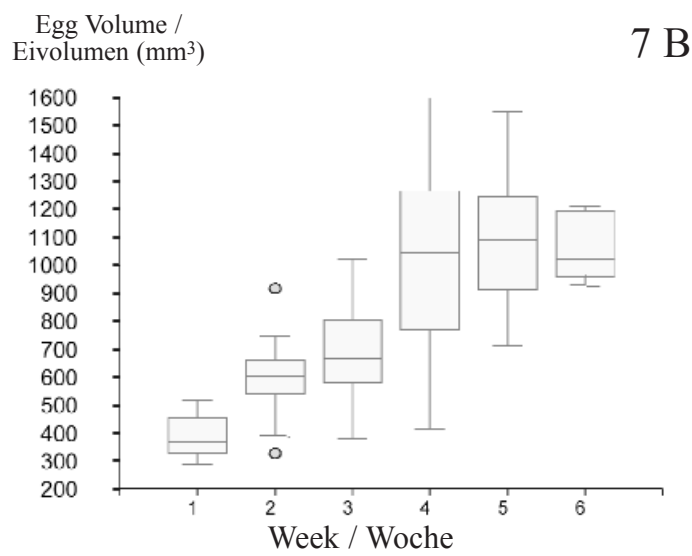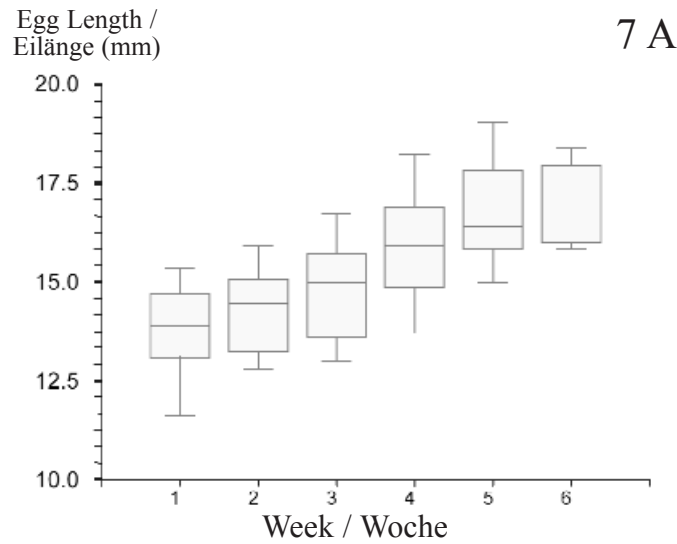
Egg Length /
Eilänge (mm)   7 A

Week / Woche

Egg Volume /
Eivolumen (mm^3)   7 B

Week / Woche

Fig. 7: Egg growth during incubation. A - increase in egg length (mm), and B - increase in egg volume (mm^3).
The plot indicates median values, 25% and 75% percentiles (which encompass the
interquartile range [IQR] = 50% of the values measured) and the ranges of adjacent values
(i. e. 25th and 75th percentile values minus or plus, 1.5 times IQR). Severe outliers are represented by dots.

Abb. 7: Eiwachstum während der Inkubation. A – Längenzunahme (mm) und B – Volumenszunahme (mm^3).
Die Grafik zeigt die Medianwerte, 25. bzw. 75. Perzentile (deren Abstand [= Quartilsabstand, IQR]
50% der gemessenen Werte umspannt) sowie den Bereich der benachbarten Werte (25. und 75. Perzentil
± das 1,5 – fache des Quartilsabstandes). Bedeutende Extremwerte sind durch Punkte dargestellt.
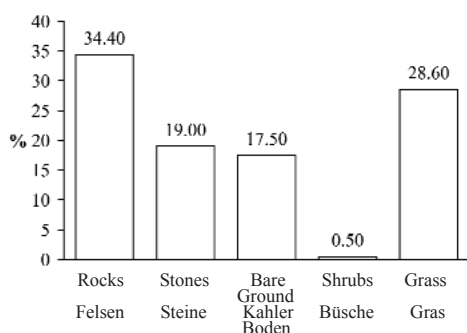
Fig. 8: Ground cover composition in the vicinity of the egg-laying sites. Mean values of 26 observations.

Abb. 8: Zusammensetzung der Bodenbedeckung in der Nähe von Eiablageplätzen. Mittelwerte aus 26 Beobachtungen.

a clutch, larvae destroy one egg after the other and frequently pupate inside the shell of the last attacked egg or close to it. The developmental cycle of the fly seems to be univoltine and synchronized to the lizard's cycle, with a diapause from mid-July until summer of the following year when adult flies emerge to infest new clutches (PAPE & ARRIBAS 1999).

Hatching process

The hatching process is of variable duration. After cutting an opening into the egg-shell with its egg-tooth, the hatchling usually remains inside the egg for a while, then the snout appears and later the whole head protrudes. The opening in the shell is usually cut into one of the egg's poles, less frequently, in a side. During this period of rest without leaving the egg-shell, vitellus from the yolk sac is reabsorbed by the lizard. If disturbed, the young can leave the egg-shell prematurely by a sudden movement dragging the rest of the yolk sac behind it. If undisturbed, the lizard leaves the egg soon after reabsorption of the yolk. The omphaloenteric duct obliterates within a few minutes (fig. 4).

Day-time and duration of the hatching process

Based on the analysis of 23 births studied in the laboratory, no day-time was signif-icantly preferred for the final hatching event. The births (irrespective of the sex of the hatchling) were evenly distributed all over the day (from 1:00 to 23:00).

The process of hatching, from the appearance of the first cut in the egg-shell until the total emergence of the lizard, last-ed from 1 to 12 hours (mean = 6.66±1.25 hours; n = 12 hatching events). There are no differences among sexes in the duration of the process of hatching. In other species as *Lacerta bilineata* DAUDIN, 1802, this pro-cess can last some hours to some days (ROL-LINAT, 1934).

Hatchlings' characteristics

Hatchling's SVL (mean±SE) was 27.57±0.3 mm (range: 26.43-29.9; n = 19) (fig. 9).

Hatchling's body mass (mean±SE) was 0.49±0.02 g (range: 0.4-0.6; n = 19).

There were no significant differences in SVL or body mass between male and female hatchlings.

Ventral scale row counts in male hatchlings (n = 15) were from 25 to 28 (mean±SE = 26.8±0.28, median = 27), and in female ones (n = 19) from 29 to 32 (mean±SE = 29.68±0.21, median = 29). There were also sexual differences in the beginning and end of the umbilical scar: in males it started at ventral scale number 19 or 20 (mean±SE = 19.8±0.16, median = 20) and ended between scales 22 or 23 (mean±SE = 22.6±0.21, median = 23). In females it started from ventral scale number 20 to 22 (mean±SE = 21.07±0.24, median = 21) and ended between scale number 23 to 26 (mean±SE = 24.46±0.24, median = 24). For coloration see figure 4.

Sex-ratio at birth

Sex ratio determined from all labora-tory-bred and sexed hatchlings (n = 34) originating from both field and laboratory clutches was 19 females versus 15 males (1 : 0.78) (χ^2 = 0.47; p = 0.4927) which is not significantly different from 1:1.

In adults the sex ratio found in the field was 1:1.21 (χ^2 = 2.14; p = 0.1433; n = 226 sexed specimens), also not differing signifi-cantly from a balanced 1:1 proportion.

Egg-tooth persistence

The premaxillar egg-tooth of the hatchling which is used for cutting the egg-shell during the birth process, drops out in the following hours. The shape of the egg-tooth was subject to considerable intraspecific variation.

In *I. aurelioi* its outline varied from semicircular to - most frequently - more or less subtriangular with round sides and the vertex (also rounded, not pointed) being curved to the rigth side. In this species the egg-tooth is comparatively greater and more protuberant than in *I. monticola* and oviparous *Z. vivipara*.

In general, the egg-tooth in reptiles is said to drop out within a few days after hatching as a rule (BELLAIRS 1970), in *Z. vivipara* (viviparous populations) it can persist up to 24 hours (SMITH 1973; STREET 1979), in *Lacerta agilis* LINNAEUS, 1758 hours to days (ROLLINAT 1934), in *L. bilineata* up to 5 days, in *Podarcis muralis* (LAU-RENTI, 1768) up to the seventh day (but most frequently second or third day) (ROLLINAT, 1934) and in *Podarcis sicula* (RAFINESQUE, 1810) from 1 up to 7 days (BRUNO 1986).

In *I. aurelioi* (n = 15 specimens controlled) the egg-tooth dropped out between 10 and 54 hours after hatching. The median value was 24 hours, and 50% of the young lost the egg-tooth 19 to 36 hours after hatching. There were no significant ($t = 0.52$, $df = 13$, $p = 0.60$) differences between sexes.

Hatchlings' behaviour

Newly hatched lizards were very vivid and agile in comparison with the adults. During the fist days of life, hatchlings of the three Pyrenean *Iberolacerta* species never autotomized their tails. This observation can be detailed only in three *I. aurelioi* newborns in which it took 6 to 8 days until the first autotomy event occurred and the most distal part of their tails broke off. As a hypothesis, this could be due to an incom-
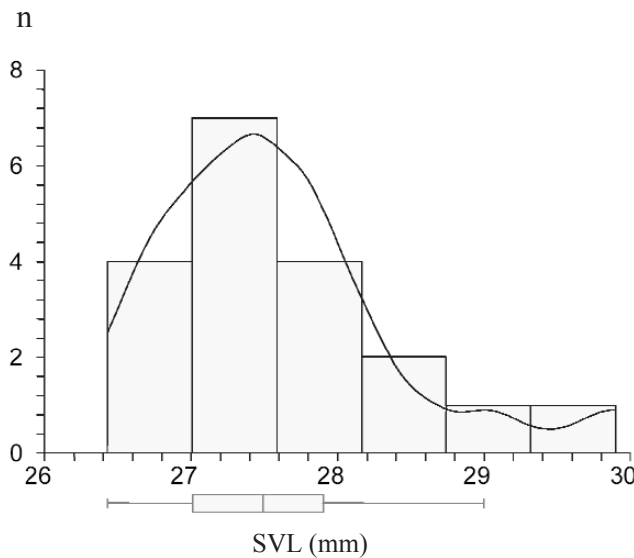

Fig. 9: Frequency distribution of SVL in 19 hatchlings of *I. aurelioi*.
Measurements were taken within 24 hours after hatching.
Abb. 9: Häufigkeitsverteilung der Kopf-Rumpf-Längen bei 19 Schlüpflingen von of *I. aurelioi*.
Die Messungen erfolgten innerhalb von 24 Stunden nach dem Schlupf.

plete development of the fracture planes of the corresponding vertebrae during the first days post hatch.

In their first days of life and for a period of unknown duration, young lizards show a particular behaviour when threatened. During the short rests interrupting their escape, they stay immobile while the distalmost part of the vividly coloured tail makes nervously winding movements, which presumably direct a potential predator's attention to the tail tip. This behaviour is not exclusive to *Iberolacerta* as it was not only noticed in *I. aranica* and *I. bonnali*

(which frequently lack vivid tail colour) but also in *Podarcis hispanica* (STEINDACHNER, 1870). This vivid motility of the tail tip is lost when growing older.

Iberolacerta aurelioi populations should be expected to be very sensible of natural or man-induced increase of adult mortality because of the lizard's delayed maturity (due to slowed growth because of the short annual activity cycle) and extremely low fecundity. The survival of *Iberolacerta aurelioi* seems to be based on its relatively long life and low number and density of enemies.

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