

THE BODY SIZE, AGE STRUCTURE AND GROWTH PATTERN
OF THE ENDEMIC BALKAN MOSOR ROCK LIZARD
(*DINAROLACERTA MOSORENSIS* KOLOMBATOVIĆ, 1886)

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The Mosor rock lizard (*Dinarolacerta mosorensis*) is a distinctly flattened endemic species that occupies discontinuously distributed rocky areas at high elevations in the Dinaric Mountains of the Balkans. The body size, age structure, longevity, survival rates and growth patterns of this species were studied using skeletochronology and back-calculation methods. The modal age was found to be 5 years for males and 6 years for females, while the maximal longevity was found to be 9 years in both sexes. The age and body length were positively correlated in both sexes. Both sexes reached maturity at 3 years, with a snout-vent length of 53.3 and 56.5 mm for males and females, respectively. The growth coefficient had significantly higher values in females (0.54) than in males (0.40). The asymptotic size of females was lower (66.01 mm) than that of males (70.82 mm). The growth rate of females decreased soon after maturation whereas males continued to grow for a longer time. Juveniles had lower survival rates than adults (0.5 vs 0.7). The effective age at maturity (13.5 months) was significantly greater than that for the small lacertid lizards living at the low altitudes of a Mediterranean climate, greater than but within the range of values predicted for those living at low altitudes of a temperate climate, and lower than but within the range of values predicted for montane small lacertids.

Key words: lacertid lizards, longevity, skeletochronology, endemic species

INTRODUCTION

Unlike morphological, physiological and behavioural characteristics, life-history traits, such as the growth rate, age of maturity, fecundity, survival and the timing of reproduction, coevolve to maximise an organism's fitness. For those with indeterminate growth, individuals must decide between allocating energy to growth, reproduction, or some combination of the two (KOZŁOWSKI 1996, HEINO & KAITALA 1999, LARDNER & LOMAN 2003). If an organism allocates energy to reproduction early in life, it will have a greater contribution to the gene pool of fu-

ture generations. Also, reproduction early in life may increase an organism's life-time reproductive success if the conditions suggest a low probability of surviving to subsequent breeding seasons (ROFF 1992, STEARNS 1992). However, if the fecundity or mating successes are strongly size-dependent (e.g. COOPER & VITT 1993, BRAÑA 1996, WIKELSKI & ROMERO 2003), individuals may attain a higher lifetime reproductive success by investing energy in growth rather than in reproduction early in life. A larger body size is related to increased success at defending a breeding territory, greater survivorship, and the production of larger clutches and/or larger offspring that may have higher survival rates than smaller offspring (reviewed by TRIVERS 1972, but see PIKE *et al.* 2008). The optimal strategy in a given environment may depend on several factors, such as size-dependent fecundity, size-dependent mortality and the mortality risk associated with reproduction (LARDNER & LOMAN 2003).

For ectotherms such as reptilians, in cold environments, the achievement of an optimal life history is additionally complicated by the fact that temperature influences many aspects of behaviour and physiology, most of which have implications for survival and fecundity (ANGILLETTA *et al.* 2002, 2004) within the framework of reproductive time constraints. Also, variation in reptilian growth rates is associated with differences in food availability and time available for foraging and thermoregulation (ANDREWS 1982).

The Mosor rock lizard (*Dinarolacerta mosorensis* KOLOMBATOVIĆ, 1886), is a small, diurnal, heliothermic, insectivorous, oviparous, saxicolous, lacertid species with a distinct flattened morphology (BISCHOFF 1984, ARNOLD & OVENDEN 2002), which is patchily distributed only at rocky sites in the Oromediterranean areas of the south-western Dinaric mountain karst in Croatia, Bosnia and Herzegovina and Montenegro (450–1900 m a.s.l., DŽUKIĆ 1989, CRNOBRNJA-ISAILOVIĆ & DŽUKIĆ 1997). Its habitats are exposed to very long, cold, snowy winters (in the northern localities, the mean annual snow cover duration is from the end of September to June), very humid autumns and springs, and hot, dry summers with extreme daytime and night-time temperature changes (between 3 °C and 25 °C) (MATVEJEV 1961). It is active from late April to early October, mating in May–June, and producing a single clutch in July, which hatches in August after prolonged an oviductal egg retention (LJUBISAVLJEVIĆ *et al.* 2007). The reproductive success of females is enhanced by an increase in the clutch size, accompanied by an enlargement of the body, but not the egg size (LJUBISAVLJEVIĆ *et al.* 2007). Apart from these aspects of reproductive biology, still very little is known regarding the other ecological characteristics of the species (e.g. BISCHOFF 1984).

The aims of this paper are to present the first data on the age structure, longevity, survival rate and growth rate patterns in the Mosor rock lizard. In particu-

lar, we tested the reliability of skeletochronology as a tool for age estimation in this species, and analysed the growth patterns in relation to maturation and reproduction by the back-calculation technique. Also, we compared the effective age and body size at maturity of the Mosor rock lizard to other small lacertids living in different environments. Thus, we provided more complete information regarding the life history of this environmentally constrained species.

MATERIALS AND METHODS

Study species and sample size

Analyses have been carried out on a population of Mosor rock lizards living at an altitude of 1350 m on Lovćen Mountain in Montenegro (in the Ivanova korita locality, 42°22'N, 18°50'E) at the south-eastern boundary of their distribution. This population inhabits cliffs and blocks of rocks surrounded by subalpine beech forest with a moderate continental climate, modified by mountain climatic conditions and with an influence from the sea, as reflected by the high precipitation levels (the average annual rainfall is 4207 mm, with the maximal rainfall occurring in November and December) (TOMIĆ-STANKOVIĆ 1970).

The sample investigated was composed of 56 adults (36 males and 20 females) and 6 subadult specimens that were collected during the reproductive season of 2006. The maturity of each specimen was determined on the basis of characterisations from previous studies (LJUBISAVLJEVIĆ *et al.* 2007, LJUBISAVLJEVIĆ *et al.* 2008): a given specimen was defined as an adult if it had enlarged testes and/or epididymides (male), or enlarged vitellogenic follicles and/or oviductal eggs and/or expanded oviducts (female). All of the specimens were collected under permits provided by the Ministry of Environmental Protection, Republic of Montenegro (no. 01–74/2) and the Institute for Nature Protection of Montenegro (nos 02–261/1 and 01–193) and were deposited as vouchers in the Herpetological Collection of the Natural History Museum of Montenegro in Podgorica.

Laboratory studies and statistical analyses

Lizard body length was measured from snout to vent (SVL) to the nearest 0.01 mm using a dial calliper. All of the data were tested for normality (Shapiro-Wilk W test) and for homogeneity of variances (Levene test). Subsequently, the data were log-transformed to ensure normality and to generate homogeneous variances (SOKAL & ROHLF 1981). If this transformation did not normalise the data, nonparametric methods were used. The age-size relationships were tested by a linear ordinary least squares regression analysis.

Skeletochronology analyses were performed following the modified standard procedure described by MIAUD (1992) and TOMAŠEVIĆ *et al.* (2008). As phalanges were insufficiently distinct to count the year rings due to the lack of sharpness and clarity of the lines of arrested growth (LAGs), we successfully applied skeletochronology on femur bones instead. Each femur bone of the right hind limb was cut, the muscle and skin were removed and the bone was washed in distilled water. The bones were then decalcified in 5% nitric acid and washed under running water. Cross sections (20 mm) from the diaphyseal region were obtained using a freezing microtome and the sections were stained with Enrich's haematoxylin. LAGs were counted and independently verified by two authors

(N. T. K and K. Lj.), to avoid possible under- or overestimation of the ages. The maximum difference for LAGs counted was one year, in which case the age was estimated as ± 1 year. The cross-sections were observed under the microscope, recorded with a digital Cannon S45 camera and processed with the image analysis software Image Tool (v. 3.0, UTHSC SA). Both the longest and shortest perpendicular axis of each LAG was measured to the nearest μm , and the square root of their product was considered to be the average diameter of the LAG. One of the factors affecting the accuracy of age estimates is endosteal resorption, which often leads to the removal of the few primary LAGs (HEMELLAAR 1985). The degree of resorption was estimated by an osteometrical analysis (SAGOR *et al.* 1998). The diameters of the innermost and second visible LAGs were compared. The cross-sections in which the innermost visible LAG had a diameter at least two standard deviations (SD) greater than the group mean were interpreted as cases of complete LAG 1 resorption. It was assumed that in *D. mosorensis*, like in other lizard species exposed to yearly cyclical environmental variations, the number of LAGs corresponds to the number of winters experienced by each individual.

A significant correlation between the SVL and femur diameter (0.87 and 0.63, $P > 0.05$ in males and females, respectively) made it possible to perform a back-calculation to determine the individual body length at the time of each LAG formation. We used the simplest back-calculation formula according to DAHL-LEA, $L_i = L_c (D_i / D_c)$, where L_i and L_c were snout-vent lengths at the time of formation of the i th LAG and at capture, while D_i and D_c are the bone diameters limited by LAG $_i$ and by the outer bone margin, respectively (MARUNOUCHI *et al.* 2000). All of the further analyses on body growth were obtained using the back-calculated data (bc SVL).

The growth was estimated using the VON BERTALANFFY'S (1938) growth equation: $S_t = S_m - (S_m - S_1) e^{-K(t-t_1)}$, where t = number of growing seasons experienced (age); S_t = average body size after having experienced t growing seasons; t_1 = age after first hibernation (fixed at one); S_1 = average back-calculated SVL at age one fixed at 45.08 mm ($N = 52$, $SD = 3.99$); S_m = average maximal body size; and K = growth coefficient, defining the shape of the growth curve such that the growth curve rises slowly towards the asymptotic length and meets it in a shallow curve when the growth coefficient is low (see ANDREWS 1982). The parameters S_m and K were estimated by non-linear least squares regression (Statistica 5.0, Statsoft Inc., U.S.A.). The two estimated parameters were considered to be significantly different when their respective confidence intervals did not overlap (e.g. MIAUD *et al.* 1999).

The adult survival rate was calculated from the age structure according to the following formula (KREBS 1999): $S = T / (\sum N + T - 1)$, where S is the average survival rate, T is the sum of the coded ages times their frequencies and $\sum N$ is the number of individuals from age classes x to $x + i$ (details in MIAUD *et al.* 1999). The respective confidence intervals (CI) were calculated according to ZAR (1984): $CI = \pm 1.96 [S(1-S) / (n-1)]^{1/2}$.

Additionally, the body size and age at maturity of the analysed population of *D. mosorensis* were compared to data available for other small lacertid lizards living in different conditions (at low altitudes in a Mediterranean climate, at low altitudes in a temperate climate, at high altitudes in a temperate climate). We only retained information pertaining to single populations or to a restricted geographical area in which no life-history differences among populations could be detected. The age at maturity was expressed in the number of months of activity (thus excluding the hibernation period) according to BAUWENS and DÍAZ-URIARTE (1997). This effective age at maturity is more equivalent to physiological time than are measures of the total number of months and are therefore more relevant for life-history patterns (BAUWENS & DÍAZ-URIARTE 1997). The separate regression equation between the female effective age and body size at maturity for the above-mentioned three groups of small lacertids was calculated. The equations were then used to calculate the predicted value of the effective age at maturity, and its 95% prediction interval, at the body size at maturity of the studied population of *D. mosorensis*. If the observed value of the studied population fell outside of the predic-

tion interval, we rejected the null hypothesis of no difference in the effective age at maturity between *D. mosorensis* and that particular group of lacertid lizards. This kind of analysis was previously used for the comparison of some reproductive traits among lacertid lizards (CASTILLA & BAUWENS 2000, GALÁN 2003). We are aware that our analysis is nonphylogenetic, and that it may lead to biased estimates of correlation and regression coefficients (GARLAND *et al.* 1992) and, hence, of the 95% prediction interval. However, we hope that analytical imperfections have not changed major results and conclusions.

RESULTS

Adult and subadult body sizes

The mean body length (SVL) was 64.71 ± 0.86 mm (with a range of 52.28–72.81 mm) in males and 63.60 ± 0.84 mm (with a range of 56.34–70.72 mm) in females. The subadult individuals had a mean SVL of 49.20 ± 0.84 mm (with range from 45.12 to 50.73 mm). No sexual size dimorphism in the SVL was found between adult males and females (*t* test, *df* = 54, *P* > 0.05, Fig. 1). The body length was significantly correlated with age in males (*n* = 36, Slope \pm EE = 0.22 ± 0.02 , Intercept \pm

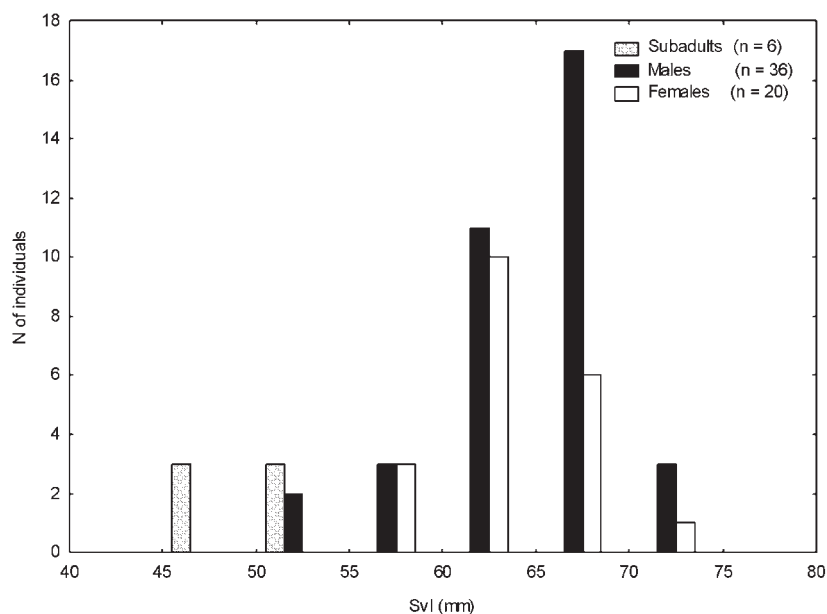


Fig. 1. The sample size and body length (SVL) distribution of Mosor rock lizard hatchlings, subadults and adults

EE = 1.65 ± 0.02 , adjusted $R^2 = 0.74$, $P < 0.001$) and females ($n = 20$, Slope \pm EE = 0.16 ± 0.03 , Intercept \pm EE = 1.68 ± 0.02 , adjusted $R^2 = 0.56$, $P < 0.001$).

Age structure

The LAGs were sharp and easily distinguishable from the broad rings of the periosteal bone deposited during the active period (Fig. 2). Double LAGs were rarely observed and were counted as a single LAG. The complete resorption of the first LAG was observed in only one male lizard (Fig. 3), while partial resorption of the first and second LAGs was found in almost all individuals.

The median age did not differ between the sexes (5 and 6 years for males and females, respectively, Mann-Whitney U test, $U = 305$, $P > 0.05$). The minimum age for adults was 3 years while the maximum age was 9 years for both sexes. The median age of subadult individuals was 3 years (range 2–3 years) (Fig. 4).

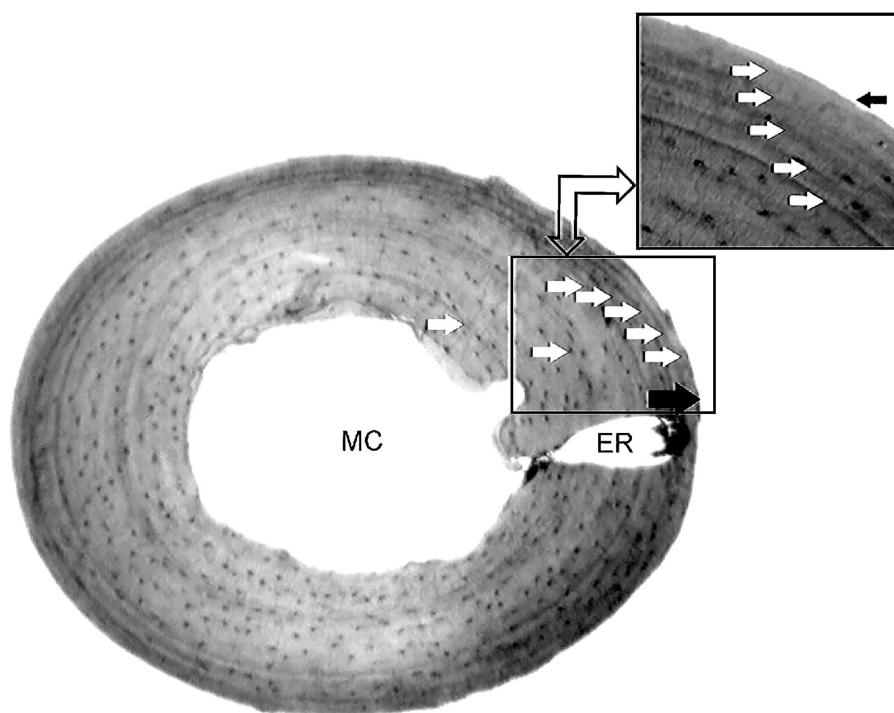


Fig. 2. A cross-section of the femur diaphysis of an adult female Mosor rock lizard. Eight LAGs are shown (LAGs appear as thin dark lines); the first LAG is partly eroded, while the outer LAGs are closely spaced (decreasing intervals between them indicate a shift in a resource allocation after sexual maturation). The arrows indicate LAGs, while mc indicates the marrow cavity

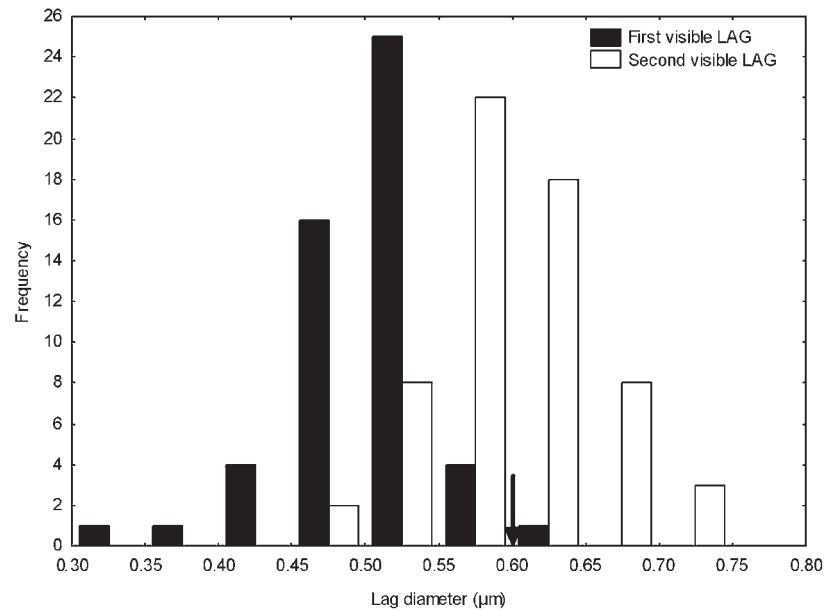


Fig. 3. The distributions of the first and second visible LAGs. The first deposited LAG has been resorbed in sections in which the diameter of the first visible LAG is greater than 0.60 µm

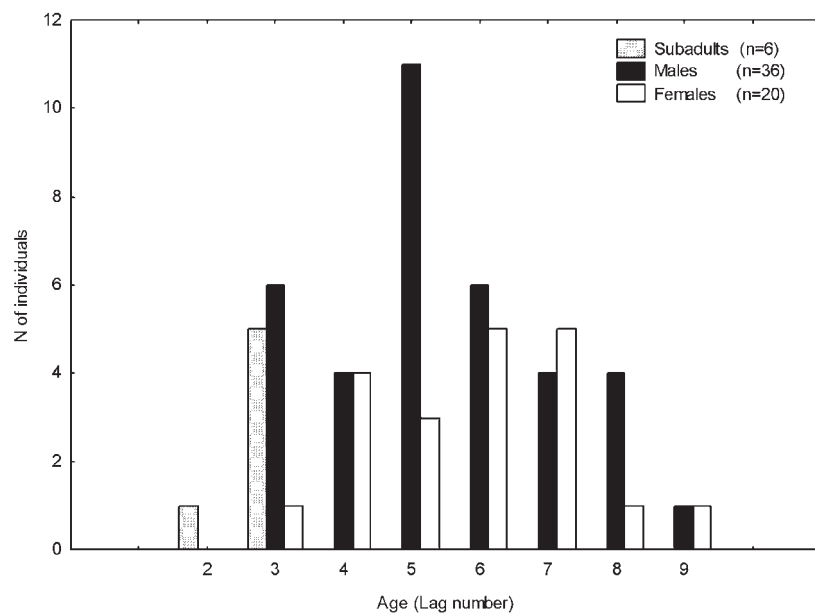


Fig. 4. The age distribution in subadult and adult Mosor rock lizards

Table 1. The von Bertalanffy equations for body growth, shown with standard errors and 95% confidence limits of the estimated parameters.

	$S_t = S_m - (S_m - S_1) e^{-Kt}$	Standard errors		95% confidence limits	
		S_m	k	S_m	K
Males	$70.82 - (70.82 - 45.08) e^{-0.40t}$	0.90	0.03	69.04–72.61	0.34–0.46
Females	$66.01 - (66.01 - 45.08) e^{-0.55t}$	0.89	0.06	64.25–67.77	0.42–0.67

Patterns of maturation and growth

The same ages of the oldest subadults and the youngest adults in the sample analysed indicated that the Mosor rock lizard matures at 3 years of age. The estimated body size at which 95% of individuals become mature was 53.32 mm and 56.51 mm for males and females, respectively. With a coefficient of multiple determination of $r^2 = 0.88$ and 88.60% of the variance explained (VE) in males and $r^2 = 0.79$ and VE = 78.75% in females, the VON BERTALANFFY growth model correctly fitted the age-body length relationship of the sampled individuals (Fig. 5).

There was a difference between the sexes in growth parameters (Table 1).

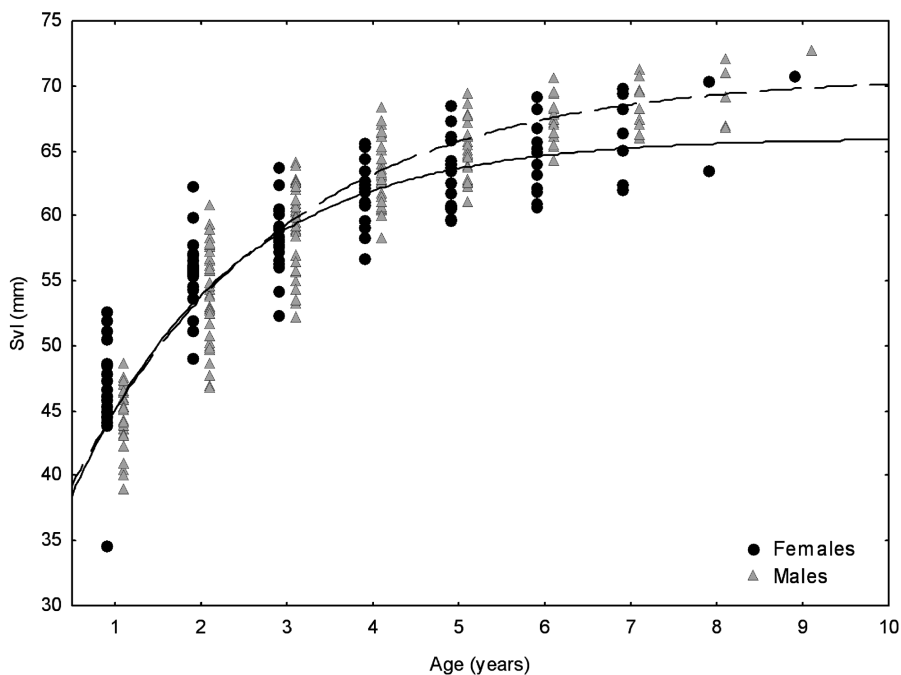


Fig. 5. The growth curves of male and female Mosor rock lizards. Age was assessed by skeletochronology, while the growth curves were fitted to VON BERTALANFFY's equation

Table 2. The body size and effective age at maturity of small lacertid lizards living at low altitudes in a Mediterranean climate (a), at low altitudes in a temperate climate (b), and at high altitudes in a temperate climate (c). The observed value for *D. mosorensis* of the Lovćen mountain population is compared to the predicted value, and the 95% prediction interval, obtained from regression equations for the other lacertids from a particular group (see text for detail). SVL = SVL at maturity (mm), EAM = Effective age at maturity (months)

Table 2a				
species/population	SVL	EAM	Locality	Reference
<i>D. mosorensis</i>				
observed	56.50	13.5	Lovćen mt. (Montenegro), 1350 m	this study
predicted		7.02		
95% prediction interval		1.18–12.86		
small lacertids at low altitudes in a Mediterranean climate				
<i>Acanthodactylus scutellatus</i>	50.0	5	Nizanim and Holon (Israel), 20 m	PERRY & DMÍEL (1994)
<i>Dalmatolacerta oxycephala</i>	53.34	9	Skadar Lake islands (Montenegro)	BEJAKOVIĆ <i>et al.</i> (1996b)
<i>Podarcis atrata</i>	51.0	7	Columbretes islands	CASTILLA & BAUWENS (2000)
<i>Podarcis hispanica</i>	42.2	7	Cíes Islands (Spain), 176–193 m	GALÁN (2003)
<i>Podarcis milensis</i>	42.0	12	Milos Island (Greece)	ADAMOPOULOU & VALAKOS (2000)
<i>Podarcis taurica</i>	52.2	9	Ionian Islands (Greece)	CHONDROPOULOS & LYKAKIS (1983)

The growth coefficient K , which shows how quickly the asymptote is reached, had significantly higher values in females (0.54) than in males (0.40). On the other hand, the average maximal body size (asymptotic size) of females was lower (66.01 mm) than those of males (70.82 mm). These results indicate that the growth rate of females decreases soon after maturation, whereas males continue to grow for a longer time (Fig. 5).

The adult survival rates were estimated to be 0.71 (CI = 0.15) and 0.75 (CI = 0.19) for males and females, respectively. The subadult survival rate was 0.5 (CI = 0.44). The differences between the survival rates were not considered to be statistically significant as the respective CIs overlapped.

Table 2b

Species/population	SVL	EAM	Locality	Reference
<i>D. mosorensis</i>				
observed	56.50	13.5	Lovćen Mt (Montenegro), 1350 m	this study
predicted		12.37		
95% prediction interval		9.79–14.97		
small lacertids at low altitudes in a temperate climate				
<i>Darevskia praticola</i>	49	11	Western Caucasus, 600 m	ORLOVA (1969)
<i>Iberolacerta monticola</i>	52.4	13	Coruña (Spain), 20–150 m	RÚA & GALÁN (2003)
<i>Podarcis bocagei</i>	44.0	8	Coruña (Spain), 90 m	GALÁN (1999)
<i>Podarcis muralis</i>	55	9	Maastricht (Netherlands), 209 m	STRIJBOSCH <i>et al.</i> (1980)
<i>Podarcis muralis</i>	54	12	Juillac, Correze (France) 280 m	BARBAULT & MOU (1988)
<i>Podarcis taurica</i>	52.5	10	Oltenia (Romania), 110 m	CRUCE (1972)
<i>Psammodromus hispanicus</i>	42	5	Salamanca (Spain)	BAUWENS & DÍAZ-URIARTE (1997)
<i>Takydromus septentrionalis</i>	56	13	Xinshau Island (China)	BAUWENS & DÍAZ-URIARTE (1997)
<i>Takydromus tachydromoides</i>	46	7	Honsu (Japan)	BAUWENS & DÍAZ-URIARTE (1997)
<i>Zootoca vivipara</i>	44	11	Antwerp (Belgium), 3 m	BAUWENS & DÍAZ-URIARTE (1997)

Comparison of effective age and body size at maturity with other small lacertid lizards

In the studied population, the observed effective age at maturity was only significantly greater than that of the small lacertid lizards living at low altitudes of Mediterranean climate (Table 2a). The observed effective age at maturity for the *D. mosorensis* population was greater but within the range of values predicted for small lacertid lizards living at low altitudes in a temperate climate, based upon the extrapolation to the female body size at maturity equal to that for the studied population (Table 2b). When compared to high altitudes populations, the observed ef-

Table 2c

Species/population	SVL	EAM	Locality	Reference
<i>D. mosorensis</i>				
observed	56.50	13.5	Lovćen Mt (Montenegro), 1350 m	this study
predicted		14.96		
95% prediction interval		9.46–20.46		
small lacertids at high altitudes in a temperate climate				
<i>Darevskia nairensis</i>	55	17	Armenia, 800–1700 m	ARAKELIAN & DANIELYAN (2000)
<i>Iberolacerta aranica</i>	50.3	18	Pyrenees (Spain), 2000–3000 m	ARRIBAS & GALÁN (2005)
<i>Iberolacerta aurelioi</i>	48.9	18	Pyrenees (Spain), 2000–3000 m	ARRIBAS & GALÁN (2005)
<i>Iberolacerta bonnali</i>	51.4	18	Pyrenees (Spain), 2000–3000 m	ARRIBAS & GALÁN (2005)
<i>Iberolacerta cyreni</i>	60	10	Avila, Segovia (Spain), 1600–2000 m	BAUWENS & DÍAZ-URIARTE (1997)
<i>Podarcis hispanica</i>	39	8	Asturias (Spain), 1100 m	BAUWENS & DÍAZ-URIARTE (1997), BRAÑA <i>et al.</i> (1991)
<i>Podarcis hispanica</i>	49	8	Salamanca (Spain), 1074 m	BAUWENS & DÍAZ-URIARTE (1997)
<i>Podarcis muralis</i>	49	12	Asturias (Spain), 1350–1500 m	BAUWENS & DÍAZ-URIARTE (1997), BRAÑA <i>et al.</i> (1991)
<i>Zootoca vivipara</i>	43	11	Asturias (Spain), 1900–2000 m	BAUWENS & DÍAZ-URIARTE (1997), BRAÑA <i>et al.</i> (1991)

fective age at maturity of *D. mosorensis* was lower, but was also within the range of values predicted for this group of small lacertids (Table 2c).

DISCUSSION

The present study provides the first information on the age structure and growth patterns in the Mosor Rock lizard. Our results revealed a growth curve pattern and an allocation of energy centred primarily on growth in immature individu-

als and on reproduction in adults, as is often observed in amphibians and reptiles (e.g. HEMELAAR 1988, ADOLPH & PORTER 1996, SORCI *et al.* 1996, MIAUD *et al.* 1999, ARAKELYAN 2002, HAENEL & JOHN-ALDER 2002, ROITBERG & SMIRINA 2006). The characteristic features of such growth patterns are an asymptotic growth up to maturity, continued growth thereafter but at a decreased rate, and large individual variation in growth- and age-specific sizes (RYSER 1988).

Body size

In the Mosor rock lizard, the body size in both sexes significantly increased with age, which appears to be a general phenomenon in lizards that exhibit indeterminate growth (BAUWENS 1999). Also, in the population under study, this lizard exhibited a low level of male-biased sexual size dimorphism (SSD) in adult animals based on the SVL. Studies have demonstrated that, apart from different selective pressures (see e.g. BRANA 1996, COX *et al.* 2003), the SSD in many adult lizards arises due to sexual differences in the growth rates before and during their first reproduction (JOHN-ALDER & COX 2007) in such a way that the larger sex grows faster than the smaller sex. Apart from other possible causes (see LJUBISAVLJEVIĆ *et al.* 2008), the observed pattern of SSD in the Mosor Rock lizard could also result from the continued growth of males after maturity and the faster growth of females prior to maturity, which influenced non-significant sex differences in adult body length. However, the positive correlation between age and body size as well as observed differences in the age distribution between the sexes (with females being slightly older than males), could also have an effect on the observed low level of male-biased SSD in SVL.

Growth trajectories, maturation and survival rates in the Mosor rock lizard

Male and female Mosor rock lizards had very different growth trajectories. Since both sexes reach sexual maturity at approximately the same age, the faster growth in the female Mosor rock lizard prior to maturity suggests that growth differences are a major factor contributing to larger size at maturity in females. Females could enlarge their size at maturity to increase reproductive success by producing larger clutches (LJUBISAVLJEVIĆ *et al.* 2007). Given that the Mosor rock lizard is a flat-bodied, crevice-dwelling species, some physical constraints from body volume on reproductive output should be expected. LJUBISAVLJEVIĆ *et al.* (2007) found that adaptations to a particular habitat-type could have placed some constraints on reproductive output in this species by producing optimal-sized offspring at some optimal, rather than maximal level, but have not constrained the

clutch size. In contrast, for males, survival to age of reproduction and the relative size among males may be more important for reproductive success than the absolute growth rate (ROFF 1992, HAENEL & JOHN-ALDER 2002). The Mosor rock lizard males and females mature at 3 years of age (in their fourth activity season), provided that they attain a given body size. If this body size is not reached, they delay reproduction until their fifth activity season. This implies that maturation is more dependent upon reaching the minimum size than on the minimum age, as has been suggested by several authors for other lacertid species (e.g. BAUWENS & VERHEYEN 1987, BAUWENS 1999, GALÁN 1999, CASTILLA & BAUWENS 2000, RÚA & GALÁN 2003). Since fecundity is size-dependent, the female strategy is to invest energy in growth rather than reproduction early in life. The major cost of delayed maturation is a decrease in the probability that a lizard will survive to reproduce. But if the benefit of increased fecundity outweighs the cost of reduced survival to maturity, delayed maturation at a relatively large size will be favoured by natural selection. The lower immature survivorship at high elevations could be more a consequence of longer winters than of predation pressure, which tends to be relatively low in those environments (SEARS & ANGILLETTA 2004).

The high predicted survival rates in adult Mosor rock lizards could indicate the benefit from their dorsoventrally flattened morphology, which allows individuals to seek refuge in narrow crevices. The observation that the flattened morphology reduces vulnerability to predation has been made in another Balkan endemic species with the same morphotype (*Dalmatolacerta oxycephala*) (BEJAKOVIĆ *et al.* 1996a). The high rate of regenerated tails in adult lizards in the analysed population (85% and 94% for males and females, respectively, authors' unpublished data) could also point to the lizards' ability to escape predators and a higher survivorship (PIANKA 1986, MEDEL *et al.* 1988 but see WILSON 1992), but aggressive interactions among lizards may also produce a greater number of specimens with an injured tail in the studied population.

Comparison with other small lacertids living in different environments

Several studies showed that the length of the activity season determines the growth patterns in small lacertids such that populations living in colder environments would exhibit a delayed age of maturation at a greater body size and a greater longevity (e.g. BAUWENS & VERHEYEN 1987, ARRIBAS 2004, ARRIBAS & GALÁN 2005). However, it could be argued that their effective life (i.e. time in activity) is not very different from lizards under less extreme conditions (see CARRETERO 2006). Our comparison of the effective age and body size at maturity of the Mosor Rock lizard and other small lacertids showed that this species had different

growth patterns relative to small Mediterranean lacertids that live under more favourable conditions, where a prolonged activity season tends to promote faster growth and early reproduction. However, the growth characteristics of the Mosor Rock lizard were not significantly different from either the high mountain populations, or the lowland populations of small lacertids of a temperate climate, which both experience seasonal restrictions of favourable conditions. Thus, although immature animals of the Mosor Rock lizard need several years to reach minimum sizes for reproduction, their effective life in activity is not significantly different from lowland lacertid populations of a temperate climate. This pattern could be related to the fact that the studied population inhabits an intermediate altitude relative to other high-altitude small lacertids such as species of *Iberolacerta* (e.g. ARRIBAS & GALÁN 2005), *Darevskia* (e.g. ARAKELYAN & DANIELYAN 2000), *Zootoca vivipara* (e.g. BRAÑA *et al.* 1991) and *Podarcis muralis* (BRAÑA *et al.* 1991), but may also relate to certain climatic characteristics of the habitats of the Mosor Rock lizard in mountains exposed to the influence of the Mediterranean climate.

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