Female life-history characteristics of the Mosor rock lizard, *Dinarolacerta mosorensis* (Kolombatović, 1886) from Montenegro (Squamata: Lacertidae)

KATARINA LJUBISAVLJEVIĆ¹, LIDIJA POLOVIĆ², NATAŠA TOMAŠEVIĆ KOLAROV¹, GEORG DŽUKIĆ¹ & MILOŠ L. KALEZIĆ¹,³

¹Department of Evolutionary Biology, Institute for Biological Research “Siniša Stanković”, Belgrade, Serbia, ²The Natural History Museum of Montenegro, Podgorica, Montenegro, and ³Institute of Zoology, Faculty of Biology, Belgrade, Serbia

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Abstract
Analysis of the female life history of the poorly studied endemic Balkan lizard species *Dinarolacerta mosorensis* was conducted on three population samples from Montenegro. One clutch is produced annually. Females mature at body sizes of 56–57 mm snout–vent length (SVL), attained at age 3–4 years. SVL increases with age. The average clutch size ranged from 4.3 to 5.2 eggs, and was significantly positively correlated with maternal SVL in two population samples. There were no trade-offs between egg size/offspring size and clutch size, nor between variation in egg size/offspring size and maternal SVL. The incubation period averaged 26.5 days, while hatching success in captivity was 72%. Significant positive correlations were found between the hatchling mass and egg mass and size, and also between the hatchling total length and egg width and volume. There was a significant negative relationship between the hatchling mass and incubation duration.

Keywords: *Dinarolacerta mosorensis*, incubation, life history, Montenegro, reproduction

Introduction
Studies that compare lower taxonomic units (i.e. populations or species) within small, monophyletic groups could help bridge the gap between broad macroevolutionary patterns and mechanistic models of life-history evolution by exploring the existence of subtle patterns and by documenting the phenotypic manifestation of trade-off functions (Bauwens and Diaz-Uriarte 1997). Life-history variables such as body size at maturation, fecundity, offspring size and reproductive frequency are central aspects of a species’ ecology. Rates of reproductive output may play a large role in determining the viability of populations in the face of pressures such as habitat destruction, predation and interspecific competition (Roff 2002; Du et al. 2005).

In spite of substantial progress during the past 20 years, detailed studies of life-history variation among conspecific populations of lizards are scarce (Bauwens 1999). For such a
study we chose the Mosor rock lizard *Dinarolacerta mosorensis* (Kolombatović, 1886), previously *Lacerta mosorensis* (see Arnold et al. 2007), which represents both a relict and a steno-endemic species of the Balkan Peninsula (e.g. Crnobrnja-Isailović and Džukić 1997a). It is a diurnal, heliothermic, insectivorous, oviparous, and a distinctly flattened saxicolous small lacertid species with a long head and a long slender tail (Arnold and Ovenden 2002). Its distribution is restricted to the south-western Dinaric mountain karst in Croatia, Bosnia and Herzegovina, and Montenegro, exposed to the influence of the Mediterranean climate. There, it is patchily distributed, restricted to altitudes ranging between 450 and 1900 m (Džukić 1989; Crnobrnja-Isailović and Džukić 1997a) within the oromediterranean biome—a complex of xeromontane ecomorphologically caused conditions with specific formation of preglacial floristic and faunistic elements (Matvejev and Puncer 1989). The main climatic characteristics of this landscape type are long, very cold snowy winters (in northern localities mean annual snow cover duration is from the end of September to June), very humid autumns and springs, and hot dry summers with extreme day and night temperature changes (Matvejev 1961; Anonymous 1969–76). Within this zone, *D. mosorensis* prefers rocky ground, but in relatively humid and shady habitats (Crnobrnja-Isailović and Džukić 1997a). As a typical petricol species, it is well adapted to mountain limestone rocks, cliffs and stones, where it regularly takes refuge in narrow crevices (Radovanović 1951; Bischoff 1984; Arnold and Ovenden 2002).

Very little is known regarding the ecology and life history of the Mosor rock lizard (e.g. Bischoff 1984). Data on the reproductive biology of this species are scarce, descriptive, based on a small number of individuals kept in captivity and consist primarily of anecdotal observations of courtship behaviour and copulation (Langerwerf 1983; Bosch 1989; Mauruschat et al. 1990). However, even such scarce data make *D. mosorensis* a distinctive species in terms of life-history traits within lacertids not least due to the very short incubation period (Langerwerf 1983; Bosch 1989; Mauruschat et al. 1990). The necessity of more in-depth study of life-history traits in different populations of this species was suggested, because a potentially ancient patchy distribution at different altitudes and in different climatic conditions might have led divergent selection pressures to act upon life-history characteristics for a long period of time (Mauruschat et al. 1990).

The aim of this study was to describe female reproductive characteristics of *D. mosorensis* from Montenegro. In particular, we provide quantitative data on: (1) body size and age at sexual maturity, clutch and hatchling characteristics and their relationships, incubation duration and hatching success in the southernmost population of the species, and (2) geographical differences in some reproductive traits. The analysis of life-history traits of the Mosor rock lizard populations should be taken into account for possible future translocation programmes concerning the number and origin of individuals for reintroductions or reinforcements. Such information is urgently needed, since, owing to small area occupancy, a severely fragmented distribution and a declining extent and quality of its habitat, the Mosor rock lizard is considered to be vulnerable (Crnobrnja-Isailović and Džukić 1997b).

**Material and methods**

**Localities and samples analysed**

The analyses of female reproductive traits and laboratory hatching study were carried out on a sample from the population of *D. mosorensis* living at 1350 m in the Lovćen Mt (Ivanova korita locality, 42°22′N, 18°50′E), at the south-eastern boundary of the
distribution range. This population inhabits the cliffs and blocks of rocks surrounded by subalpine beech forest (plant community *Fagetum montenegrinum subalpinum*) with whitebark pine (*Pinus heldreichii*) as the differential species (Tomić-Stanković 1970). The climate is moderate continental, modified by mountain climatic conditions with an influence from the sea reflected in high precipitation levels (average rainfall is 4207 mm, the maximum occurring in November and December) (Tomić-Stanković 1970).

Additionally, the oviposition period, clutch frequency, and geographic variation in female and clutch size were analysed using collection samples from the above-mentioned locality and another two localities from central (Prekornica Mt) and northern Montenegro (Durmitor Mt). On the Prekornica Mt (Ponikvica locality, 1655 m, 42°41′N, 19°16′E), specimens of the Mosor rock lizard were found most commonly along cliffs and boulders within the forest association *Pinetum heldreichii mediterraneo-montanum* (Blecic and Lakušić 1969). On the Durmitor Mt (surroundings of Zminje lake, 1495 m, 43°06′N, 19°04′E), *D. mosorensis* was found in dense populations on limestone rocks. There it occurs in a vegetation belt of mixed mountain forests of beech, Norway spruce, and silver fir *Fageto-Piceto-Abietum* (Marinković 1996).

The samples from Prekornica and Durmitor Mts came from Georg Džukić’s herpetological collection of the Institute for Biological Research, Belgrade. An additional sample of females from Lovćen Mt, deposited in the herpetological collection of the Natural History Museum of Montenegro, Podgorica, was examined for estimation of age and size at sexual maturity.

**Laboratory study**

Thirteen females near oviposition were captured from 1 to 15 July 2006 in Lovćen Mt (Ivanova korita locality) and transported to the laboratory (located in Podgorica, Montenegro at 44 m a.s.l.). Individual females were housed in individual terraria (30 × 20 cm) with a substrate of sand, while stones, pieces of bark and leaf litter were provided as sheltering sites. Food (mealworms and other insects collected in the field) and water were available *ad libitum*. The lizards were maintained under natural light and photoperiod conditions. Females were inspected almost every hour during the day and once at night. Following oviposition, females were measured (SVL, to nearest 0.01 mm) and weighed (to nearest 0.01 g). The eggs were dug up and carefully removed from the terraria, weighed (to the nearest 0.01 g) and measured (maximum length and width, to the nearest 0.01 mm), and their viability judged by the external characteristics of the eggshell. The characteristics of the eggs were, in all cases, determined within 8 h of laying. The eggs were marked and placed in plastic boxes filled with moistened vermiculite for incubation in the laboratory. The room temperature was controlled within the interval of 25–28°C during the incubation period. Moisture of the substrate was checked daily and, if necessary, distilled water was mixed evenly into substrates to compensate for water absorbed by the eggs and for losses due to evaporation. Immediately after hatching, hatchlings were weighed (to nearest 0.01 g) and measured (SVL and total length, L, to 0.01 mm).

**Sexual maturity**

The minimum size at sexual maturity was estimated for females of all three samples based on the smallest individual containing vitellogenic follicles or oviductal eggs. The age at maturity and generally the age of reproductive females could be estimated only in the
Lovčen population by the standard skeletochronological method, i.e. counting the number of lines of arrested growth deposited each year, assuming that it actually represents the number of winters the lizard has experienced (Castanet and Smirina 1990). This analysis was conducted as part of a skeletochronological study and will be described in more detail elsewhere (N. Tomašević Kolarov et al., unpublished data).

Clutch and newborn data

Egg volumes were obtained by approximating the volume of the ellipsoid: \( V = \frac{4}{3} \pi a^2 b \), \( a \) and \( b \) being half of the width and length of the egg, respectively (see Amat et al. 2000; Arribas and Galán 2005). In all cases, each clutch was unequivocally assigned to an individual female, allowing us to calculate the relative clutch mass (RCM) as the mass of the clutch (immediately after laying) divided by the female post-oviposition mass. Hatch success was estimated on the basis of the ratio of the number of eggs normally hatched to the total number of eggs in each clutch. Duration of incubation was defined as the elapsed time from egg laying to hatchling emergence. A digital caliper (0.01 mm precision) was used for the linear measurements, and mass measurements were taken with an electronic balance (accuracy 0.01 g).

Statistical procedures

Descriptive statistics (mean, standard error, range) for all traits were calculated. For subsequent analyses all variables were log-transformed, to ensure data normality and to generate homogeneous variances (Sokal and Rohlf 1981). Since some previous studies (see e.g. Galán 1997) reveal that the relationships between clutch characteristics and mother's SVL differ depending on whether oviductal or vivarium-laid eggs are considered, here, when defining clutch characteristics, we considered only the vivarium-laid eggs. Only the mean clutch size and the mean mother's SVL were estimated on the basis of data for clutches laid in the laboratory (Lovčen sample), while for the Durmitor and Prekornica samples, the data from autopsied females (oviductal eggs, enlarged vitellogenic follicles) were used. Therefore, comparisons between localities could only be made with regard to these traits. This was done according to similar studies that have found no differences between the number of vitellogenic follicles, oviductal eggs and laid eggs, with respect to female size (e.g. Amat et al. 2000; Znari et al. 2002). We used linear regression, analyses of variance (ANOVA) and covariance (ANCOVA), partial correlation analysis and Tukey's test (multiple comparisons) to analyse the corresponding data. Prior to testing for differences in adjusted means for clutch size, the homogeneity of slopes was checked. The analyses were carried out using the computer package Statistica® (Statistica for Windows, StatSoft, Tulsa, OK, USA).

Results

Sexual maturity

Of the 28 females examined from the Lovčen locality, the smallest female showing signs of sexual activity was 56.34 mm SVL, and all females larger than this size reproduced yearly. According to the skeletochronological analysis, this size was reached when the animal was 3 years old, in its fourth calendar year. In our sample, only one 3-year-old female was sexually
mature, and all other reproductive females were older. The smallest 4-year-old reproductive female was only slightly larger (56.69 mm) than the smallest 3-year-old mature female. The smallest SVL at reproduction was very similar across the three analysed population samples. The smallest reproductive females in the Durmitor sample (N=19) and Prekornica sample (N=14) had SVLs of 56.19 and 56.77 mm, respectively.

**Egg-laying period and clutch frequency**

Data from collection specimens (Durmitor and Prekornica Mts) collected in different years were mixed for each sample in order to give an overall description of the oviposition period in this species. In the Durmitor population eggs near oviposition were present in 87% of adult females collected in the middle of July, while 23% had widened oviducts (sign of postparturition). In the mid-June Prekornica sample, we found 60% of females carried enlarged vitellogenic follicles. In the laboratory, the clutches of two females from this locality were laid in the second week of July. The late-pregnant females collected during the first 2 weeks of July in the Lovćen Mt laid their clutches in the second half of July. According to these data, the oviposition period in these three populations collected in Montenegro over the years was in July.

None of the females examined exhibited the simultaneous presence of vitellogenic follicles and oviductal eggs or corpora lutea. Nor did we find other indicators of the production of more than one clutch per season.

**Age, egg and clutch characteristics of females of the Lovćen population**

Age, egg, clutch characteristics of females, and body size of newborn hatchlings of *D. mosorensis* from the Lovćen Mt based on average values for each clutch are presented in Table I, while the clutch size (CS) is given in Table II. The clutch size increased significantly with female SVL (r=0.64, F1,11=7.73, P=0.02). No significant relationship was found between the SVL and mean egg mass and sizes (EM: r=−0.07, F1,11=0.06; EL: r=−0.11, F1,11=0.12; EW: r=0.05, F1,11=0.03; EV: r=−0.06, F1,11=0.04; P>0.05 in all cases; for abbreviations see Table I). Hence, the mean egg sizes for a clutch remain constant

| Table I. Age, egg and clutch characteristics of adult female *Dinarolacerta mosorensis* from the Lovćen Mt (Ivanova korita). |
|---------------------------------------------------------------|
| **Mean ± SE** | **Range** | **N** |
| Female SVL (mm) | 63.76 ± 0.82 | 56.34–70.72 | 21 |
| Age of adult females | 5.86 ± 0.33 | 3–9 | 21 |
| Clutch mass (CM) (g) | 2.220 ± 0.130 | 1.390–2.750 | 13 |
| Relative clutch mass (RCM) | 0.380 ± 0.020 | 0.280–0.470 | 13 |
| Egg mass (EM) (g) | 0.530 ± 0.030 | 0.350–0.720 | 13 |
| Egg length (EL) (mm) | 16.28 ± 0.23 | 14.92–17.41 | 13 |
| Egg width (EW) (mm) | 7.98 ± 0.11 | 7.26–8.76 | 13 |
| Egg volume (EV) (mm³) | 546.95 ± 19.08 | 412.65–686.58 | 13 |
| Hatchling total length (L) (mm) | 70.38 ± 0.94 | 62.50–75.00 | 12 |
| Hatchling SVL (mm) | 26.75 ± 0.20 | 25.38–27.95 | 12 |
| Hatchling mass (HM) (g) | 0.430 ± 0.010 | 0.380–0.510 | 12 |
| Incubation (days) | 26.49 ± 1.22 | 20.00–34.75 | 12 |
| Hatch success (%) | 72.00 ± 7.80 | 0.00–100.00 | 13 |
with the increase in female SVL, irrespective of the number of eggs in the clutch. Also, the RCM was not significantly related to the mother’s SVL (r=0.30, F_{1,11}=1.13, P>0.05).

A partial correlation analysis showed that there was no significant egg size–clutch size trade-off within individual clutches when holding female SVL constant (EL: r=2.0.39; EW: r=0.02; EV: r=−0.15; P>0.05 in all cases). Also, the mean egg mass for a clutch decreased insignificantly with clutch size when SVL is held constant (r=−0.33, P>0.05). Hence, larger clutches were not composed of significantly smaller and lighter eggs and this relationship is independent of female SVL.

The size of reproductive females was highly significantly correlated with age (r=0.73, F_{1,19}=21.18, P<0.001) (Figure 1). However, there was no significant relationship between age of females and their egg or clutch characteristics when SVL was held constant (CS: r=−0.37; CM: r=0.13; RCM: r=0.19; EM: r=0.45; EL: 0.59; EW: r=0.02; EV: r=0.38; P>0.05 in all cases).

Geographical variation in reproductive output

The mean SVL of gravid females significantly differed among the samples (ANOVA, F_{2,28}=4.19, P<0.05) (Table II). Post hoc Tukey’s tests indicated that females from Durmitor were significantly larger than those from the other two samples (P<0.05 in both cases).

The clutch size was significantly positively correlated with maternal SVL in the Durmitor sample (r=0.65, F_{1,10}=7.40, P<0.05), as also shown above for the Lovćen sample. This relationship was non-significant in the Prekornica sample, possibly due to the small sample size (r=0.58, F_{1,4}=2.04, P>0.05).

Results of the ANCOVA revealed no difference between the regression slopes (F_{2,25}=0.10, P=0.91), but a highly significant difference between intercepts (F_{1,25}=11.43, P=0.002) (Figure 2). The size-adjusted mean clutch size was greater in the Prekornica sample than in the Lovćen sample (Tukey’s test, P<0.05) while the Durmitor sample did not differ from the other two samples in this trait (Tukey’s test, P>0.05) (Table II).

Incubation period, hatching success and hatchlings characteristics

Clutches hatched between 3 and 21 August 2006. The mean incubation period and hatch success in the laboratory, estimated from the pooled data for all clutches, were approximately equal to those given in Table I (incubation time of 40 hatched eggs of a
total of 55 laid in 13 clutches: 26.5 ± 0.6 days, range 20–35 days, hatching success 72.7%). Only in one out of 13 clutches did all eggs fail to hatch. There was no relationship between SVL of females and their offspring mass and size characteristics (L: \( r = -0.40, F_{1,10} = 1.90; \) HSVL: \( r = -0.30, F_{1,10} = 1.02; \) HM: \( r = -0.33, F_{1,10} = 1.26; P > 0.05 \) in all cases; for abbreviations see Table I). The hatchling mass was significantly positively correlated with egg mass and size (EM: \( r = 0.57, F_{1,38} = 18.49, P < 0.001; \) EL: \( r = 0.49, F_{1,38} = 11.81, P < 0.01; \) EW: \( r = 0.38, F_{1,38} = 6.41, P < 0.05; \) EV: \( r = 0.50, F_{1,38} = 12.59, P < 0.001 \)), while the hatchling total length was significantly positively correlated with egg width and volume (EW: \( r = 0.39, F_{1,38} = 6.92; \) EV: \( r = 0.35, F_{1,38} = 5.37; P < 0.05 \) in both cases). There was a significant negative correlation between the hatchling mass and incubation duration (\( r = -0.35, F_{1,38} = 4.48, P < 0.05 \)).

**Discussion**

*Sexual maturity and age effect on reproductive traits*

Our results showed that some females mature at 3 years of age (in their fourth activity season), provided that they attain a given body size, otherwise they delay reproduction until their fifth activity season. This suggests that individuals become sexually mature upon attaining a minimum body size, rather than a minimum age, as has been suggested for other lacertid lizard species (e.g. Bauwens and Verheyen 1987; Bauwens 1999; Castilla and
Bauwens 2000; Rúa and Galán 2003). Apparently, as in other mountain lizards (e.g. Arribas 2004; Arribas and Galán 2005), sexual maturity in \textit{D. mosorensis} females is delayed. It has been suggested that mountain species and populations living in areas with harsh climatic conditions attain sexual maturity at a greater body size and at an older age than the lowland species and populations (Rúa and Galán 2003; Roitberg and Smirina 2006). Their limited annual growth rate is imposed by the short annual cycle, so it takes immature animals several years to reach minimum sizes for reproduction (e.g. Shine and Charnov 1992; Adolph and Porter 1996; Arribas 2004). This explanation can be extended to our study, because other small lacertids (\textit{Podarcis muralis}, \textit{Podarcis melisellensis}, \textit{Dalmatolacerta oxycephala}, \textit{Algyroides nigropunctatus}), found in the lowlands of the Skadar Lake (at the foot of the Lovćen Mt) mature at smaller sizes and at younger ages than the Mosor rock lizard (Bejaković et al. 1996). Also, an increased size at maturity might potentially prevent females from producing offspring that will be too small to survive in a harsher environment (Ji and Wang 2005). At a given body size, species that mature late also tend to live longer as adults (Bauwens and Díaz-Uriarte 1997). Likewise, optimality models of life-history evolution predict that increased adult survival will result in delayed age at maturity (Stearns and Koella 1986). In a separate study on Lovćen population, we found that the modal age was 5 and 6 years for males and females, respectively, while the maximal longevity was 9 years in both sexes (N. Tomašević Kolarov et al., unpublished data). Thus, the mean adult age and longevity in \textit{D. mosorensis} appeared to be higher than in other lacertid species (Bauwens and Díaz-Uriarte 1997), including the mountain species (Luis et al. 2004; Roitberg and Smirina 2006), except for \textit{Iberolacerta aurelioi} (Arribas 2004).

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**Figure 2.** The relationships between clutch size and maternal SVL of \textit{Dinarolacerta mosorensis} from the three different populations.
In the Mosor rock lizard, female body size significantly increased with age, which appears to be a general phenomenon in lizards that exhibit indeterminate growth (Bauwens 1999). When the effects of body size were removed from the analyses, age had only a minor (non-significant) influence on reproductive traits. This indicated that ontogenetic increase in reproductive success is actually a function of female body length, rather than age, as has also been shown in some other lacertid species (e.g. Olsson and Shine 1996).

Reproductive cycle and clutch frequency

The reproductive cycle of *D. mosorensis* is short and delayed (Bischoff 1984), which is connected to the shortness of its annual activity cycle due to unfavourable climatic conditions in mountain environments. This pattern is also characteristic for populations of other lacertid lizards living in similar conditions (e.g. Saint Girons and Duguy 1970; Bauwens and Verheyen 1987; Rúa and Galán 2003; Arribas and Galán 2005). The activity season of *D. mosorensis* starts about 3 weeks later than in other species from the region (*D. oxycephala, P. muralis*) that are separated altitudinally (Tomassini 1889; Radovanović 1951). According to the literature (Mauruschat et al. 1990; Veith 1991), mating of the Mosor rock lizard in different localities occurs during the end of May and begins as soon as the lizards emerge from hibernation. In captivity, under an extended activity period due to unnatural favourable conditions, mating of individuals from Durmitor occurred in June (Langerwerf 1983). During the field work we observed mating between the end of May and the beginning of June over different seasons and at different localities. Our data, suggesting the oviposition period occurred in July, were in agreement with the literature (for Herzegovinian population—Tomassini 1889; for Durmitor population—Langerwerf 1983; Mauruschat et al. 1990). Some authors also suggested that the oviposition period could be extended to the beginning of August (for species as a whole—Radovanović 1951; Bischoff 1984; for Herzegovinian population—Veith 1991).

*D. mosorensis* clearly belongs to the single-clutched lizards, as indicated in our study and the literature (Langerwerf 1983; Mauruschat et al. 1990; Arnold and Ovenden 2002). In the small-sized lacertid species a single annual clutch is conditioned by the viviparous modality of reproduction (e.g. *Zootoca vivipara*, Heulin et al. 2000), or by the period of annual and reproductive activity (e.g. Saint Girons and Duguy 1970; Arribas and Galán 2005). In the case of the Mosor rock lizard, the production of a single clutch is both conditioned by the prolonged egg retention inside the female body (see below) and the climatic factors that limit the duration of the reproductive period.

Clutch size and egg size relationship

The existence of trade-offs (inverse relationships) is a central concept in evolutionary biology (Uller and Olsson 2005). Under the assumptions that the amount of energy available is limited and the egg size is not invariant, the clutch size should be inversely correlated with egg size in each clutch, because of energy and space constraints (Roff 1992; Bauwens and Díaz-Uriarte 1997; Doughty and Shine 1997; Ji and Braña 2000). Also, if eggs of reptiles are not optimized, the egg size should vary as a function of maternal size and clutch size (e.g. Olsson and Shine 1997; Ji et al. 2002). On the other hand, trade-offs are not always observed in nature (Roff 1992, 2002; Stearns 1992). The failure to provide evidence for trade-offs is probably not because they do not exist, but rather because their existence is more complex than earlier believed (Uller and Olsson 2005). Unsurprisingly,
we found that larger and heavier eggs gave rise to larger and heavier hatchlings, suggesting that the hatchling mass and size are good estimators of the energy content of an egg, as has been reported for a number of other lizards (reviewed by Bauwens 1999; Bauwens and Diaz-Uriarte 1997). However, this study revealed no evidence of the predicted trade-off between egg size/offspring size and clutch size, and variation in egg size/offspring size associated with maternal SVL. Our results could indicate that that there may be an “optimal” egg size or an egg size that produces a sufficiently viable hatching (Znari et al. 2002), as a consequence of its adaptive responses to local environments. Furthermore, reproductive output in D. mosorensis could be influenced by maternal body volume but at some optimal rather than maximal level, which means that eggs are less crowded together in the oviduct and clutches do not completely fill the available body volume. 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 (as shown below for RCM). In this case, the resource is not anticipated to be a limiting factor, and an increase in resource availability will not lead to reduction or elimination of the observed trade-offs (Uller and Olsson 2005). However, it should be noted that the moderate sample size of this study may impede the statistical detection of some relationships among the variables, given that some trade-offs between the egg size and the clutch size were observable but not statistically significant.

Hatchlings’ characteristics

A non significant correlation between the hatchling size and the female size has been found in some populations of cold-climate small lacertids (Z. vivipara—Bauwens and Verheyen 1987; Iberolacerta monticola—Rúa and Galán 2003). Similarly, the Mosor rock lizard appeared to adopt a strategy used by large-sized lizards with large clutch sizes (Bauwens and Diaz-Uriarte 1997), tending to increase the clutch size and not the egg size, despite the fact their body size is small and their clutch consists of less than 10 eggs. For that reason, it was even more interesting that we found a significant negative relationship between the incubation duration and the juvenile size, which obviously pointed out the benefits associated with an increment of egg and juvenile size, as has also been found in Lacerta schreiberi (Marco and Pérez-Mellado 1998). This result is opposite to those found in other lacertid lizards (Bauwens and Diaz-Uriarte 1997) and can indicate a selection pressure towards an even shorter incubation period (and consequently more extended egg retention, see below), due to the survival advantage of larger and earlier-hatched offspring over smaller and later-hatched ones in cold-climate mountain environments.

Relative clutch mass

In reptiles, the ratio of the total litter mass to maternal postpartum mass (RCM) has often been used as a useful measure of relative reproductive investment (e.g. Shine 1980; Gillis and Ballinger 1992). The species with a more advanced embryonic development at oviposition (also detected in D. mosorensis, see below) have been found to have significantly larger RCM and higher upper limits of altitudinal distribution (Braña et al. 1991). This is in agreement with our results which showed that the mean RCM value for the Lovćen population of D. mosorensis was greater than in other “widely foraging” (sensu Vitt and Congdon 1978) lacertid lizards of the lowlands of this region (see Bejaković et al. 1996). The higher values of RCM in species with more advanced egg retention (usually single-clutched species) was mainly due to
an increase in the clutch size (adjusted for female size) and not to an increase in the mass of individual eggs, which tended to be lower in relation to the female mass (Braña et al. 1991). However, the mean RCM value in *D. mosorensis* was lower than in some other montane single-clutched small lacertids (*Iberolacerta aranica*—Arribas and Galán 2005; *I. monticola*—Braña et al. 1991; Rúa and Galán 2003; oviparous populations of *Z. vivipara*—Braña et al. 1991). This could be explained either by larger clutches in the second two species or somewhat less advanced egg retention (heavier eggs in relation to female mass) in the small clutched *I. aranica* than in *D. mosorensis*. In addition, a flattened morphology of the Mosor rock lizard that fits its crevice dwelling could constrain the RCM value (Vitt 1981). However, explanations could be more complex since some recent studies suggested that, at least in some species, the changes in RCM are not related to evolution of extended egg retention (Calderón-Espinosa et al. 2006) and even a small shift in behaviour could potentially have a significant effect on the relationships between morphology, reproductive characteristics and the true “costs” of reproduction (Quallis and Shine 1997).

**Geographical variation in reproductive output**

Since the Mosor rock lizard is a single-clutched species with delayed maturity, gaining a larger body size and living for multiple seasons appear to be the main avenues for females to increase lifetime reproductive success, at least in Durmitor and Lovćen populations, where the significant positive correlation between the clutch size and the female body size was observed. Among-population variation in reproductive characteristics and natural history reflects a partly genetic divergence caused ultimately by natural selection as a consequence of adaptation to different environmental conditions at the evolutionary level, and partly phenotypic plasticity induced proximately by environmental factors such as temperature and prey availability (Dunham et al. 1988; Ji and Wang 2005). The persistence of among-population differences in the mean clutch size even after the effects of maternal body size were removed from the analysis suggested that these differences are either coded genetically or that they are influenced by events (food supply, temperature, etc.) early in a female’s life and are thereafter resistant to change (Du et al. 2005). Also, some lizards regulate litter and offspring sizes depending upon stored reproductive energy reserves in abdominal fat bodies in the preceding year (Doughty and Shine 1997). Since no significant genetic differences were observed among three populations here analysed (see Ljubisavljević et al. 2007), the distinctiveness of the Prekornica population could be due to the proximate effects of local conditions or simply to the influence of small sample size. This needs further research since the limitations of examining the collection sample did not allow us to investigate some other life-history and clutch characteristics of this population. However, even in species for which a substantial amount of data has been reported, identification of proximate and ultimate causes for life-history variation among reptile populations frequently remains obscure and could not be predicted by a single hypothesis (Dunham et al. 1988; Du et al. 2005; Ji and Wang 2005).

**Incubation and progressive egg retention**

This study, like the previous ones, indicated that the mean incubation time after oviposition was, at any temperature between 23 and 31°C, shorter in *D. mosorensis* than in other lacertids (see Mauruschat et al. 1990; Arribas and Galán 2005). Short incubation period in
**D. mosorensis** is related to the fact that eggs were laid in an advanced stage of embryonic development. Bosch (1989) determined that at the moment of oviposition the embryos have at least reached stage 30 in their development. We found that six recently laid eggs from one Prekornica female contained embryos of stage 33 (according to Dufaure and Hubert 1961). The high degree of variation in the stage at oviposition was observed within the same clutch, the same locality and among localities in *Sceloporus spinosus*, a species group with extended egg retention (Calderón-Espinosa et al. 2006). Additional research is needed to see whether a similar situation exists in *D. mosorensis*, since somewhat less synchronous hatching within a clutch and a rather large variation in the incubation period among clutches could be a relevant indicator.

Within Lacertidae, a similar retention of eggs within the female, followed by a short incubation period after laying, occurs in ovisparous populations of *Z. vivipara* on the Iberian and Balkan Peninsulas, and in the Pyrenean *Iberolacerta* species (Braña et al. 1991; Heulin et al. 2000; Arribas 2004; Arribas and Galán 2005). In these species, as well as in *D. mosorensis*, the phenomenon appears to be linked with the unfavourable thermal regimes and short annual activity period in the mountains, and presents a shift towards viviparity. According to the “cold climate model”, selective advantages of uterine retention at maternal body temperature are accelerated hatching, enhanced hatching success, increased locomotor speed of hatchlings (Shine 2002), and reduced egg mortality (Andrews 2000).

Progressive egg retention found in the Mosor rock lizard seems to support the suggestion of Arribas and Galán (2005) that this phenomenon occurs in similar geographical areas, the mountain slopes of Southern European Peninsulas, which were near the northern limit of the glacier refuges and presumably have harsher conditions than other southernmost areas. The ability to retain eggs is associated with the evolutionary and geographic history of the group (Calderón-Espinosa et al. 2006), but an adaptative explanation for this phenomenon could also be included (Arribas and Galán 2005). Braña et al. (1991) found that the degree of intrauterine embryogenesis was lower in the populations of *Podarcis* than those of relict mountain populations of *Iberolacerta* and *Zootoca*. The species with prolonged egg retention have a higher capacity of colonization or a competitive advantage in areas with cool climate (Braña et al. 1991). This could have helped *D. mosorensis* to colonize and survive at higher altitudes in the mountains, under the spreading of wall lizards and probably *D. oxycephala* (Ljubisavljević et al. 2007).

**Peculiarities in life-history strategy of the Mosor rock lizard**

On the basis of data presented in this study, *D. mosorensis* appeared to have a rather unique life-history strategy. At first glance it falls into the relatively long-lived, late-maturing reproductive strategy (Dunham et al. 1988), reaching sexual maturity after the second year of life and producing one clutch per year. Species that are viviparous generally fall into this category (Vitt and Cooper 1985), and apparently those with prolonged oviductal egg retention such as the Mosor rock lizard. However, some of these traits and some other characteristics such as the tendency to increase the clutch size rather than the egg size and higher RCM values found in the analysed population of *D. mosorensis* were also recognized as characteristic of large-sized lizards (Bauwens and Díaz-Uriarte 1997). Furthermore, adaptations to a particular habitat-type could have placed some constraints on reproductive output in this species, producing optimal-sized offspring at some optimal, rather than maximal level (Vitt 1981; Ji et al. 2002). Phylogenetic inertia could be an additional factor potentially influencing the directions that natural selection might take in
moulding life-history and reproductive characteristics (Vitt and Congdon 1978; Vitt and Cooper 1985). A high degree of singularity in the life-history strategy of *D. mosorensis* sits well with its distinctive place in the phylogenetic tree of Lacertidae (Arnold et al. 2007).

**Conservation considerations**

As the results of this study pointed to low fecundity and delayed sexual maturity, the viability of *D. mosorensis* populations will be based on adult survival, due to the scarce and late incorporation of immature animals into the reproductive population. Thus, they should be expected to be very vulnerable to any kind of natural and anthropogenically induced mortality or disappearance of adult specimens (Arribas 2004; Arribas and Galán 2005). For that reason, it will be necessary to take into consideration these and other characteristics related to reproductive and population dynamics for planning further conservation and protection measures for this greatly evolutionary and zoogeographically significant species of European herpetofauna.

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