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FEMALE REPRODUCTIVE LIFE HISTORY TRAITS OF THE MEADOW LIZARD, *DAREVSKIA PRATICOLA* (EVERSMANN, 1834) (SQUAMATA: LACERTIDAE) FROM THE WESTERNMOST BOUNDARY OF THE SPECIES RANGE

ABSTRACT: We presented the first data on female reproductive traits of the meadow lizard *Darevskia praticola* from the westernmost boundary of the species range (Peridanubian Serbia). Mating occurs during April and May, oviposition period occurs in June, and hatching takes place in July. Females mature at body sizes of 49.5 mm of snout-vent length (SVL). One clutch is produced annually. The average clutch size of 5.7 eggs (range 4 – 8) represents the largest recorded for this species. Clutch size and clutch mass increased significantly with the mother's SVL. There was no evidence of the predicted trade-off between egg size and clutch size, as well as of variation in egg size associated with maternal SVL. The relative clutch mass (RCM) was rather high (0.60) for lacertid species and was not correlated with female size.

KEY WORDS: oviposition period, clutch characteristics, *Darevskia praticola,* Serbia

1. INTRODUCTION

Recent studies of reptiles have accentuated the necessity of having independent data sets from different populations and reptilian taxa in order to understand both the general patterns of covariation among life-history traits, and the relationships between these and environmental factors (e.g. Adolph and Porter 1993, Du *et al.* 2005, Ji and Wang 2005). The meadow lizard (*Darevskia praticola* Eversmann, 1834) (Fig. 1) appears to be a particularly suitable object for this kind of study on the basis of its two in many respects different characteristics. Firstly, as the meadow lizard is a species of the forest lizards group of *Darevskia* genus (Arribas 1999), the knowledge of reproductive life history traits of this species is of general interest, considering the paucity of such studies dealing with small forest lacertids (e.g. Orlova 1969). Secondly, the meadow lizard provides a specific opportunity to study the possible interrelation between complex disjunctive distribution patterns with different evolutionary lineages and differences in life history traits. Namely, the current taxonomical structure of the meadow lizard includes structuring at the subspecies level (e.g. Darevsky 1997, Ljubisavljević *et al.* 2006, but see Arnold *et al.* 2007). A nominotypical subspecies (*D. p. praticola*) occurs in northeastern Caucasus and Transcaucasus, while the *D. p. pontica* is distributed in northwestern Caucasus and in southeastern Europe. In southeastern Europe the meadow lizard inhabits southwestern and southeastern Romania, Serbia, Bulgaria and Thrace in

Fig. 1. Female *Darevskia praticola* from Vršački breg, Serbia.

Turkey and Greece (A r n o l d a n d O v e n d e n 2002). There it presents a patchy distribution connected to broad-leaved woodlands exposed to the influence of Submediterranean climate, restricted mainly to middle altitudes rarely exceeding 600 m (S t u g r e n 1984).

To date, there are several studies which have yielded information on reproduction of the meadow lizard in the eastern portion of its range (Z h u k o v 1941, O r l o v a 1969, M u s h e l i s h v i l i 1970, O r l o v a a n d T e r - t y s h n i k o v 1979). Reproductive life history traits of southeastern European populations, apart from the limited descriptive data for the Romanian population (M é h e l y 1895, F u h n a n d V a n c e a 1961), are poorly known.

Here, we present the first basic study on female reproductive characteristics of the meadow lizard from the westernmost boundary of its distribution range. Knowledge of the reproductive potential of these edge populations with a severely fragmented distribution is valuable for their conservation and protection.

2. MATERIAL AND METHODS

2.1. Localities and sampling

The analysis of female reproductive traits was carried out on samples collected from three different localities in Peridanubian Serbia in 2002 and 2003: Vršački breg (340 m above sea level, 45°08'N, 21°21'E); Avala (250 m, 44°41'N, 20°31'E); Trešnja (250 m, 44°36'N, 20°34'E).

Because the preliminary analysis showed no statistical differences in female snout-vent length (SVL), clutch size and clutch and egg characteristics between localities (ANOVA for female SVL and ANCOVA with SVL as the covariate, $F_{2,7} = 0.05 - 16.74$, $P > 0.05$ for all variables), we pooled the data in order to achieve a reasonable sample size. In the study area, the meadow lizard occurs in hilly terrain in and around the open broad-leaved woods of the Hungarian and Turkey oak forest association *Quercetum-frainetto-cerris* (R a d o v a n o v i ć 1951, M a t v e j e v 1961).

2.2. Data collection in the laboratory

In the first half of June of 2002 and 2003, twelve late-pregnant females were collected from the study area and transported to the laboratory. 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. The females were inspected almost every hour during daytime and once during the night. Following oviposition, the females were measured (snout-vent length, SVL) and weighed. The eggs were dug up and carefully removed from the terraria, weighed and measured (maximum length and width), and their viability judged by the external characteristics of the eggshell. A digital calliper (0.01 mm precision) was used for the linear measurements, while mass measurements were taken with an electronic balance (accuracy 0.001 g). The characteristics of the eggs were, in all cases, determined within 8 h of laying. The estimate of egg volume (V=4/3π a^2b, a and b being half of the width and length of the egg, respectively) was taken as an overall measure of egg size. In all cases each clutch was unequivocally assigned to an individual female, allowing us to calculate the relative clutch mass (RCM) as the ratio of clutch mass to postparturition body mass.

2.3. Statistical procedures

Descriptive statistics (mean, standard error, standard deviation, 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) revealed that the relationships between clutch characteristics and maternal SVL differ depending on whether oviductal or vivarium-laid eggs are taken into account, here we considered only the vivarium-laid eggs. Only the mean clutch size was estimated on the basis of data for 12 clutches laid in the laboratory and additional oviductal clutches from five autopsied females. These individuals were part of a larger sample of 41 females which were examined for estimation of size at sexual maturity based on the smallest individual containing vitellogenic follicles or oviductal eggs. The mean maternal SVL was calculated on 28 specimens from this sample determined to be mature. The sample came from Georg Džukić's herpetological collection of the Institute for Biological Research, Belgrade.

We used multiple regression, analyses of variance (ANOVA) and covariance (ANCOVA) to analyse the corresponding data. The analyses were carried out using the computer package Statistica˚ (STATISTICA for Windows. StatSoft, Inc., Tulsa, OK).

3. RESULTS

3.1. Sexual maturity

Ovaries of immature females of the meadow lizard consisted of transparent follicles up to 1.6 mm in diameter. Somewhat larger follicles (>2 mm) showed signs of vitellogenesis and were used as an indication of the first sign of reproductive activity of the females. According to this criterion and on the basis of 41 collection specimens examined, the minimum size at which the females from Serbia attained sexual maturity was 49.5 mm in SVL, and all females larger than this size reproduced. Percentage of mature females in the analysed sample was 68%.

3.2. Oviposition and clutch frequency

The data obtained through fieldwork and from specimens already preserved in collection gathered in different years were pooled together in order to give an overall description of the oviposition period in this species. At the end of April the females bore small to medium vitellogenic follicles. Specimens from all three study localities carried oviductal eggs during May, while in all cases the clutches were laid during June in the laboratory. None of the examined females exhibited a simultaneous presence of enlarged vitellogenic follicles and oviductal eggs or *corpora lutea*. We neither found other indicators for

Table 1. Egg and clutch characteristics of female *Darevskia praticola* from Serbia based on average values for each clutch. The mean ± SE, SD, range and number of adult females or clutches analysed (N) are shown.

	mean ± SE	± SD	range	N
Female SVL (mm)	54.74 ± 0.60	3.16	49.49 – 60.51	28
Clutch size	5.71 ± 0.29	1.21	4 – 8	17
Clutch mass (g)	1.508 ± 0.090	0.311	1.184 – 2.220	12
Relative clutch mass (RCM)	0.601 ± 0.028	0.097	0.454 – 0.771	12
Egg mass (g)	0.264 ± 0.008	0.029	0.215 – 0.332	12
Egg length (mm)	10.67 ± 0.17	0.59	9.62 – 11.69	12
Egg width (mm)	6.61 ± 0.07	0.23	6.21 – 6.94	12
Egg volume (mm³)	244.76 ± 7.40	25.65	194.08 – 282.87	12

the production of more than one clutch per season.

3.3. Clutch characteristics

Reproductively active females had, on average, 54.7 ± 0.6 mm in SVL, and the clutch size of 4 to 8 eggs (mean ± SE = 5.7 ± 0.3). The laid eggs had a mean length of 10.7 ± 0.2 mm, a mean width of 6.6 ± 0.1 mm, and a mean mass of 0.26 ± 0.01 g. The relative clutch mass ranged from 0.45 to 0.77, with the mean value of 0.60 ± 0.03 (Table 1).

The clutch size and clutch mass increased significantly with female SVL (clutch size: $r = 0.67$, $F_{1,15} = 12.55$, $P < 0.01$, Fig. 2; clutch mass: $r = 0.58$, $F_{1,10} = 4.97$, $P < 0.05$). No significant relationship was found between the SVL and mean egg mass and sizes (egg mass: $r = -0.08$, $F_{1,10} = 0.07$, egg length: $r = -0.41$, $F_{1,10} = 1.99$, egg width: $r = 0.22$, $F_{1,10} = 0.51$, egg volume: $r = -0.07$, $F_{1,10} = 0.05$, $P > 0.05$ in all cases). Hence, the mean egg sizes for a clutch remain constant 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 ($r = -0.04$, $F_{1,10} = 0.02$, $P > 0.05$).

We statistically removed the effects of maternal SVL by calculating the residual scores from separate regressions of egg variables and clutch size on female SVL, respectively. Overall, the relative fecundity showed a non-significant negative correlation with the mean egg mass ($r = -0.34$, $F_{1,10} = 1.32$, $P > 0.05$), egg length ($r = -0.49$, $F_{1,10} = 3.23$, $P > 0.05$), egg width ($r = -0.21$, $F_{1,10} = 0.50$,

$P > 0.05$) and egg volume ($r = -0.37$, $F_{1,10} = 1.58$, $P > 0.05$) which indicates that there was no significant egg size-clutch size trade-off within individual clutches when holding female SVL constant. Hence, larger clutches were not composed of significantly smaller and lighter eggs and this relation is independent of female SVL.

4. DISCUSSION

4.1. Clutch frequency

Populations of *D. p. pontica* are single clutched, as indicated in our study and the literature (Orlova 1969), while *D. p. praticola* appear to be able to lay two clutches per year in Armenia (Orlova 1969) and Georgia (Mushelishvili 1970). Production of single or multiple clutches within the same season is primarily related to female body size and to the timing of oviposition (Galán 1997, Rúa and Galán 2003). Apart from this, generally in the small-sized lacertid species a single annual clutch is conditioned by the viviparous modality of reproduction (e.g. *Z. 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 *D. p. pontica*, production of a single clutch is probably the result of adoption of different life-history strategy, since, at least in South European part of the range, the temperate climatic conditions are presumably more favorable than in the mountain regions of Armenia and Georgia where *D. p. praticola* occurs.
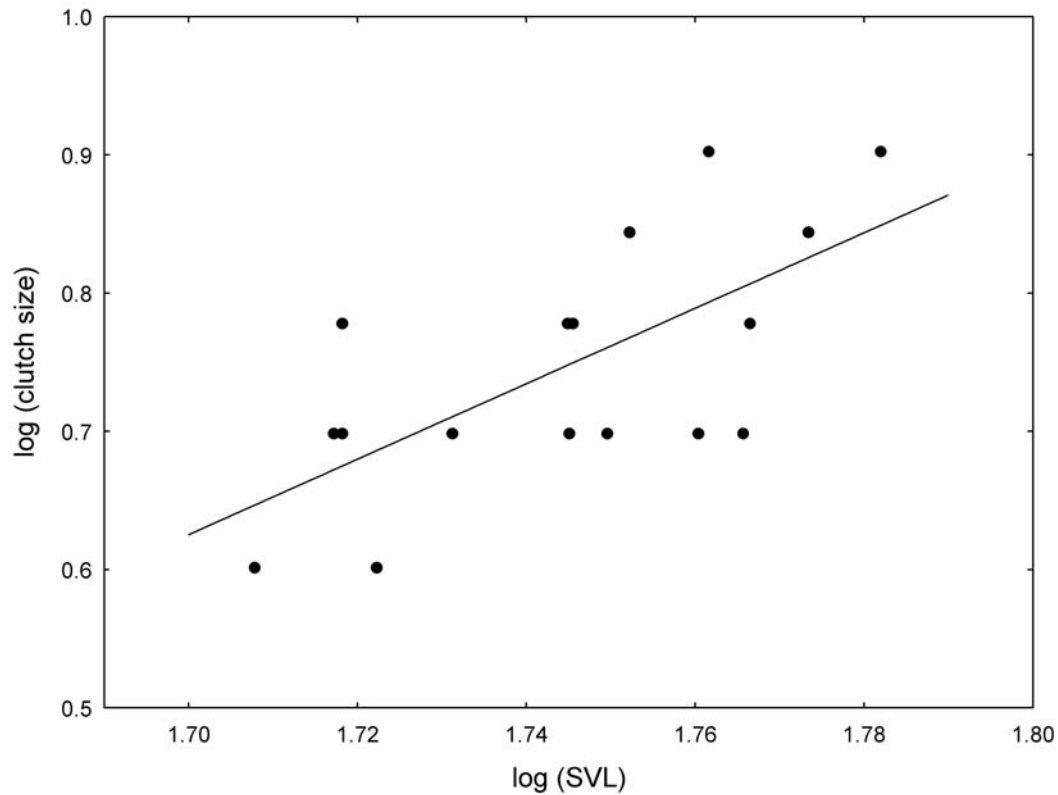
Fig. 2. The relationship between clutch size and maternal snout-vent length (SVL) of *Darevskia praticola* from Serbia.

4.2. Clutch size and clutch characteristics

The mean clutch size (4–5.7– 8 eggs) recorded in this study for the Serbian populations of the meadow lizard represents the largest recorded for this species (4–6 and 4 – 5 eggs Méhely 1895, Fuhn and Vancea 1961, respectively for the Romanian population; 2–4.4–6 eggs Orlova 1969, Orlova and Tertyshnikov 1979, for the central Caucasian population of *D. p. pontica*; 3 eggs Mushelishvili 1970, for the Georgian population of *D. p. praticola*). Since the present study showed that clutch size was significantly correlated with maternal size, geographical variation in reproductive output could be linked to geographical variation in adult body size, as reported previously for other reptile species (e.g. Ji and Wang 2005). Different reproductive strategies for production of one large or two small clutches generally found in *D. p. pontica* vs. *D. p. praticola* are accompanied by considerable morphological and particular genetical differences

(Ryabinina *et al.* 2002, Ljubisavljević *et al.* 2006). However, proximate factors that apparently vary among localities (local conditions of weather and food supply) could also be important determinants of the observed life-history variation.

Our data showed that maternal size was the main determinant of reproductive investment in the meadow lizard, with larger females producing more offspring. A trade-off between egg size and numbers (usually arises as a consequence of space constraints or limited food resources), although widespread in numerous lizard species (e.g. Bauwens and Díaz-Uriarte 1997, Doughty and Shine 1997, Ji and Braña 2000, Castilla and Bauwens 2000, Arribas and Galán 2005), was not detected in this study. However, trade-offs are not always observed for a variety of reasons. For example, failure to take into account covariates, and high variation in resource acquisition relative to variation in resource allocation, can obscure the underlying trade-off (Uller

and Olsson 2005). Also, eggs may be well optimised for size as a consequence of their adaptive responses to local environments or influenced by maternal body volume but at some optimal rather than maximal level (Ji *et al.* 2002, Ljubisavljević *et al.* 2007). Finally, Bauwens and Díaz-Uriarte (1997) noted that the sample size and the strength of the relationship between the residuals of two variables should be very large to make that relation detectable. Therefore, the moderate sample size of this study may impede the statistical detection of some relations among the size-free variables, given that some trade-offs between the egg size and the clutch size were observable but not statistically significant.

The mean RCM value recorded in the present study (0.6) was much higher than has been reported previously for most of the small sized lacertids (Braňa *et al.* 1991, Bejaković *et al.* 1996, Galán 1997, Arribas and Galán 2005). To our knowledge, higher mean RCM values have been recorded only in populations of *Z. vivipara* (Bauwens and Thoen 1981, Pilorge *et al.* 1983). In reptiles, RCM has been interpreted as an adaptation for optimal reproductive expenditure and a constraint imposed by the maternal body shape (amount of space available in the maternal abdominal cavity) (e.g. Tinkle 1969, Vit and Congdon 1978, Shine 1992). Species with a lower number of clutches per season could be expected to increase their energetic investment in each of them and variation in RCM is mainly due to an increase in clutch size (Braňa *et al.* 1991). This may be one of the reasons for the higher RCM value found in the analysed single-clutched populations of the meadow lizard with a large clutch size. Other reasons could be referred to specific characteristics related to escape tactics, vulnerability to predation, mobility and foraging mode of this forest lizard. Certain limitations of the "widely foraging" strategy and the "flight" anti-predator tactic (sensu Vitt and Congdon 1978, Greene 1988) in densely vegetated areas as the structural habitat type of *D. praticola* (Van Damme and Vanhooydonck 2002) and its cylindrical morphology could increase the RCM value (Vitt 1981).

4.3. Peculiarities in life-history strategy of the meadow lizard from the westernmost boundary of the range

Some species in their patterns of geographic variation and covariation in life-history characters (see Bauwens and Thoen 1981, Dunham *et al.* 1988, Bauwens and Díaz-Uriarte 1997, Rúa and Galán 2003, Ljubisavljević *et al.* 2007) do not conveniently fit the dichotomies in the theory of r – and K – selection (Pianka 1970), the foraging mode ("sit-and-wait" vs. "active" foragers, Vitt and Congdon 1978), the escape tactics ("cryptic" vs. "flight", Vitt and Price 1982) or time of maturation ("early" vs. "late maturing" Tinkle *et al.* 1970). The populations of *D. praticola* studied here appeared to adopt the strategy of large-sized "sit and wait" lizards having a relatively large (in comparison to other populations) single clutch with the tendency to increase the clutch size rather than the egg size and high RCM value. In addition, they presumably have a late-maturing reproductive strategy, reaching sexual maturity after the second year of life (as it is documented in populations of the same subspecies in northwestern Caucasus by Smirina *et al.* 1984, and our field observations). Adoption of this strategy, despite the fact that it actually belongs to small "widely foraging" lacertids with the clutch consisting of less than ten eggs, may be interpreted as an adaptation to a particular habitat-type (more forested habitat instead of more open areas in Caucasian region, Ljubisavljević 2004) or other environmental factors affecting different predation rates (Dunham *et al.* 1988).

Relict populations close to the range boundary often exhibit relatively low rates of population increase and low densities (e.g. Berlingd 2005). However, peripheral populations need not inevitably suffer lower fecundity with regard to central ones (e.g. Carretero and Llorente 1995, Díaz *et al.* 2005) as shown in our study. Morphological peculiarities of individuals within the analysed edge populations have already been identified (Ljubisavljević *et al.* 2006, authors unpublished data), which could be a reflection of intensive selection at the border of the species range, while their genetic

status still needs to be checked. Channell and Lomolino (2000) showed that peripheral populations are no more "doomed to extinction" than populations in the centre of a species' range, and in fact often less so. They often exhibit unique genetic characteristics (e.g. in lizards Gullberg *et al.* 1998, Böhme *et al.* 2007) that make them especially valuable for the evolutionary potential of the species and biodiversity conservation (Lesica and Allendorf 1995). In the analysed populations of the meadow lizard the threatening factors are likely to be extrinsic (habitat loss and degradation) and this is according to Araujo and Williams (2001) a strong reason for directing conservation management priorities towards these kinds of populations.

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