

Female reproductive characteristics of the Balkan sand lizard *Lacerta agilis bosnica* (Schreiber, 1912)

Authors: Ljubisavljević, Katarina, Anđelković, Marko, Urošević, Aleksandar, and Roitberg, Evgeny S.

Source: Revue suisse de Zoologie, 129(1) : 147-153

Published By: Muséum d'histoire naturelle, Genève

URL: <https://doi.org/10.35929/RSZ.0069>

BioOne Complete (complete.BioOne.org) is a full-text database of 200 subscribed and open-access titles in the biological, ecological, and environmental sciences published by nonprofit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Complete website, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/terms-of-use.

Usage of BioOne Complete content is strictly limited to personal, educational, and non - commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

BioOne sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

Female reproductive characteristics of the Balkan sand lizard *Lacerta agilis bosnica* (Schreiber, 1912)

Katarina Ljubisavljević^{1,*}, Marko Anđelković¹, Aleksandar Urošević¹, Evgeny S. Roitberg²

¹ University of Belgrade, Institute for Biological Research “Siniša Stanković” - National Institute of the Republic of Serbia, Department of Evolutionary Biology, Bulevar Despota Stefana 142, 11060 Belgrade, Serbia

² Zoological Research Museum Alexander Koenig, Adenauerallee 160, 53113 Bonn, Germany

* Corresponding author: katarina.ljubisavljevic@ibiss.bg.ac.rs

Abstract: The sand lizard (*Lacerta agilis*), which occupies a large part of temperate Eurasia and includes several morphologically and genetically distinct lineages, is a model species for life-history studies. Yet, for major parts of the species range, basic data on female reproductive traits are lacking. Here we present the first data on female reproductive traits of *Lacerta agilis bosnica*, a poorly studied lineage inhabiting montane areas of the Balkan Peninsula. Ten females caught in mid-June 2017 on Mt. Maljen (950 m a.s.l.) in western Serbia were monitored and examined in the lab, as well as their eggs and hatchlings. We additionally examined the state and number of oocytes in 31 females from scientific collections. Mean clutch size is quite high (8.0 ± 0.4 eggs) in relation to small mean snout-vent length of gravid females (74 ± 1 mm), mean relative clutch mass is relatively low (0.37 ± 0.02), and egg incubation period (51 ± 1 days at $24-26$ °C) is rather long for *L. agilis*. While mean values of the above traits are within the variation range found across conspecific populations studied thus far, mean values for egg size (mass, 0.42 ± 0.02 g; length, 11.8 ± 0.2 mm; width, 7.7 ± 0.1 mm) and hatchling size (mass, 0.47 ± 0.03 g; SVL, 25.0 ± 0.5 mm; tail length, 30.4 ± 1.6 mm) are clearly smaller than in all previously studied populations of this species.

Keywords: Clutch size - egg size - hatchling size - life-history - lacertid lizard - female reproductive output - Balkan Peninsula.

INTRODUCTION

The quantity and quality of the offspring a female produces determine her evolutionary fitness and ultimately the viability of the population. Therefore, offspring body size, offspring number, and other characteristics of female reproductive output are primary targets of evolutionary and ecological studies (Roff, 2002). Lizards exhibit a pronounced variation in reproductive traits within and among species, and they belong to model groups for studying the evolution of life-histories (Vitt & Pianka, 1994; Bauwens & Díaz-Uriarte, 1997; Shine, 2005).

The sand lizard (*Lacerta agilis* Linnaeus, 1758), which occupies a large part of temperate Eurasia and includes several morphologically (Bischoff, 1984, 1988) and genetically (Kalyabina-Hauf & Ananjeva, 2004; Joger *et al.*, 2007; Andres *et al.*, 2014) distinct lineages (subspecies), exhibits pronounced variation in reproductive traits among individual females and

over years within populations (Olsson & Shine, 1996, 1997a, b; Olsson & Madsen, 2001; Olsson *et al.*, 2018; Shine *et al.*, 2018), as well as between geographically distinct subspecies (Roitberg *et al.*, 2015). Yet, the available reproductive data for *L. agilis* are still far from appropriate covering the major geographic areas and taxonomical units, especially for relative clutch mass and offspring size (Roitberg *et al.*, 2015). For instance, for a large portion of the species range from the Pyrenees to western parts of Russia inhabited by *L. a. agilis* (sensu lato), *L. a. bosnica* (Schreiber, 1912) and *L. a. chersonensis* (Andrzejowski, 1832) (see fig. 1 in Roitberg *et al.*, 2015 for geographic ranges of the widely recognized subspecies), data on these traits are only available for South Sweden (Olsson & Shine, 1997a; Olsson & Madsen, 2001) and Middle Europe (Rykena, 1988a), the latter region being represented by a small compound sample. Specifically, for *L. a. bosnica*, a distinct lineage restricted to higher elevations in montane areas of the Balkan Peninsula (Bischoff, 1984,

1988; Andres *et al.*, 2014), any reproductive data are lacking. The reproductive life-history of this potentially endangered form (e.g. Sterijovski & Arsovski, 2019), which occupies the southern limits of the species range (Korsós & Bischoff, 1997), is important from a nature protection perspective. Furthermore, data on this lineage could help to disentangle the effects of ancestry and those of environmental and spatial factors in range-wide comparative studies on *L. agilis* (Roitberg, 2007; Roitberg *et al.*, 2015). This is because *L. a. bosnica* is geographically adjacent to the western subspecies group (*L. a. agilis* sensu lato and *L. a. chersonensis*), while being phylogenetically closer to the eastern subspecies group (*L. a. exigua* Eichwald, 1831, sensu lato) (Kalyabina-Hauf & Ananjeva, 2004; Joger *et al.*, 2007; Andres *et al.*, 2014).

Here we present the first data on female reproductive traits of *L. a. bosnica* obtained via monitoring field-caught females and their eggs in the lab and via inspecting the reproductive state of preserved specimens from scientific collections. The main site was Mt. Maljen (44°06'N, 19°59'E; ca. 950 m a. s. l.) located on the Divčibare plateau in western Serbia (Fig. 1). This area has a humid temperate continental climate influenced by the proximity of higher mountains (Popović & Obratov-Petković, 2005). Sand lizards inhabit meadows (*Poa molinieri* - *Plantaginietum holostei* association) surrounded by pine forest (*Pinetum nigrae* – *P. sylvestris* association).

MATERIAL AND METHODS

Our data consist of two parts. A full set of female reproductive traits, including clutch mass and several aspects of egg and hatchling size, was studied in individuals coming from the West Serbian site Mt. Maljen (see above). Ten females at advanced stages of pregnancy caught between 8-15 June 2017 were transported to the Institute for Biological Research “Siniša Stanković” in Belgrade and housed individually in terraria (50 × 30 × 30 cm) with a substrate of sand, with pieces of bark, moss and leaf litter serving as shelters. The terraria were exposed to natural and additional artificial light that created a thermal gradient of ca. 18-40 °C from 7 a.m. to 7 p.m. Food (mealworms and maggots) and water were provided *ad libitum*. The females were inspected daily. Following oviposition, they were measured for snout-vent length (SVL) and weighed. Within 12 hours after oviposition, eggs were dug up, weighed, and measured for maximum length and width.

The eggs were marked and placed in plastic boxes filled with moistened vermiculite (volume ratio of vermiculite to water was 10:1). The eggs were checked daily to verify their viability. The moisture of the substrate was also checked daily and, if necessary, distilled water was added to compensate for water absorbed by the eggs and for losses due to evaporation. Room temperature was kept

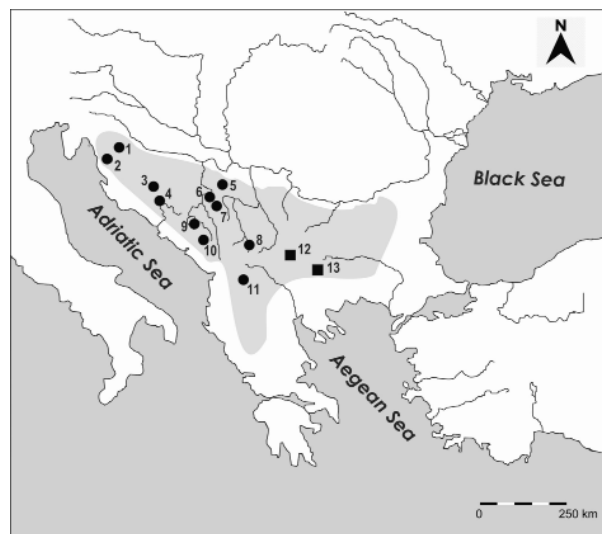


Fig. 1. Geographic range of *Lacerta agilis bosnica* (after Bischoff, 1988) and our study samples belonging to Dinaric (circles) and Balkan-Rhodope (squares) mountain systems. Numbers correspond to those in Appendix.

within 24-26 °C during the incubation period. Hatchlings were weighed and measured for SVL and total length within 12 hours after their emergence. The incubation time was defined as the number of days elapsed from egg-laying to hatchling emergence.

The second part of our data comes from recording the reproductive status and the number of oocytes in 31 gravid females of *L. a. bosnica* collected in different localities and deposited in zoological collections (see Fig. 1 and Appendix). By relating the oocyte stages (enlarged vitellogenic follicles, oviductal eggs) and internal marks of recent oviposition (widened oviducts and *corpora lutea*) to the capture dates we could roughly estimate the timing of consecutive events of the female reproductive cycle, i.e. the reproductive phenology. Specifically, a simultaneous occurrence of vitellogenic follicles and oviductal eggs or *corpora lutea* would argue for the occurrence of multiple clutches. For assessing reproductive phenology only specimens with precise collection dates were used. Considering that means of clutch size computed for different oocyte stages (enlarged follicles vs. oviductal eggs vs. laid eggs) did not differ significantly in *L. agilis* (Amat *et al.*, 2000; Roitberg *et al.*, 2015), counting enlarged follicles or oviductal eggs provided additional data on the clutch size - female size relationship. Linear measurements were taken with a digital caliper (0.01 mm precision), while mass was measured with an electronic balance (accuracy 0.001 g). Descriptive statistics (range, mean ± standard error, standard deviation) were calculated for original data. To avoid the problem of statistical non-independence of data collected from siblings, we used the mean value

for each clutch as the observation unit for egg and hatchling traits (e.g. Olsson & Shine, 1997a; Olsson & Madsen, 2001; Li *et al.*, 2013; Roitberg *et al.*, 2015). However, considering each hatchling as an independent observation did not significantly bias the results (Sorci & Clobert, 1999; Roitberg *et al.*, 2013, 2015). Hence, when comparing our data with those from other *L. agilis* populations (see Discussion) we considered studies derived with both approaches. The slope of the clutch size - female size relationship was estimated using the reduced major axis regression (see Roitberg *et al.*, 2015 for details and references). For other statistical analyses, all variables were log-transformed to approach data normality and homogeneity of variances (Sokal & Rohlf, 1981). Specifically, using general linear models (GLMs), we tested whether clutch size, maternal SVL, and their relationship differ between the following samples: I, living females from Mt. Maljen; II, preserved females from other sites in the Dinaric mountain system; III, preserved females from the Balkan-Rhodope mountain system (see Fig. 1 for geographic affinities of the three samples). All computations were done in the Statistica 10.0 for Windows package (StatSoft, Tulsa, OK, USA).

RESULTS

Seasonal variation in the reproductive stage in autopsied females from zoological collections with precise collection dates and those monitored in laboratory conditions is summarized in Fig. 2. Females with enlarged vitellogenic follicles were recorded from the second half of April to the first half of May. Capture dates of females with oviductal eggs ranged from the second half of May to the end of June. Oviposition in laboratory conditions took place in the second half of June. None of the examined females exhibited a simultaneous presence of enlarged vitellogenic follicles and oviductal eggs or *corpora lutea*; no other evidence for iteroparity was found.

Neither mean clutch size, nor mean maternal SVL differed significantly among the three study samples (Mt. Maljen females, other Dinaric females, Balkan-Rhodope females): ANOVA: $F_{2,38} = 0.86$, $p = 0.43$ and $F_{2,38} = 0.56$, $p = 0.58$ for clutch size and maternal SVL, respectively. GLM with clutch size as the response variable and maternal SVL as the covariate also exhibited no significant effect of the sample identity both in a separate slope model (Sample, $F_{2,35} = 0.12$, $p = 0.89$; Sample \times Maternal SVL, $F_{2,35} = 0.10$, $p = 0.91$; Maternal SVL, $F_{1,35} = 28.44$, $p < 0.001$) and in ANCOVA (Sample,

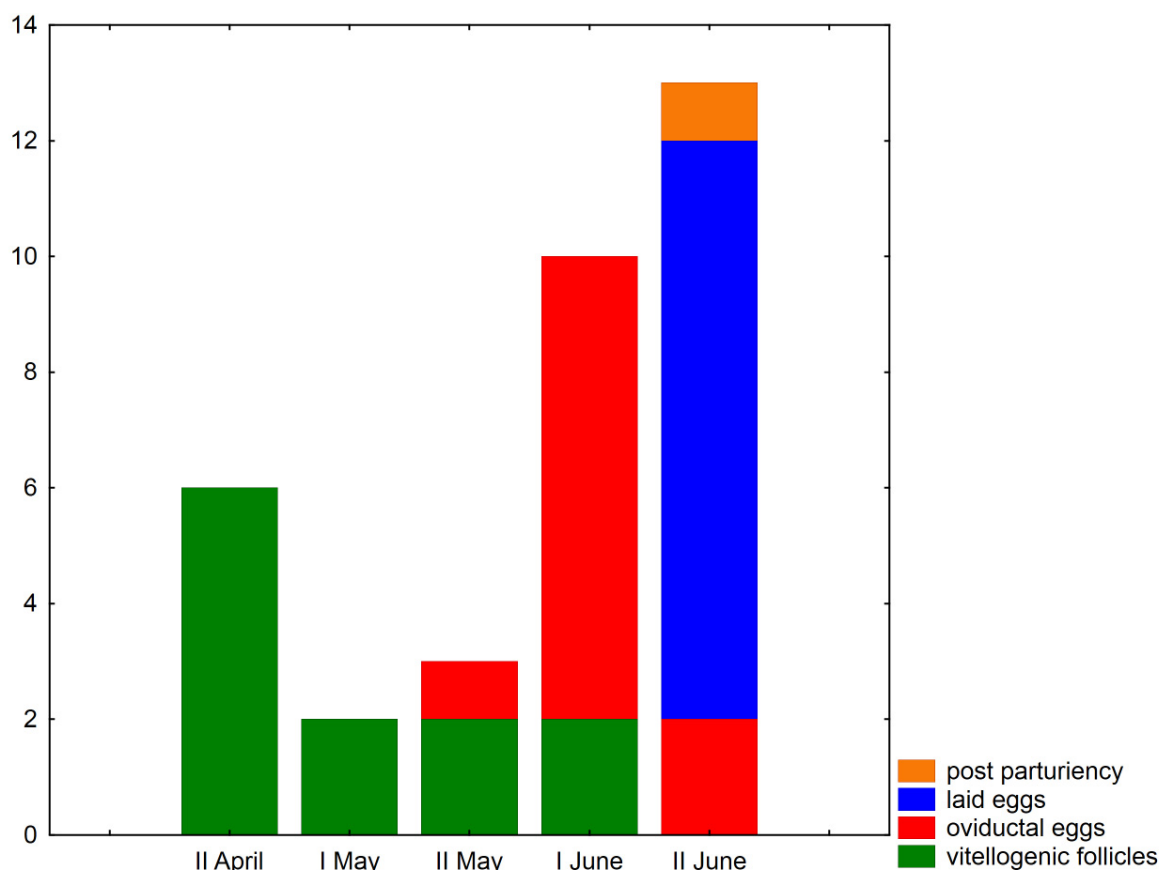


Fig. 2. Number of *L. a. bosnica* adult females in different reproductive stages during three months, presented for half-month periods.

$F_{2,37} = 0.76$, $p = 0.48$; Maternal SVL, $F_{1,37} = 48.45$, $p < 0.001$). Therefore, RMA regression slope of clutch size on maternal SVL and Pearson correlation coefficient (r) between the two traits were computed for the pooled sample: slope, 0.38 ± 0.04 ; correlation, 0.76 ± 0.10 ; $n = 41$. Fig. 3 visualizes the results presented above.

Table 1 describes the variation of 12 reproductive traits studied in ten living females from Mt. Maljen. While SVL of the post-oviposition females from Mt. Maljen is less variable than SVL of females which carry oviductal eggs or enlarged follicles and come from diverse localities (70–81 vs. 63–84 mm), the mean values of the two samples are very similar (75.2 vs. 74.2 mm). The clutch size of the Mt. Maljen females studied in the lab was similar to that in the sample from collections for both the ranges (5–12 vs. 4–12) and the means (7.8 vs. 8.0). Thus, as regards the clutch size and maternal SVL central tendencies, the ten females studied for a full set of traits are well representative for the whole study sample.

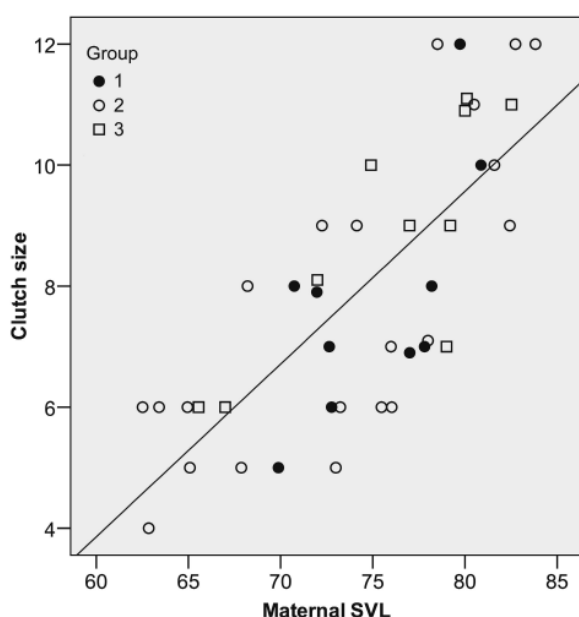


Fig. 3. Clutch size and maternal SVL for 41 studied females of *Lacerta agilis bosnica*. Regression line is shown for the pooled sample only, because no differences in the clutch size – maternal SVL relationship between the three groups were found (see text for details). Groups: 1, living females from Mt. Maljen; 2, preserved females from the Dinaric mountain system; 3, preserved females from the Balkan-Rhodope mountain system (see Fig. 1 for geographic affinities of the three samples).

DISCUSSION

Data on reproducing females collected at different dates (Fig. 2) show that each oocyte stage (enlarged follicles, oviductal eggs or *corpora lutea*) is associated with a moderate range of capture dates (five weeks or less).

This pattern, and particularly the lack of simultaneous presence of different oocyte stages in individual females, argue that female *L. a. bosnica* apparently lay a single clutch annually, oviposition likely occurring from early June to early July.

Mean clutch size is quite high in relation to small mean SVL of gravid females (Kidov *et al.*, 2012, 2014; Kidov & Kovrina, 2015; Kidov & Matushkina, 2017; Roitberg *et al.*, 2015 and references therein), mean RCM is relatively low (Roitberg *et al.*, 2015 and references therein), and egg incubation period is rather long for *L. agilis* (Li *et al.*, 2013; Rykena, 1988b and references therein; Warnecke, 2000; Sobocinski & Mašlak, unpubl. data).

While mean values of the above traits are within the variation range found across conspecific populations studied thus far, mean values for egg and hatchling size are smaller than in all previously studied populations of this species. So in *L. a. agilis* sensu lato, the lineage exhibiting the smallest egg and offspring size (Roitberg *et al.*, 2015), mean egg mass ranged from 0.56 to 0.60 g (Amat *et al.*, 2000; Rykena, 1988a; Olsson & Madsen, 2001), mean hatchling mass from 0.57 to 0.59 g (Rykena, 1988a; Olsson & Shine, 1997b; Olsson & Madsen, 2001), mean hatchling SVL from 28.3 to 30.7 mm (Rykena, 1988a; Langford, 1985; Barus & Oliva, 1992). Bosch & Bout (1998) reported a mean hatchling SVL of 24.6 mm which is slightly lower than in our study. However, this value might well be wrong, since the corresponding means for egg mass, hatchling mass, and tail length (respectively, 0.66 g, 0.70 g, 41.5 mm; Bosch & Bout, 1998) are much larger than in our *L. a. bosnica* sample. Recently Georgieva & Vergilov (2020) reported a mean hatchling mass of 0.49 g (*L. a. chersonensis*, Western Bulgaria) which is only slightly larger than in our study. Yet, their report is based on a single clutch; moreover, the mean SVL of this clutch (30.3 mm) was markedly higher than all clutch means of the Mt. Maljen sample (Table 1). A deviation in any particular trait, especially linear measurements, can be caused by inter-observer bias (Roitberg *et al.*, 2011 and references therein) and other systematic differences which might exist among studies (e.g. they might differ in mean time between oviposition and measuring eggs). However, small egg and hatchling size in our study sample can hardly be solely explained by such biases considering that six different traits show lower mean (and minimum) values than those in all previously studied populations, which range from the Pyrenees to Siberia and China and represent three distinct lineages (*L. a. agilis* sensu lato, *L. a. exigua* sensu lato, and *L. a. boemica* Suchow, 1929). Taking into account that our egg and hatchling size data come from ten females collected during eight days of a single year within a small area of 100 ha, statistical distributions of the studied traits (except clutch size and SVL of gravid females which we obtained from a larger and more diversified sample) might have been impacted by a local or temporal fluctuation. Yet, the small offspring size in our study

Table 1: Variation of female reproductive traits in *Lacerta agilis bosnica* from Mt. Maljen, Serbia.

Trait	N	range	mean \pm SE	SD
Female SVL (mm)	10	69.88 – 80.87	75.16 \pm 1.26	3.87
Clutch size	10	5 – 12	7.8 \pm 0.63	1.99
Post-oviposition female body mass (PM, g)	10	6.990 – 12.393	8.778 \pm 0.523	1.655
Clutch mass (CM, g)	10	2.003 – 5.591	3.279 \pm 0.321	1.014
Relative clutch mass (RCM = CM/PM)	10	0.287 – 0.451	0.369 \pm 0.019	0.059
Egg mass (g)	10	0.354 – 0.499	0.418 \pm 0.015	0.047
Egg length (mm)	10	10.60 – 13.10	11.75 \pm 0.22	0.70
Egg width (mm)	10	7.19 – 8.34	7.67 \pm 0.12	0.37
Hatchling SVL (mm)	9	22.23 – 27.13	25.01 \pm 0.48	1.44
Hatchling tail length (mm)	9	20.03 – 36.34	30.43 \pm 1.59	4.80
Hatchling mass (g)	9	0.298 – 0.608	0.473 \pm 0.029	0.086
Incubation duration (days)	9	48 – 53	50.81 \pm 0.51	1.53
Duration in captivity prior to oviposition (days)	10	7-16	11.00 \pm 0.94	2.98

sample is unlikely to be solely a fluctuation of this kind. In a *L. a. agilis* population (Asketunnan, South Sweden), which was studied over 20 years, mean hatchling mass was recorded in 561 clutches of 353 individual females (Ljungström *et al.*, 2016), thus providing exceptionally reliable estimates of the variation range. The minimum value of the mean hatchling mass in this huge sample was 0.42 g (Ljungström *et al.*, 2016), which is much higher than in our study (0.30 g – Table 1). Furthermore, neither the sampling year (2017) nor the previous one appeared to exhibit markedly deviating weather conditions in the Mt. Maljen study site. The time in captivity from capture to oviposition, a factor known to negatively affect egg and offspring size in squamates (King, 1993; Recknagel & Elmer, 2019; Roitberg & Eplanova, unpubl. data) was quite low (Table 1), and thus hardly influential, in our study.

Apart from low egg and hatchling size, the studied *L. a. bosnica* shows an unusual trait combination: higher clutch size relative to female size, as well as smaller egg and offspring size resemble it to the western lineage *L. a. agilis*. In contrast, lower relative clutch mass and longer egg incubation period found in the Mt. Maljen females are proper to the eastern forms *L. a. exigua* and *L. a. boemica* (Roitberg *et al.*, 2015 and references therein). To conclude, the presented data argue for a distinct reproductive strategy in *L. a. bosnica*, but further life-history studies, preferably involving multiple localities with contrasting environments, will show to what extent the revealed reproductive pattern reflects some stable characteristics of a distinct life-history strategy in this interesting but understudied lineage.

ACKNOWLEDGEMENTS

We are grateful to the curators and staff of several museums (Appendix 1) for access to the collections and

permission to dissect gravid females. We would like to acknowledge the constructive improvements suggested by an anonymous reviewer. Living lizards were collected under permits by the Ministry of Agriculture and Environmental Protection, Republic of Serbia (no. 353-01-55412017-17). Laboratory work was approved by the Ethical Committee of the Institute for Biological Research “Siniša Stanković” (no. 02-06/17). This study was supported by the Ministry of Education, Science and Technological Development of the Republic of Serbia (Contract No. 451-03-9/2021-14/200007). ESR was financed by the German Research Foundation (grant RO 4168/1–3).

REFERENCES

- Amat F., Llorente G.A., Carretero M.A. 2000. Reproductive cycle of the sand lizard (*Lacerta agilis*) in its southwestern range. *Amphibia-Reptilia* 21: 463-476.
- Andres C., Franke F., Bleidorn C., Bernhard D., Schlegel M. 2014. Phylogenetic analysis of the *Lacerta agilis* subspecies complex. *Systematics and Biodiversity* 12: 43-54.
- Andrzejowski A. 1832. Reptilia inprimis Volhyniae. Podoliae, et Gubernii Chersonensis. *Nouveaux Mémoires de la Société Impériale des Naturalistes de Moscou*, 2: 320-346.
- Barus B., Oliva O. 1992. Plazi-Reptilia. *Academia, Prague*, 224 pp.
- Bauwens D., Diaz-Uriarte R. 1997. Covariation of life-history traits in lacertid lizards: a comparative study. *The American Naturalist* 149: 91-111.
- Bischoff W. 1984. *Lacerta agilis* Linnaeus 1758 - Zauneidechse (pp. 23-68). In: Böhme W. (ed). *Handbuch der Reptilien und Amphibien Europas*, Band 2/1, Echsen II, *Aula-Verlag, Wiesbaden*, 416 pp.
- Bischoff W. 1988. Zur Verbreitung und Systematik der Zauneidechse, *Lacerta agilis* Linnaeus, 1758. *Mertensiella* 1: 11-30.
- Bosch In den H.A.J., Bout R.G. 1998. Relationships between maternal size, egg size, clutch size, and hatchling size in

- European lacertid lizards. *Journal of Herpetology* 32: 410-417.
- Eichwald E. 1831. Zoologia specialis quam expositis animalibus tum vivis, tum fossilibus potissimum Rossiae in universum, et Poloniae in specie, in usum lectionum publicarum in Universitate Caesarea Vlnensi. Pars posterior. *Zawadzki, Vilnae*, 404 pp.
- Georgieva S., Vergilov V. 2020. Notes on some biometrical data on hatchlings of *Lacerta agilis* (L.) (Squamata: Lacertidae) in Western Bulgaria. *North-Western Journal of Zoology* 16: 246-247.
- Joger U., Fritz U., Guicking D., Kalyabina-Hauf S., Nagy Z.T., Wink M. 2007. Phylogeography of western Palaearctic reptiles - spatial and temporal speciation patterns. *Zoologischer Anzeiger* 246: 293-313.
- Kalyabina-Hauf S.A., Ananjeva N.B. 2004. Phylogeography and intraspecific structure of wide distributed sand lizard, *Lacerta agilis* L., 1758 (Lacertidae, Sauria, Reptilia). *Proceedings of Zoological Institute in St Petersburg* 302: 1-108.
- Kidov A.A., Kovrina Ye.G. 2015. Reproduction of the Boehme lizard, *Lacerta boemica* Suchow, 1929 on the western periphery of the range. *Vestnik of Buryat State University* 84: 67-74.
- Kidov A.A., Matushkina K.A. 2017. Reproduction of the sand lizard (*Lacerta agilis* L.) in the Stavropol upland. *Izvestiya Timiryazevskoy Sel'skhozvaystvennoy Akademii* 4: 81-89.
- Kidov A.A., Timoshina A.L., Kovrina Ye.G., Matushkina K.A., Pyhov S.G. 2012. Reproductive characteristics of eastern sand lizard (*Lacerta agilis exigua* Eichwald, 1831) (Reptilia, Squamata, Sauria: Lacertidae) in Kuma-Manich depression. *Natural and Technical Sciences* 1: 81-83.
- Kidov A.A., Timoshina A.L., Khairutdinov I.Z., Kovrina E.G., Matushkina K.A. 2014. Age, growth and reproduction of the Bohme's lizard, *Lacerta agilis boemica* Suchow, 1929 (Reptilia: Lacertilia: Lacertidae) in the foothills of North Ossetia. *Vestnik of Buryat State University* 4: 49-52.
- King R.B. 1993. Determinants of offspring number and size in the brown snake, *Storeria dekayi*. *Journal of Herpetology* 27: 175-185.
- Korsós Z., Bischoff W. 1997. *Lacerta agilis* Linnaeus, 1758 (pp. 230-231). In: Gasc J.P., Cabela A., Crnobrnja-Isailović J., Dolmen D., Grossenbacher K., Haffner P., Lescure J., Martens H., Martínez-Rica J.P., Maurin H., Oliviera M.E., Sofianidou T.S., Veith M., Zuiderwijk A. (eds). *Atlas of Amphibians and Reptiles in Europe. Societas Europaea Herpetologica and Museum National d'Histoire Naturelle, Paris*, 495 pp.
- Langford M. 1985. Husbandry and captive breeding of the sand lizard (*L. agilis*) as an adjunct to habitat management in the conservation of the species in Britain. *British Herpetological Society Bulletin* 13: 28-36.
- Li H., Zhou Z.S., Ding G.H., Ji X. 2013. Fluctuations in incubation temperature affect incubation duration but not morphology, locomotion and growth of hatchlings in the sand lizard *Lacerta agilis* (Lacertidae). *Acta Zoologica* 94: 11-18.
- Linnaeus C. 1758. Systema Naturae per regna tria naturae, secundum classis, ordines, genera, species cum characteribus, differentiis, synonymis, locis. 10th ed. Vol. 1. *Laurentii Salvii, Stockholm*, 824 pp.
- Ljungström G., Stjernstedt M., Wapstra E., Olsson M. 2016. Selection and constraints on offspring size-number trade-offs in sand lizards (*Lacerta agilis*). *Journal of Evolutionary Biology* 29: 979-990.
- Olsson M., Madsen T. 2001. Between-year variation in determinants of offspring survival in the sand lizard, *Lacerta agilis*. *Functional Ecology* 15: 443-450.
- Olsson M., Shine R. 1996. Does reproductive success increase with age or with size? - A case study using sand lizards (*Lacerta agilis*). *Oecologia* 105: 175-178.
- Olsson M., Shine R. 1997a. The seasonal timing of oviposition in sand lizards (*Lacerta agilis*): why early clutches are better. *Journal of Evolutionary Biology* 10: 369-381.
- Olsson M., Shine R. 1997b. The limits to reproductive output: offspring size versus number in the sand lizard (*Lacerta agilis*). *The American Naturalist* 149: 179-188.
- Olsson M., Loeb L., Lindsay W., Wapstra E., Fitzpatrick L., Shine R. 2018. Extreme plasticity in reproductive biology of an oviparous lizard. *Ecology and Evolution* 8: 6384-6389.
- Popović I., Obratov-Petković D. 2005. Phyto-geographycal analysis of Divčibare. *Glasnik šumarskog fakulteta* 91: 193-206.
- Recknagel H., Elmer K.R. 2019. Differential reproductive investment in co-occurring oviparous and viviparous common lizards (*Zootoca vivipara*) and implications for life-history trade-offs with viviparity. *Oecologia* 190: 85-98.
- Roff D.A. 2002. Life History Evolution. *Sinauer Associates, Sunderland*, 527 pp.
- Roitberg E.S. 2007. Variation in sexual size dimorphism within a widespread lizard species (pp. 143-217). In: Fairbairn D.G., Blanckenhorn W.U., Székely T. (eds). *Sex, Size, and Gender Roles: Evolutionary Studies of Sexual Size Dimorphism. Oxford University Press, New York*, 280 pp.
- Roitberg E.S., Orlova V.F., Kuranova V.N., Bulakhova N.A., Zinenko O.I., Ljubisavljevic K., Shamgunova R.R., Carretero M.A., Clasen A., Fokt M., Böhme W. 2011. Inter-observer and intra-observer differences in measuring body length: a test in the common lizard, *Zootoca vivipara*. *Amphibia-Reptilia* 32: 477-484.
- Roitberg E.S., Kuranova V.N., Bulakhova N.A., Orlova V.F., Eplanova G.V., Zinenko O.I., Shamgunova R.R., Hofmann S., Yakovlev V.A. 2013. Variation of reproductive traits and female body size in the most widely-ranging reptile species: testing the effects of reproductive mode, lineage, and climate. *Evolutionary Biology* 40: 420-438.
- Roitberg E.S., Eplanova G.V., Kotenko T.I., Amat F., Carretero M.A., Kuranova V.N., Bulakhova N.A., Zinenko O.I., Yakovlev V.A. 2015. Geographic variation of life-history traits in the sand lizard, *Lacerta agilis*: testing Darwin's fecundity-advantage hypothesis. *Journal of Evolutionary Biology* 28: 613-629.
- Rykena S. 1988a. Ei- und Gelegemaße bei *Lacerta agilis*: ein Beispiel für innerartliche Variabilität von Fortpflanzungsparametern. *Mertensiella* 1: 75-83.
- Rykena S. 1988b. Innerartliche Differenzen bei der Eizeitigungsdauer von *Lacerta agilis*. *Mertensiella* 1: 41-53.
- Schreiber E. 1912. Herpetologia Europea. Eine systematische Bearbeitung der Amphibien und Reptilien welche bisher in Europa aufgefunden sind. *Verlag Gustav Fischer, Jena*, 960 pp.
- Shine R. 2005. Life-history evolution in reptiles. *Annual Review of Ecology, Evolution and Systematics* 36: 23-46.

- Shine R., Wapstra E., Olsson M. 2018. Seasonal shifts along the oviparity–viviparity continuum in a cold-climate lizard population. *Journal of Evolutionary Biology* 31: 4-13.
- Sterijovski B., Arsovski D. 2019. Sand lizard (*Lacerta agilis*). In: The National Red list of North Macedonia. Ministry of Environment and Physical Planning. Republic of North Macedonia. [<http://redlist.moepp.gov.mk/sand-lizard/>]
- Sokal R.R., Rohlf F.J. 1981. Biometry. *Freeman, San Francisco*, 859 pp.
- Sorci G., Clobert J. 1999. Natural selection on hatchling body size and mass in two environments in the common lizard (*Lacerta vivipara*). *Evolutionary Ecology Research* 1: 303-316.
- Suchow G.F. 1929. Description of a new species of lizards from the environs of Vladicaucasus (*Lacerta boemica* sp.nov.). *Académie des Sciences de l'Ukraine Mémoires de la Classe des Sciences Physiques et Mathématiques* 13 (1): 117-119.
- Vitt L.J., Pianka E.R. 1994. Lizard Ecology: Historical and experimental perspectives. *Princeton University Press, Princeton*, 403 pp.
- Warnecke R. 2000. Auswertung erster Nachzuchtergebnisse von *Lacerta agilis boemica* Suchow, 1929 im Vergleich zu anderen Unterarten der Zauneidechse. *Die Eidechse* 11: 28-38.

APPENDIX 1

Localities of population samples, including geographical coordinates, altitude, sample size and zoological collection. IBISS – Institute for Biological Research, Belgrade, Serbia; MTD - Senckenberg Natural History Collections Dresden, Germany; ZFMK - Zoological Research Museum A. Koenig Bonn, Germany; ZSM - Zoological State Collections Munich, Germany. 1. Croatia, Mt. Mala Kapela, Plitvička lakes (44.8696°N, 15.6280°E, 675 m, 2, IBISS); 2. Croatia, Mt. Velebit hinterland, Bužim village (44.5755°N, 15.2524°E, 562 m, 1, IBISS); 3. Bosnia & Herzegovina, Mt. Cincar, Gornja Malovan village (43.9277°N, 17.2003°E, 1140 m, 1, IBISS); 4. Bosnia & Herzegovina, Mt. Čvrsnica, Lake Blidinje (43.6179°N, 17.4702°E, 1205 m, 1, IBISS); 5. Serbia, Mt. Maljen, Divčibare plateau (44.1085°N, 19.9889°E, 950 m, 1, IBISS); 6. Serbia, Mt. Tara, Golubovac and Karaiča bare (43.8884°N, 19.4491°E, 1245m, 3, IBISS); 7. Serbia, Mt. Zlatibor (43.7175°N, 19.7062°E, 1007 m, 7, IBISS); 8. Serbia, Mt. Kopaonik, Trepča (42.9423°N, 20.9221°E, 840 m, 1, IBISS); 9. Montenegro, Mt. Durmitor (43.1564°N, 19.1136°E, 1417 m, 1, IBISS); 10. Montenegro, Mt. Prekornica, Srednja Ponikvica (42.6739°N, 19.2671°E, 1400 m, 1, IBISS); 11. North Macedonia, Mt. Bistra, Galičnik (41.6269°N, 20.6854°E, 1600 m, 1, IBISS) and Mt. Dešat, Lake Lokuvsko (41.6352° N, 20.5604°E, 1582 m, 1, IBISS); 12. Serbia, Mt. Dukat, Karamanica (42.3537°N, 22.3155°E, 1417 m, 2, IBISS); 13. Bulgaria, Mt. Pirin, (Pirin s.l. 5, ZFMK; Banderija, Khomutivskiyi Step, 41.7779°N, 23.4370°E, 1650 m, 1, ZSM; Begovitza Chalet, 41.6739°N, 23.4274°E, 2000-2200 m, 2, MTD).