Age and Sex-related Differences Determine Microhabitat Use in *Lacerta agilis bosnica* Schreiber, 1912 (Reptilia: Lacertidae) in Western Bulgaria

Steliyana Popova[1], Emiliya Vacheva[2], Diana Zlatanova[1] & Nikolay Tzankov[2]†

[1] Faculty of Biology, Sofia University "St. Kliment Ohridski", 8 Dragan Tsankov Blvd., 1164 Sofia, Bulgaria
[2] National Museum of Natural History, Bulgarian Academy of Sciences, 1 Tsar Osvoboditel Blvd., 1000 Sofia, Bulgaria

Abstract: Habitat selection is an important mechanism for alleviation and reduction of inter- and intraspecific competition in lizards. We examined the poorly studied Balkan subspecies of the sand lizard – *Lacerta agilis bosnica*, as a target taxon to define the importance of grass height and density, which are key microhabitat features that shape sand lizard's distribution. The study was conducted in three mountains in western Bulgaria during 2014–2019. A total of 350 (190 adults and 160 immatures) lizards were examined. We established a diverse microhabitat use in different age classes as well as some differences between sexes. Adult males were attached to the most suitable and secure microhabitats, those with higher vegetation, while adult females and both immature groups occupied less optimal microhabitats. The importance of vegetation height and density should be taken into account during planning and application of conservation measures for *L. agilis bosnica*.

Key words: Sauria, habitat structure, ontogenetic shifts, vegetation density, Balkans

Introduction

Spatial distribution of lizards, as ectotherms, is not uniform in the temperate climate zone. Geographic and climatic factors are the main variables that determine species distribution in Europe (GUISAN & HOFER 2003). Within species ranges, habitat quality additionally shapes habitat use (MÄRTENS et al. 1996), as resources are not equally distributed and all species strive to occupy the most suitable habitat to maximise their fitness and reproductive success (PILORGE 1987, PATERSON & BLOUIN-DEMERS 2018). A complex of factors influences habitat selection in lizards (HEATWOLE 1977). These factors could be a result of a structure-function relationship (ARNOLD 1998, VANHOOYDONCK & VAN DAMME 1999, KALIONTZOPOULOU et al. 2010, HERREL et al. 2001, TOYAMA 2017), or due to interspecific competition (EDWARDS & LAILVAUX 2013). They may also be associated with antipredator behaviour (VANHOOYDONCK & VAN DAMME 2002), with the necessity to reduce inter- and intraspecific competition (VANHOOYDONCK et al. 2000, DELANEY & WARNER 2017). Thus, species require structurally complex habitats, containing different patches for thermoregulation, foraging, avoiding predators and egg-laying. The habitat selection in the most diverse group of lizards in Europe, the lacertids (Lacertidae), is a focus of

---

*Corresponding author: steliyanski@gmail.com

many studies (e.g., Martín & Salvador 1995, Diego-Rassila & Pérez-Mellado 2003, Prieto-Ramirez et al. 2018).

The sand lizard, being the second most widespread lizard species (Bischoff 1984, Speybroeck et al. 2016), occupies a large variety of habitats from sand dunes on the sea level to meadows at high altitude (Corbett & Tamarind 1979, Bischoff 1984). Because of its wide distribution, the preferred habitats differ throughout its range, leading to numerous studies on habitat use (Corbett & Tamarind 1979, Stumpel 1988, Borczyk 2001, Nemes et al. 2006, Čeirāns 2007a, b, Ekner et al. 2008, Grozdanov et al. 2014, Heltai et al. 2015, Kirbiš 2015). Often, populations from periphery display higher specialisation and sensitiveness due to habitat changes and fragmentation (Henle et al. 2017). In addition, it must be noted that in the southern range of *L. agilis*, habitat differs from those in the northern populations (Amat et al. 2003). The most important microhabitat features that shape the sand lizard distribution are vegetation height and density (Glandt 1991, Török 1998, 2002).

At least nine subspecies of *Lacerta agilis* are known throughout its range (Andres et al. 2014). In Bulgaria, the species is represented with two subspecies: the lowland *L. agilis chersonensis* Andrzejowski, 1832 and *L. agilis bosnica* Schreiber, 1912, which occupies higher altitudes. The latter has a very limited distribution, restricted to the Balkan Peninsula only, and in Bulgaria it is known from isolated mountainous locations in the western part of the country (Stojanov et al. 2011).

Having in mind the low effort given to this exact subspecies, it is poorly studied. To our knowledge, no previous research on its habitat use has been done. The main aim of this study is to identify the microhabitat preferences of *L. a. bosnica*, in regards to age and sex differences.

Materials and Methods

The study sites were situated in three mountains in Western Bulgaria (Fig. 1) and their main characteristics were as follows: 1) Plana Mts.: a complex of meadows and open patches complemented with shrubs and small trees (approximate coordinates N42.473º, E23.405º, 1100-1150 m a.s.l.); 2) Vitosha Mts.: a wide meadow surrounded with beech forest (N42.627º, E 23.223º, 1200 m a.s.l.); 3) Osogovo Mts.: four meadows near to each other and surrounded with juniper shrubs and coniferous forest (N42.194º, E22.593º, 1600-1700 m a.s.l.). The field studies were conducted in the period 2014–2019 during the months from April to September but the individual visits were not equally distributed per months and sites (total 16 visits in Osogovo, 14 – in Plana, and 19 – in Vitosha).

Lizards were registered by a visual survey and captured for a closer evaluation, sexing and measuring (snout-vent length (SVL)). Two age classes were defined as follows: immatures – a combined group of juvenile and subadult lizards (SVL up to 55 mm) and adults – sexually mature lizards (SVL
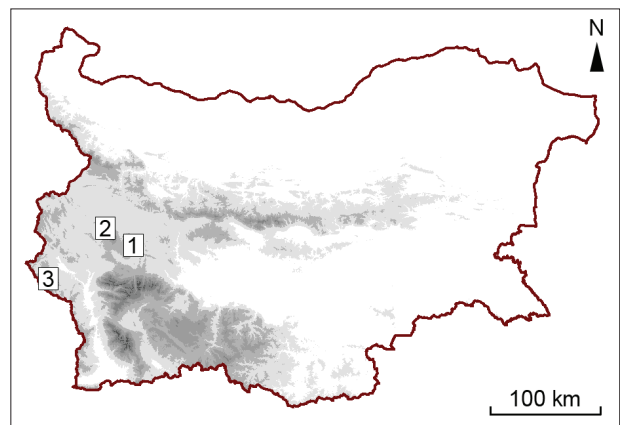
Fig. 1. Location of the studied sites: 1. Plana Mts; 2 Vitosha Mts.; 3. Osogovo Mts.

Table 1. Chi-square test results for the difference between the age-sex groups of *L. agilis bosnica* (Chi-square values, degrees of freedom number, and p-values).

	Plana		Vitosha		Osogovo	
	Chi-sq. (df)	p	Chi-sq. (df)	p	Chi-sq. (df)	p
M/F	6.287 (5)	0.2791	1.719 (5)	0.8864	6.754 (7)	0.4554
M/imM	7.311 (4)	0.1201	8.474 (6)	0.2054	7.504 (7)	0.3780
M/imF	12.739 (5)	0.0262*	9.095 (5)	0.1051	7.293 (7)	0.3991
F/imM	10.469 (6)	0.1064	12.252 (6)	0.0572	15.741 (6)	0.0151*
F/imF	10.943 (5)	0.0532	12.523 (5)	0.0284*	13.587 (6)	0.0350*
imM/imF	6.328 (5)	0.2764	6.612 (6)	0.3581	3.843 (4)	0.4282
ad/im	15.706 (6)	0.0154*	17.203 (6)	0.0093**	19.936 (7)	0.0064**
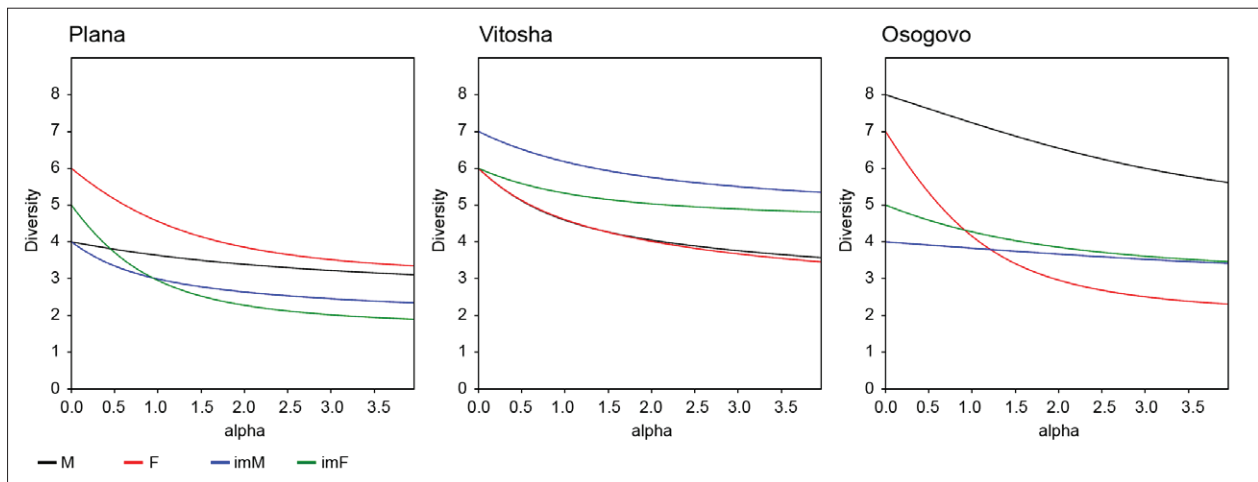
Fig. 2. Diversity profiles of the age-sex groups of *L. agilis bosnica*, according to the abundance in the individual microhabitat classes.

> 55 mm) (see Popova et al. 2019). The sex of the captured lizards was determined based on coloration pattern (green colored sides of the body in males vs. brown in females; a large count of black dots on the abdominal side of the body in males vs. absence or only very small count in females), number of ventral scales (larger in females), and size of the femoral pores (larger in males) (e.g. Darevsky et al. 1976, Majláth et al. 1997). Thus, four age-sex groups were defined: adult males (M), adult females (F), immature males (imM) and immature females (imF).

For each of the captured lizards, the grass height and density (at a radius of 5-6 m around the observation point) were categorised according to Grozdanov et al. (2014), i.e.: 1) Grass height: up to 20 cm (H1), 20–40 cm (H2), and 40–60 cm (H3); 2) Grass density: low (D1 – more than 90% of the soil surface visible), medium (D2 – respectively about 50%), dense (D3 – respectively about 10%), very dense (D4 – no soil visible). The categories of grass height and density were combined in aim to define specific microhabitat classes, appropriate for analysis (e.g. the combination "H1D4" means a patch, where the grass is low but very dense).

On the basis of the frequency of lizards in the separate microhabitat classes, the age-sex groups were compared through a Chi-square test. The diversity of microhabitats used by the separate age-sex groups was exposed by Rényi's diversity profiles. In addition, the Shannon diversity index was calculated, and it was tested for differences between age-sex groups by a permutation test (only for the pairs, in which no intersection of diversity profiles observed). The similarity between age-sex groups with respect to microhabitat choice was estimated

Table 2. Values of Shannon diversity index (H') of the age-sex groups and results (p-values) of the permutation test for differences between groups by H' (significant differences are marked with an asterisk).

		Plana	Vitosha	Osogovo
H'	M	1.29	1.52	1.98
	F	1.52	1.53	1.42
	imM	1.09	1.82	1.34
	imF	1.08	1.67	1.45
p	M/F	0.309	n/a	0.142
	M/imM	0.366	0.036*	0.025*
	M/imF	n/a	0.248	0.076
	F/imM	0.047*	0.047*	n/a
	F/imF	0.028*	0.269	n/a
	imM/imF	n/a	0.189	n/a

Table 3. Similarity (Morisita index) between the age-sex groups of *L. agilis bosnica*.

Plana	M	F	imM	imF
M	1	0.92	0.85	0.69
F	0.92	1	0.91	0.78
imM	0.85	0.91	1	0.94
imF	0.69	0.78	0.94	1
Vitosha	**M**	**F**	**imM**	**imF**
M	1	0.98	0.85	0.83
F	0.98	1	0.86	0.81
imM	0.85	0.86	1	0.87
imF	0.83	0.81	0.87	1
Osogovo	**M**	**F**	**imM**	**imF**
M	1	0.77	0.64	0.74
F	0.77	1	0.49	0.67
imM	0.64	0.49	1	0.78
imF	0.74	0.67	0.78	1

3

through Morisita index and the same index was used for the cluster analysis (through UPGMA algorithm). A Correspondence analysis was used to expose the ordination of age-sex groups and microhabitat classes. All statistical procedures were done using PAST 3.1 (Hammer et al. 2001) and STATISTICA 10 (StatSoft Inc. 2011).

Results

Collected data for the microhabitat choice relate to the total of 350 specimens of *L. agilis bosnica* (see Appendix 1). Chi-square test (Table 1) did not show statistically significant differences between sexes (neither in adults nor in immatures), because of that, the comparison of adults and immatures was performed also regardless of sex affiliations (the last row in Table 1). The differences between adults and immatures were statistically significant for each of the studied sites.

According to Rényi's profiles (Fig. 2), the diversity in microhabitat choice was highest in adult males in Osogovo, adult females in Plana, and immature males in Vitosha. Statistically significant differences by Shannon diversity index (Table 2) were observed between adult males and immature males (in Osogovo and Vitosha), between adult females and immature males in Plana and Vitosha, as well as between adult and immature females (in Plana).

The similarity between the age-sex groups in regard to the number of specimens, found in the separate microhabitat classes (Table 3), was high in most of the combinations. The highest similarity was observed between adult males and adult females (in Vitosha) and between immature males and immature females (in Plana and Osogovo). The cluster analysis (Fig. 3) showed a grouping of the adults and immatures in separate, relatively well-differentiated clusters, for each of the study sites.

The results from the Correspondence analysis (Fig. 4) were similar to those, obtained on the basis of similarity and diversity indices. In all cases, the first two axes explained more than 84% of the total dispersion. According to the values of the first axis, there was a clear differentiation between adults and immatures (for each study site), and according to the second axis – between the sexes, both for adults and immatures (in Plana), and only for adults (in Osogovo) or immatures (in Vitosha). Adult males could be associated with the patches, where the grass was most high and dense (especially in Osogovo and Plana), and adult females – with the patches, where the grass was dense or very dense, regardless of its height. In all cases, the immatures could be associated with the patches, covered by low, but dense or very dense grasses.

Discussion

When comparing the analysis results of the three surveyed territories, both similar and different trends in the choice of microhabitat were observed. The differences are hardly to be explained unambiguously: they can be dependent on the influence of site-specific environmental factors (e.g. altitude, microrelief, etc.), as well as on the subjective factors (e.g. insufficiency in sample sizes, and/or absence
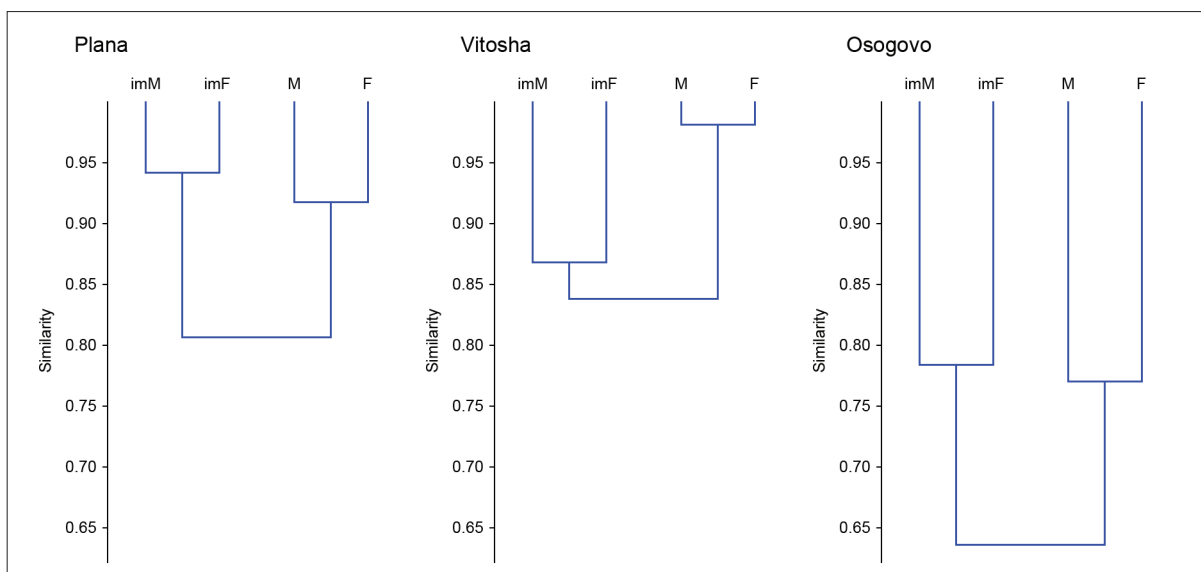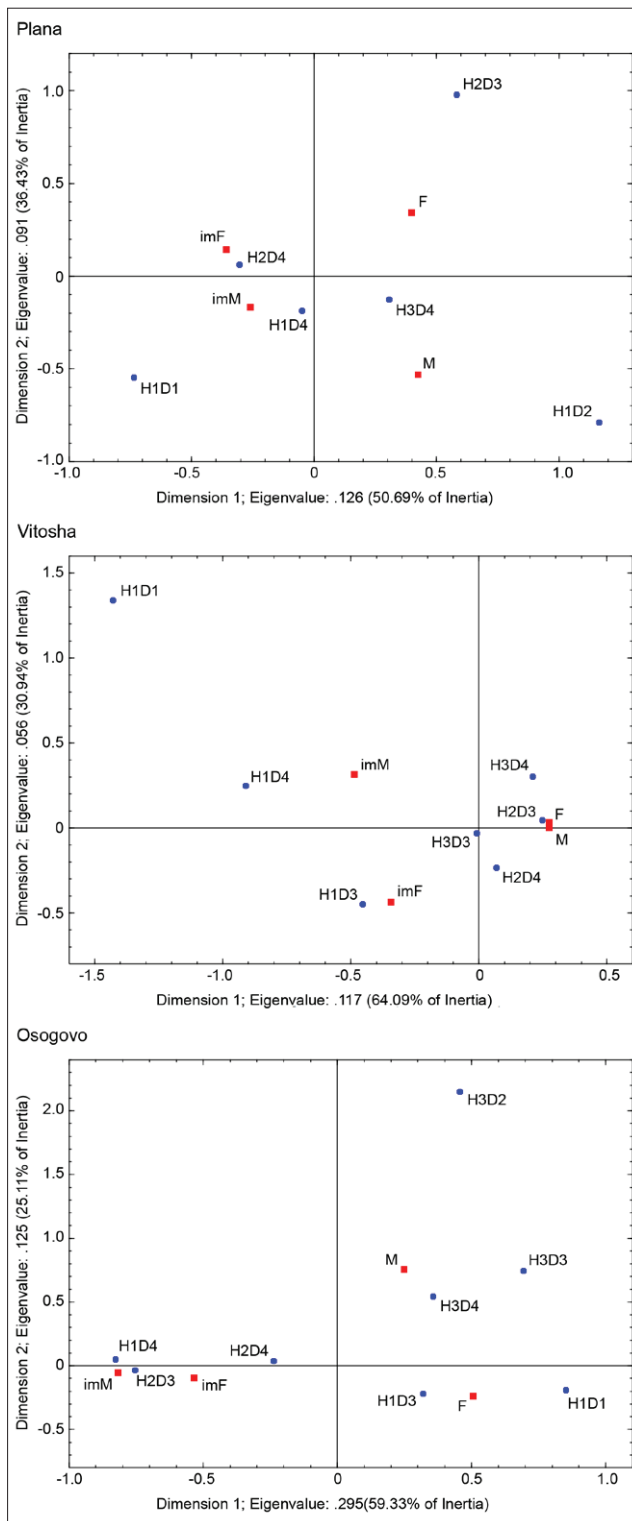

Fig. 3. Clustering of the age-sex groups of *L. agilis bosnica*, based on the Morisita index.

Fig. 4. Ordination (correspondence analysis) of the age-sex groups and microhabitat classes in the space, defined by the first two dimensions.

of uniformity in the time framework of the field researches).

In view of the results obtained, it can be argued that in the studied populations of *L. agilis bosnica*, there is a clear ontogenetic differentiation in microhabitat choice (corroborated by each of the used analytical methods for each of the three studied sites). Adults mostly choose high grass patches, and immatures – low grass patches. A similar tendency is observed also in the other subspecies (*L. agilis chersonensis*), which occurs in Bulgaria (see GROZDANOV et al. 2014). It should be taken into account, that the density of the grasses may impact the ability of the researcher to detect the immature lizards, but in our case this is unlikely, because all of the age groups of lizards were detected mainly by their movement and not by observation of immobile specimens. Data for the Sand lizard ecology in the neighbouring countries are very scarce, and only the study of NEMES et al. (2006) is comparable to our research. According to the cited authors, the microhabitat selection showed some segregation between the age groups with regard to ontogenetic shifts and age-related differences. These could be due to the morphological differences between adults and immatures (EKNER et al. 2008), their different thermal requirements in respect to size (PAULISSEN 1988, AMAT et al. 2003, MARTÍN & LÓPEZ 2003, HERCZEG et al. 2007), or competition avoidance of the adults from the juveniles (DELANEY & WARNER 2017). Age-related habitat selection is observed in many lizard species (CARRASCAL et al. 1990, NEMES et al. 2006, KOVÁCS & KISS 2016). Larger lizards have greater thermal inertia which makes them able to inhabit less exposed microhabitats than smaller conspecifics, which need more open habitats to ensure proper thermal regulation (PAULISSEN 1988). In contrast to adults, the immatures inhabit suboptimal habitats, due to competition avoidance of the more dominant adults or to avoid direct threat, as well as cannibalism, a trait well documented in *Lacerta* spp. (ANGELICI et al 1997, SAGONAS et al. 2018). Some authors state the negative influence of bushy patches to hatchlings (AMAT et al. 2003, NEMES et al. 2006, KOLANEK et al. 2019). These patches are usually occupied by adults which might result in possible cannibalism. Therefore in immatures, there is a prominent shift to the less suitable microhabitats as those with the lowest grass height were preferred by the immature females. Some studies on the northwesternmost populations, where the sand lizards prefer low-density cover of grass with bushes spread along patches of bare ground (CORBETT & TAMARIND 1979, GLANDT 1979, STRIJBOSCH 1986, WOUTERS et al. 2012, READING & JOFRÉ 2016) showed that sand and bare soil were the most preferred habitats for females and hatchlings in connection with egg lying. In our study patches with no grass or scarce grass cover could not be associated with any of age-sex

groups. The possible explanation, in this case, could be that those patches were not providing secure places to hide, as well the lack of artificial shelters in them, and lizards are driven to choose more secured nesting sites.

The difference between sexes in regard to microhabitat preferences in the studied populations of *L. agilis bosnica* was comparatively weakly expressed (supported only by the Correspondence analysis, moreover not for each of the used combinations). It seems that in *L. agilis chersonensis*, the difference between sexes is more clear, but supported also by Correspondence analysis only (see GROZDANOV et al. 2014). On the other hand, namely the multivariate analyses are considered to give more detailed picture about lizards habitat use and to be more sensitive than the classical "goodness of fit" tests (NEMES et al. 2006, GROZDANOV et al. 2014). Results from the present study suggest that the adult males, as a dominant group, often occupied the most suitable microhabitat patches (highest and densest grass cover), while the adult females were observed mainly in the patches where the grass cover was dense, but its height varied (i.e. suboptimal microhabitat); in immatures, the sex-related differences in microhabitat choice hardly to be expressed. To a large extent, that corresponds to the species ecological requirements for occupying the most appropriate and secured natural shelters, as stated by GLANDT (1991). Sex-related differences in the habitat use may be related to sexual dimorphism (BUTLER et al. 2000, MOLINA-BORJA et al. 2010, KALIONTZOPOULOU et al. 2015): males have longer bodies, tails, fore- and hind limbs, which has been observed in *L. a. bosnica* (see POPOVA et al. 2019), and that gives them greater opportunity in locomotion and sprint speed, thereby making them capable to inhabit sites with higher vegetation, shrubs etc. Behavioural differences could also shape the microhabitat occupancy: males have to explore and guard their territories (OLSSON 1986) or search for mates (OLSSON 1993). They often are exposed to higher predation risk (COOPER & VITT 2002), hence they have to choose those microhabitats that increase the probability to avoid predators, thus can provide them with greater success during the breeding season, or in our case, were those patches with higher vegetation. In contrast to males, adult females have different thermal necessities related to the nesting period (ANGILLETTA et al. 2009). Their microhabitat choice is most probably related to the reproduction and pregnancy: pregnancy affects locomotor performance (BAUWENS & THOEN 1981) and restricts climbing abilities, making females more vulnerable

toward predators (BRODIE 1989, SCHWARZKOPF & SHINE 1992, DOWNES & BAUWENS 2002). Therefore females have to choose more cryptic microhabitats, thus the dense vegetation gives them a better opportunity to flee or/and hide from predators, as well as provides for their thermoregulation needs (NEEL & MCBRAYER 2018). Other factors, such as feeding behaviour, may also influence habitat selection, but more researches are needed to clarify their role.

Conclusion

The microhabitat selection in *Lacerta agilis bosnica* depends mainly on ontogenetic stage, while the sex-related differences seem to be of less importance. In general, *L. agilis bosnica* is a taxon related to open habitats, but the structure of grass cover is crucial, which make this subspecies sensitive to habitat change caused by habitat management, processes of succession and pasture abandonment. On the other hand, intense land use and overgrazing could also have a negative impact, due to the specific requirement of this species to avoid sites with lowest grass cover. The importance of vegetation height and density should be taken into account for *L. agilis bosnica* when conservation measures are planned and applied.

References

AMAT F., LORENTE G.A. & CARRETERO M.A. 2003. A preliminary study on thermal ecology, activity times and microhabitat use of *Lacerta agilis* (Squamata: Lacertidae) in the Pyrenees. Folia Zoology 52 (4): 413–422.

ANDRES C., FRANKE F., BLEIDORN C., BERNHARD D. & SCHLEGEL M. 2014. Phylogenetic analysis of the *Lacerta agilis* subspecies complex. Systematics and Biodiversity 12 (1): 43–54.

ANGELICI F.M., LUISELLI L. & RUGIERO L.1997. Food habits of the green lizard, *Lacerta bilineata*, in central Italy and a reliability test of faecal pellet analysis. Italian Journal of Zoology 64: 267–272.

ANGILLETTA JR. M.J., SEARS M.W. & PRINGLE R. M. 2009. Spatial dynamics of nesting behaviour: Lizards shift microhabitats to construct nests with beneficial thermal properties. Ecol-

ogy 90 (10): 2933–2939.

ARNOLD E.N. 1998. Structural niche, limb morphology and locomotion in lacertid lizards (Squamata, Lacertidae); a preliminary survey. Bulletin of the British Museum 64: 63–89.

BAUWENS D. & THOEN C. 1981. Escape tactics and vulnerability to predation associated with reproduction in the lizard *Lacerta vivipara*. Journal of Animal Ecology 50: 733–743.

BISCHOFF W. 1984. *Lacerta agilis* Linneaus 1758-Zauneidechse. In: BOHME W. (ed.): Handbuch der Reptilien und Amphibien Europas. Wiesbaden: Aula Verlag, pp. 23–68..

BORCZYK B. 2001. The effects of flood on an isolated population of Sand lizards (*Lacerta agilis*) in Wroclaw (SW Poland). Herpetological Bulletin 78: 28–30.

BRODIE E. D. III 1989. Behavioral modification as a means of reducing the cost of reproduction. The American Naturalist 134: 225–238.

BUTLER M.A., SCHOENER T.W. & LOSOS J.B. 2000. The relationship between sexual size dimorphism and habitat use in Greater Antillean Anolis lizards. Evolution 54: 259–272.

CARRASCAL L.M., DÍAZ J.A. & CANO C. 1990. Habitat selection in *Psammodromus algirus* (Linnaeus, 1758) (Sauria: Lacertidae): age related differences. Acta Zoologica Cracoviensia 33: 3 –10.

ČEIRĀNS A. 2007a. Distribution and habitats of the Sand Lizard (*Lacerta agilis*) in Latvia. Acta Universitatis Latviensis 723: 53–59.

ČEIRĀNS A. 2007b. Microhabitat Characteristics For Reptiles *Lacerta agilis*, *Zootoca vivipara*, *Anguis fragilis*, *Natrix natrix*, and *Vipera berus* in Latvia. Russian Journal of Herpetology 14 (3): 172–176.

COOPER W.E. &VITT L.J. 2002. Increased predation risk while mate guarding as a cost of reproduction for male broad-headed skinks (*Eumeces laticeps*). Acta Ethologica 5: 19–23.

CORBETT K.F., TAMARIND D.L. 1979. Conservation of the sand lizard, *Lacerta agilis*, by habitat management. British Journal of Herpetology 5: 799–823.

DAREVSKY I.S., SHCHERBAK N.N. & PETERS G.1976. Systematics and intraspecific structure. In: Prytkaya yashcheritsa. In: YABLOKOV A.V. (Ed.), Moscow: Nauka Publishing House, pp. 53–95 (In Russian).

DELANEY D.M. & WARNER D.A. 2017. Adult Male Density Influences Juvenile Microhabitat Use in a Territorial Lizard. Ethology 123: 157–167.

DIEGO-RASSILA F.J. & PÉREZ-MELLADO V. 2003. Home range and habitat selection by *Podarcis hispanica* (Squamata, Lacertidae) in Western Spain. Folia Zoology 52 (1): 87–98.

DOWNES S.J. & BAUWENS D. 2002. Does reproductive state affect a lizard's behaviour toward predator chemical cues? Behavioral Ecology and Sociobiology 52: 444–450.

EDWARDS J.R & LAILVAUX S.P. 2013. Do interspecific interactions between females drive shifts in habitat use? A test using the lizards *Anolis carolinensis* and *A. sagrei*. Biological Journal of the Linnean Society 110: 843–851.

EKNER A., MAJLÁTH I., MAJLÁTHOVÁ V., HROMADA M., BONA M., ANTCZAK M, BOGACZYK M & TRYJANOWSKI P. 2008. Densities and Morphology of Two Co-existing Lizard Species (*Lacerta agilis* and *Zootoca vivipara*) in Extensively Used Farmland in Poland. Folia Biologica 56 (3-4): 165–171.

GLANDT D. 1979. Beitrag zur Habitat-Ökologie von Zauneidechse (*Lacerta agilis*) und Waldeidechse (*Lacerta vivipara*) im nordwestdeutschen Tiefland, nebst Hinweisen zur Sicherung von Zauneidechsen-Beständen. Salamandra 15 (1): 13–30.

GLANDT D. 1991. The vegetation structure preferred by the sand lizard (*Lacerta agitis*) and the common lizard (*Lacerta vivipara*) in an experimental outdoor enclosure. Acta Biologica Benrodis 3: 79–86.

GROZDANOV A.P., TZANKOV N.D., ANDRES C., POPOVA S. 2014. Microhabitat use in Sand lizard - *Lacerta agilis chersonensis* (Squamata, Lacertidae) as an indicator for planning of different management practices for pastures. Bulgarian Journal of Agricultural Science 20 (6): 1386–1391.

GUISAN A. & HOFER U. 2003. Predicting reptile distributions at the mesoscale: relation to climate and topography. Journal of Biogeography 30 (8): 1233–1243.

HAMMER Ø., HARPER D.A.T. & RYAN P.D. 2001. PAST: Paleontological statistics software package for education and data analysis. Palaeontologia Electronica 4 (1): 1–9.

HEATWOLE H. 1977. Habitat selection in reptiles. In: GANS C. & TINKLE D. (Eds.): Biology of Reptilia Vol. 7. New York: Academic Press, pp. 137–155.

HELTAI B., SÁLY P., KOVÁCS D. & KISS I. 2015. Niche segregation of sand lizard (*Lacerta agilis*) and green lizard (*Lacerta viridis*) in an urban semi-natural habitat. Amphibia-Reptilia 36: 389–399.

HENLE K., ANDRES C., BERNHARD D., GRIMM A., STOEV P., TZANKOV N. & SCHLEGEL M. 2017. Are species genetically more sensitive to habitat fragmentation on the periphery of their range compared to the core? A case study on the sand lizard (*Lacerta agilis*). Landscape Ecology 32 (1): 131–145.

HERCZEG G., TÖRÖK J. & KORSÓS Z. 2007. Size-dependent heating rates determine the spatial and temporal distribution of small-bodied lizards. Amphibia-Reptilia 28: 347–356.

HERREL A., MEYERS J. & VANHOOYDONCK B. 2001. Correlations between habitat use and body shape in a phrynosomatid lizard (*Urosaurus ornatus*): a population-level analysis. Biological Journal of the Linnean Society 74 (3): 305–314.

KALIONTZOPOULOU A., CARRETERO M.A & ADAMS D.C. 2015. Ecomorphological variation in male and female wall lizards and the macroevolution of sexual dimorphism in relation to habitat use. Journal of Evolutionary Biology 28 (1): 80–94.

KALIONTZOPOULOU A., CARRETERO M.A. & LLORENTE G.A. 2010. Intraspecific ecomorphological variation: linear and geometric morphometrics reveal habitat-related patterns within *Podarcis bocagei* wall lizards. Journal of Evolutionary Biology 23: 1234–1244.

KIRBIŠ N. 2015. Effect of Floods and Space Heterogenity on Population density of Sand Lizard (*Lacerta agilis*) M. Sc. Thesis. Ljubljana University, Biotechnological Faculty (In Slovenian).

KOLANEK A., BURY S., TURNIAK E. & SZYMANOWSKI M. 2019. Age-Dependent Utilization of Shelters and Habitat in Two Reptile Species with Contrasting Intraspecific Interactions. Animals 9 (11): 995: 1–12.

KOVÁCS D. & KISS I. 2016. Microhabitat use of different age groups of snake-eyed skink and Eastern green lizard. Amphibia-Reptilia 37 (2): 191–198.

MAJLÁTH I., ŠMAJDA B. & KUNDRÁT M. 1997. Biometric analysis of morphological traits in Sand Lizard (*Lacerta agilis*) from East Slovakia. Folia Zoologica 46 (3): 253–262.

MÄRTENS B., HENLE K., KUHN W., KRUG R., JOST K., GROSSE W.

R. & Wissel C. 1996. Survival of the sand lizard (*Lacerta agilis* Linnaeus, 1758) (Sauria, Lacertidae) in relation to habitat quality and heterogeneity. In: Settle J., Margules C.R., Poschlod P. & Henle K (Eds.): Species Survival in Fragmented Landscapes. Dordrecht: Springer, pp. 241–247.

Martín J. & López P. 2003. Ontogenetic variation in antipredator behaviour of Iberian rock lizards (*Lacerta monticola*): effects of body-size-dependent thermal-exchange rates and cost of refuge use. Canadian Journal of Zoology 81: 1131–1137.

Martín J. & Salvador A. 1995. Microhabitat selection by the Iberian rock lizard *Lacerta monticola*: effects on density and spatial distribution of individuals. Biologival Conservation 79: 303–307.

Molina-Borja M., Rodríguez-Domínguez M.A., González-Ortega C. & Bohórquez-Alonso M. L 2010. Sexual Size and Shape Dimorphism Variation in Caesar's Lizard (*Gallotia caesaris*, Lacertidae) from Different Habitats. Journal of Herpetology 44 (1): 1–12.

Neel L.K. & McBrayer L.D. 2018. Habitat management alters thermal opportunity. Functional Ecology 32: 2029–2039.

Nemes S., Vogrin M., Hartel T. & Öllerer K. 2006. Habitat selection at the sand lizard (*Lacerta agilis*): ontogenetic shifts. North-Western Journal of Zoology 2 (1): 17–26.

Olsson M. 1986. Spatial distribution and home range size in the Swedish sand lizard during the mating season. In: Roček Z. (ed.): Studies in Herpetology pp. 597–600.

Olsson M. 1993. Contest success and mate guarding in male sand lizards, *Lacerta agilis*. Animal Behaviour 46: 408–409.

Paterson J.E. & Blouin-Demers G. 2018. Density-dependent habitat selection predicts fitness and abundance in a small lizard. Oikos 127: 448–459.

Paulissen M.A. 1988. Ontogenetic and Seasonal Shifts in Microhabitat Use by the Lizard *Cnemidophoruss exlineatus*. Copeia (4): 1021–1029.

Pilorge T. 1987. Density, Size Structure, and Reproductive Characteristics of three populations of *Lacerta vivipara* (Sauria: Lacertidae) Herpetologica 43 (3): 345–356.

Popova S., Vacheva E., Tzankov N. 2019. Sexual size dimorphism in the Balkan subspecies of the Sand lizard *Lacerta agilis bosnica* Schreiber, 1912 (Reptilia: Lacertidae) in Bulgaria. Annual of Sofia University "St. Kliment Ohridski" Faculty of Biology 4 (104): 141–153.

Prieto-Ramirez A.M. Pe'er G., Rödder D. & Henle K. 2018. Realized niche and microhabitat selection of the eastern green lizard (*Lacerta viridis*) at the core and periphery of its distribution range. Ecology and Evolution 8 (22): 11322–11336.

Reading C. J. & Jofré G. M. 2016. Habitat use by grass snakes and three sympatric lizard species on lowland heath managed using 'conservation grazing'. The Herpetological Journal 26 (2): 131–138.

Sagonas K., Valakos E.D., Lymberakis P. & Pafilis P. 2018. Traits of reproduction and feeding of the european Green lizard, *Lacerta viridis* (Laurenti, 1768), at the southern edge of its distribution (Squamata: Sauria: Lacertidae). Herpetozoa 30 (3/4): 115–129.

Schwarzkopf L. & Shine R. 1992. Costs of reproduction in lizards: Escape tactics and susceptibility to predation. Behavioral Ecology and Sociobiology 31: 17–25.

Speybroeck J., Beukema W., Bok B. & Van Der Voort J. 2016. Field Guide to the Amphibians and Reptiles of Britain and Europe. London, United Kingdom, Bloomsbury Publishing.

StatSoft Inc. 2011. STATISTICA (data analysis software system), version 10. www.statsoft.com.

Stojanov A., Tzankov N. & Naumov B. 2011. Die Amphibien und Reptilien Bulgariens. Frankfurt am Main: Chimaira, pp. 338–346.

Strijbosch H. 1986. Niche segregation in Sympatric *Lacerta agilis* and *L. vivipara*. In: Roček Z. (Ed.), Studies in Herpetology. Prague: SEH, pp. 449–454.

Stumpel A.H.P. 1988. Habitat selection and management of the Sand lizard, *Lacerta agilis* L., at the Utrechtse Heuvelrug, Central Netherlands. Mertensiella 1: 122–131.

Török Z. 1998. Interactions between habitat characteristics and ecological density of the natural populations of sand lizards (*Lacerta agilis* Linnaeus 1758) from Razim-Sinoe lagoonary system (Romania). Part I-Vegetation. Analele Stincifice ale Institutului Delta Dunari 6 (1): 167–179.

Török Z. 2002. Interactions between habitat characteristics and ecological density of the natural populations of sand lizards (*Lacerta agilis* Linnaeus 1758) from Razim-Sinoe lagoonary system (Romania). Part II-Accesibility of shelters. Analele Stincifice ale Institutului Delta Dunari 2002: 191–195.

Toyama K.S. 2017. Interaction between morphology and habitat use: A large-scale approach in tropidurinae lizards. Breviora 554 (1): 1–20.

Vanhooydonck B. & Van Damme R. 1999. Evolutionary relationships between body shape and habitat use in lacertid lizards. Evolutionary Ecology Research 1: 785–805.

Vanhooydonck B. &Van Damme R. 2002. Relationships between locomotor performance, microhabitat use and antipredator behaviour in lacertid lizards. Functional Ecology 17: 160–169.

Vanhooydonck B., Van Damme R. & Aerts P. 2000. Ecomorphological correlates of habitat partitioning in Corsican lacertid lizards. Functional Ecology 14: 358–368.

Wouters B., Nijssen M., Geerling G., Van Kleef H., Remke E. & Verberk W.2012. The effects of shifting vegetation mosaics on habitat suitability for coastal dune fauna: a case study on sand lizards (*Lacerta agilis*). Journal of Coastal Conservation 16: 89–99.

Appendix 1: Percent distribution of the captured specimens (in age-sex groups) per microhabitat classes ("n" denotes number of captured lizards; for the other abbreviations see section "Material and Methods").

		M	F	imM	imF
Plana (n = 125)	H1D1	0.00	0.00	2.70	0.00
	H1D2	10.00	2.94	0.00	0.00
	H1D3	0.00	8.82	0.00	2.94
	H1D4	25.00	11.76	16.22	20.59
	H2D3	0.00	8.82	0.00	2.94
	H2D4	25.00	32.35	51.35	61.76
	H3D4	40.00	35.29	29.73	11.76
Vitosha (n = 155)	H1D1	0.00	0.00	3.13	0.00
	H1D3	3.03	6.56	9.38	20.69
	H1D4	3.03	1.64	18.75	10.34
	H2D3	36.36	37.70	21.88	20.69
	H2D4	21.21	13.11	9.38	20.69
	H3D3	21.21	22.95	21.88	24.14
	H3D4	15.15	18.03	15.63	3.45
Osogovo (n = 70)	H1D1	8.33	16.67	0.00	0.00
	H1D3	25.00	53.33	18.18	29.41
	H1D4	8.33	3.33	36.36	11.76
	H2D3	8.33	3.33	18.18	35.29
	H2D4	16.67	13.33	27.27	17.65
	H3D2	8.33	0.00	0.00	0.00
	H3D3	8.33	3.33	0.00	0.00
	H3D4	16.67	6.67	0.00	5.88