

Habitat segregation patterns of reptiles in Northern Dinaric Mountains (Slovenia)

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Abstract. We have surveyed sympatric reptiles in a diverse and preserved montane environment in the Northern Dinaric region (Southern Slovenia) to determine the assemblage structure and assess the patterns of habitat segregation. Altitude and habitat type contributed the most to segregations between the most abundant species. The most similar were species pairs of *L. viridis/bilineata* and *P. muralis*, and *I. horvathi* and *V. ammodytes*. In snakes, significant segregation patterns have been observed between all species. Among lizards, we have found strong altitudinal segregation between two morphologically and ecologically most similar species; *P. muralis* was most abundant at low and *I. horvathi* at higher elevations. This result indicated a potential competitive interaction between these species.

Keywords: habitat use, reptiles, Slovenia, spatial segregation pattern.

Species habitat selection is influenced by diverse biotic and abiotic factors. Both are important, but act differently regarding species ecology and trophic level (e.g. Langkilde and Shine, 2004; Vrezec and Tome, 2004). Habitat use patterns studied between sympatric species can uncover the most influential factors and reveal habitat segregations. To study habitat segregations within species assemblages it is necessary to assess the biotic interactions which can influence species densities and distributions (Araújo and Luoto, 2007; Heikkinen et al., 2007). In reptiles it has been shown that ecological segregation occurs in habitat use (e.g. Langkilde and Shine, 2004) or diet preferences (e.g. HENDERSON, 1982; Carretero, 2004; Luiselli, 2006).

In SE Europe and especially in the Dinaric region, habitat use of reptiles is still understudied despite the high species diversity reported (Dzukić and Kalezić, 2004). We aim to deter-

mine the assemblage structure and assess the patterns of habitat segregation in the reptile assemblage of a diverse montane environment in the Northern Dinaric region in Southern Slovenia. We expected that habitat segregation would be strongest among ecologically similar species occupying the same area (Begon et al., 1996), since interactions are expected to be more intense between species with a similar ecological niche than between species with a different ecological niche (Root, 1969; Schoener, 1982).

We studied an area of 135 km² in the northern part of the Dinaric region, Southern Slovenia (lat. 45°29'N, long. 14°49'E; fig. 1). The altitudinal span ranged from 135 m a.s.l. to 1066 m a.s.l. Landscape was karstic with prevalence of carbonate stoneware. Mean temperature in the hottest month of the year (July) was 18°C (Puncer, 1980). The study area had about 80% coverage of forest, mainly Dinaric beech-fir forest (*Omphalodo-Fagetum* s. lat.; Perko and Orožen Adamič, 1998).

On the basis of preliminary field visits we selected eight habitat types according to the main habitat extent found in the area. Two types were natural forest clearings (natural rock and water bank), four human made forest clearings (urban area, agricultural land, road and artificial rock), and two forested areas (open forest and closed forest). Sixty-six transect lines were distributed in eight habitat types to cover the whole altitudinal span of the study area (see supplementary table S1). We used ArcMap 9.2 (ESRI, 2004) to create a buffer zone of 10 m around each transect line and divided them into 10 m long segments, each covering an area of 200 m². Thereafter we applied the following habitat variables to each surveyed segment: (i) altitude at the middle point of the segment (DMR layer, source: Geodetska uprava RS), (ii) habitat type (field observation),

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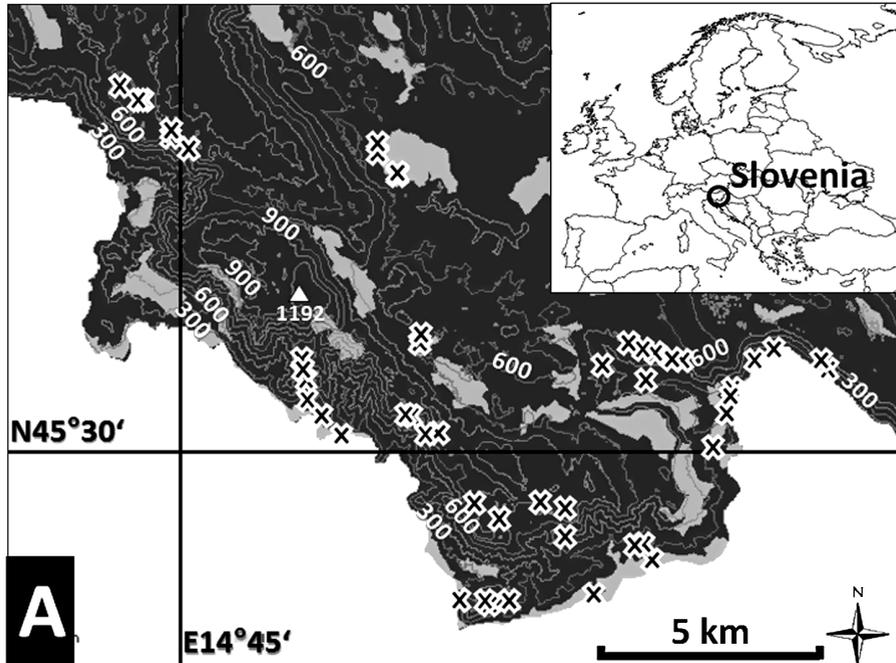


Figure 1. Geographical position of the study area in Europe (top right corner) with a detailed map of the study area representing forest (dark grey) and non-forested (light grey) areas with CORINE Land Cover 2000 maps of Europe (CLC, 2000) and altitude with 100 m altitudinal contours labelled with values of 300, 600, 900 and 1192 m a.s.l. Middle locations of the 66 surveyed transect lines are represented with black crosses outlined in white.

(iii) proportion of the area covered with forest (CLC, 2000), and (iv) exposition (topographic maps of 1:25 000, source: Geodetska uprava RS). Some forest clearings had narrow properties and were in some proportion also covered with forest, but never 100%.

Reptile surveys had been conducted between April and September in three consecutive years: 2006, 2007 and 2008. Reptiles were searched by visually inspecting the area while moving along the transect line in an equal slow pace (Buckland et al., 1993). Each transect line was surveyed three times: two times in spring (April-June) and once in summer (July-September) in all considered years, in optimal weather conditions (sunny or partly sunny days) and in the time of the day when most of the reptile species are active. During the study, the first author also noted other records of reptiles within the study area that contributed to the results of assemblage structure presented in Appendix 1. All individuals were identified to the species level except green lizards (*Lacerta viridis/bilineata*) where two species of green lizard (*L. viridis* and *L. bilineata*) were considered as one operative taxonomic group (Sneath and Sokal, 1973), due to the fact that both members of this species complex could occur in the Northern Dinaric region (Böhme et al., 2006), but are difficult to distinguish in the field.

Rare species in the area have been excluded from further analysis due to small sample size obtained. Seven species were used in further analysis of habitat segregation patterns which had been investigated with the discriminant

function analysis (DFA) after the backward stepwise procedure ($\alpha = 0.01$), a multivariate statistical method that separated groups of individuals according to measurements on several variables (Manly, 1994). For data from transect lines the maximal count on each transect was used to avoid pseudo-replication. All four habitat variables were inserted in the DFA, but from them only two were selected by the final model (altitude and habitat type), forest cover (Wilks' lambda = 0.3334, $P = 0.04$) and exposition (Wilks' lambda = 0.3235, $P = 0.001$) were rejected. Canonical variate analysis of each variable was used to derive a matrix of Mahalanobis distances that allows estimating dissimilarity in species (Manly, 1994). These analyses were done using Statistica 10 (STATSOFT, 2011). Variables contributing the most to the discrimination (altitude and habitat type) were afterwards additionally analysed to examine the habitat selection pattern for each species separately. We used buffered 10 m segments of surveyed transect lines to which we assigned the species presence/absence. Then we compared the habitat variables of occupied versus unoccupied habitat segments. Wilcoxon rank sum test was used to test the differences between segments for continuous variable (altitude) and Chi-square test for categorical variable (habitat type), all done using R package (R Development Core Team, 2008).

In total ten species with 551 sights were recorded during the sampling period, among

which 427 sights and nine species were recorded at transect line surveys (Appendix 1). The most abundant lizard species were the common wall lizard (*Podarcis muralis*), green lizard (*Lacerta viridis/bilineata*) and Horvath's rock lizard (*Iberolacerta horvathi*), and among snakes the grass snake (*Natrix natrix*), dice snake (*Natrix tessellata*) and nose-horned viper (*Vipera ammodytes*).

Discriminant function had power to separate between habitat selection patterns of the most abundant studied reptile species (Wilks' lambda = 0.3482, $F_{10,584} = 38.089$, $P < 0.0001$) with altitude and habitat type being the only variables contributing to the discrimination between species (table 1). Root 1 explained larger part of the variability with altitude as the parameter contributing the most to the discrimination (table 1). Four out of seven species showed significant selection pattern according to the altitude (table 1), with *N. tessellata* and *P. muralis* confined to low, and *I. horvathi* and *V. ammodytes* to high elevations. *L. viridis/bilineata* and *N. natrix* did not show any altitudinal preferences and *N. natrix* was the species recorded in the largest altitudinal span. The most similar habitat preferences considering both factors (altitude and habitat type) were

found between two pairs: *L. viridis/bilineata* and *P. muralis*, and between *I. horvathi* and *V. ammodytes*, while *N. natrix* and *N. tessellata* were significantly separated from all (table 1). More detailed habitat selection analyses are provided in supplementary table S2.

Our results showed that altitude and habitat type influenced the habitat segregation patterns between reptiles in the montane and highly forested area of the Northern Dinarics in Slovenia. The variables that were excluded by the model were exposition and forest cover and clearly do not influence the segregation. Indeed all species were in majority found on localities with southern expositions and in areas with low forest cover (open habitat types).

In the case of snakes, the three most abundant species in the studied assemblage were habitat segregated which coincides with their ecological characteristics that define them as members of different guilds (Luiselli and Rugiero, 1991; Luiselli, 2006). The largest habitat segregation pattern was found between *V. ammodytes* and both *Natrix* species. Nonetheless, also both *Natrix* species exhibited segregation pattern; *N. tessellata* was recorded only in lowlands and almost exclusively on the water banks, whereas *N. natrix* was found through-

Table 1. Results of the discriminant function and canonical variate analyses for seven sympatric reptile species from Northern Dinaric region with two habitat variables used by the model: altitude and habitat type (upper part) and habitat segregations between species pairs measured with squared Mahalanobis distances (D^2 ; above the diagonal) and P values (below the diagonal): *Lacerta viridis/bilineata* are counted as two species, * = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$ (bottom part).

Variable	Wilks' lambda	F	P	Root 1	Root 2
Altitude	0.72	58.83	<0.001	-0.94	0.36
Habitat type	0.48	20.36	<0.001	-0.45	-0.90
Eigenvalue	-	-	-	1.30	0.25
Cumulative	-	-	-	0.84	1.00

	<i>Iberolacerta horvathi</i>	<i>Lacerta viridis/bilineata</i>	<i>Podarcis muralis</i>	<i>Natrix natrix</i>	<i>Natrix tessellata</i>	<i>Vipera ammodytes</i>
<i>Iberolacerta horvathi</i>	-	7.2	8.3	4.9	13.2	0.2
<i>Lacerta viridis/bilineata</i>	***	-	0.04	2.7	5.0	5.2
<i>Podarcis muralis</i>	***	N.S.	-	2.9	4.7	6.1
<i>Natrix natrix</i>	***	***	***	-	2.0	3.2
<i>Natrix tessellata</i>	***	***	***	**	-	10.2
<i>Vipera ammodytes</i>	N.S.	***	***	***	***	-

out the entire area. *V. ammodytes* is exclusively a terrestrial predator, *N. natrix* a semi-aquatic predator, and *N. tessellata* a specialized piscivorous and mostly aquatic predator (e.g. Luiselli and Rugiero, 1991; Luiselli, 2006). The dietary differences most likely determined differential habitat use and consequently the observed segregation. Therefore we suggest that segregation pattern observed between snakes was a result of their pre-adaptive characteristics or even of ghost-of-competition (i.e. in the case of *Natrix* species, Guicking et al., 2006), but not of actual competitive interactions.

On the other hand, in the case of lacertids, we have found significant habitat segregation between *I. horvathi* and *P. muralis* that are morphologically and ecologically most similar species in the studied assemblage (Richard and Lapini, 1993; Žagar et al., 2012), whereas the biggest lacertid, *L. viridis/bilineata*, was segregated from *I. horvathi* but not from *P. muralis*. Lacertids are mostly active searching foragers, more rarely “sit-and-wait” predators, that feed mainly on arthropods (Carretero, 2004) with their food niches differentiated according to the size of prey they can consume (Angelici, Luiselli and Rugiero, 1997; Carretero, 2004). According to this size-related diet differentiation we can assign smaller lacertids of the studied assemblage (*I. horvathi* and *P. muralis* with adult SVL 55-65 mm; Žagar et al., 2012) to one guild and green lizard (*L. viridis/bilineata* with adult with >83 mm in SVL; Angelici, Luiselli and Rugiero, 1997) to another. We observed that, habitat segregation wise, intra-guild differences appeared to be much larger than inter-guild. In fact, *L. viridis/bilineata* and *P. muralis* were both most abundant at low to mid-elevations and occupied in large proportion same habitat types. But in the case of *P. muralis* and *I. horvathi*, the species were strongly segregated by altitude (*P. muralis* confined mainly to low and *I. horvathi* to high elevations), but not regarding the habitat type since both species selected for similar habitat types (natural and artificial rocks). Even in syntopic populations

habitat use differences between the species are very slight and only differ by *I. horvathi* more often using vertical rocks than *P. muralis* (Cabela, Grillitsch and Tiedemann, 2007). We suggest that observed altitudinal segregation pattern between small lacertids was not a reflection of pre-adaptive differences since they are in fact morphologically and ecologically very similar (De Luca, 1989; Lapini, Richard and Dall’Asta, 1993; Richard and Lapini, 1993; Cabela, Grillitsch and Tiedemann, 2007; Žagar et al., 2012), but can be viewed as an indication of potential competitive interaction, as suggested for the species of the same guild (Schoener, 1982; Crochet et al., 2004; Hochkirch, Groning and Bucker, 2007).

In future studies the focus should be to assess the processes driving the observed segregation patterns of ecologically similar species in order to better understand its reasons and outcomes.

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Appendix 1. Eleven reptile species recorded with the transect line method in eight different habitat types. Given are: total number of finds in each habitat type (sum of three repeated transect surveys), number of coincidental finds (C. FINDS) and the summed number of all finds (SUM). Number in brackets in the second row represent the maximum number of times a species was recorded in the same transect (once: 1, twice: 2 or three times: 3). *Lacerta viridis/bilineata* are counted as two species.

Species	Habitat type								C. FINDS	SUM
	Natural rock	Open forest	Closed forest	Water bank	Artificial rock	Road	Agricultural land	Urban area		
<i>Anguis fragilis</i>	1 (1)	3 (3)	1 (1)	1 (1)	/	/	/	/	10	16
<i>Iberolacerta horvathi</i>	48 (3)	2 (1)	/	/	9 (2)	/	/	/	2	61
<i>Lacerta viridis/bilineata</i>	6 (2)	17 (2)	/	3 (1)	2 (1)	4 (1)	4 (2)	12 (3)	20	68
<i>Podarcis muralis</i>	38 (3)	18 (2)	/	6 (2)	78 (3)	58 (3)	1 (1)	50 (3)	47	296
<i>Zootoca vivipara</i>	/	/	/	3 (1)	/	/	/	/	/	3
<i>Coronella austriaca</i>	1 (1)	/	/	/	2 (2)	/	/	1 (1)	1	5
<i>Natrix natrix</i>	5 (2)	/	/	10 (1)	4 (1)	/	/	1 (1)	26	46
<i>Natrix tessellata</i>	/	/	/	7 (1)	/	/	1 (1)	1 (1)	12	21
<i>Zamenis longissimus</i>	/	/	/	/	/	/	/	/	4	4
<i>Vipera ammodytes</i>	21 (3)	2 (2)	/	1 (1)	4 (2)	/	/	1 (1)	2	31
TOTAL										551