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Selected microhabitat and surface temperatures of two sympatric lizard species

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Abstract. Many small lizards live in structurally and thermally heterogeneous environments where they can select preferred microhabitats and surface temperatures to optimize their activity. We examined microhabitat selection and analyzed surface temperatures selected by two ecologically similar lacertid species, *Iberolacerta horvathi* and *Podarcis muralis*, at three sites and in different ecological contexts: allotopic and syntopic conditions. We examined their microhabitat and spatial thermal selection by using high-precision geolocation techniques to locate the lizards and record surface temperatures with temperature data loggers. Microhabitat and thermal availability differed among sites: the *I. horvathi* allotopic site had more rock surfaces and was coldest; the *P. muralis* allotopic site had more ground surfaces and was warmer; and the syntopic site had the greatest surface and thermal heterogeneity. Our results highlight the differences in microhabitat selection between the two species, most notably in surface selection, but also in thermal characteristics. *I. horvathi* preferentially and almost exclusively selected rocks. *P. muralis* chose soil, but with a more general use of microhabitats. *I. horvathi* lizards chose colder temperatures than those available, while *P. muralis* chose higher temperatures than those available. Both species showed no differences in microhabitat selection between allotopic and syntopic sites, which could not be explained by differences between sites. Our results provided new insights into the difference in surface temperature selection between two lizard species that may be adapted to different environments.

Keywords. lizards, habitat use, thermoregulation, interspecific interaction, competition

1. INTRODUCTION

As ectothermic terrestrial animals, lizards live in a thermally heterogeneous environment and use thermoregulation through behaviour and physiology to achieve body temperatures within a narrow thermal range during their activity (Huey, 1982; Angilleta, 2009). Body temperature itself has important implications for several aspects of animal ecology and behaviour: escape from predators, ability to forage, metabolise food, defend territories, successfully mate, optimize embryonic development in pregnant females, and maintain homeostasis (e.g., Christian and Tracy, 1981; Angilletta, 2001; Angilletta et al., 2002; Carretero et al., 2005; Kondo and Downes, 2007; Lou et al., 2010). Thus, attaining the preferred body temperature has a direct impact on an individual's fitness (Angilletta, 2001). Consequently, lizard microhabitat selection is determined by many factors, of which thermoregulatory behavior is one of the most important (Huey, 1982).

In small-bodied lizards, thermoregulation occurs primarily through shuttling behaviour, i.e., moving from colder to warmer microhabitats in a thermally heterogeneous environment (e.g., Sears and Angilletta, 2015). Thus, the thermal environment plays an important role in determining the ability to thermoregulate effectively. The main environmental factors that influence the ability to thermoregulate are: abiotic factors such as temperature and humidity (Sannolo and Carretero, 2019) and biotic factors such as the abundance of predators and prey (Brana, 1993; Diaz and Carrascal, 1991) and the presence of interspecific competitors. The nature and magnitude of an animal's response to environmental factors (abiotic and biotic) can vary among species and populations (e.g., Carretero et al., 2006; Verissimo and Carretero, 2009; Carneiro et al., 2017).

Most microhabitat studies of lizards have been conducted using nonspatial techniques (e.g., Carrascal et al., 1989). Only after the Selective Availability bug was removed from GPS devices in May 2001 was it readily possible to conduct full spatial analyses of how lizards use their microhabitats because GPS devices were able to geolocate individuals with a small error (< 5 m) without further processes (i.e., post-differential correction). Also, advances in geographic information systems provided the tools to perform spatial analyses such as geostatistics (interpolations) and spatial statistics (Sillero et al., 2018; Sillero et al., 2021 a). In addition, most studies on lizard habitat have neglected the thermal aspect of the environment. The use of small temperature measurement devices, such as temperature data loggers, allows us to record in situ the microhabitat conditions that lizards experience. Both the loggers and the lizards experience similar temperature because they are on the same surface (Bakken and Angilletta, 2014). Because the precise use of microhabitats by lizards and the actual thermal properties of these microhabitats are studied in parallel, thermal selection can be explored at a very fine spatial scale. With these methodological and software advances, ecological niche models (Sillero, 2011; Sillero et al., 2021 b) are becoming powerful techniques for analysing relationships between the environment and the distribution of individuals at broad and micro scales (Sillero et al., 2020; Sillero et al., 2021 a).

The Horvath's rock lizard, *Iberolacerta horvathi* (Méhely 1904), and the common wall lizard, *Podarcis muralis* (Laurenti 1768), are small lacertids that occur sympatrically throughout much of their range (Žagar et al., 2013; Žagar, 2016). Both species overlap geographically in Slovenia (Krofel et al., 2009), with *P. muralis* more common at lower altitudes and *I. horvathi* at higher altitudes (Žagar, 2008, Krofel et al., 2009). The wall lizard inhabits a wide range of natural and anthropogenic habitats (Speybroek et al., 2016) and in contrast, with some exceptions, the Horvath's rock lizard usually inhabits rocky areas at higher elevations (Žagar et al., 2016). At the local level, these two species may overlap with some separation in terms of microhabitat, but exhibit high trophic overlap (Richard and Lapini, 1993; Žagar et al., 2013). Some authors suggest that *I. horvathi* also uses more vertical surfaces than *P. muralis*, which has been associated with different climbing abilities (Arnold, 1987; Cabela et al., 2007); however, a study of locomotor performance found no differences in climbing speed between species (Žagar et al., 2017). A comparative range size study of *I. horvathi* and *P. muralis* showed that *P. muralis* has a larger range, especially males during the breeding season (Lapini et al., 2004), which may also influence the range of microhabitats used.

The aim of this study was to investigate microhabitat selection and surface temperatures of sympatric *I. horvathi* and *P. muralis* in two ecological contexts: under allotopic (occurrence of only one species) and syntopic (occurrence of both species) conditions, using GPS equipment of high-accuracy and spatial analyses. We tested the hypothesis that the more generalist species (*P. muralis*) uses microhabitats and thermal spaces less selectively than the more specialized species (*I. horvathi*). Therefore, we expected that the two species would differ in the diversity of microhabitats used and surface temperatures selected, which would reflect their specific ecophysiological and habitat niches. Therefore, our study is also important to understand the specific characteristics of microhabitat selection of ecologically similar species so that better conservation measures can be taken in the future when populations are under pressure.

2. MATERIAL AND METHODS

2.1 Study area

We conducted fieldwork at three study sites in the Kočevsko region of southern Slovenia (Fig. 1). The study area is characterized by a large altitudinal gradient (200-1,100 m a.s.l.), heterogeneous topography, high forest cover, and a mosaic of open areas with exposed rocky areas, riverbanks, roads, and villages, providing suitable habitats for the studied species (Žagar et al., 2013). The climate is temperate continental with an alpine climate influence from the north and an Adriatic Sea influence from the southwest (Puncer, 1980). We selected the three study sites hosting the studied species: P. muralis occurring alone (AlloPMUR), I. horvathi occurring alone (AlloIHOR), and both species occurring together (Syntopic) (Table 1, Fig. 1). All three sites are open sites in the forest area. The AlloPMUR site was located at the edge of a forest clearing with a rocky slope covered with grass and shrubs. The AlloIHOR site was also located on the forest road, but on a steep slope with vertical walls and rocks, with only small patches of grass and shrubs. The syntopic site was located on the edge of a cliff where rocks covered the ground and trees extended to the edge, providing heterogeneous shade. All sites are similar in size, are at similar elevations, and have the same climatic conditions (Table 1).

Table 1. Information on site location (WGS latitude and longitude coordinates), species, elevation, and size of the study area.

Site	Location	Coordinates	Species	N	Elev. (m a.s.l.)	Size (m^2)
AlloIHOR	Mala gora	N 45.675 E 14.708	*Iberolacerta horvathi*	233	1,005	6,125
AlloPMUR	Velike Bele stene	N 45.691 E 14.683	*Podarcis muralis*	389	741	4,025
Syntopic	Kuželjska stena	N 45.484 E 14.823	*Iberolacerta horvathi* *Podarcis muralis*	56 9	840	3,700

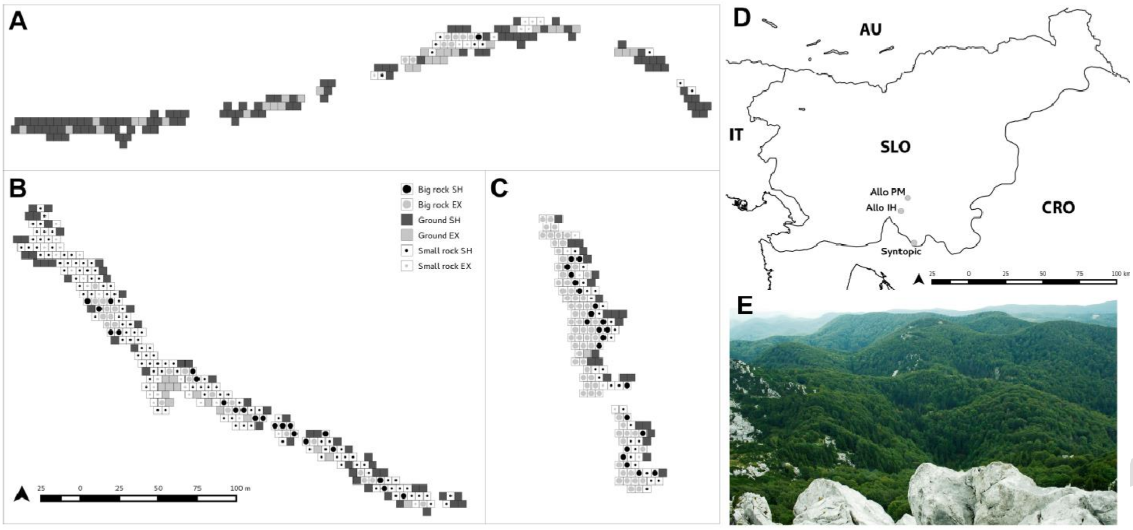

Fig. 1. Representation of microhabitats on a 5×5 m raster grid where each grid shows the microhabitat surface (see legend): (A) allotopic Podarcis muralis (AlloPMUR), (B allotopic Iberolacerta horvathi (AlloIHOR), and (C) syntopic population (Syntopic). Three study sites were located in Kočevsko region, Slovenia (D). Photo taken from the syntopic site, Kužejska stena, photo credits: Miha Krofel (E).

2.2 Lizard surveys

We conducted field studies on lizards in the summer of 2012. We collected all observations on three consecutive sunny days without wind at each site. Surveys lasted all day, beginning at 7:00 am and ending at 7:00 pm, to capture all lizard activity time. The observer (all three authors conducted the fieldwork) moved from one side of the survey area to the other at a steady walking pace to search for lizards. When finished, the observer paused for 15 minutes before continuing in the opposite direction. This was repeated many times throughout the day. Repeating surveys in the same population can be considered pseudo-replication, but that is not the case here. Pseudo-replication occurs when multiple observations of the same object (in our case, the same individual) are made in a single repetition of a treatment (here, each survey; Hurlbert, 1984; Heffner et al., 1996; Millar and Anderson, 2004). Pseudo-replication is defined as "the failure to acknowledge sequential measurement of multiple observations on the same treatment replicate" (Millar and Anderson, 2004). Thus, in our case, pseudo-replication should occur when multiple observations of the same individual were recorded within each survey but not across surveys. We recorded each individual only once per survey (walk).

2.3 Data collection

At each sighting of a lizard, the observer stopped and noted time, location (using an accurate GPS Trible GeoExplorer HX; error ~10 cm after post-differential correction), species, age class (by estimating SVL: juvenile, subadult, or adult), sex (if possible), microhabitat (selected from given categories: large rock, small rock, and soil), sun exposure (fully exposed to sun or shaded), and air and surface temperature (using a Fluke® 68 portable infrared thermometer, accuracy 0.1ºC; accuracy ±1% according to the manufacturer). At the syntopic site, we recognised species by the position of the scales on the head or the coloration of the throat region, which serve as reliable taxonomic characteristics to distinguish the species studied (Tome, 1999; Arnold and Ovenden 2004). We determined the species immediately or later from the photograph when possible. The sample size of juvenile lizards was too small to include in the analysis, so we considered only adults. We made the same decision for sexes, as we were only able to determine the sex of approximately 50% of all adults. Therefore, the sample size for each sex was too small to perform a meaningful analysis, and we included all adults in the analysis regardless of sex.

2.4 Microhabitat description

We assigned each lizard sighting to a GPS point; we assigned the microhabitat at that location to one of six microhabitat categories (see below) based on the description of the main features of the substrate and shading in the 5×5 m area. We designated substrate as rock, which was calcareous rock in all study areas, if more than 50% of the substrate in a 5×5 m grid was covered with rock. We considered large rocks to be rocks larger than 50 cm in the longest direction and small rocks if they were less than 50 cm. If more than 50% of the surface area within the 5×5 m was without rocks, this was referred to as soil, which was always covered with either grass or shrubs. We designated shading in the 5×5 m grid cell as sun-exposed if more than 75% of the surface was exposed to the sun, and part shade when more than 25% of the surface was in shade. We used these point data to create 5×5 m microhabitat grid maps of the study areas. First, we calculated a 5 m buffer around lizard locations (GPS points) in each study area to delineate the study area. Next, we interpolated categorical habitat data from lizard habitat records with Voronoid polygons within the buffer area and assumed that habitat is continuous between two lizard records with the same habitat category, but additionally confirming this with visual inspection of orthophoto maps. Next, we gridded the study areas into 5×5 m grid cells. We assigned each grid cell to one of six microhabitat categories according to surface area and sunlight exposure: i) large rock in sun, ii) large rock in partial shade, iii) small rock in sun, iv) small rock in partial shade, v) soil in sun, and vi) soil in partial shade (Fig. 1).

2.5 Surface temperature survey and analysis

We measured surface temperatures (Te) with data loggers (Maxim iButtons DS1921G) placed in six different microhabitats at all three study sites: on large and small rocks in the same positions as the observed lizards; on the soil, in the same way as the moving lizards; on top of the grass and under the bushes. The data loggers remained at each location for one month, continuously recording temperature data at 20-minute intervals. From the total data set of temperatures recorded by the data loggers (30 days), we selected the 10 warmest days that represented optimal conditions for lizard activity and had similar conditions when we conducted the lizard surveys. We calculated the mean temperature of each hour for the period of lizard activity from 8:00 to 18:00 for each microhabitat at each study site. Next, we interpolated the surface temperature data (Te) using Inverse Distance Weighted (IDW) with a power of 2 in R software (R Core Team, 2020) to create spatial thermal maps of surface temperatures for each hourly interval for all three sites (Suppl. M. A).

2.6 Data analysis

We used Chi-square tests for microhabitat surface category selection. To analyse surface temperature selection across the day, we conducted ANOVA analyses with factor selection/availability and hour and factor interaction, followed by a post-hoc Tukey test. Whenever necessary, we log-transformed the data to homogenise variances before testing. We performed all analyses using R software (R Core Team, 2020).

3. RESULTS

3.1 Microhabitat

We collected 687 observations of lizards: 389 at the AlloPMUR site, 233 at the AlloIHOR site, and 65 (56 *I. horvathi* and 9 *P. muralis*) at the Syntopic site. At AlloIHOR, the most common microhabitats available were shaded small rocks (45%) and shaded soil (22%), followed by shaded and sun-exposed big rocks (both 9%) and sun-exposed small rocks (9%) (Fig. 2A). At the AlloPMUR site, the highest proportion of microhabitats was sun-exposed and shaded soil (63% and 20%, respectively), followed by a low proportion of shaded small rocks (6%) and sun-exposed small and large rocks (both 5%) (Fig. 2B). At the Syntopic site, the most common microhabitat was sun-exposed large big rocks (46%), followed by shaded small rocks (18%), shaded soil (16%) and shaded big rocks (15%) (Fig. 2C). Lizards used microhabitats at a different ratio than available at all sites (all pairwise Chi-square comparisons were P < 0.001, Table 2).

Table 2. Results of Chi-square tests comparing lizard's microhabitat use to the available microhabitat in the respective study area. χ^2: Chi-square value, df: degrees of freedom, P: corresponding p-value. Significant effects are marked in bold letters.

Site	Species	χ^2	df	P
AlloIHOR	*Iberolacerta horvathi*	104.73	5	**<0.0001**
AlloPMUR	*Podarcis muralis*	363.10	5	**<0.0001**
SynIHOR	*Iberolacerta horvathi*	166.63	5	**<0.0001**
SynIHOR	*Podarcis muralis*	267.33	5	**<0.0001**

At the AlloIHOR site, *I. horvathi* lizards occurred most frequently on shaded big and small rocks (33% and 39%, respectively) and on sun-exposed big rocks (21%) (Fig. 2A). At the AlloPMUR site, *P. muralis* lizards occurred almost equally in different microhabitats: sun-exposed big rocks (25%), sun-exposed soil (21%) and shaded small rocks (19%), followed by shaded big rocks (15%) and sun-exposed small rocks (13%) (Fig. 2B). At the Syntopic site, *I. horvathi* lizards occurred predominantly on shaded and sun-exposed big rocks (61% and 23%, respectively) (Fig. 2C), whereas *P. muralis* lizards occurred on shaded big rocks (67%) and shaded soil (33%, Fig. 2C), but the sample size of *P. muralis* was very small (N = 9).

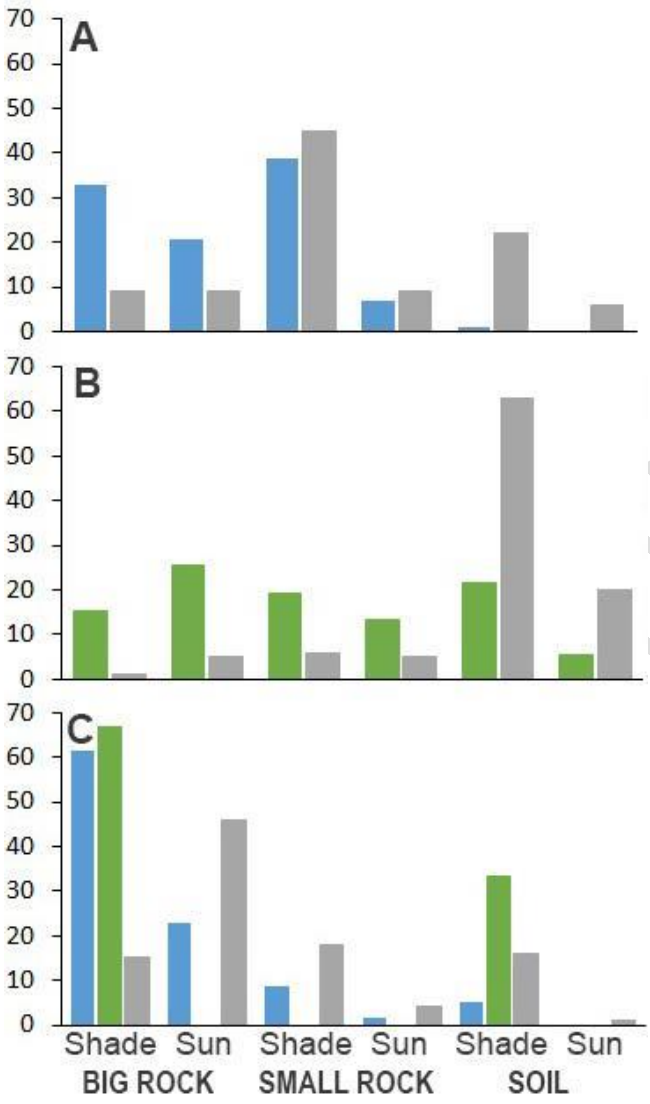

Fig. 2. Microhabitat availability (grey) and lizard use of *Iberolacerta horvathi* (blue) and *Podarcis muralis* (green) in three study sites: (A) AlloIHOR, (B) AlloPMUR, and (C) Syntopic. Labels: SHADED = partly shaded and SUN = exposed to the sun.

3.2 Surface temperature

Surface temperatures during lizard activity were lowest in AlloIHOR (mean between 9h and 17h: 26.9ºC), highest in the syntopic area (mean between 9h and 17h: 40.9ºC) and medium-high in AlloPMUR (mean between 8h and 18h: 31.4ºC, Suppl. M. B). The mean surface temperature of the selected sites of I. *horvathi* at the AlloIHOR site was also lowest (26.0ºC), medium-high for the sites of *P. muralis* at the AlloPMUR site (31.3ºC), and highest for the sites of *I. horvathi* and *P. muralis* at the Syntopic site (43.0ºC and 37.8ºC, respectively, Suppl. M. B). In AlloIHOR, surface temperatures of *I. horvathi* sites differed from those available at 14 and 15 h, when lizards chose lower surface temperatures than those available (Table 3, Fig. 3A). In contrast, *P. muralis* at AlloPMUR chose higher surface temperatures than available between 12-14 h and at 16 h (Table 3, Fig. 3B). At the Syntopic site, *I. horvathi* chose lower surface temperatures than available on average (Table 3, Fig. 3C), while we were unable to perform a statistical analysis for *P. muralis* due to missing values in the hourly intervals and small sample size.

Table 3. Results of ANOVA analyses of surface temperatures using factors Hour and lizard selection Selection/Availability that were compared to available surface temperatures in three study sites and two species: AlloIHOR = allotopic *Iberolacerta horvathi*, AlloPMUR = allotopic *Podarcis muralis* and Syntopic – here analysis was done only for *I. horvathi* because the sample size for *P. muralis* did not allow it (N=9). df: degrees of freedom, F = F statistics, P: corresponding p-value. Significant effects are marked in bold letter.

		Sum of Squares	df	F	P
AlloIHOR	Hour	18093.3	8	1731.2	**< 0.001**
Iberolacerta horvathi	Selection	7.3	1	5.6	**0.018**
	Hour ✻ Selection	108.1	8	10.4	**< 0.001**
	Residuals	213194.4	163187		
AlloPMUR	Hour	77758.0	10	3071.6	**< 0.001**
Podarcis muralis	Selection	1100.0	1	434.3	**< 0.001**
	Hour ✻ Selection	1098.0	10	73.4	**< 0.001**
	Residuals	518984.0	205011		

Syntopic *Iberolacerta horvathi*	Hour	5400.2	8	110.7	**< 0.001**
	Selection	64.1	1	10.5	**0.001**
	Hour ✻ Selection	26.7	8	0.5	0.821
	Residuals	531062.7	87113		

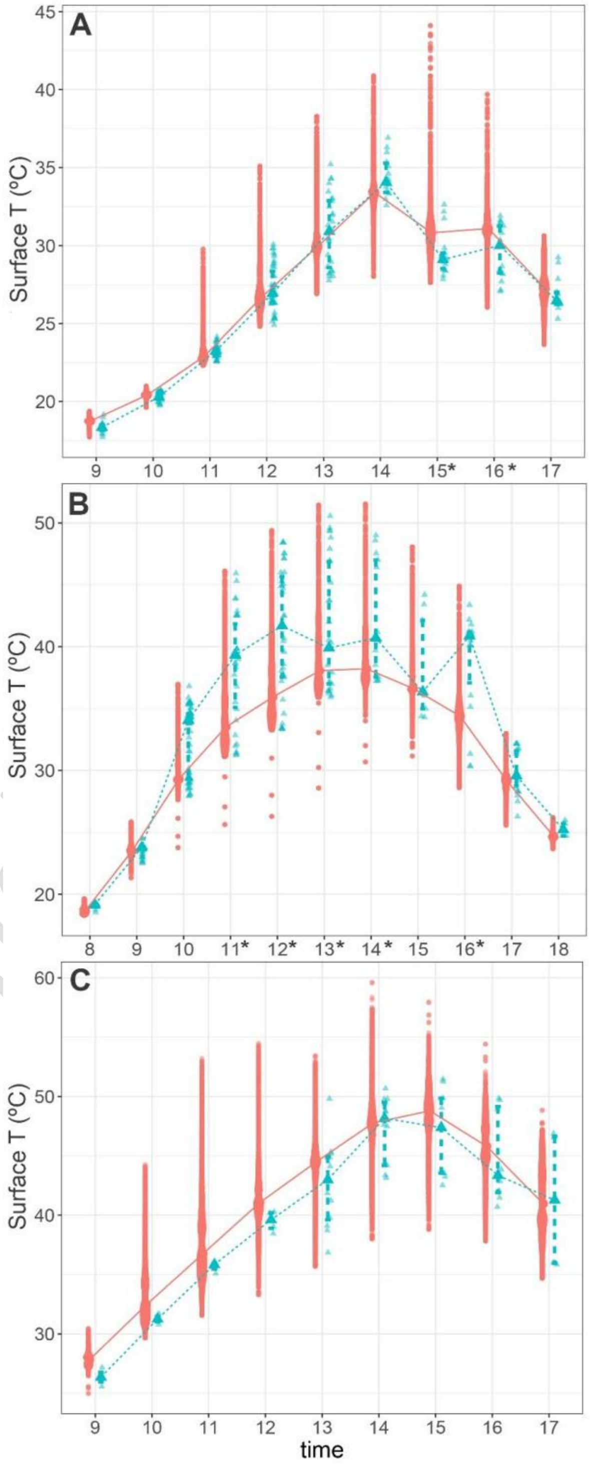

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Fig. 3. Surface temperatures obtained for each hour of the day during the lizard activity. Red colour presents the available surface temperatures measured with data-loggers and blue colour are surface temperatures selected by lizards of *Iberolacerta horvathi* and *Podarcis muralis* in the three study sites (A) allotopic *Iberolacerta horvathi* (AlloIHOR), (B) allotopic *Podarcis muralis* (AlloPMUR), and (C) syntopic population (Syntopic) – here selection is presented only for I. horvathi because the sample size for P. muralis was very small (N=9). Asterisks (*) next to the hour label indicate a significant result of the Tukey post-hoc test meaning a significant difference between available and lizards' selected surface T.

4. DISCUSSION

Microhabitat use by sympatric *I. horvathi* and *P. muralis* differed at the three study sites, reflecting site-specific conditions in surface temperatures but not in substrate use. Both species selected a specific substrate (rock or soil or both), so substrate may be the most important factor limiting species presence. We confirmed our hypothesis that the more generalist species (*P. muralis*) used both rock and soil substrate, whereas the rock-specialized species, *I. horvathi* (Arnold, 1987), selectively used rocky substrate. Rocks are also less densely vegetated, so these results are consistent with some previous findings, e.g., that *I. horvathi* generally selects sites with lower vegetation cover than *P. muralis* (Lapini et al., 1993; Cabela et al., 2007).

Using the high-precision GPS locations of the lizards and creating thermal surface maps from the data logger data, we were able to analyze the selection of surface temperatures during daily lizard activity at each site. We found that activity duration generally followed the pattern of surface temperatures at each study site: At the allotopic *P. muralis* site, where surface temperatures warmed more rapidly in the morning and cooled more slowly in the afternoon, activity was 2 hours longer than at other sites (from 8 am to 6 pm). *I. horvathi* at the allotopic site was active from 9 am to 5 pm, which was due to low surface temperatures. The syntopic site was characterized by the highest average surface temperatures, but lizards were still only active between 9 am and 5 pm, as this site is the most west-facing of the three. Lacertid lizards are diurnal and exhibit either a unimodal or a bimodal pattern of diurnal activity depending on the climatic characteristics of the habitat in which they live (Pianka and Vitt, 2003). The species we studied, *I. horvathi* and *P. muralis*, were previously thought to have a similar diurnal activity pattern, with their diurnal activity pattern being mostly bimodal (De Luca, 1992; Lapini et al., 1993), but may become unimodal in spring (De Luca, 1992). In this sense, our study brings some new results: Both species had a unimodal activity pattern, despite very high temperatures in summer.

In addition, a comparison of available surface temperatures with those used by the lizards showed that selection occurs in certain hours of the day, depending on location and species. The allotopic *I. horvathi* lizards selected for lower than available surface temperatures in the afternoon. The allotopic *P. muralis* selected higher than available surface temperatures during most of the day. And at the syntopic site, *I. horvathi* consistently selected lower than available temperatures throughout the day, while we were unable to conduct an analysis for *P. muralis* due to the low density at this site and associated small sample size. The results that *I. horvathi* prefers cooler and *P. muralis* prefers warmer surface temperatures are consistent with known ecophysiological differences between these two species. For example, *P. muralis* chooses a higher tpref in spring than *I. horvathi* and exhibits less precise thermoregulatory behaviour (wider range and seasonal differences in preferred body temperatures; Osojnik et al., 2013). *I. horvathi* has higher metabolic potential and resistance to dehydration, representing ecophysiological and behavioural adaptation to thermoregulation in more thermally restrictive environments (Osojnik et al., 2013; Žagar et al., 2015a,b). Thus, the most important finding from the selection of surface temperatures in our study was that species reflect their ecophysiological differences in their thermal use of space.

Importantly, by acquiring datasets with high-precision GPS receivers and GIS interpolation tools from ground measurements (i.e., temperate and habitat types), we were able to analyze spatial patterns at very high spatial resolution (Sillero et al., 2020). Previous studies have used LiDAR data (Sillero and Gonçalves-Seco, 2014) or orthophotos and data loggers (Sillero et al., 2021 a). But we show here that it is also possible to perform spatial analyzes without using remote sensing imagery with a very high spatial resolution, which can be very costly (Perotto-Baldivieso et al., 2009). However, our study is limited by the environmental data we were able to measure and the small sample size at some study sites. First, access to remote sensing imagery with very high spatial resolution (from satellites or aerial photographs) will improve our ability to analyze the relationship between species and microhabitats in the future. In any case, spatial analyzes open new opportunities to better analyze which environmental factors determine species distributions at local scales (Sillero et al., 2014; Sillero et al., 2021 a). Second, because of the small sample size, our analysis was only partially possible (for one species at one of the three sites), so the results presented for other sites nevertheless provide valuable new information that expands knowledge about the ecology of the species studied. In addition, they provide a novelty in terms of the microscale of habitat use and linkage to thermal conditions that has rarely been explored.

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6. CRediT author statement

Anamarija Žagar: Conceptualization, Methodology Lizard and temperature surveys, Data curation, Writing-Original draft preparation, Visualization, Investigation. Neftali Sillero: Conceptualization, Methodology Spatial analysis, Data curation, Visualization, Investigation, Writing- Reviewing and Editing. Veronica Gomes: Conceptualization, Validation, Writing-Reviewing and Editing.

7. REFERENCES

Angilletta, M.J. (2001): Thermal and physiological constraints on energy assimilation in a widespread lizard (*Sceloporus undulatus*). Ecology 82: 3044-3056.

Angilletta, M.J., Hill, T., Robson, M.A. (2002): Is physiological performance optimized by thermoregulatory behavior?: a case study of the eastern fence lizard, *Sceloporus undulatus*. Journal of Thermal Biology 27: 199-204.

Angilletta, M.J. (2009): Thermal adaptation: a theoretical and empirical synthesis. Oxford, University Press.

Arnold, E.N. (1987): Resource partition among lacertid lizards in southern Europe. J. Zool. Ser. B 1: 739-782.

Arnold, E.N., Ovenden, D. (2004): A field guide to the reptiles and amphibians of Britain and Europe. Collins, London.

Bakken, G.S., Angilletta Jr, M.J. (2014): How to avoid errors when quantifying thermal environments. Functional Ecology 28: 96-107.

Braña, F. (1993): Shifts in body temperature and escape behaviour of female *Podarcis muralis* during pregnancy. Oikos 66: 216-222.

Cabela, A., Grillitsch, H., Tiedemann, F. (2007): Habitatpraferenzen von *Podarcis muralis* (Laurenti, 1768) und *Iberolacerta horvathi* (Mehely, 1904) bei gemeinsamem Vorkommen. Herpetozoa 19: 149-160.

Carneiro, D., García-Muñoz, E., Žagar, A., Pafilis, P., Carretero, M.A. (2017): Is ecophysiology congruent with the present-day relictual distribution of a lizard group? Evidence from preferred temperatures and water loss rates. Herpetological Journal 27: 47-56.

Carrascal, L.M., Cano, C., Diaz, J.A. (1989): Habitat selection in Iberian *Psammodromus* species along a Mediterranean successional gradient. Amphibia-Reptilia 10: 231-242.

Carretero, M., Roig, J., Llorente, G. (2005): Variation in preferred body temperature in an oviparous population of *Lacerta* (*Zootoca*) *vivipara*. The Herpetological Journal 15: 51-55.

Carretero, M.A., Marcos, E., de Prado, P. (2006): Intraspecific variation of preferred temperatures in the NE form of *Podarcis hispanica*. In: Mainland and Insular Lacertid Lizards: a Mediterranean Perspective, p. 55-64. Corti, C., Lo Cascio, P., Biaggini, M., Eds., Firenze University Press, Florence.

Christian, K.A., Tracy, C.R. (1981): The effect of the thermal environment on the ability of hatchling Galapagos land iguanas to avoid predation during dispersal. Oecologia 49: 218-223.

De Luca, N. (1992): Notes on biology and ecology of the Horvath's rock lizard (*Lacerta horvathi* Méhely, 1904, Reptilia: Lacertidae). In: Proceeding of the Sixth Ordinary General Meeting of the Societas Europaea Herpetologica, Budapest 1991, p. 129-135. Korsós, Z., Kiss, I., Eds., Hungarian Natural History Museum, Budapest.

Diaz, J.A., Carrascal, L.M. (1991): Regional distribution of a Mediterranean lizard: influence of habitat cues and prey abundance. Journal of Biogeography: 291-297.

Heffner, R.A., Butler, M.J., Reilly, C.K. (1996): Pseudoreplication revisited. Ecology 77: 2558-2562.

Huey, R.B. (1982): Temperature, physiology, and the ecology of reptiles. In: Biology of the Reptilia 12, Physiology C., p. 25-91. Gans, C., Pough, F.H., Eds., Academic Press, London.

Hurlbert, S.H. (1984): Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211.

Kondo, J., Downes, S.J. (2007): Does social behaviour reliably reflect temperature-dependent physiological capacity in geckos? Animal Behaviour 74: 873-880.

Krofel, M., Cafuta, V., Planinc, G., Sopotnik, M., Šalamun, A., Tome, S., Vamberger, M., Žagar, A. (2009): Distribution of reptiles in Slovenia: a review of data collected until 2009. Natura Sloveniae 11: 61-99.

Langkilde, T., Shine, R. (2004): Competing for crevices: interspecific conflict influences retreat-site selection in montane lizards. Oecologia 140: 684-691.

Lapini, L., Richard, J., Dall'Asta, A. (1993): Distribution and ecology of *Lacerta horvathi* Mehely, 1904 (Reptilia, Lacertidae) in North-Eastern Italy. Atti di Museo Civico di Storia Naturale Trieste 14: 213-230.

Lapini, L., Dall'Asta, A., Luiselli, L., Nardi, P. (2004): *Lacerta horvathi* in Italy: a review with new data on distribution, spacing strategy and territoriality (Reptilia, Lacertidae). Bollettino di Zoologia 71: 145-151.

Luiselli, L. (2006): Resource partitioning and interspecific competition in snakes: the search for general geographical and guild patterns. Oikos 114: 193-211.

Luo, L.-G., Ding, G.-H., Ji, X. (2010): Income breeding and temperature-induced plasticity in reproductive traits in lizards. Journal of Experimental Biology 213: 2073-2078.

Millar, R.B., Anderson, M.J. (2004): Remedies for pseudoreplication. Fisheries Research 70: 397-407.

Osojnik, N., Žagar, A., Carretero, M.A., Garcia-Munoz, E., Vrezec, A. (2013): Ecophysiological dissimilarities of two sympatric lizards. Herpetologica 69: 445-454.

Perotto-Baldivieso, H.L., Melendez-Ackerman, E., Garcia, M.A., Leimgruber, P., Cooper, S.M., Martinez, A., Calle, P., Gonzales, O.M.R., Quinones, M., Christen, C.A. (2009): Spatial distribution, connectivity, and the influence of scale: habitat availability for the endangered Mona Island rock iguana. Biodiversity and Conservation 18: 905-917.

Pianka, E.R. (1973): The structure of lizard communities. Annual review of ecology and systematics: 53-74.

Pianka, E.R., Vitt, L.J. (2003): Lizards: windows to the evolution of diversity. Univiversity of California Press, Berkley and Los Angeles, California.

Puncer, I. (1980): Dinarski jelovo bukovi gozdovi na Kočevskem. Razprave SAZU XII: 407-561.

R Core Team (2020): R: A Language and Environment for Statistical Computing. https://www.R-project.org/. R Foundation for Statistical Computing, Vienna, Austria.

Richard, J., Lapini, L. (1993): Trophic niche overlap in syntopic populations of *Lacerta horvathi* and *Podarcis muralis* (Reptilia, Lacertidae). Atti di Museo Civico di Storia Naturale Trieste 45: 151-157.

Sannolo, M., Carretero, M.A. (2019): Dehydration constrains thermoregulation and space use in lizards. PLoS One 14: e0220384.

Sears, M.W., Angilletta, M.J. (2015): Costs and Benefits of Thermoregulation Revisited: Both the Heterogeneity and Spatial Structure of Temperature Drive Energetic Costs. The American Naturalist 185: E94-E102.

Sillero, N. (2011): What does ecological modelling model? A proposed classification of ecological niche models based on their underlying methods. Ecological Modelling 222: 1343-1346.

Sillero, N., Goncalves-Seco, L. (2014): Spatial structure analysis of a reptile community with airborne LiDAR data. International Journal of Geographical Information Science 28: 1709-1722.

Sillero, N., Gomes, V. (2016): Living in clusters: the local spatial segregation of a lizard community. Basic and Applied Herpetology 30: 61-75.

Sillero, N., Argaña, E., Freitas, S., Garcia-Munoz, E., Arakelyan, M., Corti, C., Carretero, M. (2018): Short term spatial structure of a lizard (*Darevskia* sp.) community in Armenia. Acta Herpetologica 13: 155-163.

Sillero, N., Argaña, E., Matos, C.t., Franch, M., Kaliontzopoulou, A., Carretero, M.A. (2020): Local Segregation of Realised Niches in Lizards. ISPRS International Journal of Geo-Information 9: 764.

Sillero, N., Dos Santos, R., Teodoro, A., Carretero, M. (2021a): Ecological niche models improve home range estimations. Journal of Zoology 313: 145-157.

Sillero, N., Arenas-Castro, S., Enriquez-Urzelai, U., Vale, C.G., Sousa-Guedes, D., Martinez-Freira, F., Real, R., Barbosa, A.M.r. (2021b): Want to model a species niche? A step-by-step guideline on correlative ecological niche modelling. Ecological Modelling 456: 109671.

Speybroeck, J., Beukema, W., Bok, B., Van Der Voort, J. (2016): Field guide to the amphibians and reptiles of Britain and Europe. Bloomsbury publishing.

Tome, S. (1999): Razred: Plazilci, Reptilia. In: Ključ za določanje vretenčarjev Slovenije, p. 284-305. Kryštufek, B., Janžekovič, F., Eds., DZS, Ljubljana.

Veríssimo, C.V., Carretero, M.A. (2009): Preferred temperatures of *Podarcis vaucheri* from Morocco: intraspecific variation and interspecific comparisons. Amphibia-Reptilia 30: 17-23.

Žagar, A. (2008): The lowest altitudinal record of Horvath's Rock Lizard (*Iberolacerta horvathi*) in Slovenia. Natura Sloveniae 10: 59-61.

Žagar, A., Kos, I., Vrezec, A. (2013): Habitat segregation patterns of reptiles in Northern Dinaric Mountains (Slovenia). Amphibia-Reptilia 34: 263-268.

Žagar, A., Carretero, M.A., Osojnik, N., Sillero, N., Vrezec, A. (2015a): A place in the sun: interspecific interference affects thermoregulation in coexisting lizards. Behavioral Ecology and Sociobiology 69: 1127-1137.

Žagar, A., Simčič, T., Carretero, M.A., Vrezec, A. (2015b): The role of metabolism in understanding the altitudinal segregation pattern of two potentially interacting lizards. Comp. Biochem. Physiol. Part A: Molecular & Integrative Physiology 179: 1-6.

Žagar, A. (2016): Altitudinal distribution and habitat use of the common wall lizard *Podarcis muralis* (Linnaeus, 1768) and the Horvath's rock lizard *Iberolacerta horvathi* (Méhely, 1904) in the Kočevsko region (S Slovenia). Natura Sloveniae 18: 47-62.

Žagar, A., Carretero, M.A., Vrezec, A., Drašler, K., Kaliontzopoulou, A. (2017): Towards a functional understanding of species coexistence: ecomorphological variation in relation to whole-organism performance in two sympatric lizards. Functional Ecology 31: 1780-179.