UNIVERSITY OF LJUBLJANA
BIOTECHNICAL FACULTY

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INTERSPECIFIC COMPETITION BETWEEN THE COMMON WALL LIZARD (*Podarcis muralis* [Laurenti 1768]) AND THE HORVATH'S ROCK LIZARD (*Iberolacerta horvathi* [Méhely 1904])

MEDVRSTNO TEKMOVANJE MED POZIDNO (*Podarcis muralis* (Laurenti 1768)) IN VELEBITSKO KUŠČARICO (*Iberolacerta horvathi* (Méhely 1904))

DOCTORAL DISSERTATION

Ljubljana, 2016

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AB The understanding of mechanisms of interspecific competition between ecologically similar sympatric species is often lacking from studies predicting the impact of future climate changes. However biotic interactions are known to be key factors influencing the community structure. We studied interspecific competitive mechanisms in two species: the Horvath's rock lizard (*Iberolacerta horvathi* [Méhely, 1904]) and the common wall lizard (*Podarcis muralis* [Laurenti, 1768]). At first we examined the potential for competition between studied species by comparing their realised niches in the sympatric area and their morphological, physiological and ecological traits (species' fundamental ecological niches). Altitude contributed the most to the segregation pattern in their distribution. Both species have similar general habitat use and were morphologically similar, except for the head height, which might have reprecursions in segregation in the use of refuge sites. Species were similar in the mean of preferred body temperatures and metabolic rates, but differed in the precision of thermoregulation and the potential metabolic activity. Thus, *I. horvathi* might have eco-physiological competitive advantages over *P. muralis* in thermally restrictive (cold) environments. Furthermore, species were found to compete for limited resource (sun-exposed areas) via direct agonistic interactions, indicating an asymmetric interspecific interaction (*P. muralis* showed to be in adavnatge over *I. horvathi*). We have also assesed the role of common predators as mediators on the interaction between lizards as prey species. We suggest that “a more cautious” anti-predator behavioural response of *I. horvathi* might provide direct benefits (higher survival rates) but only in populations where predation pressure was high, otherwise it carries substantial time and thermoregulatory costs. Overall results of the dissertation improved our understanding of interspecific competition between studied sympatric species. Such information may also be used for improving results of modelling predictions of the effect of future climate changes on the distribution of these protected species.

KLJUČNA DOKUMENTACIJSKA INFORMACIJA

ŠD Dd
DK UDK 591:598.112.23(043.3)
KG višinska segregacija/medvrstna kompeticija/fundamentalna ekološka niša/ realizirana ekološka niša/tekmovanje s posredovanjem/termoregulacija/kuščarica/ *Iberolacerta horvathi*/velebitska kuščarica/*Podarcis muralis*/pozidna kuščarica
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OP XIII, 123 str., 8 sl., 2 tab., 178 vir.
IJ en
JI en/sl
AI Razumevanje mehanizma medvrstnega tekmovanja med ekološko podobnimi vrstami, ki živijo v simpatriji, pogosto manjka v raziskavah, ki napovedujejo vplive prihodnjih podnebnih sprememb na strukturo živalskih združb, kljub temu, da so biotske interakcije eden od ključnih dejavnikov, ki nanjo vplivajo. V naši raziskavi smo raziskovali mehanizem medvrstnega tekmovanja med dvema vrstama, velebitska kuščarica (*Iberolacerta horvathi* (Méhely, 1904)) in pozidna kuščarica (*Podarcis muralis* (Laurenti, 1768)). Sprva smo raziskali potencial za medvrstno tekmovanje s primerjavo rabe prostora in morfoloških, fizioloških in ekoloških značilnosti njunih temeljnih ekoloških niš. Nadmorska višina je najbolj prispevala k razumevanju vzorca prostorske segregacije med vrstama. Obe vrsti imata v splošnem podobno rabo prostora in sta morfološko podobni, razen v višini glave, ki bi lahko vplivala na ločevanje pri uporabi skrivališč. Vrsti imata podobne povprečne izbrane telesne temperature in stopnjo metabolizma, vendar se razlikujeta v natančnosti termoregulacije in potencialu metabolizma. *I. horvathi* ima morda eko-fiziološke konkurenčne prednosti pred *P. muralis* v termalno omejujočih (hladnejših) okoljih. Ugotovili smo tudi, da vrsti lahko tekmujeta za omejen vir (soncu izpostavljena mesta) preko neposrednih agonističnih interakcij, ki so bile asimetrične (*P. muralis* bi lahko bila v prednosti pred *I. hrovathi*). V zadnji raziskavi smo ugotavljali vlogo skupnih plenilcev kot mediatorjev na interakcijo med plenskima vrstama. "Bolj previden" odziv v protiplenilskem vedenju pri *I. horvathi* bi lahko tej vrsti zagotovil večje neposredne koristi (večjo stopnjo preživetja), vendar le v populacijah, kjer je plenilski pritisk večji, sicer pa nosi velike energetske stroške. Rezultati disertacije so izboljšali naše razumevanje medvrstnega tekmovanja med simpatričnimi vrstami, ki bodo lahko uporabljeni v prihodnosti za izboljšanje modelov, ki se uporabljajo za predvidevanje vplivov prihodnjih podnebnih sprememb.

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ABBREVIATION AND SYMBOLS

df	degree of freedom
EWL	evaporative water loss rate
Tb	body temperature
Tp	preffered body temperature

LIST OF SCIENTIFIC ARTICLES AND AUTHORSHIP RIGHTS

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Article I:

ŽAGAR Anamarija, KOS Ivan, VREZEC, Al (2013): Habitat segregation patterns of reptiles in Northern Dinaric Mountains (Slovenia). Amphibia-Reptilia 34: 263-268. doi:10.1163/15685381-00002889

Article II:

ŽAGAR, Anamarija, OSOJNIK, Nadja, CARRETERO, Miguel A., VREZEC, Al (2012): Quantifying the intersexual and interspecific morphometric variation in two resembling sympatric lacertids: *Iberolacerta horvathi* and *Podarcis muralis*. Acta Herpetol. vol. 7, no. 1: 29-39. doi: 10.13128/Acta_Herpetol-9602

Article III:

OSOJNIK, Nadja, ŽAGAR, Anamarija, CARRETERO, Miguel A., GARCÍA-MUÑOZ Engrique, VREZEC, Al (2013): Ecophysiological dissimilarities of two sympatric lizards. Herpetologica, Allen Press Publishing Services, 69: 445-454. doi: 10.1655/HERPETOLOGICA-D-13-00014

Article IV:

ŽAGAR, Anamarija, SIMČIČ, Tatjana, CARRETERO, Miguel A., VREZEC, Al (2015): The role of metabolism in understanding the altitudinal segregation pattern of two potentially interacting lizards. Comparative Biochemistry and Physiology Part A: Molecular & Integrative Physiology 179: 1-6. doi: 10.1016/j.cbpa.2014.08.018

Article V:

ŽAGAR, Anamarija, CARRETERO, Miguel A., OSOJNIK, Nadja, SILLERO, Neftalí, VREZEC, Al (2015): A place in the sun: interspecific interference affects thermoregulation in coexisting lizards. Behavioral Ecology and Sociobiology 69: 1127-1137. doi: 10.1007/s00265-015-1927-8

Article VI:

ŽAGAR, Anamarija, BITENC, Katja, VREZEC, Al, CARRETERO, Miguel A. (2015): Predators as mediators: Differential antipredator behavior in competitive lizard species in a multi-predator environment. Zoologischer Anzeiger: A Journal of Comparative Zoology 259: 31-40. doi: 10.1016/j.jcz.2015.10.002

“Lizards have held a prominent place in indigenous art and myth, have been hunted and eaten, have been raised for food, have become the basis for a multimillion dollar pet trade, and are important components of most natural ecosystems. If you haven’t yet had an intimate relationship with a lizard, you should!”

(Eric R Pianka and Laurie J Vitt, Lizards: windows to the evolution of diversity, 5th ed., 2003)

»Oba, znanstvenik in pisatelj, lahko pri iskanju svoje zgodbe zaupata zgolj intuiciji, ki edina lahko namigne, da se prav v določenem literarnem motivu, v določenem znanstvenem vprašanju, skriva dovolj pomenljiva zgodba, da jo je vredno počasi, drobec za drobcem odkrivati, čistiti, sestavljati, se ji čuditi in jo povsem po človeško imeti rad.«

(Anton Ihan, Platon pri Zobozdravniku. Eseji, 1997)

1 INTRODUCTION

Ecosystems are usually composed of multiple species organised in communities where they interact with each other. Members of the community (species) that share resources in the same way belong to the same ecological guild (Root 1969). In communities where two or more members of the same ecological guild coexist and resources that they utilize are limited, they will either segregate in one or more dimensions of ecological niche to avoid interspecific interactions or they will interact (Begon et al., 2006). Interspecific interactions, direct or indirect, have been identified as one of the most important processes determining the structure of natural communities (Cody and Diamond, 1975; Bonsall and Hassell, 1997; Vrezec and Tome, 2004).

In this dissertation we studied the mechanism and possible outcomes of interspecific competition between two species, which belong to the same ecological guild and exhibit sympatric distribution across the range of at least one species. We used a multidisciplinary approach including fields of morphometry, eco-physiology, behaviour and ecology. Studied lizards are small, active, diurnal and abundant. This allowed us to make direct observations, keep lizards in captivity and use them in in experimental studies. The species studied are ectotherms with limited dispersal ability thus are likely to be strongly impacted by rapid climate changes. Understanding species interactions and how they can be affected by future climate change is important for future planning of conservation activities of potentially threatened species.

1.1 DISTRIBUTION PATTERNS OF TWO SPECIES OF THE SAME GUILD

The current distribution of a species is a result of species’ biogeographical history and dispersal abilities and can be affected by current biotic and abiotic factors (e.g. Lomolino et al., 1989; Langkilde and Shine, 2004; Vrezec and Tome, 2004; Mallet et al., 2009). Competition is one of the most important biotic factors influencing species distributions (Schoener, 1977) and climate changes are considered to be most influential among abiotic factors (Tylianakis et. al, 2008).

Species that completely segregate in space have allopatric distributions and species that coexist in the same area live in sympatry (Fig. 1). Species generally coexist when interspecific competition is less important than intraspecific (both species have less competitive effect on the other species than they have on themselves) and a stable equilibrium combination is reached (Begon et al., 2006). Allopatry is most often sustained with a natural barrier that prevents secondary contact between ecologically similar species (Begon et al., 2006). In some cases, allopatry can be a consequence of competitive exclusion, where the competitively stronger species causes extinction of the inferior species in areas of overlap. Inferior species can only survive in areas where a competitively stronger species is not able to arrive. When ancestors of two species were in competition for long periods in the past, this may have influenced co-evolutionary adaptations in such a way that species evolved differences in their ecological niches. When two species sufficiently diverged in their ecological niches, this can either promote their coexistence (sympatry) or dispersal that will lead to complete spatial segregation (allopatry). Such outcomes are a phenomenon termed as “the ghost of competition” (Langkilde et al., 2005).

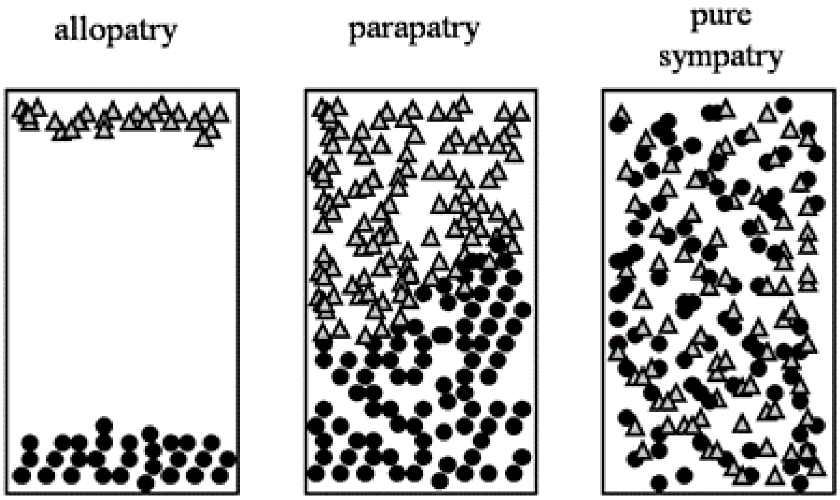

Figure 1: Simplified schematic representation of three options of species distribution patterns for two species: allopatry, parapatry and sympatry. In parapatry two species distributions overlap in the middle zone of overlap, where is a high likelihood for interspecific interaction (Mallet et al., 2009: 2334).

Slika 1: Poenostavljena shematska predstavitev treh tipov prostorske razporeditve dveh vrst: alopatrična, parapatrična in simpatrična razporeditev. Pri parapatrični razporeditvi v vmesnem območju dve vrsti živita skupaj, kjer je velika verjetnost, da bo med njima prišlo do tekmovanja (Mallet s sod., 2009: 2334).

Lastly, when two species live in allopatry, but their distribution ranges do not completely exclude each other, they exhibit a parapatric distribution pattern (Fig. 1). Each species will occur in allopatry and both will occur in a (usually narrow) zone of overlap. In this zone of overlap, both species can share the same space and utilize the same resources and these populations are termed syntopic. In such syntopic populations two ecologically similar species are likely to come in competition. Generally the zone of overlap in parapatric distribution of two species decreases with increasing competition between the two species (Begon et al., 2006). Parapatric distribution patterns are often found along environmental gradients, such as altitudinal, latitudinal or climatic gradients (e.g. Vrezec and Tome, 2004; Monasterio et al., 2009), which is often a consequence of migration of species along a gradient that results in secondary contact with another species (Begon et al., 2006).

1.2 SPECIES' ECOLOGICAL NICHE

The niche is defined as a multidimensional space, including abiotic and biotic factors that influence the fitness of phenotypes in a population of organisms (Hutchinson, 1957; Whittaker et al., 1973).

Ecological niche of a lizard is defined by the following variables following Pianka and Vitt (2003):

1. Spatial niche
    a. habitat
    b. microhabitat
2. Temporal niche
    a. time of activity
    b. nocturnal vs. diurnal species
    c. thermoregulatory tactics (thermoconformers vs. thermoregulators)
3. Trophic niche
    a. dietary niche breadth
    b. mode of foraging
    c. anatomical correlates: head length vs. prey size

4. Reproductive tactics
5. Predator escape tactics

The fundamental niche of a species is the sum of all dimensions of the ecological niche, which the species is genetically suited to and is defined by the combination of conditions and resources that allow the species to maintain a viable population (Hutchinson, 1957; Whittaker et al., 1973). The concept of a fundamental niche is also viewed as the niche of a species in the absence of interactions with other species (i.e. competitors, parasites, predators, symbionts etc.; Gause, 1934; Tome, 2006). For example, in presence of competitors, the species' fundamental niche may become restricted to a realized ecological niche (Hutchinson, 1957). This occurs when a species can no longer survive or reproduce successfully in some parts of its fundamental niche due to interspecific competition (Hutchinson, 1957). Two processes cause the restriction of species' fundamental niche: "niche shrink" or "niche differentiation" (Tome, 2006). When the realized niche of the superior competitor completely fills the area of inferior competitor's fundamental niche, competitive exclusion occurs (Begon et al., 2006).

Moreover, a species may be unable to use the whole potential fundamental niche due to other limitations; for example, limitations in dispersal ability (Holt, 2003). When taking into account all constraining factors of the realized niche and dispersal limitations of a species, we should refer to this as the occupied niche, which is smaller than the realized one (Pearson, 2010).

1.3 INTERSPECIFIC COMPETITION

Interspecific competition is a relationship between species, defined as a collection of reciprocal negative effects among ecologically similar species that results in a reduction of fecundity, growth and/or survivorship due to resource exploitation or interference (Smith and Smith, 1998). Interspecific competition can be either symmetric or asymmetric. It is symmetric when species induce the same interaction influence one to another. In the case of asymmetric competition, one species has a competitive advantage over the other under a certain set of factors (Smith and Smith, 1998). Prerequisites for competition in two species are: they occupy the same space (occur in a zone of sympatry), are active in the same time and their fundamental niches overlap (at least partly) (Smith and Smith, 1998; Begon et al., 2006).

Species that belong to the same predator guild, exhibit morphological similarity, and have a parapatric distribution pattern with zone of overlap, where they occur in syntopic populations, are ideal candidates for studying competition. All these characteristics apply to the species we studied along an altitudinal gradient in Kočevsko region, Slovenia.

1.3.1 Types of competitive interactions between two species

Interference competition is when one competitor interferes with another's access to a resource. It is direct and aggressive (Smith and Smith, 1998). Exploitation competition reduces the abundance of shared resources; each species indirectly reduces the abundance of the other species. For example, Petren and Case (1996) found that due to exploitative competition, the native gecko species (nocturnal lizards from the family Gekkonidae) numerically declined after the invasive gecko invaded urban habitats. Diet overlap between species was nearly complete and food was the limiting resource for both gecko populations. Invasive geckos were more efficient in catching prey than the native species, which reduced the rate of resource acquisition by native geckos, which translated into significant reductions in their body condition, fecundity, and survivorship (Petren and Case, 1996). Interference or exploitative competition is magnified when its costs are small, its effects are high, and resource overlap between species is large (Case and Gilpin, 1974; Smith and Smith, 1998). Apparent competition is an indirect type of interaction when two species are negatively affected by a common enemy (predator, parasite etc.; Bonsall and Hassell, 1997). Two species can also indirectly compete via a third species on the same trophic level, where the third species is a competitor of one and a mutualist of the other (Begon et al., 2006).

1.3.2 Factors influencing competition

In the first mathematical model of competition, the Lotka-Volterra model of interspecific competition, it was proposed that the effect of competition is modulated by the relationship between intra- and inter-specific competitions (Lotka, 1910; Volterra, 1926). The possible outcomes of competition between two species are the following (Tome, 2006):

- strong interspecific competitors outcompete weak interspecific competitors (when species A is competitively stronger than species B, and vice versa),
- when intraspecific competition is greater in both species than interspecific, the species will coexist, and
- when interspecific competition is strong in both species, but intraspecific competition is weak, we cannot predict the outcome (other factors such as species' densities, parasite prevalence, etc. can affect the competitive outcome).

In reality, however, the environment is not sufficiently constant for the outcome of competition to be determined only by the competitive abilities of the competing species. Environment usually represents a combination of favourable and unfavourable habitats and their availability changes in time and space. Direct and indirect factors (abiotic or biotic) which can influence competition are: species' carrying capacity, intrinsic rates of increase, arrival time to new resource patch, resource availability, common predators, parasites, etc. For example, malaria infected two competing similar sized species of *Anolis* lizards and causeed important pathology that had a negative fitness effect on lizards (Schall, 1992). It very rarely infected one lizard species while it was a very common infection in the other (Schall, 1992). The result was that the less infected lizard was the dominant competitor in the interspecific interaction (Schall, 1992). Thus malaria mediated competition between the two species which was reflected in their distribution (Schall, 1992). The influence of various environmental (biotic or abiotic) factors on interspecific competition can lead to unpredictable outcomes of competition and should be incorporated in study designs to improve the understanding of competition (Smith and Smith, 1998; Begon et al., 2006).

2 ECOLOGY OF STUDIED SPECIES WITH LITERATURE REVIEW

The Horvath's rock lizard, *Iberolacerta horvathi*, Méhely 1904, and the Common wall lizard, *Podarcis muralis,* Laurenti 1768, are members of a diverse group of ectotherm vertebrates belonging to class Reptilia, paraphyletic to Aves, order Squamata and in the lower rank to the group of Lacertoidea (Pianka and Vitt, 2003; Pyron et al., 2013). Lizards comprise of over 3000 species in 21 families (Pianka and Vitt, 2003) with a diverse range in size and ecology (Pianka and Vitt, 2003; Meiri, 2008). Studied species classified to the family Lacertidae (commonly known as "lacertid lizards") are native to Europe, Africa and Asia (Arnold et al., 2007). Lacertids lizards are small-bodied lizards, mostly having snout-to-vent length (SVL) smaller than 8 cm (Arnold and Ovenden, 2004).

2.1 PHYLOGEOGRAPHY AND DISTRIBUTION

The Horvath's rock lizard is one of eight species currently recognized in the genus *Iberolacerta* Arribas 1997 (Mayer and Arribas, 1996; Odierna et al., 1996; Arribas, 1999a, 1999b; Almeida et al., 2002; Mayer and Arribas, 2003; Arribas and Carranza, 2004; Carranza et al., 2004; Crochet et al., 2004; Arribas et al., 2006; Arnold et al., 2007; Galán et al., 2007; Mayer and Pavlicev, 2007). Seven of these species live in the Pyrenees and in northern and central mountains of the Iberian Peninsula. Only one, our study species *I. horvathi,* occurs in the Central and South-eastern Europe (Gasc et al., 1997; Arnold et al., 2007; Sillero et al., 2014). It is geographically isolated from the other members of its genus and its relations with the Iberian members of the genus are still unsolved (Carranza et al., 2004; Crochet et al., 2004; Arnold et al. 2007), although we know that the diversification of the genus date back to the Miocene (around 8.4 Mya). Evolutionary history of *I. horvathi* is so far completely unknown thus we lack information on the structuring of its genetic diversity. This is in stark contrast to the ample information available for other members of this relictual genus (e.g. Mouret et al., 2011; Remón et al., 2013; Arribas et al., 2014; Ferchaud et al., 2015).

The Common wall lizard has the largest distribution range among species of the genus *Podarcis* Wagler 1830 (Gasc et al., 1997; Sillero et al., 2014). The species originated from multiple glacial refugia (Gassert et al., 2013; Salvi et al., 2013) and multiple lineages were identified within the three Mediterranean peninsulas – Iberia, Apennine and the Balkans - where the highest species genetic diversity was observed, as well as in some more northern areas (Salvi et al., 2013). Both genera, *Iberolacerta* and *Podarcis*, diverged from other genera in the sub-family Lacertini around about 16-12 million years ago (Arnold et al., 2007; Pavlicev and Mayer, 2009) and radited simultaneously; the start of radiation occurred around about 8 million years ago in both (Arnold et al., 2007; Pavlicev and Mayer, 2009).

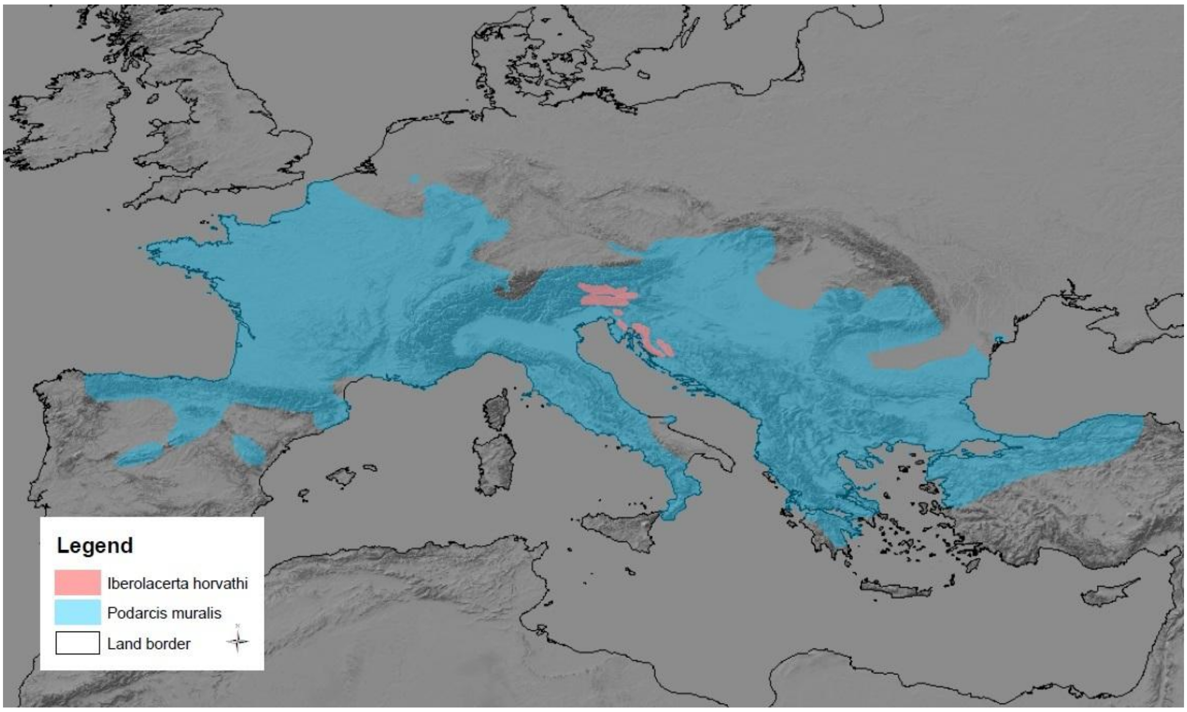

Figure 2: Distribution of the studied species: *Podarcis muralis* and *Iberolacerta horvathi*. Based on Böhme et al. (2009) and Vogrin et al. (2009).

Slika 2: Razširjenost pozidne (*Podarcis muralis*) in velebitske kuščarice (*Iberolacerta horvathi*). Povzeto po Böhme s sod. (2009) in Vogrin s sod. (2009).

Today, *I. horvathi* has a relatively small range in eastern Alps and northern Dinaric Mountains located in the Central and South-eastern Europe (Bischoff, 1984; Sillero et al., 2014). It occurs at least in four countries: Italy, Austria, Slovenia and Croatia (Fig. 2). The species likely occurs in Bosnia and Hercegovina, but has not been discovered there yet

(Žagar et al., 2014). The population found in Karwendel Gebirge in south Germany (Capula and Luiselli, 1990) was strongly disputed (Bischoff, 1991; Faberl and Faberl, 1991; Tiedemann, 1992; Capula and Luiselli, 1993; Franzen et al., 1993; Schmidtler and Schmidtler, 1996) and has not been recently re-confirmed (Cabela et al. 2004). The northernmost confirmed population is known from the Frauenbachtal valley in northern Austria (Cabela et al., 2004). In Austria the species occurs also in the state Carinthia (Grillitsch and Tiedemann, 1986; De Luca, 1989; Tiedemann, 1992; Grillitsch et al., 2001; Cabela et al., 2002, 2004, 2007). In Italy it is distributed in a narrow belt of the Alpine and pre-Alpine area in the North-Easternmost part of the country (Lapini and Dolce, 1983; De Luca, 1989; Lapini et al., 1993, 2004; Lapini and Dal Farra, 1994; Rassati, 2010). In Slovenia, the distribution stretches in a NW-SE direction, from the Julian Alps and Karavanke, pre-Alpine area, to Northern Dinaric Mountains (Brelih, 1954; Brelih and Džukić, 1974; De Luca, 1989; Tome, 1996; Mršić, 1997; Tome, 2001; Krofel et al., 2009; Cafuta, 2010). In Croatia is the *locus typicus* (type locality) of the species at Jasenak on Velika Kapela (Méhely, 1904; Karaman, 1921). There, species is distributed from the border with Slovenia in the north to the Dinara Mountain in the south (Arnold, 1987; De Luca, 1989; Tvrtkovic and Veen, 2006; Kryštufek et al., 2008; Jelić, 2014), where the southernmost population has been recently found (Žagar et al., 2014).

P. muralis has a widespread distribution that expands across most of Central Europe, northern part of Iberian Peninsula, majority of the Apennine and the Balkan Peninsula and in the east into northern Turkey (Fig. 2). In Slovenia it is relatively common and widespread (Tome, 1996; Mršić, 1997; Tome, 2001; Krofel et al., 2009). It is more frequent at lower altitudes compared to higher altitudes (Žagar, 2008a; Krofel et al., 2009).

2.2 HABITAT USE

The general habitat use is highly similar between both species in sympatry (Cabela et al., 2007). They both preferentially use rocky substrates with sparse vegetation and sun exposed microhabitats (Arnold, 1987; Arnold and Ovenden, 2004; Arnold et al., 2007). However, *I. horvathi* generally selects for sites with less vegetation cover than *P. muralis* (Lapini et al., 1993; Cabela et al., 2007). Some authors hypothesize that *I. horvathi* also uses more vertical surfaces than *P. muralis,* which was linked with different climbing abilities (Arnold, 1987; Cabela et al., 2007), but no experimental performance test has been done. Comparative study of the home range sizes of syntopic *1. horvathi* and *P. muralis* showed that *P. muralis* had larger home ranges, especially males in the breeding period (Lapini et al., 2004).

2.3 SYMPATRIC OCCURRENCE

Distribution range of *I. horvathi* overlaps completely with *P. muralis*, thus at the macro-scale species are considered sympatric. Syntopic populations of *I. horvathi* and *P. muralis* have been most frequently found at low and middle altitudes (Bischoff, 1984 in Italy Lapini et al., 1993; Richard and Lapini, 1993; Lapini et al., 2004; Rassati, 2010; in Austria Grillitsch et al., 2001; Cabela et al., 2002, 2007; in Croatia Arnold, 1987; De Luca, 1989 and in Slovenia Brelih, 1954; Žagar et al., 2007, 2008a; Krofel et al., 2009). During a reptile study conducted in southern Slovenia, *P. muralis* was found to be more abundant at lower altitudes and *I. horvathi* at higher altitudes (Žagar, 2008a), which is also a general rule across the country (Krofel et al., 2009).

The species tandem studied here is not unique, since other *Iberolacerta-Podarcis* species pairs with completely/partly attitudinally segregated distributional patterns have been observed in the Iberian Peninsula. For example, *I. monticola* and *P. guadamarrae* (Moreira et al., 1999), *I. cyreni* and *P. muralis* (Monasterio et al., 2010), *I. galani* and *P. bocagei* (Arribas et al., 2006), *I. aranica and P. muralis* (Arribas, 2015a), and *I. martinezricai* and *P. guadamarrae* (Arribas, 2015b). Observed spatial segregation between these lacertid species is commonly understood as a consequence of competition (e.g. Crochet et al., 2004) and areas of sympatry provide an ideal situation for the study of interspecific interactions between ecologically similar species.

2.4 COMPARATIVE BIOLOGY AND ECOLOGY

2.4.1 Morphology

Competitive outcomes between lacertid lizards often depend on body size, with larger lizards out-competing smaller ones in agonistic interactions (Langkilde et al., 2005; Sacchi et al., 2009). Cases where aggressiveness was more important than size are scarce (e.g. Cejudo et al., 1999). Both studied species are similar in their body size, with average SVL in adults ranging between 55-65 mm (De Luca, 1989; Aleksić and Ljubisavljević, 2001). Both species are similar also in shape and colouration (Fig. 3). Both have slender rather flattened bodies with tails on average 2-times longer than the body, and legs with long fingers (Arnold and Ovenden, 2004). Most individuals are brownish with darker dorsolateral stripes (flanks) (Fig. 3), with a white-yellowish belly side in *I. horvathi* (both sexes), white-reddish in female *P. muralis*, and white-dark red in male *P. muralis* (Arnold and Ovenden, 2004). High morphological similarity seems evident also from frequent misidentifications of *I. horvathi*, misidentified as *P. muralis*. Many of such occurrences prolonged the time of discovery of *I. horvathi* in several localities across its range (e.g. Brelih, 1954; De Luca, 1989; Lapini et al., 2004; Žagar et al., 2007). Even the description of the species was delayed by a misidentified (as *P. muralis*) specimen brought to the Hungarian National Museum in 1901 (Méhely, 1904).

Sexual dimorphism in size and shape occurs in majority of lacertid lizards, including both studied species. Described for *P. muralis* were male-biased (e.g. Strijbosch et al., 1980) and female-biased sexual dimorphism (e.g. Gracceva et al., 2008). Sexual dimorphism in *I. horvathi* was studied to a lesser extent and in one case female-biased sexual size dimorphism was observed (De Luca, 1989). However, these are ambiguous results because several populations from NW Slovenia and Croatia were pooled together before analysis.

On the other hand, in a population of *I. horvathi* from the Carnic Alps in Italy, no sexual dimorphism in SVL was found (Capizzi, 1999).

Figure 3: Adult females of Horvath's rock lizard (*Iberolacerta horvathi*) (left) and common wall lizard (*Podarcis muralis*) (right) from the study area in Kočevsko region, Slovenia (photos: Anamarija Žagar).

Slika 3: Odrasli samici velebitske kuščarice (*Iberolacerta horvathi*) (levo) in pozidne kuščarice (*Podarcis muralis*) (desno) iz območja raziskovanja na Kočevskem (fotografiji: Anamarija Žagar).

Lizards' morphology and sexual dimorphism in size and shape varies among populations due to sexual and natural selection pressures (Kaliontzopoulou et al., 2010, 2012a). Also in both studied species, inter-population variation in morphology has been already observed (De Luca, 1989; Gracceva et al., 2008; Aleksić et al., 2009). Local competitive pressures between competing species might also have an effect on morphology; such morphological divergence is referred to as "character displacement" (Begon et al., 2006).

2.4.2 Diet

Studied species are both predators and have a high overlap in their diets observed in syntopic populations (De Luca, 1992; Richard and Lapini, 1993; Capizzi, 1999). The most common prey of both species are ground-dwelling and flying arthropods. They use active foraging in combination with a sit-and wait predatory strategy (De Luca, 1992; Capizzi, 1999), common for most small-sized rupicolous lacertid lizards (Carretero, 2004). From the study area there are also reported cases of cannibalism and intraspecific oophagy in *P. muralis* (Žagar and Carretero, 2012; Žagar et al., 2016). Rare dietary events, such as cannibalism, have been observed in lacertids connected with high population densities, temporary food scarcity or the combination of both (Carretero, 2004). Strong overlap in the dietary niche between species, suggests a high potential for interspecific exploitative competition for food resources.

2.4.3 Activity period

Lacertid lizards are diurnal in their activity and have either unimodal or bimodal daily activity pattern, depending on climatic properties of the habitat where they live (Pianka and Vitt, 2003). In areas with high temperatures some species have a window of inactivity in the days of extreme hot conditions, which is called aestivation (Pianka and Vitt, 2003). In temperate zones lizards become inactive during winter; a behavioural response in ectotherms called brumation (Pianka and Vitt, 2003). Both, aestivation and brumation are evolutionary consequences of avoiding mortality in long-term due to extreme environmental temperature conditions unfavourable for their activity (Pianka and Vitt, 2003). Brumation locations can be underground, inside rock outcrops, under soil, under various objects or in any cavity providing adequate temperatures to survive cold periods (Vitt and Caldwell, 2014).

Studied species, *I. horvathi* and *P. muralis*, do not significantly differ in their seasonal or daily activity patterns. They start their activity period in March/April and go to brumation in October/November (De Luca, 1992; Lapini et al., 1993). Their daily activity pattern is mostly bimodal (De Luca, 1992; Lapini et al., 1993), but can become unimodal in spring

(De Luca 1992). Since high overlap in the time dimension of studied species' ecological niche exits, there is a high potential for interspecific interactions in syntopic populations.

2.4.4 Physiology

Lizards are generally well equipped to cope with water stress in dry environments. Keratinized scales and pigments in their skin prevent desiccation, protect them from UV radiation and retain heat (Pianka and Vitt, 2003). Lacertid lizards are heliothermic ectotherms with an ability to precisely thermoregulate using basking and shuttling behaviour between warm and cold places (Pianka and Vitt, 2003). To raise their body temperature they predominately use sunlight in comparisons to other available heat resources (Fig. 4). Basking in the sun is one of the most typical thermal behaviours in reptiles in general (Carrascal et al., 1992; Gvoždik, 2002).

In optimal conditions without restrictions, lizards will thermoregulate to achieve body temperature in a narrow range of species' preferred body temperature (Tp) (Huey, 1982). Tp has been found to correlate with several physiological optima and is directly related with fitness (Huey and Bennett, 1987). Thermal preferences of lacertid lizards have been considered species' specific for a long time. For example, several studies showed that Tp was similar between populations of the same species under different climate regimes (Van Damme et al., 1990; Gvoždik and Castilla, 2001; Carretero et al., 2005). However, others found intra-population or intraspecific variation in Tp affected by factors such as habitat use, parasitation etc. (e.g. Brown and Griffin, 2003; Aguado and Braña, 2014; Paranjpe et al., 2014), season (e.g. Van Damme et al., 1986) or reproductive status (e.g. Carretero et al., 2005). Moreover, Tp may change even on the individual level as a function of body condition (e.g. Aguado and Braña, 2014). For example, thermal optima of gravid females tend to be lower than those of non-gravid females, apparently to ensure optimal embryo development (e.g. Carretero et al., 2005).

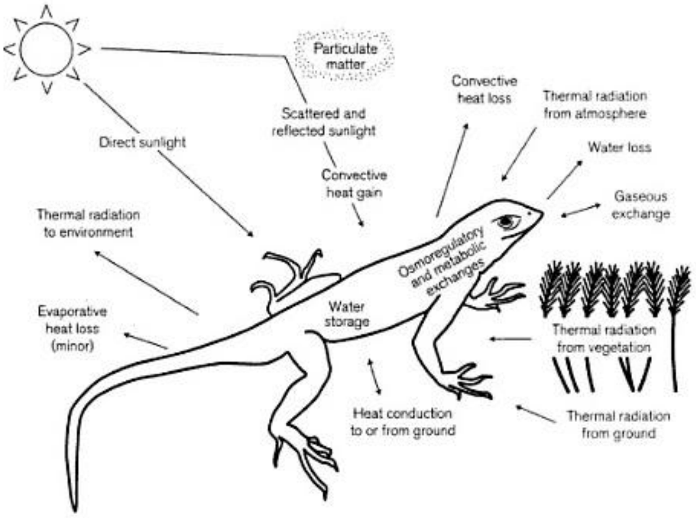

Figure 4: Schematic representation of heat gain (sources) and losses involved in thermoregulation of a diurnal lizard. (Pianka and Vitt, 2003: 35)

Slika 4: Shematska predstavitev virov in izgub toplote vključenih v termoreglacijo dnevno aktivnega kuščarja. (Pianka and Vitt, 2003: 35)

In areas where sun-exposed basking sites are limited and habitat varies in the quality for thermoregulation (low heterogeneity in space), interference competition for basking sites may occur between lizards (e.g. Case and Gilpin, 1974; Hertz, 1992; Sears and Angilletta, 2015). Interference is common on islands with high lizard densities (Downes and Bauwens, 2004). Since basking in the sun rapidly affects body temperature of small-bodied lizards (Stevenson, 1985), they use the best basking places to efficiently exploit thermal energy. Lizards often defend preferred basking sites (Marler et al., 1995) and engage in social agonistic interactions with conspecifics or ecologically similar heterospecifics (Langkilde et al., 2005). We expect interference competition for basking sites between *I. horvathi* and *P. muralis* in our study area due to their ecological similarity and low availability of suitable basking sites in limited sun-exposed areas inside highly forested landscape (Perko and Orožen Adamič, 1998).

Thermal ecology of *P. muralis* has been studied in several populations across Europe (e.g. Braña, 1991; Tosini and Avery, 1993; Grbac and Bauwens, 2001) but not in this part of species' range. For *I. horvathi* only field activity body temperatures were measured (De Luca, 1992). Thus there is still no information on the range of Tp for both species from our study area. Together with the thermal physiology, also water physiology (rates of evaporative water loss (EWL)) (Mautz, 1982), and the metabolism importantly define the limits of species' physiological fundamental niche (Vitt and Caldwell, 2014). So far, to our best knowledge, the EWL and metabolism have not been experimentally defined for the studied species. If species have adapted their physiology to current climatic conditions of their distributions, we expect to find interspecific differences in their physiology because of observed altitudinal segregation pattern; high-altitude species (*I. horvathi*) compared to lowland species (*P. muralis*).

2.4.5 Reproduction

Lacertid lizards reach sexual maturity and start reproducing during the second or third calendar year (Arnold and Ovenden, 2004). Females lay one or more clutches per year depending on species and length of annual activity periods (Arnold and Ovenden, 2004). In most species the number of eggs correlates with female body size as has been also observed for our studied species (De Luca, 1992; Ji and Braña, 2000). Females can mate with several males, which results in clutches with higher hatchling success while avoiding costs associated with male choice (Olsson and Madsen, 1995). There is no paternal care involved after the female deposits eggs and common ovipositon sites can be used by several different females (e.g. Peñalver-Alcázar et al., 2015). Male reproductive success was in some populations positively connected with their head and body size, body condition and colour intensity (e.g. López et al., 2002; Bajer et al., 2010), but not in others (e.g. Olsson and Madsen, 1995).

Species of the genus *Iberolacerta* from the Iberian Penninsula showed a low fertility, delayed sexual maturation and prolonged egg retention, which was interpreted as an advanced stage in the tendency towards viviparity (Arribas, 2004; Arribas and Galán, 2005). Syntopic *I. horvathi* and *P. muralis* showed similar reproductive traits; both reproduced in May and oviposition occured in mid-July (De Luca, 1992; Lapini et al., 1993). Clutch size of *I. horvathi* varied between 3-5 eggs in Italy (Lapini et al., 1993) and 1-5 eggs in Slovenia and Croatia (De Luca, 1992; Ljubisavljević et al., 2012). Clutch size of a rather small sample size of *P. muralis* (n = 6) from syntopic population in Italy had 3-

4 eggs (Lapini et al., 1993). *I. horvathi* seemed to be monoestrous (De Luca, 1992; Lapini et al., 1993) and no second clutch in the same activity period has been reported so far. While in syntopic *P. muralis* two females carried mature eggs at the end of May, which was hypothezised as possible evidence that they may have a second clutch later in the same season (Lapini et al., 1993). Reproductive output directly affects organisms' fitness (Roff, 2002), thus, if interspecific differences in reproduction strategies exist between species in competition they may have an influence on their competitive interaction (Begon et al., 2006).

2.4.6 Predators

Lizards are situated in an intermediate position in the food web (Pianka and Vitt, 2003). Lacertid lizards can be preyed on by several birds species (e.g. Castilla et al., 1999; Steen et al., 2011; Pérez-Mellado et al., 2014), wild carnivores (e.g. Castilla et al., 1999), snakes (e.g. Luiselli, 1996), and by domestic cats in urban environs (e.g. Woods et al., 2003). Some snake species are specialized in searching for inactive lizards in their shelters (e.g. Luiselli, 1996) and often represent the most important predators. They are also preyed upon opportunistically by larger lacertid species (Arnold and Ovenden, 2004) or conspecifics (e.g. Žagar and Carretero, 2012). In the study area the most potential predator species are saurophagous snakes, larger lizard species, and kestrel (*Falco tinnunculus*) (pers. observ.).

In such multi-predator environments, lacertids are expected to have evolved complex antipredator avoidance strategies (e.g. Amo et al., 2005). Lacertid lizards use avoidance (cryptic coloration) and/or escape to a safe refuge to avoid predation (e.g. Carretero et al., 2006). While hiding in a shelter, a lizard might become exposed to saurophagous snakes. Several species (including *P. muralis*) have the ability to discriminate between chemicals from potential (saurophagous) or non-potential (non-saurophagous) snakes and thus avoid dangerous predators (Amo et al., 2004a, 2004b, 2004c, 2004d). Differences in antipredator tactics can modulate predation pressure between different prey species. In the case of common predators of competing prey species different predator pressure can have an effect on interspecific relationships (through indirect interactions, see also chapter 1.3.1).

3 WORKING OBJECTIVES AND HYPOTHESES

The main goal of my dissertation was to develop an understanding of the mechanisms of competition between ecologically similar and sympatric species. I used two species of lacertid lizards, where competition was expected on the basis of observed general distribution pattern and known general morphological and ecological similarity.

We tested the following hypotheses for my doctoral dissertation:

- Potential for competition between the common wall lizard (*P. muralis*) and the Horvath's rock lizard (*I. horvathi*) is high due to high zone of overlap in their distribution (with existing syntopic populations) and habitat use in the study area (article I, results in paragraph 5.1 and Annex 7,8 and 9).

- The two species have highly similar fundamental niches and traits:
  - species resemble in morphology (article II),
  - species resemble in thermal and water physiology (article III),
  - species resemble in metabolism (article IV).

- Realized niches of both potentially competing species diverge in areas of sympatric occurrence compared to allopatry as a consequence of realization of a larger part of species fundamental niche in allopatry ("competitive release"):
  - realized body temperatures differ from species' preferred body temperatures when in different social context: alone, conspecific pair or heterospecific pair (article V).

- Direct competition between species is expressed in male-male social agonistic interactions (article V).

- Indirect effects of common predators on the competitive interaction exist if species differ in their antipredatory tactics (article VI).

4 SCIENTIFIC ARTICLES

4.1 PUBLISHED SCIENTIFIC ARTICLES

4.1.1 Article I

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

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Amphibia-Reptilia, **2013**, 34, 263-268, DOI:10.1163/15685381-00002889

ABSTRACT
We have surveyed sympatric reptiles of a diverse and natural 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 the segregation between the most abundant species. The most similar were 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.

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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. Langklide 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. Langklide 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 determine 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 km^2 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 Oroženˇ 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 m^2. 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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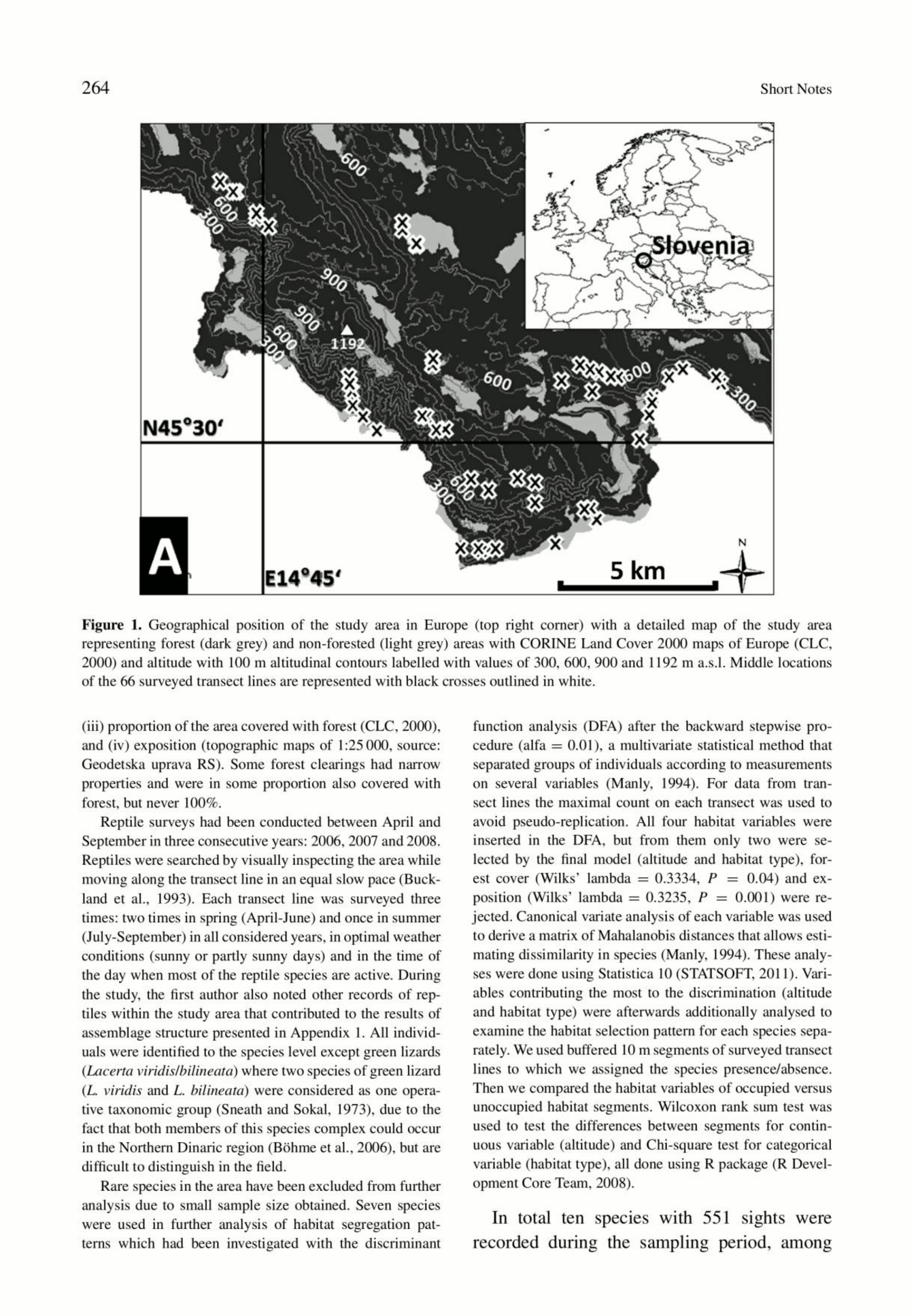


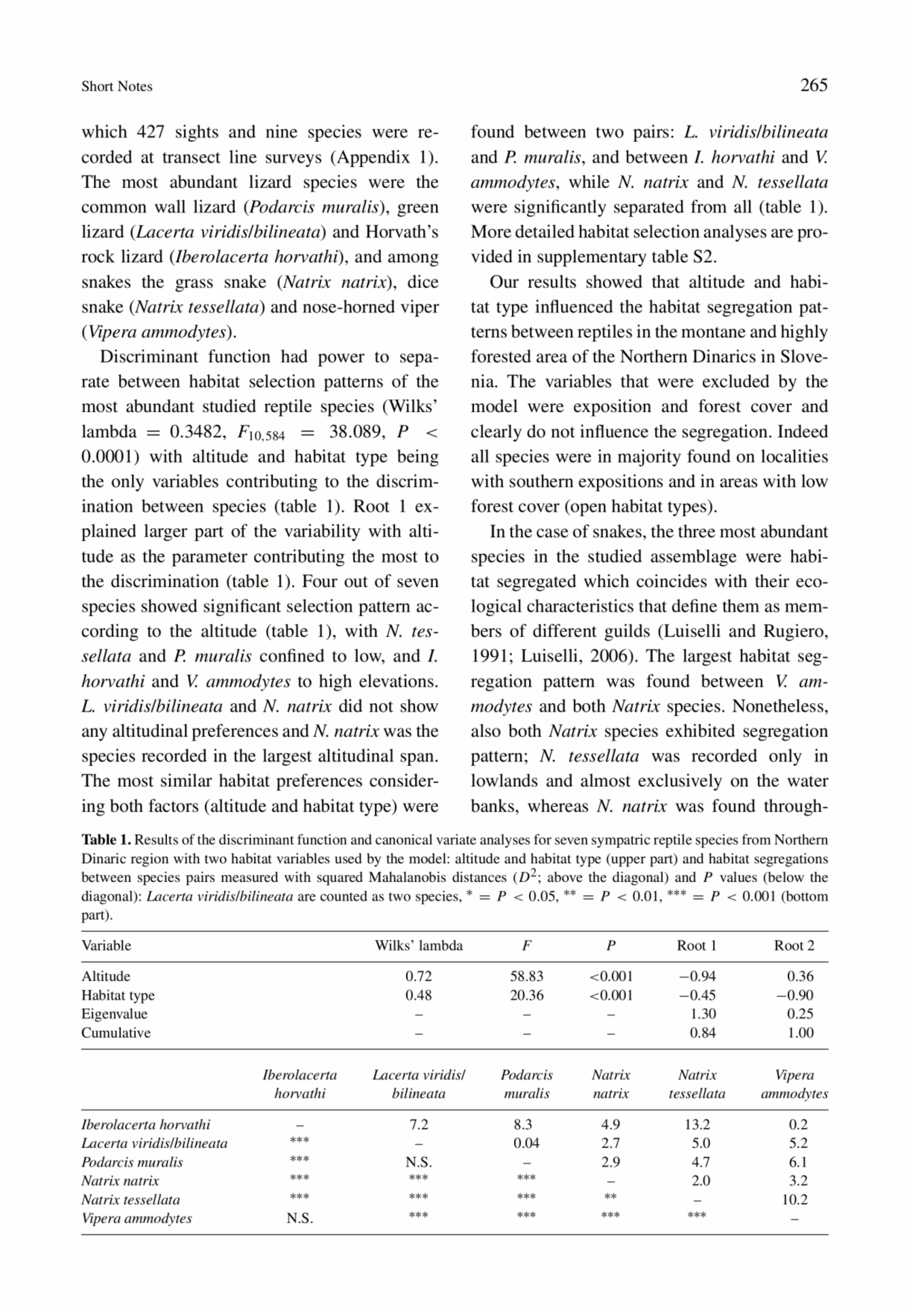
Figure 1. Geographical position of the study area in Europe (top right corner) with a detailed map of the study area representing forest (dark grey) and non-forested (light grey) areas with CORINE Land Cover 2000 maps of Europe (CLC, 2000) and altitude with 100 m altitudinal contours labelled with values 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 (alfa = 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

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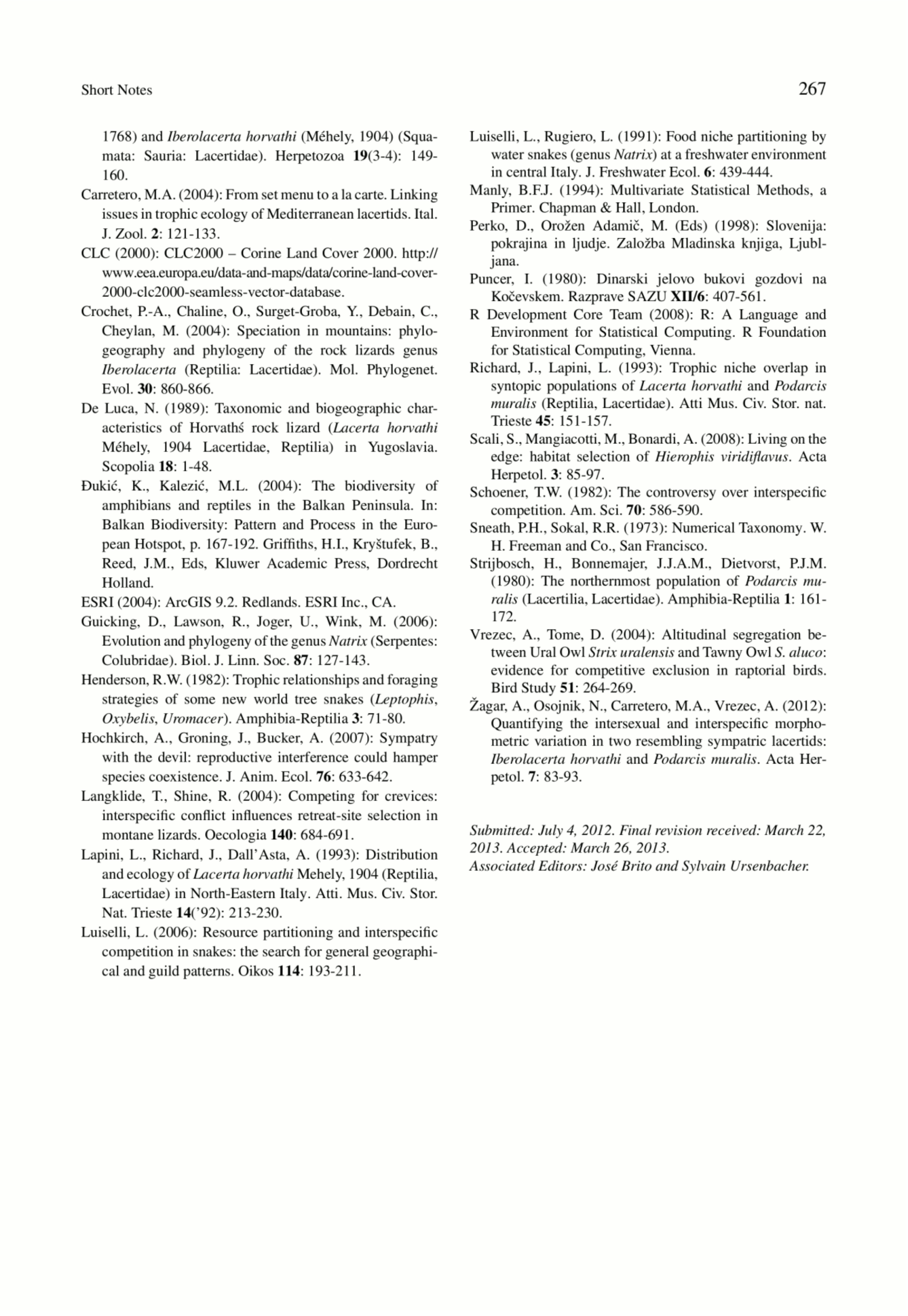

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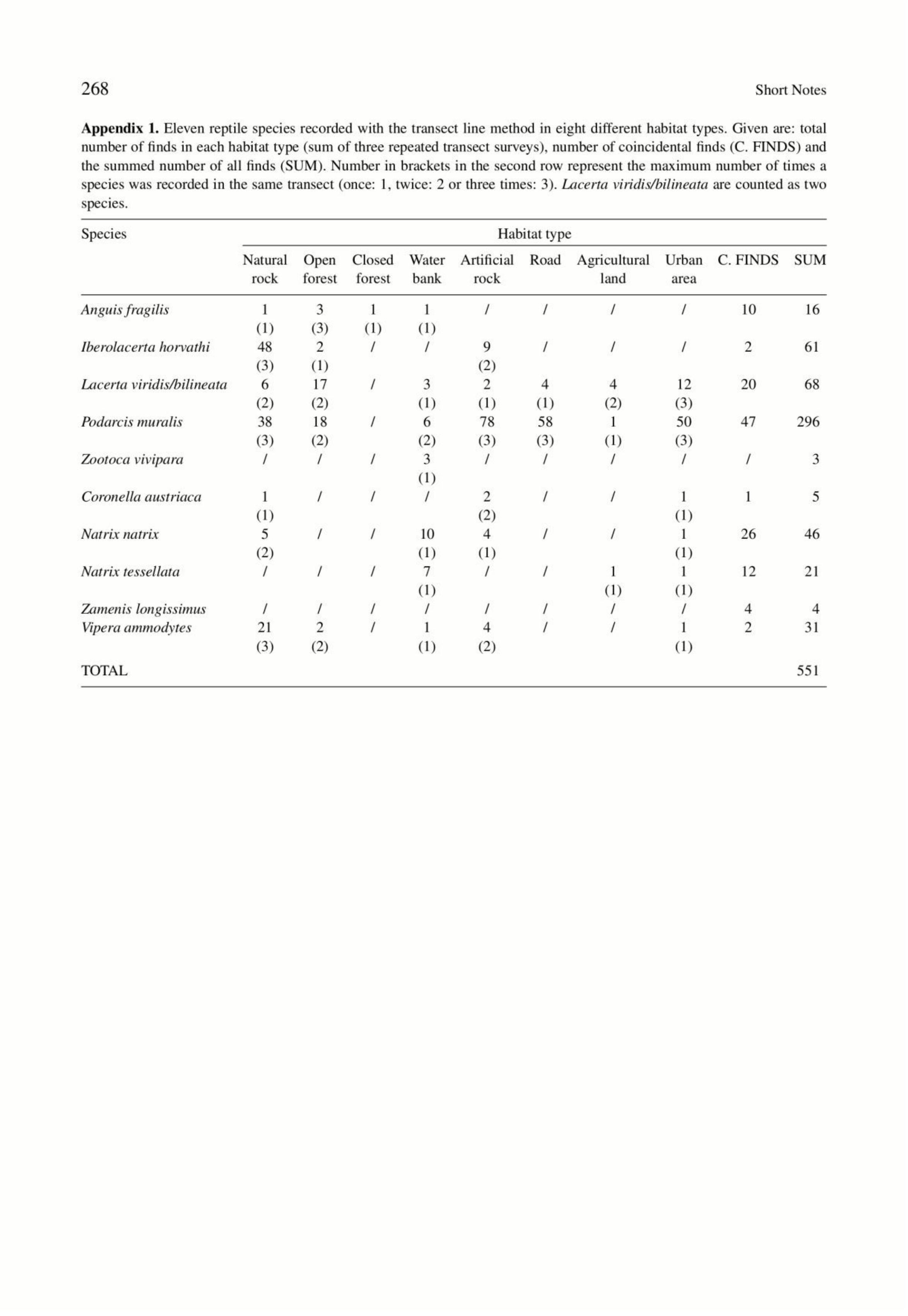
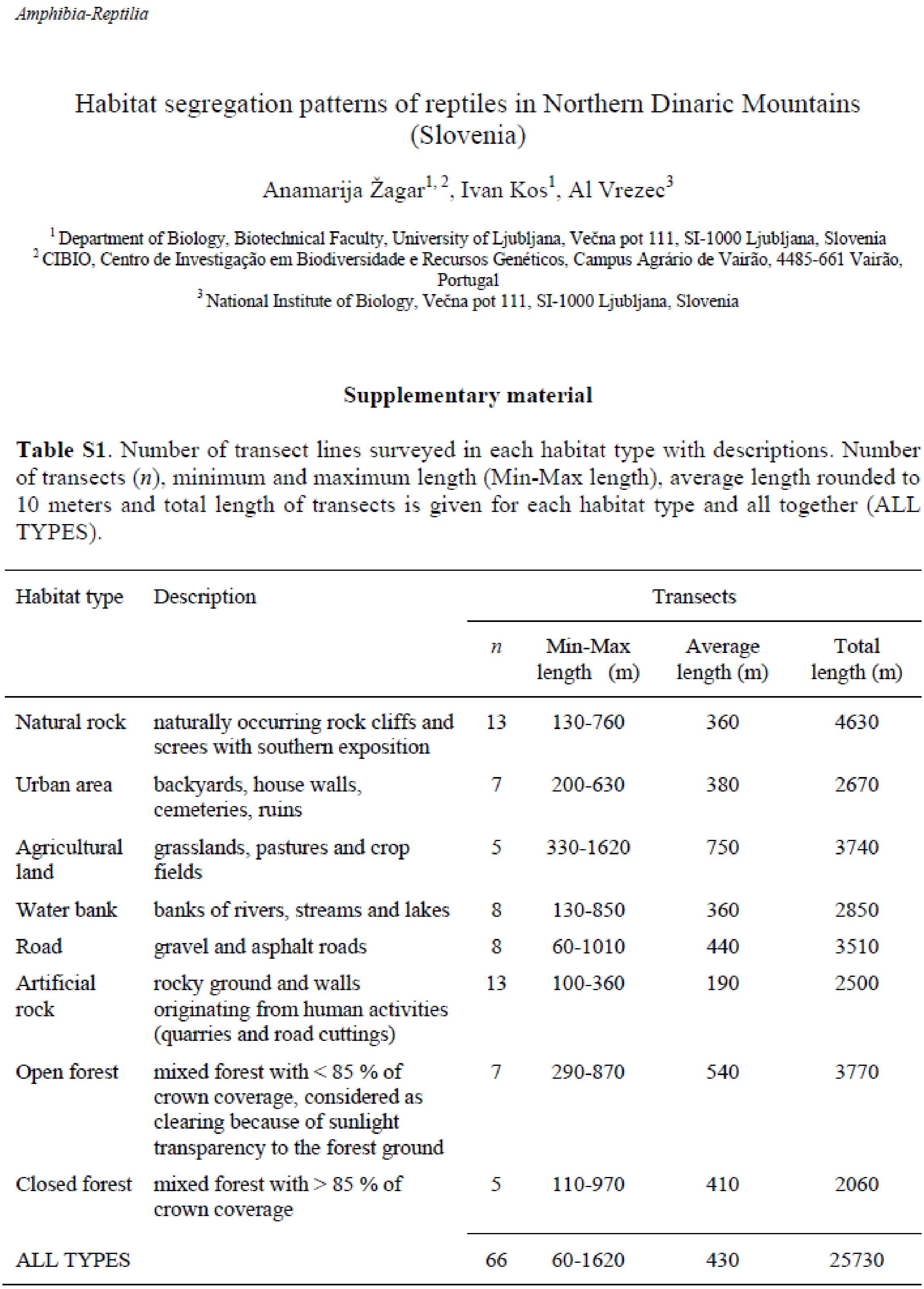


Appendix 1. Eleven reptile species recorded with the transect line method in eight different habitat types. Given are: total number of finds in each habitat type (sum of three repeated transect surveys), number of coincidental finds (C. FINDS) and the summed number of all finds (SUM). Number in brackets 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									
	Natural rock	Open forest	Closed forest	Water bank	Artificial rock	Road	Agricultural land	Urban area	C. FINDS	SUM
Anguis fragilis	1	3	1	1	/	/	/	/	10	16
	(1)	(3)	(1)	(1)						
Iberolacerta horvathi	48	2	/	/	9	/	/	/	2	61
	(3)	(1)			(2)					
Lacerta viridis/bilineata	6	17	/	3	2	4	4	12	20	68
	(2)	(2)		(1)	(1)	(1)	(2)	(3)		
Podarcis muralis	38	18	/	6	78	58	1	50	47	296
	(3)	(2)		(2)	(3)	(3)	(1)	(3)		
Zootoca vivipara	/	/	/	3	/	/	/	/	/	3
				(1)						
Coronella austriaca	1	/	/	/	2	/	/	1	1	5
	(1)				(2)			(1)		
Natrix natrix	5	/	/	10	4	/	/	1	26	46
	(2)			(1)	(1)			(1)		
Natrix tessellata	/	/	/	7	/	/	1	1	12	21
				(1)			(1)	(1)		
Zamenis longissimus	/	/	/	/	/	/	/	/	4	4
Vipera ammodytes	21	2	/	1	4	/	/	1	2	31
	(3)	(2)		(1)	(2)			(1)		
TOTAL										551



Amphibia-Reptilia

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

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Supplementary material

Table S1. Number of transect lines surveyed in each habitat type with descriptions. Number of transects (*n*), minimum and maximum length (Min-Max length), average length rounded to 10 meters and total length of transects is given for each habitat type and all together (ALL TYPES).

Habitat type	Description	Transects			
		n	Min-Max length (m)	Average length (m)	Total length (m)
Natural rock	naturally occurring rock cliffs and screes with southern exposition	13	130-760	360	4630
Urban area	backyards, house walls, cemeteries, ruins	7	200-630	380	2670
Agricultural land	grasslands, pastures and crop fields	5	330-1620	750	3740
Water bank	banks of rivers, streams and lakes	8	130-850	360	2850
Road	gravel and asphalt roads	8	60-1010	440	3510
Artificial rock	rocky ground and walls originating from human activities (quarries and road cuttings)	13	100-360	190	2500
Open forest	mixed forest with < 85 % of crown coverage, considered as clearing because of sunlight transparency to the forest ground	7	290-870	540	3770
Closed forest	mixed forest with > 85 % of crown coverage	5	110-970	410	2060
ALL TYPES		66	60-1620	430	25730

Table S2. Habitat selection regarding altitude and habitat type for all finds of seven species surveyed with transect line method. Abbreviations of habitat types: AL = agricultural land, AR = artificial rock, NR = natural rock, OF = open forest, RO = road, UA = urban area and WB = water bank. *Lacerta viridis/bilineata* are counted as two species.

	Altitude (m)		Habitat type	
	Mean ± SD Min-Max	Wilcoxon test	Proportion of sights in each habitat type	Chi-square test
Iberolacerta horvathi	858.6 ± 179.6 500-1060	$W = 16489$ $P < 0.001$	NR = 81.4% AR = 15.2% OF = 3.4%	$\chi^2 = 143.88$ $P < 0.001$
Lacerta viridis/ bilineata	408.5 ± 158.2 225-780	$W = 66107$ $P = 0.41$	OF = 35.4% UA = 25.0% NR = 12.5% RO = 8.3% AL = 8.3% WB = 6.3% AR = 4.2%	$\chi^2 = 32.08$ $P < 0.001$
Podarcis muralis	376.2 ± 157.9 200-865	$W = 350495$ $P < 0.001$	AR = 31.3% RO = 23.3% UA = 20.1% NR = 15.3% OF = 7.2% WB = 2.4% AL = 0.4%	$\chi^2 = 185.33$ $P < 0.001$
Natrix natrix	493.5 ± 305.6 195-1025	$W = 28504$ $P = 0.61$	WB = 50.0% NR = 25.0% AR = 20.0% UA = 5.0%	$\chi^2 = 35.93$ $P < 0.001$
Natrix tessellata	208.9 ± 13.6 195-230	$W = 21595$ $P < 0.001$	WB = 77.8% UA = 11.1% AL = 11.1%	$\chi^2 = 32.01$ $P < 0.001$
Vipera ammodytes	763.6 ± 265.3 220-1055	$W = 12944$ $P < 0.001$	NR = 48.3% AR = 13.8% OF = 6.9% UA = 3.4% WB = 3.4%	$\chi^2 = 43.38$ $P < 0.001$

4.1.2 Article II

Quantifying the intersexual and interspecific morphometric variation in two resembling sympatric lacertids: *Iberolacerta horvathi* and *Podarcis muralis*

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ABSTRACT

Podarcis muralis and *Iberolacerta horvathi* are sympatric, frequently syntopic, lacertids through the entire range of *I. horvathi* and very similar in their general body size and shape, as well as in most ecological traits. We morphologically compared adults from the area of sympatry using biometric measurements and performed analyses to investigate their sexual size and shape dimorphism. A total of 34 males and 24 females of *I. horvathi*, and 25 males and 23 females of *P. muralis*, all adult individuals, were measured. Both species showed sexual size dimorphism with females being longer (snout-vent length, SVL) than males. After SVL correction (ANCOVA), head width, length and height and mass showed to be sexually dimorphic in both species. Males carry relatively wider, longer and higher heads and were heavier than conspecific females. *I. horvathi* heads were more flattened than those of *P. muralis* and *P. muralis* were heavier than *I. horvathi*. Both species displayed the same pattern of sexual dimorphism regarding body size, head size and shape not only in direction but also in magnitude. All results confirm that both species are very similar in studied biometric characters and, together with their ecological similarities, these suggest in absence of other factors they are likely to interact when living together.

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Quantifying the intersexual and interspecific morphometric variation in two resembling sympatric lacertids: *Iberolacerta horvathi* and *Podarcis muralis*

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Abstract. *Podarcis muralis* and *Iberolacerta horvathi* are sympatric, frequently syntopic, lacertids through the entire range of *I. horvathi* and very similar in their general body size and shape, as well as in most ecological traits. We morphologically compared adults from the area of sympatry using biometric measurements and performed analyses to investigate their sexual size and shape dimorphism. A total of 34 males and 24 females of *I. horvathi,* and 25 males and 23 females of *P. muralis*, all adult individuals, were measured. Both species showed sexual size dimorphism with females being longer (snout-vent length, SVL) than males. After SVL correction (ANCOVA), head width, length and height and mass showed to be sexually dimorphic in both species. Males carry relatively wider, longer and higher heads and were heavier than conspecific females. *I. horvathi* heads were more flattened than those of *P. muralis* and *P. muralis* were heavier than *I. horvathi*. Both species displayed the same pattern of sexual dimorphism regarding body size, head size and shape not only in direction but also in magnitude. All results confirm that both species are very similar in studied biometric characters and, together with their ecological similarities, these suggest in absence of other factors they are likely to interact when living together.

Keywords. Biometric characters, sexual dimorphism, southern Slovenia, *Podarcis muralis*, *Iberolacerta horvathi*, Lacertidae

INTRODUCTION

The Common wall lizard (*Podarcis muralis*) and Horvath's rock lizard (*Iberolacerta horvathi*) are sympatric and frequently syntopic lacertids through the entire range of *I.*

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horvathi (Tiedemann, 1997). The range of latter as known today extends from pre-alpine and alpine part of north eastern Italy, to north western Slovenia (Lapini et al., 2004; Rassati, 2010) and southern Austria (Cabela et al., 2007), and Dinaric Alps of central and southern Slovenia and Velebit in Croatia (De Luca, 1989; Krofel et al., 2009). Allotopic *I. horvathi* populations are only known from high elevations where *P. muralis* is absent; in the north of its distributional range above 900 m a.s.l. (e.g., Lapini et al., 1993; Cabela et al., 2007). Both species are said to be very similar in their general body size and shape, the average snout-vent length of adults being between 55-65 mm (e.g. De Luca, 1989; Aleksić and Ljubisavljević, 2001). Reproductively, *I. horvathi* is monoestrous while *P. muralis* may lay a second clutch when conditions are favourable (Lapini et al., 1993; Capula et al., 1993). The dietary niches of both species are highly overlapping (De Luca, 1992; Richard and Lapini, 1993). In the area of sympatry both species start their activity period in March/April and go to hibernation in October/November, exhibiting the diurnal activity pattern typical of lacertids in temperate zone (De Luca, 1992; Lapini et al., 1993). The overall habitat use of both species is also highly similar (Cabela et al., 2007). They mostly occupy rocky habitats with sparse vegetation or open rocky screes in forests. On the microhabitat scale, some differences in slope and vegetation cover selection between species have been detected, *I. horvathi* tending to use more rocks and vertical surfaces than *P. muralis* (Arnold, 1987; Lapini et al., 1993; Cabela et al., 2007). Moreover, similarity in the overall appearance between both species has frequently led to misidentification in the past (e.g. Brelih, 1954; De Luca, 1989). To determine the species it is usually necessary to catch or make a close-up photograph of the individual to see the position of rostral and frontonasal scales that are frequently in contact in *I. horvathi* and separated in *P. muralis* (e.g. Arnold et al., 2007). Because of that, recent intensive studies discovered unknown populations of *I. horvathi* in many parts of its range where the species had previously been misidentified as *P. muralis* or not recorded yet (Lapini et al., 2004; Žagar, 2008 a, b; Krofel et al., 2009; Cafuta, 2010; Rassati, 2010).

Sexual dimorphism in size and shape occurs in most species of lacertids. Size (snout-vent length and body mass) can be either male- or female-biased (e.g., Kaliontzopoulou et al., 2007; Kratochvíl et al., 2003) and males in most species have bigger and wider heads and longer limbs (e.g. Herrel et al., 1996). Such sexual differentiation in lacertids is hypothesised to be derived from different selection pressures: males having bigger head proportions to have a firm grasp of a female's trunk during copulation and females having longer trunks to hold the eggs (Kaliontzopoulou et al., 2007, 2008 a, b). In the case of *P. muralis*, instances of both male-biased (Strijbosch et al., 1980; Barbault and Mou, 1988; Braña and Ji, 2000; Allan et al., 2006; Bruner and Constantini, 2007; Gracceva et al., 2008; Aleksić et al., 2009) and female-biased (Gracceva et al., 2008; Kaliontzopoulou and Carretero, unpublished) sexual dimorphism have been described. In contrast, for *I. horvathi* a single comparative study of sexual dimorphism published so far showed a female-biased sexual size dimorphism (De Luca, 1989) as described for some other species of this genus (e.g. for *I. galani*; Arribas et. al., 2006).

The main aim of our study is to reveal morphometric (dis)similarity in two very resembling species of lacertids, *P. muralis* and *I. horvathi* living in the area of sympatry. In the past, most comparisons of size and shape of both species only referred to descriptive, often qualitative data and were not targeted to biometric characters in order to detect possible subtle interspecific differences. We aimed to compare differences at intra- (intersexual) and interspecific level in order to evaluate morphological divergences of considered sympatric lacertids. For the first time, we quantitatively investigate biometric characters of these two species from a sympatric area in southern Slovenia. Intersexual differences in size and shape in lacertids are a result of sexual selection rather than resulting from niche segregations (Carretero, 2004) and therefore we expect it exists in both species.

MATERIAL AND METHODS

Study area and individuals studied

Lizards were captured at 19 localities in the sympatric area of *P. muralis* and *I. horvathi* in Kočevsko region, Southern Slovenia (45˚28'37"N, 14˚48'34"E) in spring and summer periods between 2007 and 2010 (Fig. 1). The maximal distance between locations was 30 km that ensured similar environmental conditions. Climate was moderate continental and mountainous influenced by Mediterranean, inland and Atlantic ocean (Kordiš, 1993) with total annual precipitation of 1600 to 1800 mm and mean temperature in July 17.9 °C and in January -2.8 °C (Puncer, 1980). Typical habitats of both lacertid species in the region are natural or artificial rock cliffs with no or sparse vegetation and rocky outcrops on the forest edge (Žagar, 2008 a). Sampling sites were chosen to have similar microhabitat characteristics. All individuals caught were measured and photographed, and released afterwards on the same location. Sex was verified by inspection of colouration, cloacal region and femoral pores.

Biometric characters

To quantify intra- and interspecific differences we measured six biometric characters: snout vent length (SVL), head length (HL) from the tip of the snout to the posterior border of the collar, pileus length (PL), head width (HW), head height (HH), and mass (M) (only for specimens caught in 2010, measuring scheme after Kaliontzopoulou et al., 2007). All linear measurements were taken to the closest 0.1 mm, using digital callipers and mass was measured to the closest 0.1 g, using scale with a hook type Pesola max. 30 g.

Statistical analysis

Variables were logarithmically transformed to meet the assumptions of normality and homogeneity of variances. Considering that sexual dimorphism either in size (SSD) or in shape (SShD) is common in lacertids (see Introduction) sex was taken into account in all analyses. Differences in SVL were tested through a two-way ANOVA with sex and species as factors. Differences for the other measurements were relativized to SVL by using a two-way ANCOVA design with sex and species as factors and SVL as covariate for size correction. All statistical analyses have been done using Statistica 10 (STATSOFT, 2011).

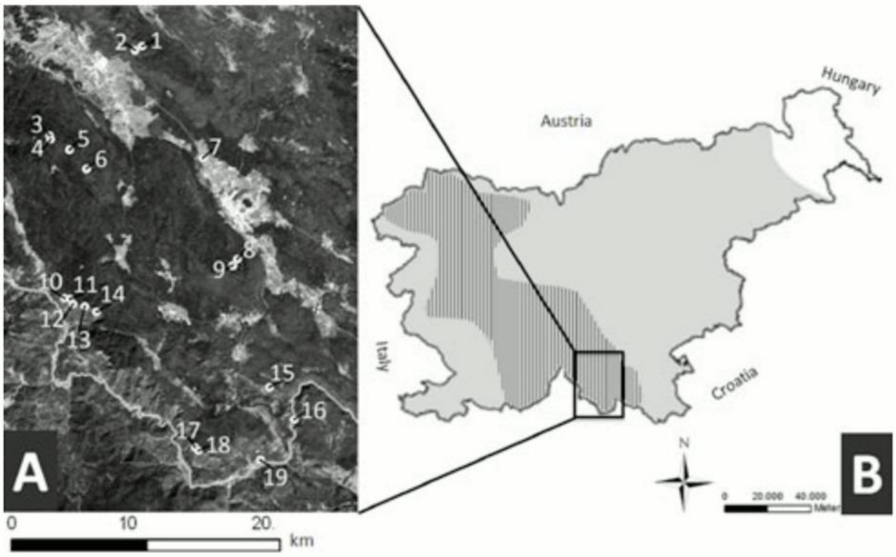


Fig. 1. Locations of the sampling sites (A) of Common wall lizards (*Podarcis muralis*, numbers 1, 2, 7-9, 16 and 19) and Horvath's rock lizards (*Iberolacerta horvathi*, numbers 3-6, 10-15, 17 and 18) and the location of the study area in Slovenia (B) with distributions of both species (*P. muralis* in grey and *I. horvathi* in black stripes).

RESULTS

A total of 34 males and 24 females of *I. horvathi,* and 25 males and 23 females of *P. muralis*, all adult individuals, were measured (Tab. 1). Both species showed sexual size dimorphism with females being longer (SVL) than males, but no interspecific differences either in SVL or in sexual dimorphism were found (Tab. 1 and 2). After size correction (ANCOVA), only PL did not show to be dependent on sex, but HW, HL, HH and M proved to be sexually dimorphic in both species (Tab. 2). In fact, males of both species had relatively wider, longer and higher heads and were heavier than the conspecific females (Tab. 1). Moreover, for both sexes, *I. horvathi* heads were more flattened than those of *P. muralis* and *P. muralis* were heavier than *I. horvathi* but no interspecific differences were found for the remaining variables (Tab. 2).

DISCUSSION

Our results comparing body size, head size and head shape of adult *P. muralis* and *I. horvathi* form the area of sympatry, indicated both sexual dimorphism and (limited) interspecific variation which were independent one from another. We have also confirmed that species were similar to each other in their external appearance. Considering each sex

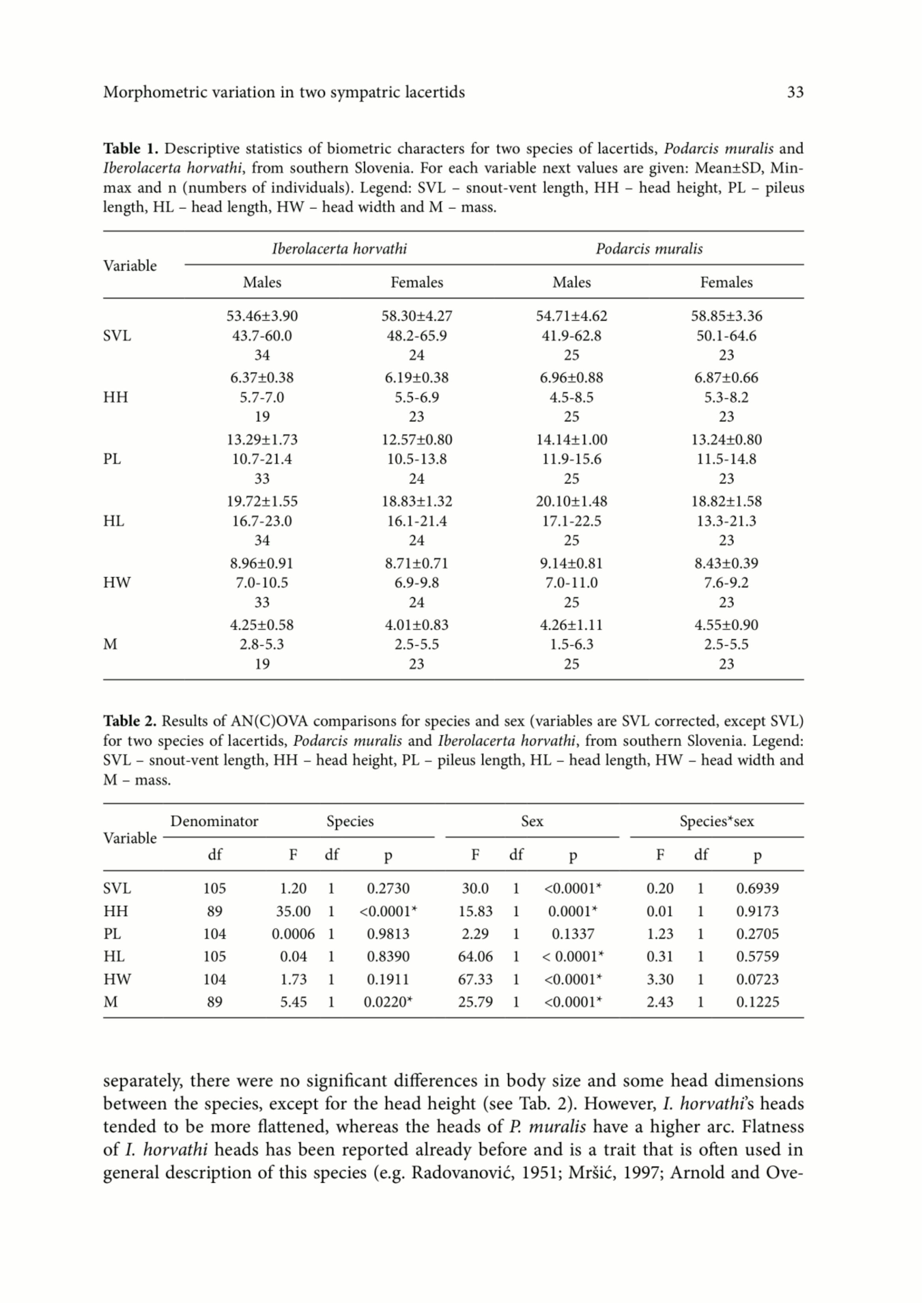


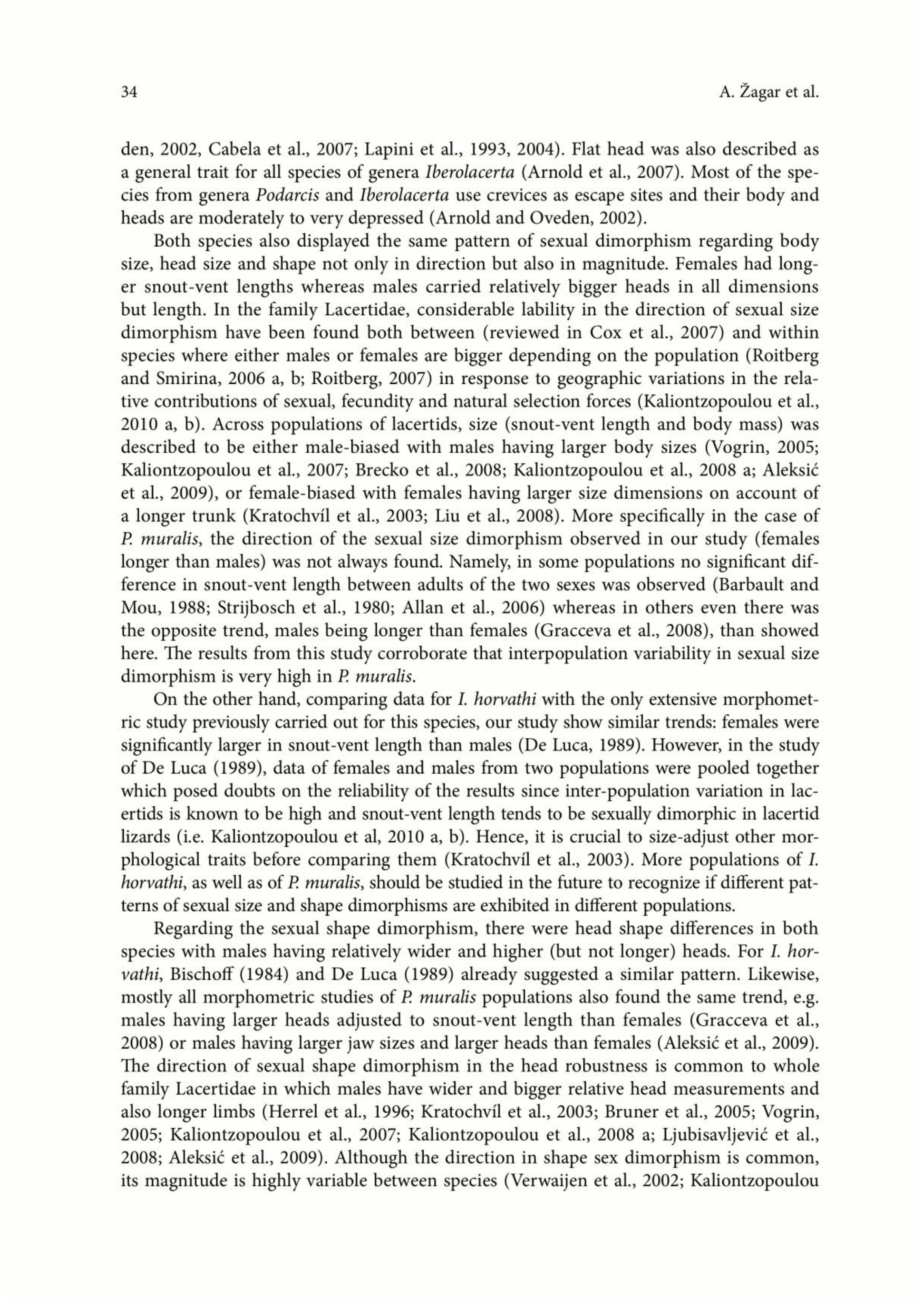
Table 1. Descriptive statistics of biometric characters for two species of lacertids, *Podarcis muralis* and *Iberolacerta horvathi*, from southern Slovenia. For each variable next values are given: Mean±SD, Min-max and n (numbers of individuals). Legend: SVL – snout-vent length, HH – head height, PL – pileus length, HL – head length, HW – head width and M – mass.

Variable	*Iberolacerta horvathi*		*Podarcis muralis*	
	Males	Females	Males	Females
SVL	53.46±3.90 43.7-60.0 34	58.30±4.27 48.2-65.9 24	54.71±4.62 41.9-62.8 25	58.85±3.36 50.1-64.6 23
HH	6.37±0.38 5.7-7.0 19	6.19±0.38 5.5-6.9 23	6.96±0.88 4.5-8.5 25	6.87±0.66 5.3-8.2 23
PL	13.29±1.73 10.7-21.4 33	12.57±0.80 10.5-13.8 24	14.14±1.00 11.9-15.6 25	13.24±0.80 11.5-14.8 23
HL	19.72±1.55 16.7-23.0 34	18.83±1.32 16.1-21.4 24	20.10±1.48 17.1-22.5 25	18.82±1.58 13.3-21.3 23
HW	8.96±0.91 7.0-10.5 33	8.71±0.71 6.9-9.8 24	9.14±0.81 7.0-11.0 25	8.43±0.39 7.6-9.2 23
M	4.25±0.58 2.8-5.3 19	4.01±0.83 2.5-5.5 23	4.26±1.11 1.5-6.3 25	4.55±0.90 2.5-5.5 23

Table 2. Results of AN(C)OVA comparisons for species and sex (variables are SVL corrected, except SVL) for two species of lacertids, *Podarcis muralis* and *Iberolacerta horvathi*, from southern Slovenia. Legend: SVL – snout-vent length, HH – head height, PL – pileus length, HL – head length, HW – head width and M – mass.

Variable	Denominator	Species			Sex			Species*sex		
	df	F	df	p	F	df	p	F	df	p
SVL	105	1.20	1	0.2730	30.0	1	<0.0001*	0.20	1	0.6939
HH	89	35.00	1	<0.0001*	15.83	1	0.0001*	0.01	1	0.9173
PL	104	0.0006	1	0.9813	2.29	1	0.1337	1.23	1	0.2705
HL	105	0.04	1	0.8390	64.06	1	< 0.0001*	0.31	1	0.5759
HW	104	1.73	1	0.1911	67.33	1	<0.0001*	3.30	1	0.0723
M	89	5.45	1	0.0220*	25.79	1	<0.0001*	2.43	1	0.1225

separately, there were no significant differences in body size and some head dimensions between the species, except for the head height (see Tab. 2). However, *I. horvathi*'s heads tended to be more flattened, whereas the heads of *P. muralis* have a higher arc. Flatness of *I. horvathi* heads has been reported already before and is a trait that is often used in general description of this species (e.g. Radovanović, 1951; Mršić, 1997; Arnold and Ove-



den, 2002, Cabela et al., 2007; Lapini et al., 1993, 2004). Flat head was also described as a general trait for all species of genera *Iberolacerta* (Arnold et al., 2007). Most of the species from genera *Podarcis* and *Iberolacerta* use crevices as escape sites and their body and heads are moderately to very depressed (Arnold and Oveden, 2002).

Both species also displayed the same pattern of sexual dimorphism regarding body size, head size and shape not only in direction but also in magnitude. Females had longer snout-vent lengths whereas males carried relatively bigger heads in all dimensions but length. In the family Lacertidae, considerable lability in the direction of sexual size dimorphism have been found both between (reviewed in Cox et al., 2007) and within species where either males or females are bigger depending on the population (Roitberg and Smirina, 2006 a, b; Roitberg, 2007) in response to geographic variations in the relative contributions of sexual, fecundity and natural selection forces (Kaliontzopoulou et al., 2010 a, b). Across populations of lacertids, size (snout-vent length and body mass) was described to be either male-biased with males having larger body sizes (Vogrin, 2005; Kaliontzopoulou et al., 2007; Brecko et al., 2008; Kaliontzopoulou et al., 2008 a; Aleksić et al., 2009), or female-biased with females having larger size dimensions on account of a longer trunk (Kratochvíl et al., 2003; Liu et al., 2008). More specifically in the case of *P. muralis*, the direction of the sexual size dimorphism observed in our study (females longer than males) was not always found. Namely, in some populations no significant difference in snout-vent length between adults of the two sexes was observed (Barbault and Mou, 1988; Strijbosch et al., 1980; Allan et al., 2006) whereas in others even there was the opposite trend, males being longer than females (Gracceva et al., 2008), than showed here. The results from this study corroborate that interpopulation variability in sexual size dimorphism is very high in *P. muralis*.

On the other hand, comparing data for *I. horvathi* with the only extensive morphometric study previously carried out for this species, our study show similar trends: females were significantly larger in snout-vent length than males (De Luca, 1989). However, in the study of De Luca (1989), data of females and males from two populations were pooled together which posed doubts on the reliability of the results since inter-population variation in lacertids is known to be high and snout-vent length tends to be sexually dimorphic in lacertid lizards (i.e. Kaliontzopoulou et al, 2010 a, b). Hence, it is crucial to size-adjust other morphological traits before comparing them (Kratochvíl et al., 2003). More populations of *I. horvathi*, as well as of *P. muralis*, should be studied in the future to recognize if different patterns of sexual size and shape dimorphisms are exhibited in different populations.

Regarding the sexual shape dimorphism, there were head shape differences in both species with males having relatively wider and higher (but not longer) heads. For *I. horvathi*, Bischoff (1984) and De Luca (1989) already suggested a similar pattern. Likewise, mostly all morphometric studies of *P. muralis* populations also found the same trend, e.g. males having larger heads adjusted to snout-vent length than females (Gracceva et al., 2008) or males having larger jaw sizes and larger heads than females (Aleksić et al., 2009). The direction of sexual shape dimorphism in the head robustness is common to whole family Lacertidae in which males have wider and bigger relative head measurements and also longer limbs (Herrel et al., 1996; Kratochvíl et al., 2003; Bruner et al., 2005; Vogrin, 2005; Kaliontzopoulou et al., 2007; Kaliontzopoulou et al., 2008 a; Ljubisavljević et al., 2008; Aleksić et al., 2009). Although the direction in shape sex dimorphism is common, its magnitude is highly variable between species (Verwaijen et al., 2002; Kaliontzopoulou et al., 2007; Ljubisavljević et al., 2008), but even though, in our case almost no differences in the amount of sexual shape dimorphism were detected between both species living in the area of sympatry. Actually, the analysis revealed that sexual dimorphism was in general higher (significant differences in all but one biometric characters) than species variation (significant differences only in head height and relative body mass, Tab. 2).

Summarizing, the lacertids *P. muralis* and *I. horvathi* show remarkable similarities not only in general size and shape (and in colouration; De Luca, 1989; Arnold and Oveden, 2002), but also in their sexual dimorphism patterns. Our study comparison of inter- and intraspecific sexual dimorphism patterns form localities in the sympatric area confirmed that *P. muralis* and *I. horvathi* are very similar. Together with their ecological similarities these facts suggest that, in absence of other factors, they are likely to be in interaction when living together. With our analysis we could not yet identify what type of interspecific interaction is present between both species, but most probably acts as interference which is commonly found in predator guilds (e.g. Carothers and Jaksić, 1984; Robinson and Terborgh, 1995; Linnell and Strand, 2000), and even in lacertids (Downes and Bauwens, 2002, 2004). In this perspective, results suggest potential for competition between species since interspecific effects in sympatric populations were not expressed in morphological, i.e. coevolved divergences. Perhaps such effects are expressed in other phenotypic or ecological adaptations, e.g. spatial segregation or resource partitioning (Tokeshi, 1999) that need to be investigated in the future. Thus, biometric comparisons could provide a first evaluation of competitive potential between lacertids of similar size belonging to the same predator guild (Valverde, 1967). If interspecific size differences are smaller than intraspecific, i.e. sexual dimorphism, this might suggest species to be potential competitors. On the other hand, equal or larger interspecific size differences could indicate already coevolved niche differentiation and consequently lower competition potential, i.e. "ghost of competition" pattern (Begon et al., 2006). Multipopulation comparison of sexual dimorphism and morphological divergence between both species in allopatry and sympatry should be carried out to test the hypotheses of character displacement and relaxation of interspecific competition (Butler et al., 2007).

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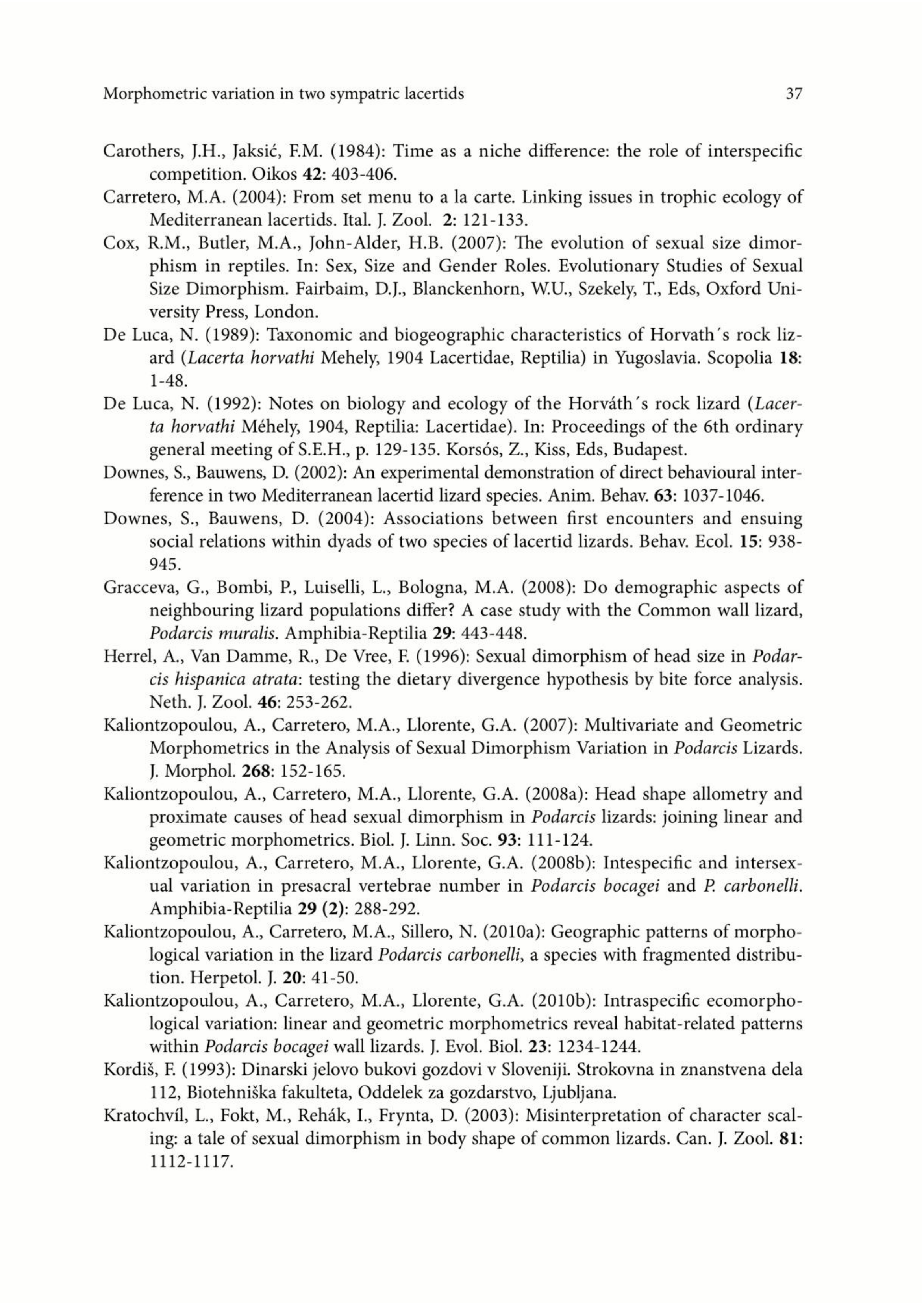

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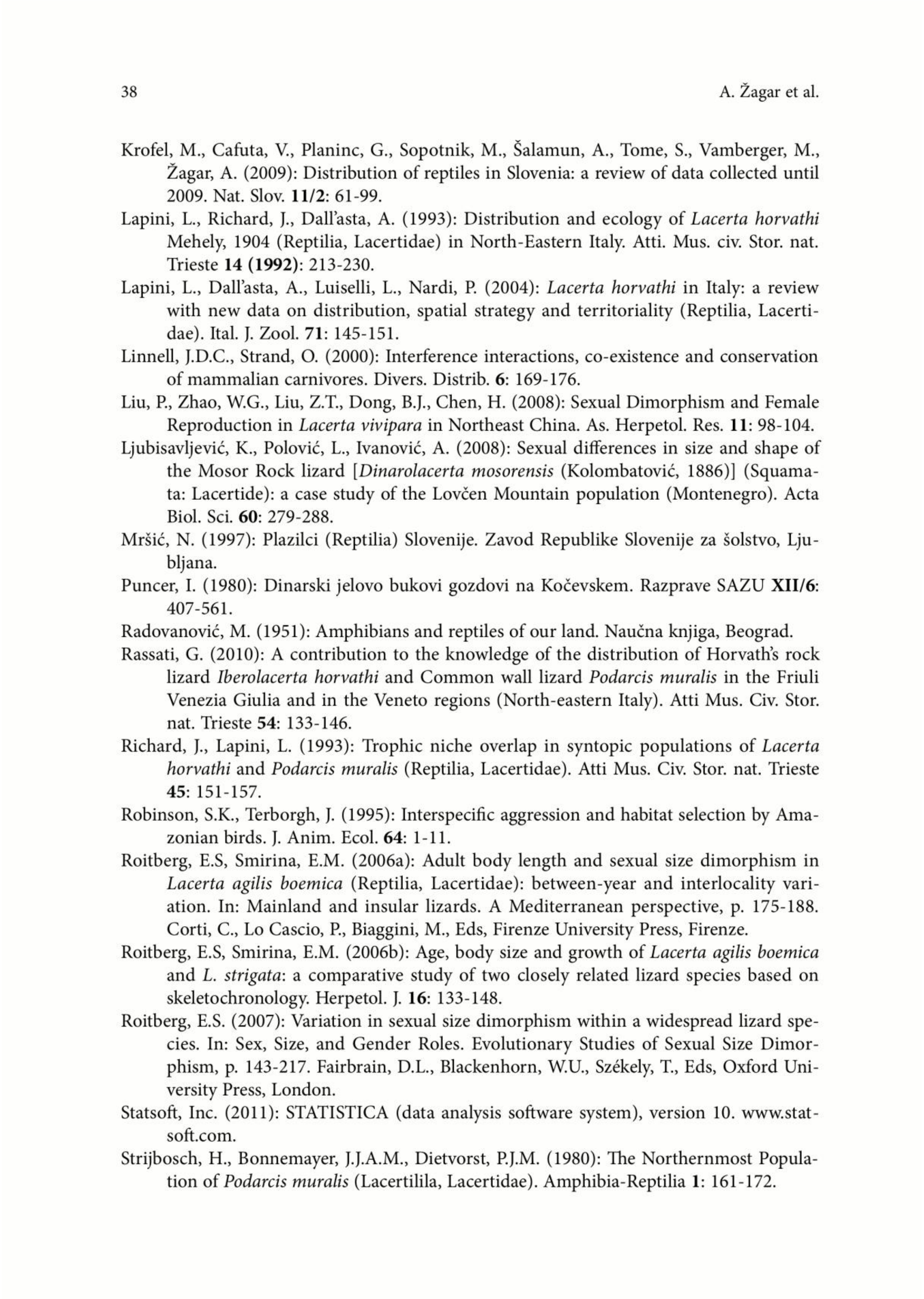

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4.1.3 Article III

Ecophysiological dissimilarities of two sympatric lizards

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ABSTRACT
The lizards *Podarcis muralis* and *Iberolacerta horvathi* display an overall similarity in morphology and ecology. Although they are widely sympatric in part of their distribution range of Slovenia, areas of altitudinal segregation have been observed. Eco-physiological traits such as preferred body temperatures (Tp) and rates of evaporative water loss (EWL) are some of the factors likely to be subjacent to this pattern. We expect the species that is more abundant in higher altitudes to have lower Tp and higher EWL (due to lower environmental temperatures at higher elevations) than the species that is more abundant in lowlands. We conducted lab experiments to determine whether intra- and interspecific variation in these two physiological traits exists. Contrary to expectations, the means of Tp were similar between the species, but their seasonal dynamics differed, which indicates that thermal accuracy might be more important. Species differed in seasonal (and daily) variation of Tp, rising from spring to summer more in *P. muralis* than in *I. horvathi*. Comparing instantaneous EWL, our results showed interspecific differences with higher values in *P. muralis* than in *I. horvathi*. Throughout a 12-h period, the accumulative EWL was also always higher for *P. muralis* than for *I. horvathi*, with the greatest differences occurring after 9−12 h of the experiment. Further studies should focus on investigating if these divergent physiological characteristics of both species are associated with their habitat use (in terms of thermal and water environment) and species interaction.

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ECOPHYSIOLOGICAL DISSIMILARITIES OF TWO SYMPATRIC LIZARDS

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ABSTRACT: The lizards *Podarcis muralis* and *Iberolacerta horvathi* display an overall similarity in morphology and ecology. Although they are widely sympatric in part of their distribution range of Slovenia, areas of altitudinal segregation have been observed. Ecophysiological traits such as preferred body temperatures (T_p) and rates of evaporative water loss (EWL) are some of the factors likely to be subjacent to this pattern. We expect the species that is more abundant in higher altitudes to have lower T_p and higher EWL (due to lower environmental temperatures at higher elevations) than the species that is more abundant in lowlands. We conducted lab experiments to determine whether intra- and interspecific variation in these two physiological traits exists. Contrary to expectations, the means of T_p were similar between the species, but their seasonal dynamics differed, which indicates that thermal accuracy might be more important. Species differed in seasonal (and daily) variation of T_p, rising from spring to summer more in *P. muralis* than in *I. horvathi*. Comparing instantaneous EWL, our results showed interspecific differences with higher values in *P. muralis* than in *I. horvathi*. Throughout a 12-h period, the accumulative EWL was also always higher for *P. muralis* than for *I. horvathi*, with the greatest differences occurring after 9–12 h of the experiment. Further studies should focus on investigating if these divergent physiological characteristics of both species are associated with their habitat use (in terms of thermal and water environment) and species interaction.

Key words: *Iberolacerta;* Lacertids; *Podarcis;* Sympatric populations; Thermal ecology; Water ecology

DISTRIBUTIONS of the lacertid lizards from the genera *Podarcis* and *Iberolacerta* in Europe have been hypothesized to derive from current and past interactions between members of both genera (Arribas, 1999; Mayer and Arribas, 2003; Carranza et al., 2004; Mayer and Pavlicev, 2007). An oft-cited example occurs in Common Wall Lizards (*Podarcis muralis* Laurenti, 1768) and Horvath's Rock Lizards (*Iberolacerta horvathi* Méhely, 1904), where the first species is widespread in Europe and the second is endemic to the Southern Alps and Dinaric Mountains (De Luca, 1989; Gasc et al., 1997; Lapini et al., 2004). Syntopic populations of both species can occur, but there is a general trend of altitudinal segregation between them (Arnold, 1987; Lapini et al., 1993; Richard and Lapini, 1993; Cabela et al., 2007). Specifically, *P. muralis* attains higher relative abundances in lowlands, whereas *I. horvathi* does so at higher elevations (Žagar et al., 2013). Both species display an overall similarity in morphometrics (Žagar et al., 2012), coloration, and several ecological characteristics (De Luca, 1989; Lapini et al., 1993; Richard and Lapini, 1993; Cabela et al., 2007).

Observed altitudinal segregation, overall similarity, and interspecific territorial aggressiveness indicate ecological interactions in lacertid lizards (Sacchi et al., 2009). To ascertain whether *P. muralis* and *I. horvathi* interact, several researchers have compared their dietary niches, habitat use, and life-history traits (De Luca, 1989; Lapini et al., 1993; Cabela et al., 2007; Ljubisavljević et al., 2012). Although these characteristics are relevant for defining similarities in species' niches (Kearney and Porter, 2009), physiolog-

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ical traits of these species still remain poorly documented.

One of the most important physiological traits of lizards is the preferred body temperature (T_p) in the absence of thermoregulatory constraints, because many species are known for the ability to precisely regulate body temperature by means of behavioral adjustments (reviewed in Huey, 1982). Being correlated with several physiological optima and directly related with fitness (Huey and Bennett, 1987), T_p is reflected in reproduction, habitat use, and geographical distribution. The thermal preferences of lacertids are recognized as relatively conservative—whereas their field activity body temperatures vary according to the environment, their T_p remain similar within species even under different climate regimes (Van Damme et al., 1990; Gvoždik and Castilla, 2001; Carretero et al., 2005). Within individual lacertids, however, T_p may change as a function of season, feeding activity, or reproductive status (Castilla et al., 1999; Grbac and Bauwens, 2001; Carretero et al., 2005). For instance, thermal optima of gravid females tend to be lower than those of nongravid females, apparently to ensure optimal embryo development (Braña, 1993; Castilla et al., 1999; Carretero et al., 2005). Although the thermal ecology of *P. muralis* has been investigated in several populations across Europe (Braña, 1993; McKeehan and Sievert, 1996; Tosini and Avery, 1996; Grbac and Bauwens, 2001), no data are available for *I. horvathi*.

In contrast to the abundant literature on lizard thermal ecology, less attention has been paid to water loss in reptiles, in spite of its expected role in the physiology of this group. Evaporative water loss (EWL) mainly occurs through the skin (cutaneous water loss) of terrestrial reptiles (Shoemaker and Nagy, 1977; Mautz, 1982a), but also through the respiratory passages (respiratory water loss) and the eyes (ocular water loss; Mautz, 1982a). Many studies have shown that cutaneous water loss rates differ between reptiles from xeric and humid habitats (Warburg, 1965; Mautz, 1982b; Eynan and Dmi'el, 1993), indicating either a current or past adaptation. Together with the thermal ecology traits, EWL is another physiological trait of a given lizard species that defines the limits of its fundamental niche, particularly when the water availability is restricted (Bowker, 1993). Therefore, integrating thermal and water-loss data may be crucial for explaining interspecific differences between reptile populations occurring in syntopy.

In this study, we compare two ecophysiological traits, preferred body temperatures and water loss rates, of two similar and sympatric lizard species. Our objectives were to: (1) determine the differences in mean T_p and ranges of T_p between species and sexes; (2) examine the seasonal variation of T_p between the species and sexes; and (3) to determine inter- and intraspecific variation in EWL. We expect our results to contribute toward understanding ecological segregation patterns found in the areas of sympatric occurrence of these two species.

MATERIALS AND METHODS

Sampling

We captured all individuals used in experiments with a noose in the area of sympatric occurrence in Kočevsko region, in southeastern Slovenia (45°28′37″N, 14°48′34″E, datum = WGS84). All individuals of one species were collected from a single population within an area of 5 km. We collected the lizards and released them at their capture sites after the experiments, and after being fed and rehydrated (see below). We collected lizards in two seasons—in spring (May and June) and summer (July and August) of 2010 for T_p experiments, and in one season (July and August) of 2011 for EWL experiments. The climate of the area is temperate continental with alpine climate characteristics at higher elevations (Kordiš, 1993), with the total annual precipitation of 1600–1800 mm, and mean temperature of 17.9°C in July, and –2.8°C in January (Puncer, 1980). Typical habitats of both lacertids in the region are natural or artificial rock cliffs with no or sparse vegetation and rocky outcrops on the forest edge (Žagar, 2008; Žagar et al., 2013).

We verified the sex of each subject by inspection of coloration, cloacal region, and femoral pores, and we checked for gravidity of females by observing the belly size, signs of

copulation marks, and palpating the eggs around the abdomen. Before experimentation, lizards were kept in individual terraria for less than 8 days with food (*Tenebrio molitor* larvae and grasshoppers) and water ad libitum, and were kept under a natural regime of light and temperature. We measured snout–vent lengths (SVL; ±0.1 mm) using a digital caliper after the experiments. Average daily temperatures (and maximum daily temperatures) collected from the nearest meteorological station (Kočevje, 45°38′24″N, 14°51′38″E, datum = WGS84) for months of lizard collections for T_{p} experiments in 2010 were: 13.1°C (23°C) in May, 17.5°C (30.6°C) in June, 20.0°C (34.7°C) in July, and 17.6°C (31.5°C) in August (ARSO, 2013).

Thermal Gradient Experiment

In an experimental terrarium (0.4 × 0.4 × 1.5 m), we exposed each lizard to a photothermal gradient between 20 and 50°C produced by a 150-W infrared reflector bulb fixed at one end of the terrarium (Veríssimo and Carretero, 2009). The bulb was switched on 1 h before we placed a lizard into the terrarium, and 2 h before the first measurement was recorded at 0900 h. We performed the experiment in a closed room to prevent wind and direct sun from affecting the temperatures in the terrarium. We monitored the thermal gradient during all experiments with DS1922L iButton temperature loggers (Maxim Integrated, San Jose, California) placed at both ends and the middle of each terrarium. At 11 consecutive hourly intervals, we measured the body temperature of each lizard (T_{p}; ±0.1°C) using a k-thermocouple probe associated with a digital portable thermometer HIBOK 14 inserted into the subject's cloaca (Veríssimo and Carretero, 2009). This procedure was chosen as a compromise between invasiveness and accuracy; namely, these species are too small to allocate permanent cloacal probes or implanted transmitters (Clusella Trullas et al., 2007), and too slender to provide accurate infrared readings (Carretero, 2012). The experiment was performed from 0800 to 1900 h Central European Time (CET), the period of daily activity of both species observed in the field (Braña, 1991; Lapini et al., 1993). To minimize thermal shifts due to stress or contact with the researcher's hand, we limited the combined time of catching the lizard and the time between the capture and the measurement of T_{p}, to no more than 10 s (Veríssimo and Carretero, 2009).

Water-Loss Experiment

For this experiment, we first placed individual lizards in small plastic boxes (15 × 10 × 5 cm) with holes in the top and the bottom. Then, we placed groups of five boxes containing lizards into a sealed chamber (60 × 40 × 30 cm) with dry conditions (relative humidity of ~25–35%) generated by the silica gel. The silica gel (~80 g) was placed in a bag made of gauze and fixed on the bottom side of the chamber lid, as well as 5 g placed at the bottom of each box containing a lizard. We conducted the experiment under controlled room temperature (~25°C). Conditions in the chamber were monitored at hourly intervals to ensure a low relative humidity using the Fluke 971 temperature humidity meter (Fluke Corporation, Everett, Washington). The amount of silica gel used ensured a low and stable relative humidity inside each box (±1%). We conducted the experiment from 0800 to 2000 h CET. Every hour, we removed the lizards from the chamber and determined the mass of each using an analytical balance (±0.0001 g; CPA model 224S, Sartorius, Bohemia, New York), and immediately placed them back in their respective boxes within the chamber. The whole measurement procedure took no longer than 20 s. The measurements of EWL experiments were first checked for detecting faults or outliers. Measuring faults were identified by an increase in the lizard's mass compared with the previous measurement, and attributed to the fact that measurements had to be conducted in a limited time during which the lizard could be moving (i.e., the scale did not stabilize within 20 s). An outlier was an extremely low value compared with the previous measurement, in one case caused by a data-entry error. These faults resulted in incomplete data sets that were excluded from analysis (for *P. muralis*: three males; for *I. horvathi*: one female and three males).

From our data, we calculated two measurements of relative water loss. The first was the accumulative water loss (EWL_a) after each hour of the experiment (from 0900 to 2000 h CET), calculated after the formula: $EWL_a = [(W_0 - W_n) / W_0] \times 100$. These values provide information on how much overall water evaporated during the course of the experiment. Second, we calculated the instantaneous water loss (EWL_i) by subtracting the mass of the lizard at a given time interval from the previous interval ($W_n - W_{n+1}$), and dividing by initial mass at 0800 h (W_0), multiplying by 100 to obtain a percentage value (%). The full formula used was $EWL_i = [(W_n - W_{n+1}) / W_0] \times 100$. EWL_i values plotted across time illustrate the pattern of losing water (either constant or variable).

Statistical Analysis

The distribution of T_p, EWL_i, and EWL_a values at each hour did not deviate from normality (Shapiro–Wilk's test, $P > 0.05$ in all cases), were homoscedastic (univariate Levene's tests and multivariate Box M, $P > 0.05$ in most cases), and the variances and means were also uncorrelated; hence, we did not transform the values before analysis. Measures of T_p were repeated for the same individual for each interval. Hence, we used analyses of covariance with repeated measures (ANCOVA-rm) to ascertain variation in T_p as a function species, sex, and season (between-subject factors) and time interval (within-subject factor), with SVL as the covariate (Carretero et al., 2005). The sphericity assumption of the data was assessed by means of Mauchly's tests. We performed post hoc Duncan's tests between groups to detect the patterns of significance. For analysis of water loss we used the calculated values of EWL_a in 12 separate one-way analyses of variance (ANOVA), using species as factor. Subsequently, P values were adjusted for multiple tests using a false discovery rate (FDR) procedure (Benjamini and Hochberg, 1995). Second, values of EWL_i were analyzed using ANCOVA-rm with sex and species as between-subject factors, time interval as the within-subject factor, and logSVL (or $\log W_0$, the initial weight of the lizard) as the covariate. All analyses were performed in Statistica 10 (Statsoft, Tulsa, Oklahoma), except FDR was performed using R software (R Developement Core Team).

TABLE 1.—Results of a repeated-measures analysis of covariance ($F_{10,670} = 1.14$, $P = 0.33$) of preferred body temperatures for *Podarcis muralis* and *Iberolacerta horvathi* using snout–vent length (SVL) as the covariate, and sex, species, and season as between-subject factors, and time interval as a within-subject factor. (* indicates statistical significance.)

Factor	F	df	P
Species	7.59	1	< 0.01*
Season	188.62	1	< 0.001*
Sex	0.07	1	0.79
Species × season	23.26	1	< 0.001*
Species × sex	3.42	1	0.07
Season × sex	0.04	1	0.85
Species × season × sex	1.12	1	0.29
Time	1.08	10	0.37
Time × species	1.34	10	0.20
Time × season	2.85	10	< 0.01*
Time × sex	0.45	10	0.92
Time × species × season	0.65	10	0.77
Time × species × sex	1.18	10	0.30
Time × season × sex	1.15	10	0.32
Time × species × season × sex	1.14	10	0.33

RESULTS

Experimental Individuals

For T_p experiments, we collected lizards in two sampling seasons. In spring, we tested 5 females and 10 males of *P. muralis*, and 10 females and 7 males of *I. horvathi*. In summer, we tested 10 females and 15 males of *P. muralis*, and 11 females and 11 males of *I. horvathi*. For EWL experiments, we collected separate samples of 10 females and 10 males of each species (in total 40 individuals) in summer 2011. To minimize the effect of gravidity, we decided to use females of the same state in the same season; in spring, all females were showing signs of gravidity, whereas in summer, none of the females was gravid. In both experiments, we pooled our results across sexes, as this was not a significant factor in analyses of either T_p or EWL.

The mean (±SD) SVL of *P. muralis* caught in spring and summer was 54.16 ± 5.95 and 55.07 ± 3.66 mm for males, respectively, and 58.95 ± 2.67 and 58.10 ± 3.41 mm for females. Measurements for male and female *I. horvathi* collected in each season (spring and

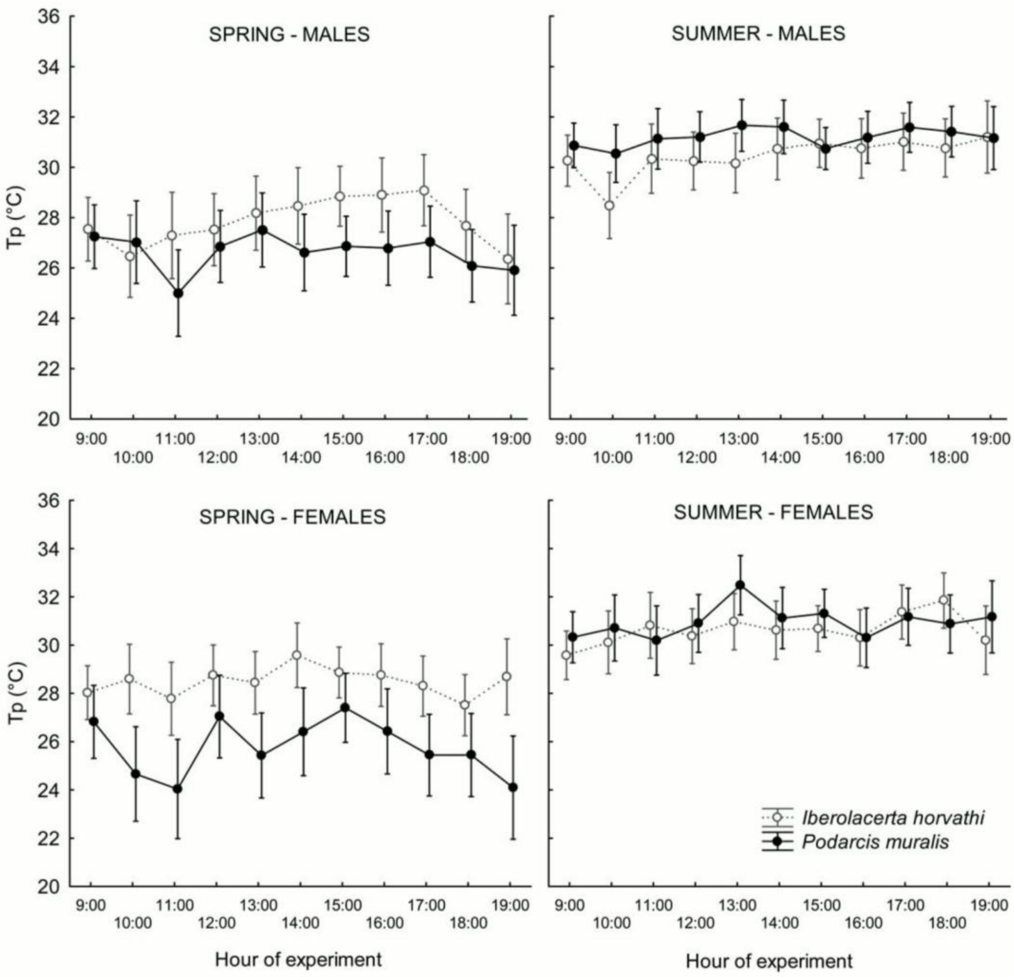

FIG. 1.—Daily variation of the preferred body temperatures of males and females of *Podarcis muralis* and *Iberolacerta horvathi* in spring and summer. The *x*-axis shows time of day (Central European Time). Displayed are median values and 95% confidence intervals.

summer) were 55.64 ± 2.54 and 55.50 ± 2.36 mm and 60.20 ± 3.66 and 57.73 ± 3.84 mm, respectively. Male and female *P. muralis* used in the EWL experiments had a mean SVL of 53.11 ± 5.68 mm and 55.13 ± 3.70 mm, respectively. Male and female *I. horvathi* measured 50.14 ± 5.41 mm and 58.16 ± 4.92 mm, respectively. For each species, we compared SVL values among all experiments for females and males separately, and determined that there were no differences in SVLs of each sex between experiments (ANOVA, females: $F_{5,59} = 1.84$, $P = 0.12$, males: $F_{5,51} = 1.77$, $P = 0.14$).

Preferred Temperatures

Both *P. muralis* and *I. horvathi* exhibited differences in T_p during each season (Table 1), with higher values in summer than in spring. The difference in T_p between seasons is lower in *I. horvathi* than in *P. muralis* (Fig. 1), but T_p values of both species differ between seasons (Duncan's test for species × season, $P < 0.001$ for both). The degree to which each species shifted its T_p between

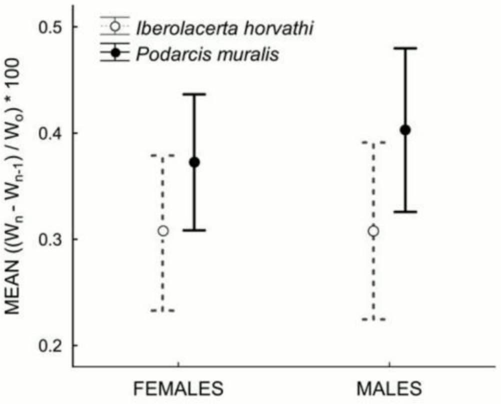

FIG. 2.—Mean instantaneous water loss of *Podarcis muralis* and *Iberolacerta horvathi* as a function of time over 12 hourly measurements (repeated-measures analysis of covariance, using snout–vent length (logSVL) as a covariate, sex and species as between-subject factors, and time interval as a within-subject factor; $F_{1,28} = 5.35$, $P = 0.03$).

changed seasons, with *I. horvathi* tending to attain higher T_p than *P. muralis* in spring, but being similar in summer (Duncan's test, $P = 0.13$). Moreover, both species displayed more daily variation in T_p values in spring than in summer, essentially consisting of higher differences between T_p attained in early morning and midday (Fig. 1).

Water Loss

Rates of EWL_i differed between species ($F_{1,28} = 5.35$, $P = 0.03$), with *P. muralis* having a higher mean EWL_i than *I. horvathi* (Fig. 2). Within each species, the rates did not differ as a function of time (i.e., across the 12-h duration of the experiment). Our analyses of EWL_a rates as a function of time showed that values of both species were progressively more divergent over the duration of the experiment (Table 2). Rates of EWL_a for *P. muralis* tended to be higher than those of *I. horvathi* after the ninth hour of the experiment, but differences were not significant after the FDR correction was applied (Table 2, Fig. 3).

DISCUSSION

Although sympatric *P. muralis* and *I. horvathi* displayed similar trends in their physiology, the species differed in their temporal patterns of T_p and water loss. In general, T_p is expected to remain similar between populations of the same species (Van Damme et al., 1989; Tosini and Avery, 1993; Gvoždik and Castilla, 2001; Carretero et al., 2005), despite divergent thermal conditions in the habitats occupied by those populations. This is only true, however, when T_p is monitored within similar periods (both seasonal and daily acclimatization have been reported; Van Damme et al., 1986; Veríssimo and Carretero, 2009). Our results indicate that lizards tended to select higher temperatures when environmental temperatures are low (in spring; mean T_p was above 30°C for all groups), suggesting that thermoregulation is

TABLE 2.—Results of an analysis of variance for accumulative water loss ($EWL_a = [(W_0 - W_n) / W_0] \times 100$) after each hour of the experiment and false discovery rate (FDR) values for *Podarcis muralis* and *Iberolacerta horvathi*. Also presented are mean values of EWL_a for each species, and the difference in mean values (mean for *I. horvathi* subtracted from the mean for *P. muralis*).

Hour of the experiment	ANOVA				Mean		Difference
	F	df	*P*	FDR	*P. muralis*	*I. horvathi*	
1	2.07	1	0.16	0.26	0.38	0.27	0.11
2	0.64	1	0.43	0.43	0.68	0.58	0.10
3	0.12	1	0.43	0.43	1.02	0.90	0.12
4	0.59	1	0.19	0.26	1.40	1.13	0.27
5	0.87	1	0.20	0.26	1.80	1.48	0.32
6	1.54	1	0.22	0.26	2.24	1.88	0.36
7	1.93	1	0.17	0.26	2.64	2.20	0.44
8	3.90	1	0.06	0.14	3.12	2.48	0.64
9	5.15	1	0.03	0.09	3.60	2.81	0.79
10	5.36	1	0.03	0.09	3.96	3.10	0.86
11	5.97	1	0.02	0.09	4.34	3.40	0.96
12	5.48	1	0.03	0.09	4.61	3.69	0.92

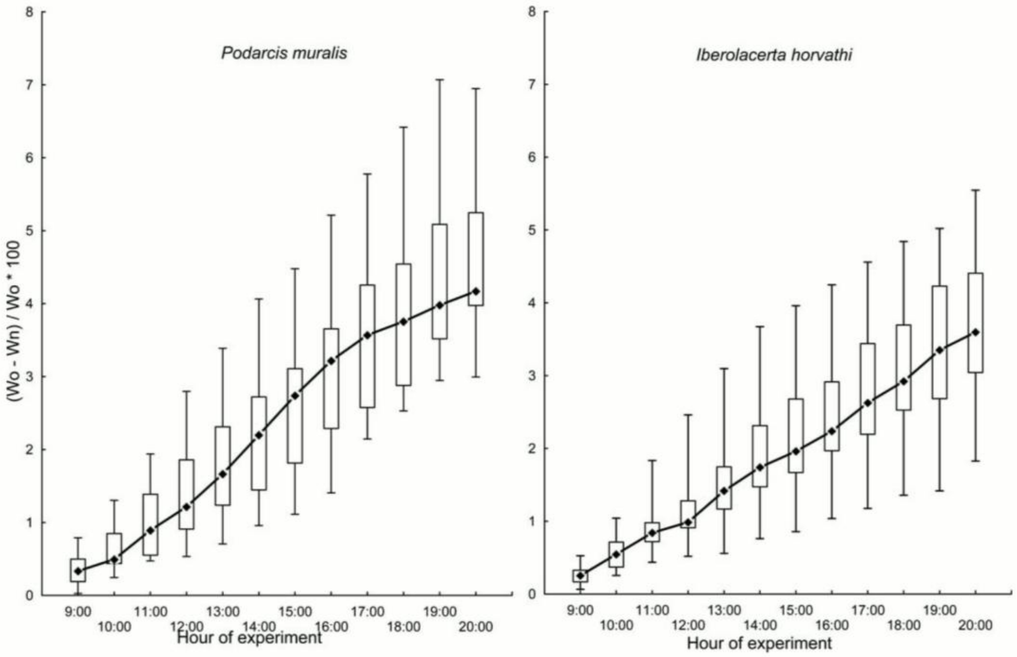

FIG. 3.—Accumulated water loss after 1 to 12 h of the experiment of *Podarcis muralis* and *Iberolacerta horvathi*. Displayed are means (diamonds) with standard errors (box) and nonoutlier minimum and maximum values (whiskers).

a priority in relation to other requirements (Carretero et al., 2005, 2006; Veríssimo and Carretero, 2009). In other words, maintaining higher temperatures in the thermal gradient in spring, when environmental temperatures are cooler, apparently takes precedence over the daily pattern. This might reflect more dramatic changes in thermal environment between seasons than between hours within a single day, but might also reflect some limitations in the capacity to change T_p. Similar seasonal changes are reported by Van Damme et al. (1986) for subadult *Zootoca vivipara*, where individuals also had higher temperatures in summer than in spring, excluding the first month after hibernation (April).

Even if both species compared here exhibited a similar direction of the trend (higher T_p in summer than in spring), the intensity of the response to the seasonal variation was different between the species. Namely, when comparing the T_p values of two seasons, *I. horvathi* has a narrower overall T_p range than *P. muralis*. With independence of this seasonal variation among lacertid species, T_p tend to be distinct and are more related to biogeographic origins (i.e., carry a substantial phylogenetic signal) than to current environmental conditions (e.g., Van Damme et al., 1986, 1990; Carretero et al., 2005).

When exposed to a long dry period, *P. muralis* had a greater EWL_a through cutaneous-respiratory evaporation than *I. horvathi*. Despite the sexual dimorphism in morphology in both species, no intersexual differences in EWL were found, whereas interspecific differences persisted when robustness (measured in either SVL or mass—values that would favor *P. muralis*, and males; Žagar et al., 2012) was statistically removed. Causes of observed differences between the species might be related to different rates of evaporation through their skin, their pharynx (also related to breathing rate), or a combination thereof. In general, when compared with those of mammals and birds, the reptilian epidermis is less permeable to water (Patil et al., 1993); our results indicate that skin permeability might also be different between closely related reptile species. The few studies on the evaporative characteristics of lizard skin do not concern any lacertid species. Kobayashi et al. (1983) compared evaporation and skin evaporative characteristics of *Anolis* maintained in dry and humid conditions, showing that lizards could reduce the rate of losing water when in dry conditions by altering their skin evaporation rates.

Following our laboratory results, field observations on thermal ecology of sympatric *P. muralis* and *I. horvathi* populations in climatically heterogenic environments are needed to determine whether macrohabitat (i.e., altitudinal gradient) and microhabitat (e.g., shaded, humid, or cool sites) traits selected by the lizards reflect, totally or in part, the ecophysiological traits of each species. This might be particularly useful in the case of the spatial distribution of the endemic *I. horvathi*. Namely, some species of *Iberolacerta* occupy areas having more damp, humid, and shaded microhabitats than species of *Podarcis* of the same regions (Galán et al., 2007; Arribas, 2009; Monasterio et al., 2009). This also applies to *I. horvathi* compared with *P. muralis* (Lapini et al., 2004; Žagar, 2008). Such comparative studies might be essential, in the light of global trends of climate change (Solomon et al., 2007), providing reliable predictions of future responses of both species, including presumed competitive interactions (Bozinovic et al., 2011).

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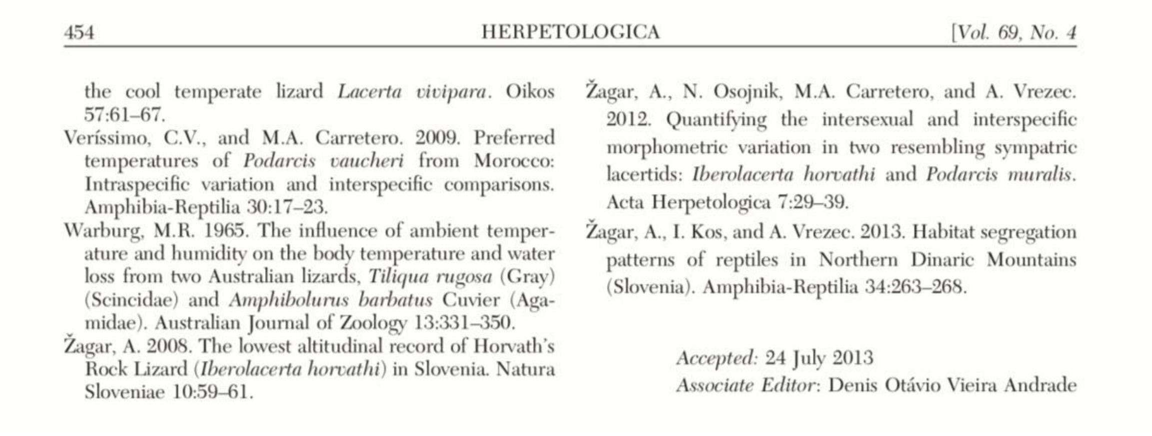

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4.1.4 Article IV

The role of metabolism in understanding the altitudinal segregation pattern of two potentially interacting lizards

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ABSTRACT
Sympatric species from the same ecological guild, that exhibit partial altitudinal segregation, can potentially interact in areas of syntopic occurrence. Besides general species' ecology, physiology can provide important answers about species interactions reflected in altitudinal patterns. Lizards *Podarcis muralis* and *Iberolacerta horvathi* exhibit partial altitudinal segregation, while they strongly resemble in overall morphology and ecology (diet, daily and seasonal activity pattern), but show certain degree of physiological dissimilarity. They have similar mean preferred body temperatures and its pattern of seasonal and daily variations but differ in the magnitude of seasonal variation. Since an ectotherm metabolism is highly dependent on body temperature, thermoregulation is expected to directly affect their metabolism. We compared metabolic rates of adult males from an area of sympatry, measured under two temperature regimes (20 °C and 28 °C). Both species increased metabolic rates with temperature in a similar pattern. We also compared electron transport activity from tail tissues which provide values of species potential metabolic activity (enzymatic capacity). Species clearly differed in potential metabolic activity; *I. horvathi* attained higher values than *P. muralis*. No difference was detected in how species exploited this potential (calculated from the ratio of electron transport activity and metabolic rates). However, we observed higher potential metabolic activity *I. horvathi* which together with the ability to thermoregulate more precisely could represent a higher competitive advantage over *P. muralis* in thermally more restrictive environments such as higher altitudes. Understanding of metabolism seems to provide valuable information for understanding recent distributional patterns as well as species interactions.

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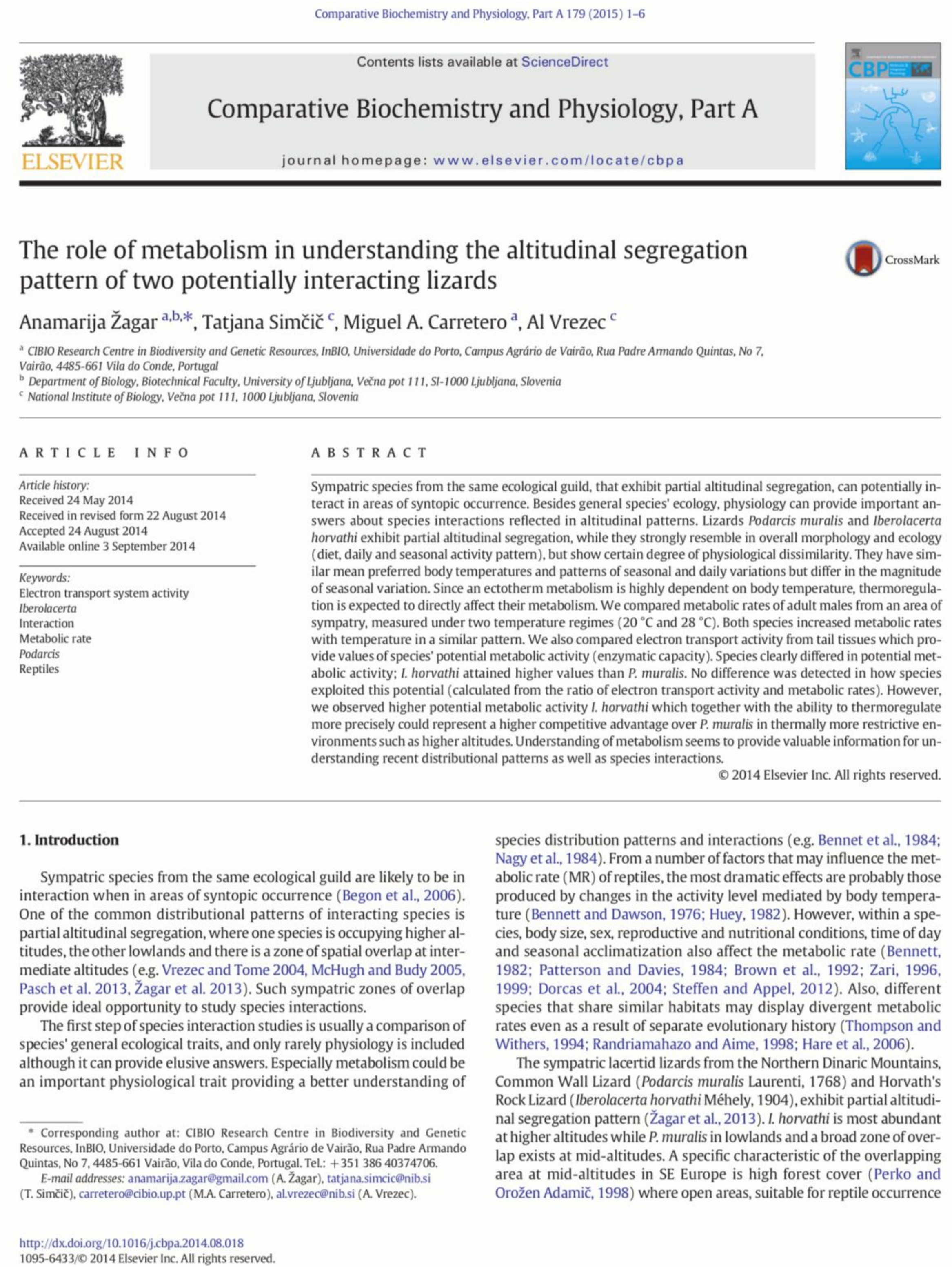

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The role of metabolism in understanding the altitudinal segregation pattern of two potentially interacting lizards

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Sympatric species from the same ecological guild, that exhibit partial altitudinal segregation, can potentially interact in areas of syntopic occurrence. Besides general species' ecology, physiology can provide important answers about species interactions reflected in altitudinal patterns. Lizards *Podarcis muralis* and *Iberolacerta horvathi* exhibit partial altitudinal segregation, while they strongly resemble in overall morphology and ecology (diet, daily and seasonal activity pattern), but show certain degree of physiological dissimilarity. They have similar mean preferred body temperatures and patterns of seasonal and daily variations but differ in the magnitude of seasonal variation. Since an ectotherm metabolism is highly dependent on body temperature, thermoregulation is expected to directly affect their metabolism. We compared metabolic rates of adult males from an area of sympatry, measured under two temperature regimes (20 °C and 28 °C). Both species increased metabolic rates with temperature in a similar pattern. We also compared electron transport activity from tail tissues which provide values of species' potential metabolic activity (enzymatic capacity). Species clearly differed in potential metabolic activity; *I. horvathi* attained higher values than *P. muralis*. No difference was detected in how species exploited this potential (calculated from the ratio of electron transport activity and metabolic rates). However, we observed higher potential metabolic activity *I. horvathi* which together with the ability to thermoregulate more precisely could represent a higher competitive advantage over *P. muralis* in thermally more restrictive environments such as higher altitudes. Understanding of metabolism seems to provide valuable information for understanding recent distributional patterns as well as species interactions.

1. Introduction

Sympatric species from the same ecological guild are likely to be in interaction when in areas of syntopic occurrence (Begon et al., 2006). One of the common distributional patterns of interacting species is partial altitudinal segregation, where one species is occupying higher altitudes, the other lowlands and there is a zone of spatial overlap at intermediate altitudes (e.g. Vrezec and Tome 2004, McHugh and Budy 2005, Pasch et al. 2013, Žagar et al. 2013). Such sympatric zones of overlap provide ideal opportunity to study species interactions.

The first step of species interaction studies is usually a comparison of species' general ecological traits, and only rarely physiology is included although it can provide elusive answers. Especially metabolism could be an important physiological trait providing a better understanding of species distribution patterns and interactions (e.g. Bennet et al., 1984; Nagy et al., 1984). From a number of factors that may influence the metabolic rate (MR) of reptiles, the most dramatic effects are probably those produced by changes in the activity level mediated by body temperature (Bennett and Dawson, 1976; Huey, 1982). However, within a species, body size, sex, reproductive and nutritional conditions, time of day and seasonal acclimatization also affect the metabolic rate (Bennett, 1982; Patterson and Davies, 1984; Brown et al., 1992; Zari, 1996, 1999; Dorcas et al., 2004; Steffen and Appel, 2012). Also, different species that share similar habitats may display divergent metabolic rates even as a result of separate evolutionary history (Thompson and Withers, 1994; Randriamahazo and Aime, 1998; Hare et al., 2006).

The sympatric lacertid lizards from the Northern Dinaric Mountains, Common Wall Lizard (*Podarcis muralis* Laurenti, 1768) and Horvath's Rock Lizard (*Iberolacerta horvathi* Méhely, 1904), exhibit partial altitudinal segregation pattern (Žagar et al., 2013). *I. horvathi* is most abundant at higher altitudes while *P. muralis* in lowlands and a broad zone of overlap exists at mid-altitudes. A specific characteristic of the overlapping area at mid-altitudes in SE Europe is high forest cover (Perko and Orožen Adamič, 1998) where open areas, suitable for reptile occurrence

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and basking, are limited (Žagar et al., 2013). Males of many species of the family Lacertidae are known to exhibit aggressiveness against other males in spatial context, namely for the best basking places and shelters (e.g. Olsson, 1994; López and Martín, 2002). Thus, while such favourable parts of the habitat are limited in the area of sympatric occurrence of the studied species, there is a high potential for interactions.

Both species strongly resemble in morphology (Žagar et al., 2012) and ecology (diet, daily and seasonal activity pattern and reproduction, De Luca, 1989; Lapini et al., 1993; Richard and Lapini, 1993; Cabela et al., 2007), but show some degree of physiological dissimilarity. Osojnik et al. (2013) recently described that both species have similar mean preferred body temperatures (T_p) and the pattern of daily and seasonal variations of T_p. The only interspecific difference detected was the magnitude of seasonal variation of T_p; the "high altitude" species, *I. horvathi*, selected similar temperatures throughout the year, while the "low altitude" species, *P. muralis*, displayed seasonal variation. This suggests that *I. horvathi* is potentially a more precise thermoregulator than *P. muralis*. Alongside, *I. horvathi* was found to lose less water than *P. muralis* when exposed to dry conditions, suggesting additional physiological trait enabling it to spend more time in sun basking without risking water stress (Osojnik et al., 2013).

Since acclimatization of preferred body temperature (T_p) in response to environmental seasonality has been demonstrated to vary between lizard species (e.g. Angilletta, 2001; Osojnik et al., 2013) and temperature is the key determinant of metabolic rate in ectotherms (Bennett, 1982), difference in metabolism between species is expected. As a general rule in ectotherms, species from cold climates tend to have a higher metabolic rate at low temperatures than those from warm climates. For example, the cold-climate lizard *Zootoca vivipara* attained higher metabolic rates than the warmer-climate lizard *Podarcis hispanica* (Patterson and Davies, 1989). With altitude, the most obvious changing environmental trait is the temperature (dropping with increase of altitudes) which has a pronounce direct effect on ectotherms, such as lizards (Huey et al., 2012).

Organisms' metabolism is constraint by the enzymatic capacity of tissues. This can be measured in several ways, most often by assessing citrate synthase activity or cytochrome *c* oxidase (e.g. Simon and Robin, 1971; Lannig et al., 2003; Seebacher et al., 2003), whereas electron transport system (ETS) activity was less frequently used (e.g. Lannig et al., 2003) but provides similar information. Measurements of ETS activity indicate the amount of oxygen consumption that would occur if multi-enzyme complexes, located in the inner membrane of mitochondria, functioned maximally (Muskó et al., 1995). The ratio between ETS activity and observed oxygen consumption (ETS/MR ratio) is an important index of an organism's metabolism (Muskó et al., 1995) because it provides a measure of the fraction of total metabolic potential that is actually exploited for respiration. Several studies also calculated the ETS/MR ratio (but only in invertebrates) and reported that it differs between species having different ecological demands and consequently inhabiting different habitats (Muskó et al., 1995; Simčič and Brancelj, 1997; Simčič et al., 2005). Measuring metabolic potential provides information on species' fundamental physiology and is therefore crucial for a comprehensive understanding of an organisms' metabolism.

Our study was set to explore the metabolic respiration, the response of metabolism to temperature change and to determine metabolic potential, which was compared between studied species to elucidate the underlying distributional pattern (partial altitudinal segregation) and the potential for interaction in syntopic populations. We measured metabolic rate (oxygen consumption) and determined metabolic potential (ETS activity) under two realistic temperature regimes: at 20 °C, which is a less favourable temperature for lizard activity, and at 28 °C, the temperature close to their T_p (Osojnik et al., 2013). If both species were adjusted to their current altitudinal ranges, the metabolic rates and potential should be higher in the mountain species (*I. horvathi*) than in the lowland one (*P. muralis*), while the use of metabolic potential (calculated from the ratio of metabolic rate and metabolic potential at the same temperature) should be lower for the mountain species ensuring a reserve for thermally critical periods. Furthermore, metabolic response to temperature was expected to differ; species with a lower precision of thermoregulation (*P. muralis*) was expected to have higher metabolic rate at lower temperatures as a consequence of compensation for attaining lower T_p in spring, when the thermal environment is more restrictive (Osojnik et al., 2013). Obtained results were linked to species ecology to provide a better understanding of potential interspecific interaction.

2. Material and methods

2.1. Field study sites and lizard collection

Lizards were collected in the area of species' sympatric occurrence (Kočevje, SE Slovenia: lat. 45°38′N, long. 14°51′E, datum = WGS8410). To discard effects of ontogeny or egg production only adult male lizards were collected. Collecting sites were similar in habitat structure and altitude (*P. muralis* site: 723 m a.s.l., and *I. horvathi* site: 986 m a.s.l.), and were located at a distance of 9.4 km one from another. Previously seasonal differences in enzymatic activity have been detected in several terrestrial species of lizards (e.g. Garland and Else, 1987; Zari, 1996, 1999), thus to avoid possible effect of season, all collections were conducted in the summer in three sampling campaigns between 26th June and 15th August 2013. Live lizards were quickly transported to the laboratory in the dark in order to reduce stress effects. Before the experiments, lizards were kept in individual housing terraria for three to five days with food (*Tenebrio molitor* larvae) and water provided ad libitum, and under a natural regime of light and temperature maintained by switching infra-red bulbs on for the period of 8 am to 18 pm (see also Osojnik et al., 2013). Food supply was interrupted two days previous to the experiment.

2.2. Collection permit and ethical procedures

All individuals used in the experiments were collected under the special licences 35601-14/2013-5 issued by the Slovenian Environment Agency. All animal handling procedures were done following the EU and Slovenian Government-established norms and procedures.

2.3. MR and ETS activity

Metabolic rate (MR, as a measure of oxygen consumption) was measured consecutively at two temperature regimes (20 °C and 28 °C). The experiment was performed in randomised trials from 08.30 to 16.30 h Central European Time (CET), the period of daily activity of both species observed in the field (Brana, 1991; De Luca, 1992). Lizards were put in 200 mL individual glass flasks with an impermeable lid and MR was measured with a fibre-optic oxygen meter (PreSens, Regensburg, Germany), each lizard individually in one flask. In the first part of the experiment, the flasks with lizards were first kept for 20 min at 20 °C to acclimatize. Then we measured the oxygen concentration at hourly intervals for four consecutive times, each time in the same order starting from flask number one, continuing until the last number. Each measuring session was done in less than three minutes to minimise disturbance of lizards during the experiment. After this, flasks were opened, with lizards remained kept inside, and moved to 28 °C where lizards were left for 20 min to heat-up. After that we closed the flasks and left it for an additional 20 min after starting the first measurement. Again we measured the oxygen concentration at hourly intervals for four consecutive times. In each series we used 18–28 flasks, depending on the number of individuals used per session. In all cases two of the flasks were left empty and represented controls. Oxygen consumption by each lizard was determined as the difference between oxygen consumption in the flask with the animal and mean oxygen consumption in control flasks. Oxygen consumption in each flask was calculated as the

difference between the oxygen concentration during incubation, multiplied by the volume of the flask which was subtracted by the animal volume, and divided by the incubation time. We used values calculated after each hourly interval and after the two last hours of the experiments when the rate has stabilized more; the latter is denoted as MR-last-2-hr. The animals were weighed to the nearest ± 0.1 mg (Sartorius, Goettingen, Germany) and measured for snout to vent length (SVL) to the nearest 0.1 mm using a digital calliper. We then removed the last third of the tail that was used for non-lethal ETS measurements. Tail tip removal has already been demonstrated to produce minimal disturbance in the subsequent lizard behaviour in the field (García-Muñoz et al., 2011). All lizards were released back at capture sites after experiments.

In a previous study it was shown that ETS activity of a whole animal can be estimated on the basis of the measured ETS activity of a part of an animal body which can be regenerated afterwards (Simčič et al., 2012). ETS activity was measured using the method originally proposed by Packard (1971) and improved by G.-Tóth (1999). A 10 mm long segment of the tail, taken from the posterior third of the whole tail was homogenized in liquid nitrogen using a mortar. A weighed amount (100–400 mg wet mass) was sonicated in 4 mL of ice-cold homogenization buffer (0.1 M sodium phosphate buffer pH = 8.4; 75 μM $MgSO_4$; 0.15% (w/v) polyvinyl pyrrolidone; 0.2% (v/v) Triton-X-100) for 20 s (4710; Cole-Parmer) and centrifuged at 8500 ×g for 4 min at 0 °C (Centrifuge Sigma). Three 0.5 mL samples from each homogenate were incubated for 40 min at 20 °C (standard temperature) in 1.5 mL substrate solution (0.1 M sodium phosphate buffer pH = 8.4; 1.7 mM NADH; 0.25 mM NADPH; 0.2% (v/v) Triton-X-100) with 0.5 mL 2.5 mM 2-(p-iodophenyl)-3-(pnitrophenyl)-5-phenyl tetrazolium chloride (INT) solution. The reaction was ended by addition of 0.5 mL of stopping solution (formalin: H_3PO_4 concentration = 1:1 v/v). Blanks (1.5 mL substrate solution and 0.5 mL INT solution) were incubated and treated as for the samples, followed by addition of 0.5 mL of homogenate. Formazan production was determined spectrophotometrically from the absorbance of the sample at 490 nm against the control blank within 10 min of stopping the reaction (WTW PhotoLabSpektral). ETS activity was calculated according to (Kenner and Ahmed, 1975). All data on ETS activity at 20 °C (ETS_{20}) were obtained directly from the measurement and for ETS activity values at 28 °C (ETS_{28}) we used a transformation formula $ETS_{28} = ETS_{20}.\ \exp^{Ea(1/T20\ -\ 1/T28)/R}$, where E_a is the activation energy (a value of 15 kcal mol^{-1} was used; Bamstedt, 1980; Packard et al., 1975), T20 and T28 are the absolute temperatures at 20 °C and 28 °C, respectively, and R the gas constant. We also calculated the ratio between ETS activity and MR (using the formula: ETS/MR-last-2-hr) to estimate the fraction of the metabolic potential that was used by the individual at two temperature regimes. Finally, the mean Q_{10} value, was calculated according to equation (Lampert, 1984): $Q_{10} = (k_2/k_1)^{(10/(T_2\ -\ T_1))}$, where k_1 and k_2 are the reaction rates (using MR-last-2-hr at 20 °C and 28 °C) at temperatures T_1 (20 °C) and T_2 (28 °C), respectively.

2.4. Statistics

Log-transformed values of SVL and weight of both species were compared by means of one-way ANOVA once normality and homoscedasticity were ensured. For data sets of MR and ETS measurements, we used Shapiro–Wilk's test and Levene's test to examine the normality of the data distribution and to assess homoscedasticity. Consequently all values (MR, ETS and ETS/MR-last 2-hr-values) were log-transformed to ensure normality and homoscedasticity (which was checked again) prior to analysis to meet the analysis criteria. To examine the effect of two temperature regimes, species and time on MR and ETS, we used a repeated measures ANOVA design (rm ANOVA) with species and temperature (Temp) as between-subject factor and time interval (Time) of the measurement as a within-subject factor. Next, we performed an analysis of MR-last-2-hr values first without (one-way ANOVA) and second including (two-tailed ANCOVA) average $\log_{10}$weight as a continuous predictor to account for size differences (Carretero et al., 2005) and species and Temp as between-subject factor. For analysis of ratios, factorial ANOVA with species and Temp as between-subject was used (ETS values were already size corrected). For pairwise post-hoc comparisons we used Duncan's significant difference test. All statistical analyses were performed with Statistica (Statsoft 2013).

3. Results

In total 32 *P. muralis* and 26 *I. horvathi* adult males were collected and used in the experiments. Individuals of both species were similar in size (logSVL: $F_{1,\ 56} = 2.80$, $P = 0.10$) but not in weight; *P. muralis* males were heavier (mean ± SE: 4.3 ± 0.1 g) than *I. horvathi* males (mean ± SE: 3.7 ± 0.1 g; $\log_{10}W$: $F_{1,\ 55} = 6.03$, $P < 0.05$). Table 1 displays descriptive statistics with sample sizes used in analysis for MR considering species, temperature regimes and measurement time interval.

First we examined the effects of species and temperature regime on MR in time (in three consecutive hourly intervals). MR of both species was higher at higher temperature with no interspecific difference (Table 2, Fig. 1). There were significant differences between consecutive measurements under the same temperature regime, but interaction between temperature and time was also significant (Table 2, Fig. 1).

Results of the second analysis using MR-last-2-hr values reconfirmed a similarity between the species at both temperatures (at 20 °C: $F_{1,\ 52} = 0.87$, $P = 0.35$ and at 28 °C: $F_{1,\ 39} = 3.20$, $P = 0.08$), also when we introduced the $\log_{10}$weight ($\log_{10}W$) as a continuous predictor to account for eventual mass-related allometry in MR (at 20 °C: species $*$ $\log_{10}W$, $F_{2,\ 50} = 0.06$, $P = 0.94$ and at 28 °C: $F_{2,\ 37} = 2.80$, $P = 0.08$).

LogETS values were significantly higher at 28 °C than at 20 °C in both species (Temp, $F_{1,\ 45} = 2.91.10^{14}$, $P < 0.001$), but were also lower in *P. muralis* than in *I. horvathi* at both temperatures (Temp $*$ Species, $F_{1,\ 45} = 4.97$, $P < 0.05$, Fig. 2). On the other hand, we did not detect interspecific differences in the ratios (ETS/MR-last-2-hr, Temp $*$ Species, $F_{1,\ 28} = 0.09$, $P = 0.76$). Nevertheless, the ratios were higher at 20 °C than at 28 °C in both species (Temp, $F_{1,\ 28} = 4.08$, $P = 0.05$, Fig. 2).

The mean Q_{10} value at 20 °C and 28 °C also did not differ between species either uncorrected (One-way ANOVA, Species, $F_{1,\ 35} = 1.62$, $P = 0.21$) or with mass-corrected analysis (One-way ANOVA, Species $*$ $\log_{10}W$, $F_{2,\ 33} = 0.84$, $P = 0.44$). The mean and standard error of Q_{10} were 2.986 ± 0.221 for *I. horvathi* and 2.628 ± 0.160 for *P. muralis*.

4. Discussion

Results of our study provide evidence for physiological dissimilarity in metabolic potentials (measured as ETS activity) of two sympatric lizard species, *I. horvathi* and *P. muralis*. The pattern of partial altitudinal segregation of the studied species that has been found across their overlapping distribution (De Luca, 1989; Lapini et al., 1993; Cabela et al., 2007; Žagar et al., 2013) was reflected in their metabolism, namely in the difference of ETS activity. *I. horvathi* had higher ETS activity determined from the tail tip tissue than *P. muralis*. However, contrarily to the initial expectation, interspecific differences were not found in measured metabolic rates (MR). Our results showed that MR was similar between species at the ranges of variation of both species at tested temperature regimes.

Weight was the morphological trait showing some variation between species (our results here and Žagar et al., 2012). Therefore weight was included as the covariate into analysis of MR to account for size differences, but similar results persisted, showing size independent similarity in MR between species. ETS activity values were already size corrected (see formula used in Section 2), thus obtained results reflect intrinsic difference between species in metabolic potentials.

Table 1
Mean metabolic rates of three consecutive hourly measurements and the mean of the last two measurements of *Podarcis muralis* and *Iberolacerta horvathi* males measured under two different temperature regimes (20 °C and 28 °C). MR-1 denotes the first, MR-2 the second and MR-3 the third of the three consecutive hourly measurements of metabolic rate. MR-last-2-hr denotes the mean of the last two consecutive hourly measurements of metabolic rate. n denotes sample size.

Species	Temp. regime	MR-1 (mg O_2/g/h ± SE) n	MR-2 (mg O_2/g/h ± SE) n	MR-3 (mg O_2/g/h ± SE) n	MR-last 2-hr (mg O_2/g/h ± SE) n
P. muralis	20 °C	0.23 ± 0.030 31	0.241 ± 0.018 31	0.226 ± 0.016 30	0.229 ± 0.013 30
	28 °C	0.724 ± 0.057 22	0.543 ± 0.034 20	0.531 ± 0.035 17	0.529 ± 0.029 19
I. horvathi	20 °C	0.307 ± 0.048 25	0.291 ± 0.028 25	0.228 ± 0.024 24	0.251 ± 0.020 24
	28 °C	0.769 ± 0.047 25	0.617 ± 0.047 23	0.592 ± 0.034 22	0.603 ± 0.030 22

Metabolism of organisms is particularly in ectotherms highly dependent on body temperatures due to the temperature dependence of involved biochemical process (Gillooly et al., 2001), thus we tested also for the response of MR to temperature change. Results of MR measured at two temperatures (20 °C and 28 °C) showed that MR values were higher at 28 °C than at 20 °C with no interspecific difference found. Our results confirm that biochemical reactions rather than eco-physiological traits govern the temperature dependence of metabolism (Randriamahazo and Aime, 1998; Angilletta, 2001; Gillooly et al., 2001).

While we found that both species possess different metabolic potentials (ETS activity) that could be exploited for energy production, we were interested in how the potential is exploited following the change in temperature. Significantly, the effect of temperature (all measures were recorded in the same season) was positive and parallel in both species. ETS activity was calculated higher for 28 °C than for 20 °C for both. Nevertheless, the interspecific difference persisted at both temperature regimes; *I. horvathi* ETS activity values were higher than *P. muralis* at 20 °C and at 28 °C. Detected higher ETS activity in *I. horvathi* than *P. muralis* at the same temperature means that former species maintains higher level of enzymes which can assure adequate production of energy when demands are increased.

By calculating the ratio between the actual metabolic rate and the ETS activity we detected that both species, with no interspecific difference, use less of the potential at 20 °C then at 28 °C. The implications of calculated ratios from other studies show that they varied with temperature (since ETS activity is a direct enzymatic process) and depended upon enzyme concentration (Bamstedt, 1980) and their characteristics (Packard, 1971). Previous studies on aquatic invertebrates also revealed that in species with high ETS/MR ratio, the capacity to increase metabolism is maintained (Fanslow et al., 2001; Simčič et al., 2005). Despite the fact that we have not detected any direct interspecific difference in ETS/MR ratio, results of higher ETS activity in *I. horvathi* than in *P. muralis*, provide evidence that *I. horvathi* has a higher capacity of metabolism.

There are evidences that thermoregulatory behaviour and thermal physiology are co-adapted in lizards (Angilletta et al., 2002), as well as both are reciprocally in connection with metabolism and performance (Angilletta, 2001). Higher thermoregulatory precision of *I. horvathi* (Osojnik et al., 2013), integrated with higher capacity of metabolism (ETS activity) as found here, could mean that *I. horvathi* can actually better exploit its greater metabolic potential due to a better ability of obtaining higher body temperatures than *P. muralis* when environmental temperatures are more restrictive, i.e. in spring. We suspect that these attributes of *I. horvathi* could pose competitive advantage against more generalist but thermoregulatory less efficient *P. muralis*, at least in colder environments, i.e. at high altitudes.

Moreover, metabolism is highly positively dependent on temperature (Bennett, 1982), reflecting in the increase of energy requirements (Angilletta, 2001) as well as in overall metabolic production of proteins. This in turn affects food intake (feeding time, feeding mode, e.g. Nagy et al., 1984; Angilletta, 2001) and other life-important activities such as reproduction, territorial defence, anti-predatory behaviour (Bennett, 1982; Patterson and Davies, 1984; Martín and López, 2001). Results from this study suggests that *I. horvathi* should in syntopic sites be able to outcompete *P. muralis*, since metabolic potential combined with more precise thermoregulation should be reflected in higher metabolic rates that are in turn reflected in other, above mentioned, life-important activities. Nevertheless, *I. horvathi* is more abundant than *P. muralis* only at higher altitudes (De Luca, 1989; Lapini et al., 1993; Cabela et al., 2007; Žagar et al., 2012), thus in the light of species interactions, the question remains why this physiological advantage of *I. horvathi* seems to only provide an advantage over *P. muralis* at higher altitudes and does not reflect also at lower altitudes. These results corroborate to suggest that interactions likely still persist in syntopic populations with *I. horvathi* as competitive subordinate species, when higher

Table 2
Results of the rm ANCOVA analysis of metabolic rates of *Podarcis muralis* (n = 17) and *Iberolacerta horvathi* (n = 19) males using temperature (Temp) and species as between-subject factors, and time interval (Time) as a within-subject factor.

Effects	F	MS	df	P
Temp	331.50	7.36	34	<0.001
Species	2.11	0.10	34	0.16
Temp ∗ Species	0.20	<0.01	34	0.66
Time	7.34	0.23	68	<0.01
Temp ∗ Time	4.98	0.14	68	<0.01
Time ∗ Species	0.39	0.01	68	0.68
Temp ∗ Time ∗ Species	0.26	0.01	68	0.77

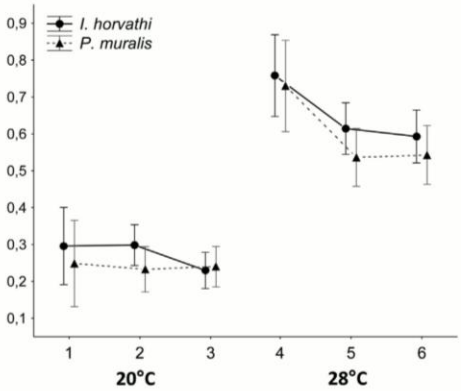

Fig. 1. Hourly metabolic rates (MR) of *Podarcis muralis* and *Iberolacerta horvathi* males measured at 20 °C and 28 °C. Metabolic rates were measured each hour as a measure of oxygen consumption with a fibre-optic oxygen meter. Lizards were kept at two temperature regimes: first at 20 °C (1, 2 and 3 on the X axis) and next at 28 °C (4, 5 and 6 on the X axis). Error bars represent 95% confidence intervals. Sample sizes used are given in Table 1.

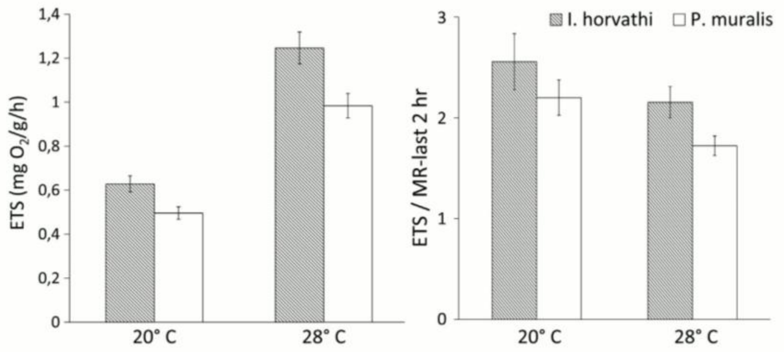

Fig. 2. The metabolic potential (left plot) and the use of metabolic potential (right plot) of *Podarcis muralis* and *Iberolacerta horvathi* males determined for 20 °C and 28 °C. We obtained the vales of electron transport system (ETS) activity (metabolic potential) under two realistic temperature regimes; at 20 °C which is a less favourable temperature for lizard activity and at 28 °C, the temperature close to their T_p for *Podarcis muralis* (n = 26) and *Iberolacerta horvathi* (n = 21) males, represented on figure A. On figure B are ratios calculated from electron transport system (ETS) activity divided by the mean metabolic rate of the last two hours of the experiment (MR-last-2-hr) for *Podarcis muralis* (n = 17) and *Iberolacerta horvathi* (n = 17). Bars represent the mean and whiskers standard error values. Measurements were done using tissue from lizards' tail tips.

environmental temperatures do not promote *I. horvathi* any metabolic advantage.

We found out yet another specialisation of *I. horvathi* that suggests its better adaptation to colder environments which to a certain level explains its distributional pattern with higher abundances at higher altitudes. On the opposite, different physiology of *P. muralis* explains its higher abundances at lower altitudes and is probably not likely to try to occupy higher altitudes. Jointly, dissimilarities in metabolic potential between studied sympatric species seem to contribute to understanding their altitudinal segregation pattern. However, we emphasize that in studies of species interactions, metabolism cannot be viewed solely and other factors (independent or connected to metabolism) will certainly play a role and provide additional explanation of the distribution pattern of both species.

In conclusion, we have shown that metabolic studies can be of prominent importance for understanding species interactions and to some extent for explaining altitudinal patterns, but need to be integrated with other results of species ecology, physiology and behaviour. Further work needs to focus on ascertaining the significance of different physiological traits in the field, especially in energy economics, which can at last reflect in different reproduction outputs which would give further explanation of the output of studied species interaction. Finally, the competitive advantage due to differences in physiological traits which suggest for a spatially limited specialisation to certain climatic conditions in the environment, i.e. to higher altitudes, raises the question of threats under future climate changes for this specialized species. The future work should be in the direction of hypothesizing what could be the effects of global warming (Sinervo et al., 2010, Huey et al., 2012) on such ectothermic reptile communities.

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4.1.5 Article V

A place in the sun: interspecific interference affects thermoregulation in coexisting lizards

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ABSTRACT
Solar radiation is in theory an unlimited resource on Earth, but can be locally limited. Heliothermic organisms use solar radiation to elevate their body temperatures, leading them to compete for sun-exposed areas, where interference for limited resource can occur. In coexisting lizard species, interference for basking sites could promote and direct interspecific interactions, which can be related to broader geographic species distribution patterns. We compared two competing lizard species (*Podarcis muralis* and *Iberolacerta horvathi*) that occupy sun-exposed gaps in a forested landscape in the Northern Dinaric Mountains (southern Europe). Both species exhibit an altitudinal segregation pattern with a high zone of overlap at middle altitudes. Using experimental thermal gradients, we tested for existence of interference competition. We used adult male lizards in three social contexts, alone as a measure of preferred body temperature (Tp) and in conspecific or heterospecific pairs as a measure of realized body temperature (Tr). *I. horvathi* achieved lower Tr compared to its Tp (alone), while Tr of *P. muralis* did not vary between social contexts. The evidence for interference found in *I. horvathi* could not be explained by a change in their general movement pattern in a thermal gradient. Our results suggest that interference was a result of direct agonistic interactions, assessed by the frequency of approaches and touches. *I. horvathi* showed higher interference-susceptibility than *P. muralis* indicating an asymmetric interaction between the two species. Sunlight (as a resource) is an important factor influencing distribution patterns in assemblages of heliothermic ectotherms where sun-exposed basking sites are limited.

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ORIGINAL PAPER

A place in the sun: interspecific interference affects thermoregulation in coexisting lizards

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Abstract Solar radiation is in theory an unlimited resource on Earth, but can be locally limited. Heliothermic organisms use solar radiation to elevate their body temperatures, leading them to compete for sun-exposed areas, where interference for limited resource can occur. In coexisting lizard species, interference for basking sites could promote and direct interspecific interactions, which can be related to broader geographic species distribution patterns. We compared two competing lizard species (*Podarcis muralis* and *Iberolacerta horvathi*) that occupy sun-exposed gaps in a forested landscape in the Northern Dinaric Mountains (southern Europe). Both species exhibit an altitudinal segregation pattern with a high zone of overlap at middle altitudes. Using experimental thermal gradients, we tested for existence of interference competition. We used adult male lizards in three social contexts, alone as a measure of preferred body temperature (T_p) and in conspecific or heterospecific pairs as a measure of realized body temperature (T_r). *I. horvathi* achieved lower T_r compared to its T_p (alone), while T_r of *P. muralis* did not vary between social contexts. The evidence for interference found in *I. horvathi* could not be explained by a change in their general movement pattern in a thermal gradient. Our results suggest that interference was a result of direct agonistic interactions, assessed by the frequency of approaches and touches. *I. horvathi* showed higher interference-susceptibility than *P. muralis* indicating an asymmetric interaction between the two species. Sunlight (as a resource) is an important factor influencing distribution patterns in assemblages of heliothermic ectotherms where sun-exposed basking sites are limited.

Keywords Interference · Heliothermic ectotherms · Thermoregulatory behavior · Social interactions · Agonistic behavior · Competition

Introduction

Interspecific competition is defined as a collection of reciprocal negative effects among competing species that reflects in a reduction of fecundity, growth or survivorship as a result of resource exploitation or interference (Begon et al. 2006). It has been thought to be one of the most important processes determining the structure of natural communities (Cody and Diamond 1975). However, there are several abiotic and biotic factors that play a role in interspecific interactions (e.g., Holt 1977; Hinch et al. 1991; Hudson and Greenman 1998). Interference occurs when one species obtains a benefit by using a resource that would have otherwise been used by another (Case and Gilpin 1974). To favor the interference,

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its cost must be small, its effect must be high, and the resource overlap with the species interfered against should also be high (Case and Gilpin 1974).

As a resource, solar radiation is in theory an unrestricted resource for life on Earth, but it can be locally limited, leading to competition for solar energy between organisms as in the well-known case of shading in plants (e.g., Black 1958; Weihe and Neely 1997). On the other hand, less attention has been paid to competition for solar energy in other organisms such as heliothermic ectotherms. Heliothermic reptiles use solar radiation to elevate their body temperatures to optimize their activity and physiological function (Huey and Slatkin 1976; Seebacher 2005). Basking in the sun is one of the most typical thermal behaviors in reptiles (Carrascal et al. 1992; Gvoždík 2002). If suitable basking places (representing solar energy resource) are limited and vary in quality, then interference for basking sites is promoted (Case and Gilpin 1974).

Interference is common on islands with high lizard densities (Downes and Bauwens 2004), but can also be found in other limited areas like sun-exposed spots within large forest stands. The mountainous areas of central and south-east Europe are highly forested (Perko and Orožen Adamič 1998), where sun exposed gaps occur either because of topographic characteristics of the area (cliffs, cave entrances, mountain tops, etc.) or because of endogenous tree mortality. The latter can be produced through periodic exogenous disturbances such as wind throw or heavy snow break (Rozenbergar et al. 2007; Nagel and Svoboda 2008), or from human activities such as clear cutting or road construction. Such sun exposed areas are characterized by being small and spatially isolated and may promote interference for limited basking sites between lizards in the same way as on islands.

South-Eastern forests of Europe are home of several species of small lacertid lizards (family Lacertidae). This family of lizards typically are found living in open areas either segregated in space, or in coexisting populations of two or more species (e.g., Žagar et al. 2013). These species are small heliotherms and require high thermoregulatory precision (e.g., Huey 1982; Osojnik et al. 2013), achieved by basking and shuttling behavior from hot to cold areas (Bowker et al. 2010). In the mountainous forest landscape of the Northern Dinaric Mountains, the common wall lizard (*Podarcis muralis* Laurenti, 1768) and Horvath's rock lizard (*Iberolacerta horvathi* Méhely, 1904) cohabitate in rocky, sun-exposed areas. Both live at mid-elevations, but also exhibit altitudinal segregation: the common wall lizard is more abundant at lower altitudes and Horvath's rock lizard in higher altitudes (Žagar et al. 2013). Furthermore, the common wall lizard is widespread across a large part of Europe whereas the Horvath's rock lizard is confined only to Southern Alps and Dinaric Mountains (Sillero et al. 2014). The partial segregation pattern suggests that species potentially compete in areas of cohabitation, but possible competitive mechanisms behind this interaction are not yet fully understood. Since basking in the sun rapidly affects body temperature of small lizards (Stevenson 1985), it is crucial for them to use the best basking places to efficiently exploit thermal energy. For lizards in general, preferred basking sites are often defended (Marler et al. 1995) and social interactions may occur with ecologically similar heterospecifics found within their home ranges (Langkilde et al. 2005). We expect this is likely to be the case with the two species we are studying since they are ecologically similar and basking sites in their habitat are scarce and limited (De Luca 1989; Lapini et al. 1993; Cabela et al. 2007; Žagar et al. 2012).

Body temperature for lizards can be important for overall fitness. (e.g., Lamprecht et al. 1991; Carrascal et al. 1992; Bauwens et al. 1995; Braña and Ji 2000; Amo et al. 2007). Therefore, interference competition for basking sites may indirectly affect realized body temperatures (T_r) of lizards, which influence important life processes such as metabolism, growth rate, and reproduction (Downes and Bauwens 2004). Despite the general similarity in morphology and ecology, the common wall lizard and Horvath's lizard are different in thermal physiology. The Horvath's lizard is a more precise thermoregulator, and the common wall lizard appears to be more tolerant to variation in environmental temperature (Osojnik et al. 2013). In this context, we would expect that the species with more precise thermoregulation requirements would be more susceptible to any interference in thermoregulation. Huey and Slatkin (1976) suggested that thermoregulation only occurs if the costs associated with this behavior do not outweigh the physiological benefits; if thermoregulatory costs are high, less precise thermoregulation is expected. Less precise thermoregulation may result in lower or higher body temperatures (realized body temperature, T_r) compared to the species' preferred temperatures (T_p).

To test for possible interference at basking sites, we designed a two-level experimental study. Our main goals of this study was to test whether interference had an effect at the physiological level; in the capability of attaining species' physiological set points (i.e., preferred body temperature (T_p, Osojnik et al. 2013)), and on the behavioral level; the lizards' ability to optimally regulate body temperature through behavioral thermoregulation. We used three social contexts: single individual (alone) as a measure of preferred body temperature (T_p) and conspecific or heterospecific pairs as a measure of different realized body temperatures (T_r) under interference interaction. Our null hypothesis predicts no interference and no deviation in physiology and behavior when in the presence of another lizard in the thermal gradient. In other words, lizards' T_r is the same as species' specific T_p. If interspecific interference effectively occurred, there could be two expected possible outcomes: (1) if interference was symmetrical, we should find an equivalent deviation in thermoregulation in both species and (2) if interference was asymmetrical, one of the species should show more deviation than the other. It is also predicted that intraspecific interference should be greater than interspecific due to greater similarities between conspecifics. Finally, to evaluate the importance of social interactions in interference, we observed both species to measure direct social agonistic interactions.

We hope to provide insight into the magnitude and effects of interactions that affect thermoregulation in lizards. Furthermore, we have also taken into account contrasting distribution patterns of studied species. Thermoregulation as a key physiological trait of ectothermic organisms is directly reflected in their life history, which in turn can shape geographical distributional patterns of species (e.g., Pianka 1973). As we have mentioned before, *P. muralis* is a generalist with a wide-range distribution while *I. horvathi* is a range-restricted endemic species (Sillero et al. 2014). Hence, if we find conclusive evidence that interference competition for basking sites provides competitive advantage for the generalist and disfavors the specialist, this could provide better understanding of the general distribution patterns found across lizard species.

Materials and methods

Species and study area

I. horvathi and *P. muralis* are both small saxicolous lizards. Snout-vent length (SVL) of males in this study area ranges between 41.9 and 62.8 cm and does not differ between species (Žagar et al. 2012). Lizards were collected in the sympatric area in Kočevsko region in the North Dinaric Mountains, SE Slovenia (Kočevje, 45° 38′ 29″ N, 14° 51′ 14″ E). Approximately, 80 % of the study area is Dinaric beech-fir forest (*Omphalodo-Fagetum* s. lat., Perko and Orožen Adamič 1998). Typical habitats of both lacertids in the region are limited open areas in the forest, typically represented by natural rock cliffs, rocky outcrops or human-made stone walls with sparse or no vegetation (Žagar et al. 2013).

Experimental animals and captive conditions

We captured only similarly sized male lizards by noose for our study. Males exhibit aggressiveness with other males making them ideal candidates for studying interference (e.g., Downes and Bauwens 2004). We verified the sex of each lizard by inspecting coloration, cloacal region, and femoral pores. Once an individual was captured, we quickly transported them in non-transparent transport boxes to avoid additional stress. For experiments in the linear thermal gradient, we collected 39 males of *P. muralis* and 43 males of *I. horvathi* in the summer of 2010 and 2011. For behavioral tests in the circular thermal gradient, ten *P. muralis* males and nine *I. horvathi* males were collected in the summer of 2012. Before experiments, lizards were kept in individual plastic terraria (dimensions 20×40×25 cm) with a permeable lid for less than 10 days with food (*Tenebrio molitor* larvae) and water *ad libitum*, and were kept under a natural regime of light and temperature made by infrared light bulb and sunlight coming through the window of the room where they were kept. After the experiments, we measured their SVL to 0.01 mm accuracy using a digital caliper and released them at capture sites.

Body temperature experiment

In both experimental set-ups, constructed thermal gradients provided lizards with an optimal environment for thermoregulation, excluding possible constraining factors (Verissimo and Carretero 2009). The only additional constraint added was the presence of another lizard, either a conspecific or a heterospecific, to test for interference in thermoregulation on the intra- and interspecific level. In the body temperature experiment, each lizard or lizard pair was exposed to a linear thermal gradient between 20−40 °C (experimental terrarium measurements: 0.4×0.4×1.5 m) produced by a 150-W infrared reflector bulb affixed at one end of the terrarium 30 cm above the surface. We obtained 11 consecutive measurements (one per hour) of body temperatures taken with a digital thermometer (HIBOK 14, accuracy of 0.1 °C) by inserting a probe in the cloaca (see the detailed methodology in Osojnik et al. 2013). Measurements were taken from 8 AM to 7 PM (local time, CET), to mimic natural daily activity patterns of both species (Braña 1991; Lapini et al. 1993). In order to minimize thermal shifts due to stress or contact with the researcher's hand, we minimized the time spent catching the lizard and obtaining measurement of body temperature to no more than 10 s (Verissimo and Carretero 2009). To avoid pseudoreplication, each individual was used only in one trial. For *P. muralis*, we used 10 males that were alone, 20 males (forming 10 pairs) in a conspecific pair and nine males in a heterospecific pair. For *I. horvathi*, seven males were used alone, 26 males (forming 13 pairs) in a conspecific pair, and nine males in a heterospecific pair.

Behavioral experiment

In the second experiment, we used a circular thermogradient arena (2r=1 m) with a 150-W infrared reflector bulb placed in the center and elevated 30 cm above the surface to establish a thermal gradient between 20−40 °C (Fig. 1a). This design was identical to work by Bowker et al. (2010) and Downes and Bauwens (2004). We limited the basking spot to a small 10 cm (r) circle in the middle of the arena, forcing lizards to approach one another and interact while basking. Both lizards were able to utilize this resource (basking site) at the same time. Our design was meant to mimic natural conditions where multiple

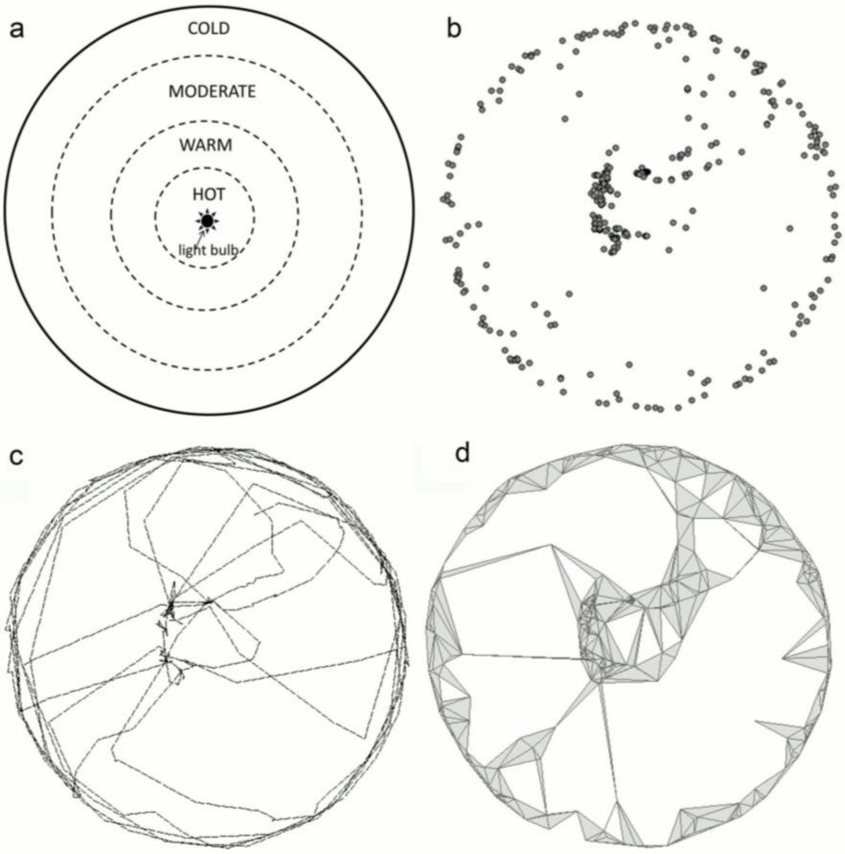


Fig. 1 **a** Top-down view of a schematic representation of the circular thermogradient (diameter=1 m) with a 150-W infrared reflector bulb placed in the center (light bulb) 30 cm above ground to establish a photo-thermal gradient between 20 and 40 °C. We schematically indicated four surface temperature (surfT) categories used in analyses. **b** Positions (n=720) of one individual lizard obtained from a 24 min video. **c** Constructed path of one lizard. **d** Estimated home range of one lizard using CHP 95

lizards bask on the same rock. We kept the experimental room at 22 °C, which is considerably lower than the range of T_p of both species (Osojnik et al. 2013) to stimulate the basking behavior.

Each day before the start of the experiment, the bulb was switched on for 30 min for the gradient to be established. Lizards were positioned randomly, either individually, or in con- or heterospecific pairs, inside the circular thermogradient. All experiments were done between 10 AM and 4 PM, which is inside the window of activity of both species (Braña 1991; Lapini et al. 1993). Lizards were first left for the 10 min of the initial acclimatization period and then video-recorded using a compact camera (Nikon Cool pix). The camera was placed above the circular gradient to cover the arena. We staged interaction experiments over a 24-min period as previous researchers have showed this as an adequate timespan to detect social behaviors in lacertid lizards (e.g., Downes and Bauwens 2004).

We matched lizard pairs according to their SVL with a maximum deviation of 3 mm. The gradient was cleaned between consecutive trials by wiping the surface with diluted ethanol (70 %) to prevent chemical cues of the previous occupants possibly influencing the results. In tests with lizard pairs, one lizard (randomly chosen species) had the dorsal side of the body painted with a bright removable marker to individually distinguish them when analyzing the videos. This paint was not expected to interfere with lizards' thermoregulation since it was only applied as a small dot-like area of 5 mm (2r) in the center of the body (Simon and Bissinger 1983).

Thermal data loggers (Thermochron e-button® DS1922L, accurate to 0.1 °C) were placed on the substrate in 10-cm intervals between the center and the rim of the circular terraria to record the surface temperatures across the circular gradient generated by the bulb. We used these measures to obtain a regression curve with the best fit. We also adjusted a regression equation for calculating values of surface temperatures (surfT) at each lizard's position (1 mm discrepancy) from the bulb to the rim of the thermal gradient. Adjusted formula used was as follows: surfT=40.119−0.041×x, where x is the distance to the bulb. Afterwards we used these values to determine four temperature areas (surfT categories) inside the circular gradient according to its surfT: cold (<25 °C), moderate (25−30 °C), warm (30−35 °C), and hot (>35 °C, see Fig. 1a

for a schematic presentation), which was used in subsequent analysis as an additional factor.

Video analyses and spatial data

Videos were processed with Max TRAQ software (2002–2012 Innovision Systems, Inc.) to obtain coordinates (*x*, *y*) of lizard positions at 2-s intervals, period long enough for a lizard to move across the whole gradient if intended. This provided 720 positions (Fig. 1b) for each 24-min long video, assigned to individual, species and social context. Using ArcMap 9.2 (ESRI 2004) we constructed paths between consecutive positions (Fig. 1c, Hawth's tools, Convert locations to paths, Beyer 2004). We extracted values for movements (in mm), which represented traveled distances in each 2-s interval (Hawth's tools, Add length tool, Beyer 2004). Using these data, we calculated the mean and the total distance traveled by each lizard. We calculated home ranges for each lizard within the circular thermogradient (Fig. 1d) using a Characteristic Hull Polygons (CHPs) method (Downs and Horner 2009). CHPs are polygons supporting concave edges, with disjoint regions, and containing empty areas inside their interiors. A Delaunay triangulation is calculated from a set of points, and the triangles are ordered according to their area (and not their perimeter). Here, we used CHPs consisting of 95 % of the smallest triangles to estimate lizards' home range in m^2 (Calenge 2006). We calculated CHPs with Adehabitat package (Calenge 2006) of R software (R Core Team 2012). Lizard positions attributed with surfT category were counted and multiplied by two (corresponding to 2 s of one video time frame) to obtain time values each lizards spent in each of the four surfT categories.

Videos with lizard pairs were systematically screened using VLC media player 1.0.2 (1996–2009 VideoLAN Team) to obtain behavioral data about social interactions. We quantified the number of directed interactions from one lizard to another during a given social context. We classified the interaction as the following: "approach" or "touch". "Approach" was when the first lizard approached the second lizard to a distance of 10 mm or less, which provoked a clear reaction (running or moving) from the second lizard. "Touch" was defined as the moment when the first lizard touched the second lizard, which again provoked a clear reaction (running or moving) from the other individual and in one case resulted in biting. Combat (or fighting) between lizards was reduced due to the size of the arena that allowed the lizard to easily escape. We also recorded the direction of approach/touch behavior with three categories: to the front, the rear, or the side of the body. This was done by observing the path of the approaching lizard and determining to which side of the body it was directed by using the nearest angle to any of the four sides of the body in the last 10-cm path of the approaching lizard. Each social agonistic interaction was also attributed with a surfT category.

Statistical analyses

Body size (SVL) variation among groups (according to species and experiment) was tested using ANOVA to ensure that individuals used in the experiments were not divergent in size. For data sets of the T_b (T_p and T_r), the mean movement distance, the total distance traveled, the home range size, and the time spent in four SurfT categories, we used Shapiro-Wilk's test and univariate Levene's test to examine the normality and homoscedasticity of the data distribution prior to analyses. Since measurements were repeated for the same individual in each social context, statistical analysis was based on analysis of variance for repeated measures (ANOVA-rm) with dependent variable and species and social context as between-subject factors. In the case of T_b analysis, the same individual was measured for 11 consecutive hours, thus we used ANOVA-rm test design with the time interval (time) as within-subject factor used to investigate the daily variation. We also used SVL as a continuous predictor to account for the possible effect of size (Carretero et al. 2005). For pairwise post hoc comparisons, we used Duncan's significant difference test. Data sets of lizard movements had a skewed distribution with predominantly zero or very short movement values, because lizards spent considerable time standing still or only repositioning their body. To account for this, we used generalized nonlinear model with Poisson distribution to investigate the effect of temperatures inside the gradient, using species and social context as factors at first, and later adding surfT category. Afterwards, we added lizard as a factor to account for individual differences. Behavioral data—counts of approach/touch—were, due to their categorical nature, used in a log-linear analysis (Jobson 1992) to identify the effects of factors or combination of factors (species, social context, surfT category, and the approach direction) on the observed behaviors. To represent factors simultaneously, we used multiple correspondence analyses (MCA, Abdi and Valentin 2007). Analyses were performed in Statistica 10 (Statsoft 2011).

Results

Experimental animals

All males used in experiments were similar in size (ANOVA, combined effect of factors species and experimental data set, $F_{7,\ 89}=1.97$, $P>0.08$). SVL (mean±SE) of *P. muralis* males used in preferred body temperature experiments was, respectively, 53.6±4.4 mm in the social context alone, 57.3±3.9 mm in conspecific pairs, and 52.9±3.8 mm in heterospecific pairs. For *I. horvathi*, the SVLs were 54.5±6.2 mm in social context alone, 53.6±4.0 mm in conspecific pairs, and 54.7±4.8 mm in heterospecific pairs. SVL (mean±SE) of males used in the behavioral experiments was 54.9±4.2 mm for *P. muralis*, and 54.7±3.3 mm for *I. horvathi*.

Body temperatures

Values of measured body temperatures (T_b) did not deviate from normality (Shapiro-Wilk's social context, $P>0.05$ in all cases), were homoscedastic (univariate Levene's tests, $P>0.05$ in all cases), and variances and means were uncorrelated. Results of ANCOVA-rm for body temperatures, using SVL as continuous predictor, were significant for social context ($F_{2,\ 670}=4.31$, $P=0.02$) and combination of factors species × social context ($F_{2,\ 670}=6.40$, $P=0.003$, Fig. 2a), but not for other factors and other combinations (species, time, time × species, time × social context or time × species × social context, all $P>0.05$). *I. horvathi* males had the highest body temperatures when thermoregulating alone (corresponding to species T_p); had lower body temperatures (T_r) in heterospecific pairs (post-hoc Duncan's test pairwise comparison alone vs. heterospecific, $P<0.04$); and even lower T_r when in the conspecific pairs in the thermal gradient (post hoc Duncan's test pairwise comparison alone vs. conspecific, $P<0.001$). This difference in T_r of *I. horvathi* between conspecific and heterospecific pair was also significantly different (post hoc Duncan's test, $P<0.03$). On the other hand, T_r of *P. muralis* males did not change under these conditions (Duncan's test pairwise comparisons, both $P>0.05$, Fig. 2a).

The use of space and movement pattern of thermoregulation

Values of the mean movement distance, the total distance traveled, and the home range size did not deviate from normality (Shapiro-Wilk's test, $P>0.05$ in all cases), were homoscedastic (univariate Levene's tests, $P>0.05$ in all cases) and variances and means were uncorrelated. Both species exhibited the same movement pattern between three social contexts: the mean movement (factor combination species × social context, $F_{2,\ 34}=1.200$, $P=0.314$, Fig. 2b), the total distance traveled (factor combination species × social context, $F_{2,\ 34}=1.909$, $P=0.164$, Fig 2c), and the home range size (factor combination species × social context, $F_{2,\ 34}=0.072$, $P=0.931$, Fig. 2d). We also did not find any interspecific difference in the temporal use (time) of thermal space inside the circular gradient depending on the presence of a conspecific or heterospecific lizard. All lizards (no interspecific differences)

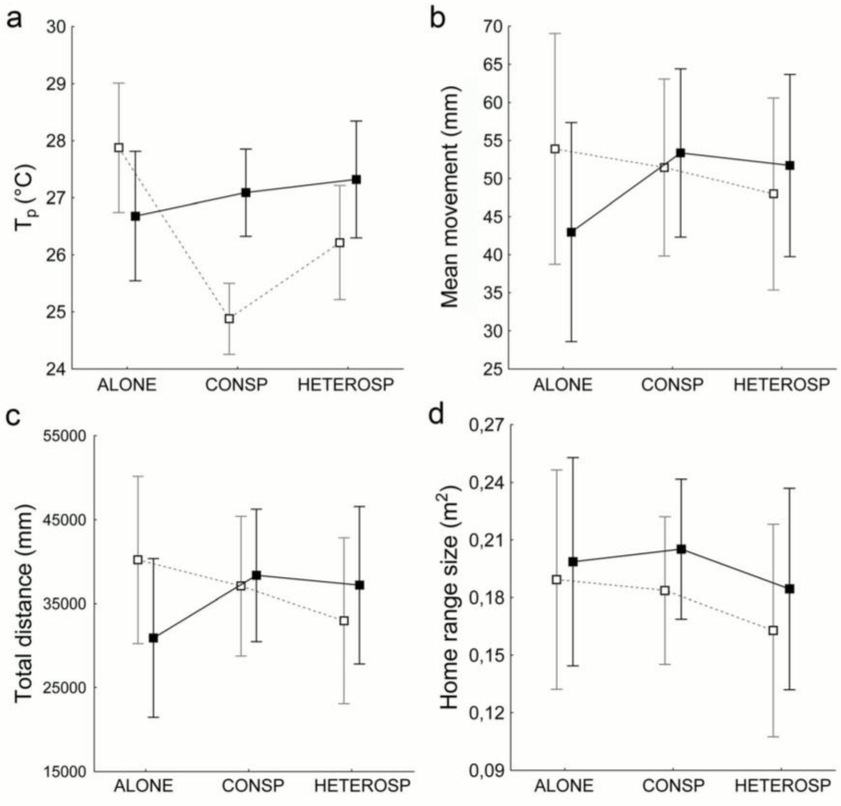


Fig. 2 **a** Plots of body temperatures (T_b), **b** mean movement distance, **c** total movement distance, and **d** home range size for *Podarcis muralis* (in black and full squares) and *Iberolacerta horvathi* (in gray and empty squares) in three social contexts: alone, in a conspecific pair, and in a heterospecific pair. Displayed are median values and 0.95 confidence intervals

spend most of the time in the coldest and hottest areas and the least time at moderate temperatures (effect of surfT category, as the only significant factor: $F_{3,\ 102}=106.57$, $P<0.001$).

Social interactions

Species differed in the frequency of physical interactions (touches and approaches) depending on the social context (conspecific or heterospecific pair) and body part (Table 1). Furthermore, these physical interactions of both species significantly differed depending on the presence of conspecific or heterospecific individual in pair (log-linear analysis, factor combination species × social context, Table 2). Plotted projections from the multiple correspondence analyses (MCA, Suppl. material 1, Fig. 3) revealed that *I. horvathi* approached and touched the other individual most frequently and with a higher intensity (Table 1) in a conspecific pair (the closest position between *I. horvathi* and conspecific pair on the MCA plot, Fig. 3). On the contrary, *P. muralis* most frequently exhibited physical interactions in a heterospecific pair (Table 1, Fig. 3). Among all groups, the approach counts were the highest for *P. muralis* when in heterospecific pairs and were twice as high compared to when in conspecific pairs (Table 1).

Factor surfT category in combination with species or social context were non-significant (Table 2), meaning physical interactions occurred equally frequently in all areas of the thermal gradient not depending on the species and social context. However, surfT category as a factor alone (surfT category) or in combination with the body part were significant (Table 2); approaches and touches were more frequently directed to the front when lizards were in the cold area of the circular thermo gradient (outskirts) and more frequently to the side of the body when lizards were in the hot area—the center of the circular thermo gradient (Fig. 3).

Discussion

Our results, using two experimental set-ups (linear thermal gradient and circular thermal gradient with limited basking area), provide evidence of existing asymmetric interference during thermoregulatory behavior of *P. muralis* and *I. horvathi* inside thermal gradients. We found that in the presence of conspecifics or heterospecifics, only *I. horvathi* had significantly lower realized body temperatures (T_r) compared to their preferred body temperature (T_p). Our results support the assumption that niche overlaps should be greater among conspecifics than heterospecifics (Begon et al. 2006) and specifically holds true for *I. horvathi*. On the other hand, T_r of *P. muralis* remained invariant across social contexts indicating no significant effects of interference on thermoregulation. These differences indicate asymmetry in interference competition between lizard species in regard to thermoregulation.

We found that interference in thermoregulation was a result of direct agonistic social interactions. *I. horvathi* males frequently stopped thermoregulating to engage in approaching and touching the other lizard inside the thermal gradient, especially with conspecifics. On the contrary, *P. muralis* physically interacted more often with heterospecifics (*I. horvathi*) than conspecifics. From the perspective of the chased lizard, the likelihood of being chased (approached or touched) inside the thermal gradient was higher for *I. horvathi* than for *P. muralis*. Lizards being approached or touched reacted by either moving away or by repositioning their body. In both scenarios, lizards subsequently moved away from the chosen spot inside the thermal gradient or changed their body position. The chosen spot inside the thermal gradient was likely the most suitable for thermoregulation in a given time and place. Behavioral reactions provoked by social agonistic situations (approaches or touches directed towards a lizard) apparently created displacement from resources (in this case thermal source). This can be attributed to the presence of interference while thermoregulating. However, it is possible that such agonistic social interactions also alter lizards' other physiological responses, for example stress levels, which result in unique neuroendocrine and other behavioral responses (Summers 2002). These results showed that interference in thermoregulation in co-existing lizards might play an important role in interspecific interactions in co-existing populations where there are limited basking resources.

The second part of the study was designed to observe thermoregulatory behavior inside the circular gradient in connection to the three social context combinations. Contrary to our expectations, there were no differences in the thermoregulatory movement patterns between species or social contexts. As a

Table 1 Cumulative counts of approaches and touches for *Iberolacerta horvathi* ($N=9$) and *Podarcis muralis* ($N=10$) by social context and body part

Species	Social context	Approaches			ALL	Touches			ALL
		Front	Side	Back		Front	Side	Back	
I. horvathi	Conspecific	18	23	3	44	8	4	2	14
P. muralis	Conspecific	13	5	9	27	11	3	1	15
I. horvathi	Heterospecific	7	17	7	31	4	2	4	10
P. muralis	Heterospecific	10	34	8	52	10	3	2	15

Table 2 Log-linear analysis results of direct agonistic interactions (touch and approach) obtained by analyzing 24-min videos of *Iberolacerta horvathi* (N=9) and *Podarcis muralis* (N=10), by social context (conspecific or heterospecific pair), and including factors: SurfT category (cold, warm and moderate, hot) and body part (front, back or side)

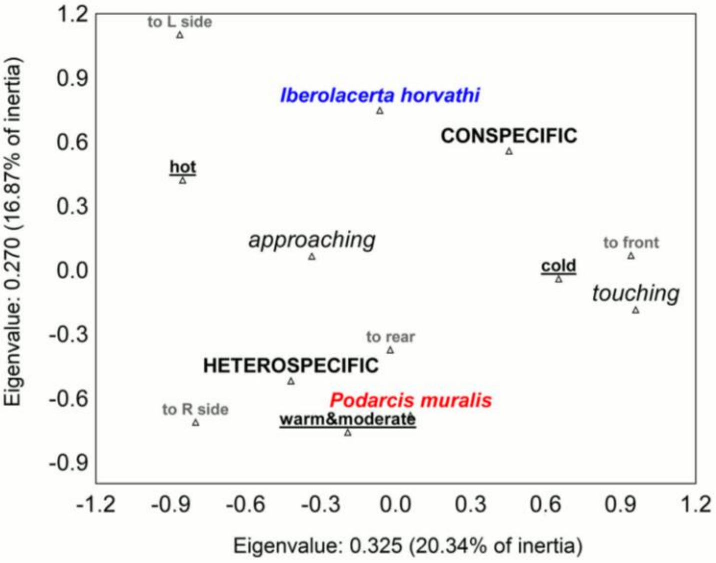
	df	Partial χ^2	*P*	Marginal χ^2	*P*
SurfT category	2	30.60	<0.0001	30.60	<0.0001
Touch/approach	1	42.22	<0.0001	42.22	<0.0001
Body part	2	22.96	<0.0001	22.96	<0.0001
Species × social context	1	8.33	0.004	7.17	0.007
Social context × body part	2	6.50	0.04	8.71	0.01
SurfT category × body part	4	20.36	0.0004	25.10	<0.0001
Touch/approach × body part	2	11.52	0.003	14.47	0.0007
Species × social context × body part	2	7.38	0.03	9.10	0.01
Log-linear model (factors used)	Social context × species, body part × surfT category, body part × touch/approach, body part × social context				
			Value	*df*	*P*
Max. likelihood χ^2			46.27	55	0.79
Pearson χ^2			47.07	55	0.77

Provided are only significant results of tests of all marginal and partial associations in the upper part of the table. In the bottom part of the table are information of the best fitted model (including two-way factor interactions) and two tests of the model. Selection of the model was automatic (see section "Materials and methods")

result, the physiological response found in *I. horvathi* (lower T_r than T_p, when in pairs) could not be explained by changes in their general movement pattern. Since we compared several movement pattern descriptors, and none were affected by presence/absence of con- or hetero-specifics, the general pattern of movements inside the gradient seems to be conserved regardless the presence of another lizard. Most probable explanation for not finding differences in the movement pattern between social contexts could be that movements in 2-s interval were not precise enough to detect effects on body temperature.

We found evidence of asymmetric susceptibility for interference (via direct agonistic interactions) in thermoregulation on the interspecific level between the two coexisting lizard species. This suggests that in the wild, one species may have a greater competitive advantage to occupy the most optimal basking sites. In general, *I. horvathi* reaches highest densities at high altitudes (De Luca 1989; Lapini et al. 1993; Žagar et al. 2013) and *P. muralis* at low altitudes (Žagar et al. 2013) with a broad zone of distributional overlap between the species. Furthermore, it is important to integrate results from this study on behavioral thermoregulation with known thermal

Fig. 3 Results of the multiple correspondence analysis (tot. χ^2= 1605.80, df=121, P<0.0001) of the counts of approach/touch behavior, represented by projections on the first two dimensions (X and Y axis)



physiology of both species. Relative costs and benefits of thermoregulation are different if species have different thermal sensitivity; a species with a broad thermal performance curve would suffer a lower cost relative to a species with a narrow thermal performance curve for the same decrease in T_b (Huey and Slatkin 1976; Angilletta 2009). Osojnik et al. (2013) showed that *I. horvathi* tends to be a high-precision thermoregulator regardless of seasonal variation in thermal properties of the environment, while conversely *P. muralis* responded with seasonal acclimatization in T_p. Combining both results, *I. horvathi* may be more sensitive to interference at basking sites than *P. muralis*. In other words, the presence of interference could decrease the fitness of one species (*I. horvathi*) but not the other (*P. muralis*), due to its negative effect on achieving T_p. We have also shown that social interactions seem to play a major role in thermoregulation of lacertids while repercussions in life history traits are also expected (Huey 1982). These findings, together with detected interspecific differences in physiological traits (Osojnik et al. 2013; Žagar et al. 2015), may help to explain why *I. horvathi* occupies cooler environments at higher elevations where reptile diversity and density is generally lower (McCain 2010; Sillero et al. 2014). We emphasize that such conclusions need verification with intensive field sampling of thermal availability and thermal use of space of both species in syntopic and allotopic populations. However, results from this experimental study provided key evidence that *P. muralis* and *I. horvathi* are actually competing species in mountainous forest landscape, where they competitively interfere for suitable basking sites.

It cannot be ruled out that similar results could be found in other sympatric pairs of partially segregated heliothermic reptile species, since in lacertids distributional overlaps (sympatry) of ecologically similar species are common (Sillero et al. 2014). In fact, our results coincide with results from two other sympatric lizard pairs from SE Iberian Peninsula. In the broadly distributed habitat generalist *Podarcis hispanica* (Carretero 2008), T_r were not different from T_p when in a conspecific or a heterospecific pair, whereas the geographically restricted habitat specialist *Algyroides marchi* (Carretero et al. 2010) attained lower T_r compared to their T_p (García-Muñoz et al. 2010). This strongly suggests that interference in thermoregulation could be a more general phenomenon than previously suspected, particularly in sympatric species with similar morphology and spatial overlap (see also Downes and Bauwens 2004).

The mechanistic basis of competitive interactions still remains a rarely addressed topic in ecological research. Thus far, few studies in reptiles have assessed and provided evidence about interference as a mechanism for competitive exclusion (e.g., Bolger and Case 1992; Downes and Bauwens 2004; Langkilde et al. 2005). Here, we highlight that results of such studies are crucial in conservation biology to be able to adequately predict future threats and conservation plans or reptiles. Future scenarios of climate change predict the rise of environmental temperatures (Solomon et al. 2007) with generally expected shifts of species distributions to higher elevations (Walther et al. 2002), which might have a direct effect on lizard assemblages (Sinervo et al. 2010). Increase of temperature might promote uphill range expansion of generalist species and consequently promote an increase of potential interference interactions in new syntopic populations with mountain restricted species. According to our findings, the already expected range constraints on *I. horvathi* owing to its conservative thermal ecology (Osojnik et al. 2013) would be amplified by the interference with a generalist competitor *P. muralis*. As suggested by Gvoždík (2012), ectothermic thermoregulation shows plasticity towards environmental variations, which may be widespread and potentially play an important role in ectotherms' adaptive response to climate change. Additionally, the cost and benefit model of thermoregulation in lizards should include heterogeneity and spatial structure of temperature (Sears and Angilletta 2015). Contributing to this, we suggest that future studies should also account for social interactions, which might play an important role through interference competition during thermoregulation as seen in interacting species.

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Compliance with ethical standards The authors declare that they have no conflict of interest. All lizards were collected and used in experiments under the special licenses No. 35601–32/2010–6 and 35601–47/2011–6 issued by the Slovenian Environment Agency. We state that the welfare of animals for research was respected during housing and experiments. All applicable international, national, and/or institutional guidelines for the care and use of animals were followed. All involved lizards were kept in individual terraria with natural light and heat regime and were provided with food and water *ad libitum*. Lizards were kept in the laboratory for a maximum of 10 days and afterwards released back at the capture sites after being fed and rehydrated.

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4.1.6 Article VI

Predators as mediators: Differential antipredator behavior in competitive lizard species in a multi-predator environment

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ABSTRACT
Prey response to different predators is complex and can include diverse antipredatory strategies. In syntopic populations of competing species common predators can play a mediator role thus influence the interaction out-come of prey-species in an indirect way. We studied differences in antipredator response in two competing lizards in syntopy in a multi-predator environment. Studied prey species, *Iberolacerta horvathi* and *Podarcis muralis*, are likely to compete in syntopic populations limited in size and have similar morphology and ecology but exhibit fine-scale ecophysiological differences. Taking into account interspecific differences in ecophysiology we expected that *I. horvathi* as a more precise thermoregulator would be less prone to use refuges that represent a thermal cost (are colder than outside). The pattern we found was the opposite of our expectations; *I. horvathi* escaped at greater distances and remained in the refuge for longer before re-emerging than *P. muralis*. Second part of the study revealed that both species were able to recognize chemical cues of predator snakes (represented as higher tongue flick rates in the presence of scents of predator snakes in comparison to control). Behavioral responses, which are linked with stressful situations connected to saurophagous snakes, were more frequent and variable in *I. horvathi*. Overall, antipredator responses seem to be more pronounced in *I. horvathi* than in *P. muralis*. While this “more cautious” attitude of *I. horvathi* should provide higher short-term benefits (higher survival rates), this would hold true only in populations where predation pressure is high. Otherwise it carries substantial time and thermoregulatory costs. For *I. horvathi*, costs of refuge use should be even higher due to narrower dimensions of their ecophysiological fundamental niche. Such divergences in antipredator behavior are expected to shape the relationships between both species in syntopic populations modulated by common predation pressure and habitat structure.

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Predators as mediators: Differential antipredator behavior in competitive lizard species in a multi-predator environment

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Prey response to different predators is complex and can include diverse antipredatory strategies. In syntopic populations of competing species common predators can play a mediator role thus influence the interaction out-come of prey-species in an indirect way. We studied differences in antipredator response in two competing lizards in syntopy in a multi-predator environment. Studied prey species, *Iberolacerta horvathi* and *Podarcis muralis*, are likely to compete in syntopic populations limited in size and have similar morphology and ecology but exhibit fine-scale ecophysiological differences. Taking into account interspecific differences in ecophysiology we expected that *I. horvathi* as a more precise thermoregulator would be less prone to use refuges that represent a thermal cost (are colder than outside). The pattern we found was the opposite of our expectations; *I. horvathi* escaped at greater distances and remained in the refuge for longer before re-emerging than *P. muralis*. Second part of the study revealed that both species were able to recognize chemical cues of predator snakes (represented as higher tongue flick rates in the presence of scents of predator snakes in comparison to control). Behavioral responses, which are linked with stressful situations connected to saurophagous snakes, were more frequent and variable in *I. horvathi*. Overall, antipredator responses seem to be more pronounced in *I. horvathi* than in *P. muralis*. While this “more cautious” attitude of *I. horvathi* should provide higher short-term benefits (higher survival rates), this would hold true only in populations where predation pressure is high. Otherwise it carries substantial time and thermoregulatory costs. For *I. horvathi*, costs of refuge use should be even higher due to narrower dimensions of their ecophysiological fundamental niche. Such divergences in antipredator behavior are expected to shape the relationships between both species in syntopic populations modulated by common predation pressure and habitat structure.

1. Introduction

Successfully avoiding attacks of a predator has obvious direct benefits, but overreacting may also involve substantial fitness costs. Because of this, antipredator behavior in lizards has been described in the context of cost benefit models (e.g., Cooper and Frederick, 2007; Martín et al., 2009). Benefits of antipredator responses for prey species are related to direct survival and costs can be associated with reduced opportunities for feeding, mating, territorial defense and thermoregulation (e.g., Cooper, 1998; Downes, 2001; Samia et al., 2015). For example fleeing from a predator attack has been frequently found to detrimentally affect lizards’ time devoted to social interactions and foraging (Samia et al., 2015). Lizards commonly occur in multiple-species populations where they can interact (compete) (Pianka, 1976). There common predators can play a mediator role thus influence the interaction out-come of prey-species in an indirect way (Holt, 1997).

Lizards play a pivotal role in the trophic webs of ecosystems where they prey upon multiple prey species and are being preyed by multiple predators (e.g., Carretero, 2004; Valverde, 1967). In Europe, small diurnal lizards can be opportunistically preyed on by a wide spectrum of predators such as raptorial birds, corvids, shrikes and gulls (e.g., Castilla et al., 1999b; Pérez-Mellado et al., 2014; Steen et al., 2011), large mammals (e.g., Castilla et al., 1999b), domestic cats in urban environments (e.g., Woods et al., 2003), and by snakes (e.g., Luiselli, 1996). While most are visual predators,

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which capture active lizards, some snakes are specialized in searching for inactive lizards in their refuges (e.g., Luiselli et al., 1996). It is known that in a multi-predator environment lizards can develop a complex antipredator avoidance strategy to cope with different kinds of predation strategies (e.g., Amo et al., 2005; Heatwole, 1968). However, it is unclear whether this is due to species specific traits or due to variations in predation pressure.

Small lacertids (Squamata: Lacertidae) lack any physical defense traits like spines or venom, and instead use avoidance with either cryptic coloration and patterns (e.g., stripes) or have conspicuous, vividly colored tails (e.g., blue tails of juveniles) to redirect predator's attention from the body to the tail, which is expendable, increasing their overall survival probability (e.g., Carretero et al., 2006; Hawlena et al., 2006; Martín and López, 1999a). Abiotic factors likely to affect the use of refuge sites in lizards depend on the type of predators, predator's size, frequency or intensity of attacks, habitat characteristics, refuge site availability or thermal properties of refuge sites and coupled with lizards' physiology and morphology (Cooper, 1998; Martín and López, 1999a,b; Samia et al., 2015). Since the use of (cooler) refuge sites is a thermal cost for active lizards it will be traded off by significance of costs and benefits involved (Samia et al., 2015).

On the other hand, lizards selecting inadequate refuges might become exposed to saurophagous snakes. Lacertids have well-developed olfactory senses and associated brain areas (Font et al., 2012) that enable them to recognize chemical cues of snakes and have a better chance of avoiding potential encounters (Greene, 1988). Some species (or populations) have been found to discriminate between chemicals from potential (saurophagous) or non-potential (non-saurophagous) snake predators (e.g., Dial and Schwenk, 1996; Downes and Shine, 1998; Van Damme and Quick, 2001). This was mostly considered more advantageous than having generalized chemical cue recognition due to the associated costs of predator avoidance (Cooper, 1997; Downes, 2001). However, cases of generalized responses do exist (e.g., Webb et al., 2009), which has been suggested to be linked with their widespread distribution and a more general habitat use (Amo et al., 2004b).

We have studied two sympatric small-sized lizards, Horvath's rock lizard, *Iberolacerta horvathi* (Méhely, 1904), and Common wall lizard, *Podarcis muralis* (Laurenti, 1768). The Common wall lizard is widespread across Europe whereas the Horvath's rock lizard is confined only to Southern Alps and Dinaric Mountains (Sillero et al., 2014). Due to several indices: great ecological similarity between species, substantial overlap in their habitat use and sympatric occurrence (Žagar et al., 2013) species show a high potential for competition in syntopic populations. Furthermore, species were shown to compete with interference when sunlight as a heat resource is limited (Žagar et al., 2015a). Both species resemble each other morphologically (Žagar et al., 2012), and have similar life history traits, but exhibit some differences in ecophysiology and thermoregulatory behavior (Cabela et al., 2007; De Luca, 1989; Lapini et al., 1993; Osojnik et al., 2013; Žagar et al., 2015b). The analysis of thermal preferences in the lab showed that *I. horvathi* had a narrower seasonal range of preferred body temperatures, while *P. muralis* seems to acclimate to seasonal changes in environmental temperature (Osojnik et al., 2013). To regulate body temperature lacertids use active behavioral thermoregulation (basking and shuttling behavior between hot and cold areas). Because of this, as *I. horvathi* seems to be capable of thermoregulating more precisely than *P. muralis*, it is also likely devoting more time to behavioral thermoregulation (Osojnik et al., 2013).

Refuge escape behavior decreases the time available for other activities (including thermoregulation) in heliothermic lizards thus representing an indirect associated cost which trades off with the direct benefits of surviving a predator attack (e.g., Martín and López, 1999b; Samia et al., 2015). Our expectation is that antipredator responses will be more costly for a species that is a more precise thermoregulator (*I. horvathi*) because it needs to devote more time to thermoregulation in general. This means that it should try to avoid higher thermal costs of escape behavior and use a refuge less often (escaping at a closer distance) and spend less time inside the refuge, than *P. muralis*.

However, this is not the only restriction that lizards have to face when selecting for refuges: lizards also assess the presence of chemical cues of potential lizard-eating snakes to avoid being predated inside the refuge (e.g., Amo et al., 2004a; see above). The ability to detect scent may, according to the spatial overlap of prey and predators, differ between species in the refinement, accuracy and reaction; for instance, a generalist prey species present in a wide variety of habitats tend to have a generalized response to potential predators e.g., do not discriminate between dangerous and non-dangerous predator snake scents (Amo et al., 2004a). In our two species system, we hypothesize that interspecific differences in habitat use and geographical distribution will be reflected in the ability to detect chemical cues of predator and non-predator snakes as well as in their behavioral response to predator scents. More specifically, we would expect *P. muralis* to have a more generalized response compared to range restricted *I. horvathi*.

From the point of interspecific competition, divergences in antipredator tactics are expected to modulate predation pressure by common predator(s) and, hence, can shape the relationships between both species in syntopic populations (Holt, 1977). Consequently, a general aim of this study is to assess antipredator responses of two competitive lacertids sharing the same multi-predator pressure while considering their differing ecophysiological traits. Our hypothesis is that if antipredator responses show discrepancy between interacting species, predators will asymmetrically influence the costs of antipredator behavior for both species in interaction. Based on obtained results we expect to gain insights on the role of predator-mediated co-existence of prey species (Tokeshi, 1999) in syntopic populations of studied lacertid species, which may be generalized to similar interacting species tandems with multiple common predators.

2. Material and methods

2.1. Study sites and species

Study site (Kočevje, SE Slovenia: lat. 45°38′N, long. 14°51′E, datum = WGS8410) is located in the area of sympatric occurrence of studied species, *I. horvathi* and *P. muralis* (Žagar et al., 2013). The area is characterized by high forest cover (Puncer, 1980) and a mosaic of open areas with exposed rocks which represent suitable habitat for both species (Žagar et al., 2013). Climate is temperate continental with an alpine climate trend at higher elevations (Kordiš, 1993). We performed the study at a representative syntopic location, where both species are occupying similar habitats and are exposed to the same predators. Suitable refuges for lizards in this area are frequent, because rocks are calcareous and thus full of crevices and holes.

I. horvathi and *P. muralis* are small, saxicolous and diurnal lizards (Žagar et al., 2012). In the study site several species are known to at least occasionally take lizards as prey: beech marten (*Martes foina* (Erxleben, 1777)) and fox (*Vulpes vulpes* Linnaeus, 1758) among mammals, both reported to only very rarely include lizards as prey in their diet (<1% of the diet mass; Bertolino and Dore, 1995; Serafini and Lovari, 1993). Regarding birds there were at least 14 species recorded in the area (data compiled from Atlas ptic, 2015; Geister, 1995; own field observations) that are known to be able to prey lizards. Remarkably, none of these species is a specialist reptile predator, the proportion of reptiles rarely exceeding 10% of their diet mass (Cramp, 1978–1994; Glutz von Blotzheim and Bauer, 2004). Species which are most prone to prey lizards in the study area are in fact two snake species, *Coronella austriaca* (Laurenti, 1768) and *Vipera ammodytes* (Linnaeus, 1758) (Lapini et al., 1993; Luiselli, 1996; Schedl and Klepsch, 1999). The smooth snake (*C. austriaca*) is well known as a specialized lizard eater (in adults they exceed 80% of their prey type frequency) (e.g., Luiselli et al., 1996) whereas adult *V. ammodytes* preys on lizards only occasionally (9.5 % of their their prey type frequency), but include them in their diet in a greater proportion when in juvenile and subadult stage (more than 82 %; Luiselli, 1996). As a control non-predator snake, we used *Natrix natrix* (Linnaeus, 1758), which predominantly preys on amphibians, but can also locally include other types of prey such as fish and terrestrial vertebrates (Luiselli and Rugiero, 1991). However, since endotherm predators' feeding rates are higher due to higher metabolic activity, they (e.g., birds) might pose higher predation pressure to lizards than ectotherm predators (e.g., snakes), despite their lower proportion in the diet (Nowak et al., 2008).

2.2. Field study of escape and recovery behavior

We conducted the study in the period between 30th May and 18th September, 2012, always between 900 and 1700, which is within the period of daily activity of both species (Braña, 1991Lapini et al., 1993). The same person, always wearing similar clothes, walked at a slow pace on random routes to cover the whole study area during the field day and made all of the observations; recorded lizard's behavioral variables and related abiotic variables using a standard protocol of refuge escape experiment (Carretero et al., 2006; Martín and López, 1999b). The approximate size of the study area was 0.5 ha and walking routes were adjusted to minimize the risk of observing the same individual twice by avoiding observations in vicinity of the points where previous observations have taken place. We excluded observations of interacting lizards because previous interactions might modify the lizard's escape behavior (Cooper, 1997; Marcellini and Jenssen, 1991). Since lizards can shift their behavior shortly after tail autotomy (Stankowich and Blumstein, 2005), we considered only individuals with either intact or long regenerated tails. All included individuals were adults to remove the possible effects of ontogeny. According to the shape of the body and secondary sexual characteristics it was also possible to determine the sex by visual inspection.

Following the protocol (for details see: Carretero et al., 2006; Martín and López, 1999b) we measured the following variables corresponding to the escape and the recovery behavior: approach distance (between observer and the lizard when the latter started to move) and distance fled (between the place from where lizard started to move and the refuge). Recovery behavior was evaluated by recording the recovery time (time spent in a refuge before emergence) and recovery distance (distance between the point of hiding and reemergence). To optimize the field work effort, the duration of each observation was limited to three minutes. Most of the lizards (>91%, 71 out of 78) re-appeared in that time period (before 3 min) and all remaining lizards had the reemergence time arbitrarily assigned as 3 min.

Because escape and recovery behavior may be thermoregulatory dependent (Bulova, 1994; Rocha and Bergallo, 1990), the air (T_a, 50 cm above ground) and substrate (T_s) temperatures (at the sighting point), as well as the refuge temperature (T_r) were recorded immediately after lizard's emergence. When lizards were seen to completely hide in the refuge, we tried to measure the T of the deepest point of the refuge and when lizards were seen to escape to refuge but remained at the entrance, we measured the temperature at the exact spot to make the best approximation of actual T_r to which lizards were exposed while inside the refuge. T_a was measured with digital thermometer (Fluke® 971) and T_s and T_r with an infrared thermometer (Fluke® 68). Precision for field measurements was 1 s for durations, 1 cm for distances, and 0.1 °C for temperatures. Following Carretero et al. (2006), the thermoregulatory costs of retreating to a refuge were estimated from the thermal quality formula (Hertz et al., 1993):

$$\delta_{\mathrm{ar}} = \frac{|T_{\mathrm{a}} - T_{\mathrm{r}}|}{T_{\mathrm{a}} + T_{\mathrm{r}}}; \quad \delta_{\mathrm{sr}} = \frac{|T_{\mathrm{s}} - T_{\mathrm{r}}|}{T_{\mathrm{s}} + T_{\mathrm{r}}}$$

where δ_{ar} and δ_{sr} were the costs considering the air and the substrate temperatures, respectively. Both variables were considered because these saxicolous lacertids combine both radiation and conduction from the substrate as heat sources (Castilla et al., 1999a).

We also collected habitat use data for all individuals at the point of first sight of the lizard. We assigned each locality to one off our pre-determined habitat categories depending on the surface and vegetation cover in a 50 cm radius of that point: (1) ground (without rock) with vegetation (grass and shrubs), (2) small rock with scarce surrounding vegetation, (3) small rocks without surrounding vegetation, and (4) large rock without surrounding vegetation.

2.3. Scent recognition tests

For chemical (scent) recognition tests only adult male lizards were collected to avoid effects of ontogeny or pregnancy on their general behavior (e.g., Bauwens and Thoen, 1981; Carretero et al., 2006). To avoid possible effects of seasonal variation, all tests were conducted within a two-month period, between late May and late July 2013. Predator chemical recognition in lizards specifically results in an increased rate of tongue flicks and several antipredator behavioral modifications (Downes and Shine, 1998; Thoen et al., 1986). In the tests we used three different snake species as scent donors, which were collected in the same study area: an adult smooth snake (*C. austriaca*), a subadult horned viper (*V. ammodytes*) and an adult grass snake (*N. natrix*). Potential predator species were *C. austriaca* and *V. ammodytes*, while *N. natrix* represented a non-predator control snake (Fillippi et al., 1996; Luiselli, 1996; Luiselli et al., 1996).

We kept the snakes and lizards separated in different rooms during the period of experiments to avoid possible contact of lizards with predators' chemical cues. Collected lizards were kept in individual housing terraria (15 × 30 × 20 cm) for three to five days before tests and snakes were kept in individual housing terraria (70 × 40 × 30 cm) for no longer than three weeks. Each housing terrarium had a wooden shelter box and a water bowl. Food (*Tenebrio molitor* Linnaeus, 1758 larvae) and water were provided ad libitum, and every lizard was observed daily to ensure they fed. Lizards underwent a fasting period one day prior to experiments. Both snakes and lizards were kept undisturbed through a regime of light and temperature which mimicked a natural day cycle, maintained by switching on infra-red bulbs from 800 to 1800 (e.g., Osojnik et al., 2013). After experiments were concluded, all individuals were released at capture sites.

Tests were conducted in a room with a constant temperature (~22 °C) under normal daylight illumination conditions (natural light coming through a window in addition to a white light bulb in the laboratory) and during the natural activity period of the lizards (Braña, 1991; Lapini et al., 1993) between 1100 and 1700. During the day all lizards were allowed to thermoregulate under infra-red (heating) lamps to the range of their preferred body temperatures (Osojnik et al., 2013) to assure lizards were active when used in the test trial. Test terraria dimensions were 40 × 50 × 30 cm. Each test terrarium was used with the same donor scent during all experimental trials. Four test terraria were as follows: CONT—control with no scent, Nnat—with the scent of *N. natrix*, Caus—with the scent of *C. austriaca*, and Vamm—with the scent of *V. ammodytes*.We cleaned the inside of the terrarium between the trials by thoroughly rinsing

Table 1
Descriptive statistics of the behavioral and environmental variables by species (*Iberolacerta horvathi* and *Podarcis muralis*) and sex. Values are means ± SE. See Section 2.2 for calculations of thermal costs (δ_{ar} and δ_{sr}).

	Iberolacerta horvathi		*Podarcis muralis*	
	Females (n = 18)	Males (n = 41)	Females (n = 13)	Males (n = 6)
Approach distance (m)	1.37 ± 0.12	1.38 ± 0.09	0.84 ± 0.14	1.07 ± 0.29
Distance fled (m)	0.34 ± 0.06	0.34 ± 0.03	0.46 ± 0.09	0.36 ± 0.08
T_a (°C)	25.9 ± 0.8	26.2 ± 0.6	26.5 ± 1.0	23.5 ± 1.8
T_s (°C)	30.1 ± 2.1	27.7 ± 1.0	27.7 ± 2.2	30.2 ± 4.1
T_r (°C)	13.3 ± 1.3	16.6 ± 1.0	19.2 ± 2.0	21.0 ± 2.8
δ_{ar}	0.34 ± 0.05	0.25 ± 0.03	0.19 ± 0.06	0.10 ± 0.02
δ_{sr}	0.39 ± 0.06	0.27 ± 0.03	0.21 ± 0.05	0.20 ± 0.04
Recovery time (s)	64.6 ± 12.9	52.3 ± 7.6	13.9 ± 5.1	34.8 ± 29.1
Recovery distance (cm)	17.9 ± 2.8	25.3 ± 4.1	8.6 ± 3.3	20.5 ± 8.4

Table 2
Results of general regression models for escape and recovery behaviors of *Iberolacerta horvathi* and *Podarcis muralis* and related environmental variables.

Dependent variable	Independent variable	df	β	t	P
Log approach distance	Log distance fled	1, 72	−0.09	−0.78	0.44
	Log T_a	1, 72	−0.33	−1.63	0.11
	Log T_s	1, 72	0.49	1.77	0.08
	Log δ_{ar}	1, 72	0.70	1.47	0.15
	Log δ_{sr}	1, 72	−0.79	−1.65	0.10
Log recovery time	Log approach distance	1, 73	0.28	2.48	0.02
	Log distance fled	1, 73	−0.02	−0.21	0.84
	Log δ_{ar}	1, 73	0.11	0.60	0.55
	Log δ_{sr}	1, 73	−0.01	−0.03	0.97
Log recovery distance	Log approach distance	1, 73	0.28	2.53	0.01
	Log distance fled	1, 73	0.02	0.19	0.85
	Log δ_{ar}	1, 73	0.13	0.68	0.50
	Log δ_{sr}	1, 73	−0.16	−0.83	0.41

it with diluted ethanol (30 %) and dried it with a clean paper towel. All terraria were fitted with a piece of paper infused with a scent, which covered the entire bottom surface and was replaced with a new sheet of paper of the same scent before each trial. In CONT terrarium a clean piece of paper was replaced between subsequent lizard exposures. In terraria with snake scents we used paper sheets that were previously rubbed against the corresponding snake and floor of their housing terrarium.

Each lizard passed all four tests in a random order and in a maximum of two trials per day. Lizard was gently placed in the middle of the terrarium, we then closed the transparent glass lid, turned on a video recorder placed one meter above the terrarium and exited the room to leave the lizards undisturbed. Each video was recorded for approximately 13 min, of which 12 min were used for analysis, discarding the first 10 s of each video to remove eventual effects of initial behavioral disturbance. Duration of videos was determined following previous similar studies (e.g., Amo et al., 2005).

2.4. *Video analysis*

We used the program VLC Media Player (VideoLAN Organisation) to forward and stop videos to record either frequencies or durations (in seconds) of the following behaviors and locomotion patterns (Amo et al., 2004a; Molina-Borja, 1981): (1) tongue flicks: the lizard extrudes and retracts its tongue, either onto the substrate or into the air, (2) reverse: the lizard rapidly shifts the body for 180°, (3) lunge: the lizard throws its body forward with a sudden jump and then stops or is followed by a quick, short run, (4) run: very fast movement, often over a short distance, (5) tail wave: the lizard moves the tail from side to side, frequently in an undulating motion, (6) foot shake: the raised forelimbs are alternately and rapidly moved up and down, (7) freezing: the lizard remains motionless, either on the floor or the walls of the test terrarium, with its venter raised or resting on the surface, (8) slow motion: the lizard moves slowly and not in a continuous way, but with stalking movements, sometimes accompanied by jerky or waving movements of the forelimbs, (9) crawl: lizard crawls with the venter in contact with or close to the substrate, (10) walk: the lizard displays continuous forward movement, with the venter raised, typically observed in unrestrained lizards, and (11) climb out: the lizard is in an upright position against the wall and attempting to climb up the wall. Among counted behaviors the following were considered to be linked with antipredator behavior: reverse, lunge, run, tail wave and foot shake (Molina-Borja, 1981; Van Damme and Quick, 2001). Lizards detecting predator's chemicals were previously also found to spend more time stationary (freezing) or in slow and crawl motion (Cooper et al., 2010, 2012).

2.5. *Statistical analyses*

Variables related with escape/recovery behavior were log-transformed to achieve normality. Homoscedasticity was assessed by means of Levene's tests ($P < 0.01$ in all cases). Models in which the putative variables (T_a, T_s, δ_{ar} and δ_{sr}, distance fled and approach distance) could modify the antipredator behavior were constructed using multiple regression analysis separately for escape and recovery behavior. Analyses of (co)variance, AN(C)OVAs, with species and sex as factors were performed for each behavioral variable, first in isolation and then considering the variable interactions by using the subsequent significant independent variables of the multiple regression analysis as covariates (Carretero et al., 2006).

Since a lizard tongue flicks much less or not at all when stationary (Van Damme and Castilla, 1996), we regressed the total number of tongue flicks (those when either active or stationary) on total time lizards were active, and we used the residuals of this regression as the estimate of tongue flicks (controlling for time being active). Data sets of tongue flicks and durations of freezing and slow motion were checked for normality and homoscedascity using Kolmogorov-Smirnov and Levene's tests, respectively. As there were no violations, the data sets were used in the analysis without prior transformations. We used General Linear Model with the repeated measures ANOVA design (rm-ANOVA), with species (between subject) and scent (within subject) as categorical predictors.

Antipredator behaviors (run, lunge, reverse, tail wave and foot shake) were counted for each lizard. Each of these behaviors is related to activity: run, lunge and reverse to being in motion, and tail wave and foot shake to stationary period. Because tail wave and foot shakes were only very rarely observed (<5 % of all individuals), we decided to only compare frequencies of run, lunge and reverse, and for latter we also pooled frequencies to avoid too many zero values in the data set. Total number of antipredator behavior was then first regressed on total time lizards were active, and we used the residuals of this regression as the estimate of frequency of antipredator behaviors (controlling for time being active) in the

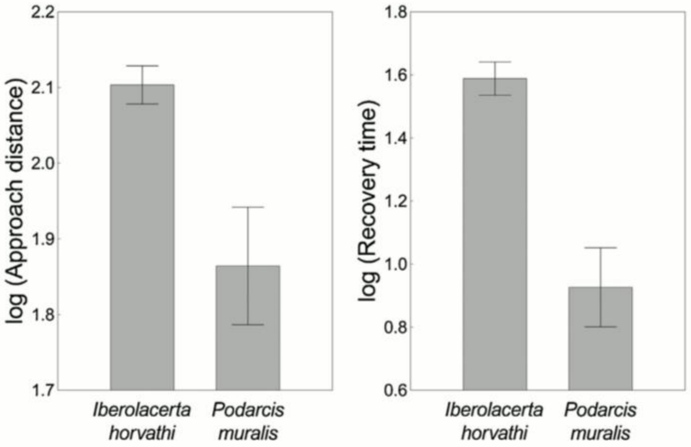

Fig. 1. Variation in approach distances (m) and recovery time (s) of adult *Iberolacerta horvathi* and *Podarcis muralis* in the study area. Both variables showed significant interspecific variation (see Table 2). Boxes represent means and whiskers standard errors.

pairwise comparisonsbetween species in the same scent test with multiple Median tests.

After the initial tests, we explored the variability of used antipredator behaviors by changing the frequency data of all five different behaviors with binary options: exhibited (value 1) or not exhibited (value 0). This data was used to classify each lizard into one of the three categories describing the variability of behavioral response: Zero response (no displayed antipredator behaviors), Medium response (one or two different antipredator behaviors) and High response (more than three different antipredator behaviors). Proportions of lizards in each category were also calculated and compared between species in the same scent test with multiple Median tests. All analyses were performed in Statistica 12 (StatSoft, 2013).

3. Results

3.1. Escape and recovery behavior

In total 59 *I. horvathi* (18 females and 41 males), and 19 *P. muralis* (13 females and six males) were approached in the field and studied for their refuge escape behavior (Table 1). In both species approach distance was not correlated with the distance fled or with any environmental variable (Table 2). Approach distance showed variation between species, but not between sexes (Table 3); *I. horvathi* started to escape at a farther distance from the simulated predator than *P. muralis* (Table 1, Fig. 1). We did not find either interspecific or intraspecific (between sexes) variation in the distance fled, meaning that both sexes of both species were at a similar distance away from refuge sites on the start of the escape behavior (Tables 1 and 3).

Both recovery time and recovery distance were not correlated with either distance fled or any environmental variable (Table 2). However, recovery behavior was positively correlated with the approach distance (Table 2). Consequently, the analyses for these two variables were run using approach distance as a covariate. Interspecific comparison of the recovery time showed that *I. horvathi* remained in the refuge for a longer time before emerging than *P. muralis*,again with no differences between sexes within both species (Fig. 1 and Table 3). By contrast, recovery distance did not differ between species and sexes (Table 3). We also examined the effect of habitat on escape and recovery behavior by introducing habitat type as a factor in the analyses of the two variables that showed significant differences between species (approach distance and recovery time). Results showed that the effect of habitat was negligible (factor habitat was n.s., Table 3) whereas the effect of species remained strong (Table 3). In other words, regardless of the habitat used at the time of escape, *I. horvathi* individuals escaped at longer approach distances and stayed in the refuge for a longer time than *P. muralis*.

Table 3
ANCOVA, and ANOVA comparisons of behavioral variables between sexes and species (*Iberolacerta horvathi* and *Podarcis muralis*), including Approach distance or Habitat type as a covariable. Significant factors are in bold.

Dependent variable	(Covariates), factors	*F* or Wilks'	df	*P*
Escape behavior				
Approach distance	**Species**	10.42	1, 74	<0.01
	Sex	0.72	1, 74	0.40
	Species × Sex	0.79	1, 74	0.38
Approach distance	**Species**	9.36	1, 72	<0.01
	Sex	0.52	1, 72	0.47
	Habitat type	0.22	1, 72	0.88
Distance fled	Species	1.29	1, 74	0.26
	Sex	0.001	1, 74	0.97
	Species × Sex	0.51	1, 74	0.48
Recovery behavior				
Recovery distance	Species	3.17	1, 74	0.08
	Sex	1.34	1, 74	0.25
	Species × Sex	0.73	1, 74	0.40
Recovery distance	(Approach distance)	2.66	1, 73	0.11
	Species	1.24	1, 73	0.30
	Sex	1.01	1, 73	0.32
	Species × Sex	0.48	1, 73	0.49
Recovery time	**Species**	27.35	1, 74	<0.001
	Sex	0.0003	1, 74	0.99
	Species × Sex	0.59	1, 74	0.45
Recovery time	(Approach distance)	0.29	1, 73	0.59
	Species	21.95	1, 73	<0.001
	Sex	0.005	1, 73	0.95
	Species × Sex	0.49	1,73	0.48
Recovery time	**Species**	32.08	1, 72	<0.001
	Sex	1.14	1, 72	0.29
	Habitat type	1.46	1, 72	0.23

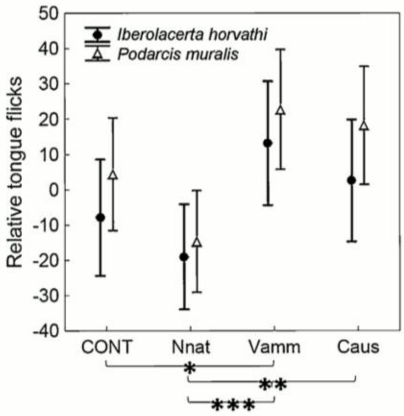

Fig. 2. Relative tongue flicks of *Iberolacerta horvathi* and *Podarcis muralis* in terraria with four scents. *X* axis shows the residuals of regression of the total number of tongue flicks on total time lizards were active to control for time being active. Symbols denote the mean value and vertical lines represent 95% confidence interval. CONT—control, Nnat—*Natrix natrix* scent, Caus—*Coronella austriaca* scent, Vamm—*Vipera ammodytes* scent. Significant post-hoc tests of pairwise comparisons are labeled in the following way: $P < 0.05$ with *, $P < 0.01$ with ** and $P < 0.001$ with ***.

3.2. *Predator chemical recognition and related antipredator behavioral responses*

The mean snout to vent length (SVL) of males used in experiments of chemical recognition was 52.5 ± 0.6 mm for *I. horvathi* ($n = 15$) and 54.1 ± 0.9 mm for *P. muralis* ($n = 16$), with no interspecific differences (independent samples *t*-test, $t_{1,29} = 1.44$, $P = 0.16$).

Tongue flicks (controlled for time when lizard was active, see Section 2.5) were not significantly different between species (rm-ANOVA, effect of factor Species, $F_{1,29} = 2.49$, $P = 0.13$, Fig. 2). However, there were significant differences between four scents (effect of factor Scent: $F_{3,87} = 8.30$, $P < 0.001$, Fig. 2), with no significant interaction between both factors (combined effect of factors Species and Scent, $F_{3,87} = 0.20$, $P = 0.89$, Fig. 2). Thus, both species resemble each other in the ability to recognize the scent of both predator snakes; *C. austriaca* and *V. ammodytes*, where both had the highest tongue flick frequencies (Fig. 2, Appendix A). Pairwise comparisons showed that tongue flick counts were higher in response to *C. austriaca* scent than in control and *N. natrix* (non-predator snake), while in response to *V. ammodytes* scent, both species had higher tongue flick count only in comparison to *N. natrix* scent but not to control (see Fig. 2 for significant results of post hoc Tukey's HSD tests).

Using rm-ANOVA design, we compared species and scents in the time spent freezing and in slow motion (descriptive data in Appendix A). There were no differences between the two controls and snake scents within any of the species (rm-ANOVA, combined effect of factors Species and Scent, for freezing, $F_{4,116} = 1.13$, $P = 0.35$, and for slow motion, $F_{4,116} = 1.07$, $P = 0.37$).

Individuals of both species exhibited different types of antipredator behaviors; the least frequent were foot shake and tail wave, followed by run, reverse and lunge (Table 4). Pooled frequencies of run, reverse and lunge were compared between species while accounting for activity time (see Section 2.5) and in the same scent test. Frequencies of antipredator behaviors were similar between species in the two controls (control: $\chi^2 = 0.82$, df = 1, $P = 0.376$, non-predator snake scent: $\chi^2 = 0.28$, df = 1, $P = 0.59$) and in terraria with *V. ammodytes* scent ($\chi^2 = 0.82$, df = 1, $P = 0.37$), but differed in terraria with *C. austriaca* scent where *I. horvathi* more frequently exhibited antipredator behaviors than *P. muralis* ($\chi^2 = 3.89$, df = 1, $P < 0.05$).

Results of comparisons in the variability of different antipredator behaviors of multiple independent samples (Scents) with Median test performed for three types of response (Zero, Medium and High response), revealed no significant differences separately for *I. horvathi* ($\chi^2 = 4.52$, df = 3, $P = 0.21$) and *P. muralis* ($\chi^2 = 4.05$, df = 3, $P = 0.26$). However, it is noteworthy that no individual of *P. muralis* exhibited a High response, whereas 13 % of *I. horvathi* individuals did, all in the terraria with *C. austriaca* scent (Fig. 3).

4. Discussion

Our results showed that antipredator responses of *I. horvathi* and *P. muralis* differ on the behavioral level. Responses to predator snake scents differed in such way, that *P. muralis* displayed less specific and intense antipredator behavioral responses than *I. horvathi*. However, the general ability to recognize scents of predator snakes was similar between species. Secondly, *I. horvathi* used physiologically suboptimal strategy of refuge use: fled at a longer approach distance and remained longer in the refuge before re-emerging. This tactics represent disproportionally higher costs for it when compared to *P. muralis*. From species' ecophysiology it was expected that the more precise thermoregulator, *I. horvathi*, would be less prone to use refuges and remain in them for a shorter time than the thermally less sensitive species, *P. muralis* (Osojnik et al., 2013). Contrary to our expectations, results showed the opposite to be true. Overall, it seems that common predators indirectly induce asymmetrical competition of studied lizard species in syntopic populations. These results provide new insights that contribute to the understanding of observed segregation pattern and interaction between the studied lizard species tandem (Žagar et al., 2013) and reinforce the importance of common predators as mediators of competing prey species (Holt, 1977).

Small lizards have low thermal inertia, which makes their heating and cooling rates fast (e.g., Pough et al., 2004; Luna and Font, 2013; Sannolo et al., 2014). New methods, such as thermal infra-red camera can be used to measure heating/cooling rates in small-sized lizards; in *P. muralis* for example it was shown that a change of 10 °C occurs in 20 min, which is at the rate of 0.5 °C per minute (Sannolo et al., 2014) and similar rate was recorded for cooling after the heat-source was removed (Pough et al., 2004; Luna and Font, 2013). Thus, once they have entered a rock crevice, where temperatures are usually lower than outside, their body temperature will decrease to sub-optimal levels the longer they stay in it, meaning the time spent in the refuge should be kept to a minimum to avoid thermal costs (e.g., Martín and López, 1999a,b). Our results showed that under the same conditions, *I. horvathi* stayed inside the refuge for longer than *P. muralis* and thermal conditions in the refuge did not influence the duration of the use of refuge for all lizards. This means that species intrinsically differed in the time spent in the refuge before re-emerging, not depending on the thermal properties of the refuge. Because all refuge sites were cooler than outside air temperature, *I. horvathi* experienced higher thermal costs than *P. muralis*. Several studies have shown that temperature influences a broad suite of phenotypic traits in Squamates. Best known is the temperature in relation to locomotor performance, i.e., sprint speed (i.e., Braña and Ji, 2000), which is essential for many lizards' activities, such as capturing prey, escape behavior (Husak, 2006; Samia et al., 2015), defending territory, agonistic interactions and mate acquisition, which directly affect reproductive fitness in males (Husak, 2006; Husak et al., 2006).

Escape behavior of *I. horvathi* and *P. muralis* did not only differ in the refuge use but also in the way lizards escaped; *I. horvathi* fled at a longer approach distance from an approaching human observer

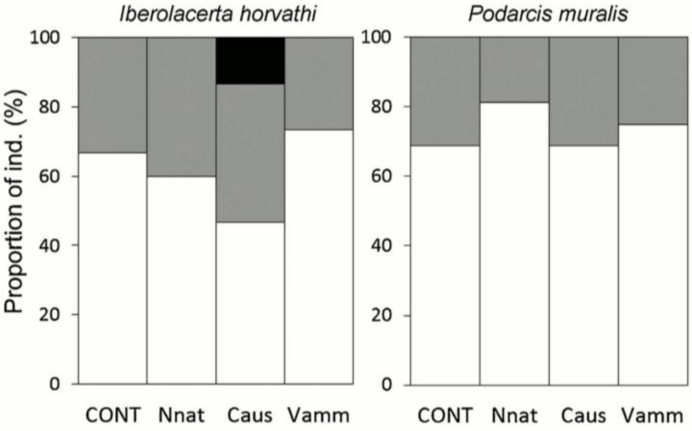

Fig. 3. Behavioral responses to chemical cues of *Iberolacerta horvathi* and *Podarcis muralis*. Presented are proportions of individuals that exhibited none (Zero response, in white), one or two different types (Medium response, in gray) or more than three different types (High response, in black) of antipredator behaviors in four scents. CONT—control, Nnat—*Natrix natrix* scent, Caus—*Coronella austriaca* scent, Vamm—*Vipera ammodytes* scent.

than *P. muralis*. These results remained unchanged regardless of variable air, surface and refuge temperatures or habitat use, which are factors influencing escape and recovery behavior in lizards (e.g., Martín and López, 1999a). Under our hypothesis we did not expect to find a more sensitive escape tactics in *I. horvathi* because it is a more precise thermoregulator (Osojnik et al., 2013) and should avoid higher thermal costs of refuge use. However, this overly cautious antipredator behavior response in escape tactics of *I. horvathi* is in parallel with results of a recent comparative study of behavioral interference in thermoregulation in studied species. The males of *I. horvathi* were more prone to displacements from resources (thermal source), which was provoked by an approach or touch by conspecifics or *P. muralis* males inside a thermal gradient, than *P. muralis* (Žagar et al., 2015a). This is again an observation of *I. horvathi* exhibiting a more sensitive behavioral response than *P. muralis*, similar to this study that showed a more sensitive response to an approaching human observer (simulating a ground predator attack).

On the contrary to the costs of refuge use, over time the probability of a predator waiting outside for prey to re-emerge drops (Martín and López, 1999a) consequently; staying in refuge might be viewed as an antipredatory advantage. If the frequency of potential predator attacks is high, a sensitive (easily-triggered) escape tactics should be beneficial. Despite several species of potential air and ground predators being present in the studied population, none of them is a specialized lizard eater (see Section 2.1 for literature review). Thus, successful avian or mammalian predator attacks causing actual mortality in lizards in the area are probably not frequent and a sensitive antipredator response might involve more costs than true benefits. Two snake species that occur in the study area are relatively common and frequent (Žagar et al., 2013 and pers. observation). As endothem's predation rate is higher because of higher metabolism demands than of ectotherm's (see Section 2.1), the high abundance of snakes does not necessarily mean higher predation pressure. Both snake species are present and lizards should employ responses to avoid predation. Our results showed that both species have a similar ability to discriminate between the scents of *C. austriaca* and *V. ammodytes* compared to control scents. Species did however differ in exhibited antipredator behavioral responses. The species *I. horvathi* was more responsive and it displayed a higher frequency and a more diverse array of behaviors typically associated with stressful situations (lunge, reverse, run, foot shake and tail waving) compared to *P. muralis*. The highest proportion of *I. horvathi* individuals exhibiting such behaviors was found in the terraria with *C. austriaca* scent. These behaviors are considered likely to have a functional significance in predator avoidance (e.g., Webb et al., 2009).

Besides benefits of escaping predation, investing energy and time in exhibiting these antipredator behaviors also imposes certain costs on lizards on account of other fitness-related activities (foraging, social interactions, thermoregulation, reproduction, etc.). The species and specifically, *I. horvathi* which was exhibiting these behaviors more frequently, is therefore expected to experience higher related costs. Similarly to previous test on refuge escape tactics, *I. horvathi* was again found to have a more sensitive antipredator behavioral response than *P. muralis*, which correlates with recent findings on behavioral responses to presence of another lizard inside the thermal arena, where *I. horvathi* exhibited direct agonistic social interactions with conspecifics more frequently than *P. muralis* (Žagar et al., 2015a).

Table 4
Mean values with standard errors (SE), minimum–maximum counts of five different counted antipredator behaviors linked to avoidance of predators recorded in 12 min video recordings when *Iberolacerta horvathi* ($n = 15$) and *Podarcis muralis* ($n = 16$) males were exposed to four different scents. CONT—control, Nnat—*Natrix natrix* scent, Caus—*Coronella austriaca* scent, Vamm—*Vipera ammodytes* scent.

	Iberolacerta horvathi				*Podarcis muralis*			
	CONT	Nnat	Caus	Vamm	CONT	Nnat	Caus	Vamm
Tail wave	0	0	1.1 ± 0.5 0 – 6	0	0	0	0.3 ± 0.3 1 – 4	0
Reverse	0.5 ± 0.3 0 – 4	0.4 ± 0.3 0 – 3	0.3 ± 0.3 0 – 4	0.1 ± 0.1 0 – 1	0.3 ± 0.1 0 – 1	0.4 ± 0.3 0 – 5	0.3 ± 0.1 0 – 2	0.2 ± 0.1 0 – 2
Lunge	0	1.1 ± 0.5 0 – 6	1.2 ± 0.5 0 – 6	0.3 ± 0.2 0 – 2	0	0	0.1 ± 0.1 0 – 1	0.3 ± 0.2 0 – 2
Run	0.1 ± 0.1 0 – 1	0.1 ± 0.1 0 – 1	0.2 ± 0.2 0 – 3	0.2 ± 0.1 0 – 2	0	0.1 ± 0.1 0 – 1	0.1 ± 0.1 0 – 1	0
Foot shake	0	0.1 ± 0.1 0 – 2	0.5 ± 0.4 0 – 6	0	0	0	0	0

Overall we may conclude that differences found in antipredator behavior, specifically in escape and refuge use and in behavioral responses to predator snake scents, probably contribute to asymmetric competition in studied lacertid species through costs related to these behaviors when syntopic species share predators, which act as competition mediators (Holt, 1977). Because *I. horvathi* as the species with higher expected costs due to its more restrictive ecophysiology did not modify behavior in a way to minimize such costs, we assume that species' ecophysiological traits do not affect antipredator behavior in studied lacertids. We conclude this with some reservation as the problem would certainly benefit from further investigation. Despite this, antipredator behavior seems to be independent, probably species or even population specific, as shown in several previous studies (e.g., Biaggini et al., 2009; Diego-Rasilla, 2003).

In conclusion, this study provided key evidence for existing predator-mediated effect in competitive small lizards. Interspecific differences found in antipredator tactics need to be integrated with species' ecophysiology and other behavioral responses to fully understand the role it is playing in the mechanisms of interspecific interactions such as competition. Antipredator behavioral responses should be taken into account in future studies because the presence of shared predators might play an important role in outcomes of interaction between co-existing prey species even through indirect effects (e.g., Bety et al., 2002; Bonsall and Hassell, 1997).

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Appendix A.

See Table A1.

Table A1
Mean values with standard errors (SE) and minimum–maximum values of the duration (s) of five different movements recorded in 12 min video recordings when *Iberolacerta horvathi* ($n = 15$) and *Podarcis muralis* ($n = 16$) males were exposed to four different scents. Behaviors linked to avoidance of predators are labelled with a star (*). CONT—control, Nnat—*Natrix natrix* scent, Caus—*Coronella austriaca* scent, Vamm—*Vipera ammodytes* scent.

	Iberolacerta horvathi				*Podarcis muralis*			
	CONT	Nnat	Caus	Vamm	CONT	Nnat	Caus	Vamm
Freeze*	362.2 ± 40.1	384.5 ± 41.9	409.3 ± 42.5	379.9 ± 34.9	493.1 ± 29.6	410.0 ± 30.0	416.2 ± 25.6	429.7 ± 29.9
Slow motion*	212.4 ± 22.470–351 70 – 35	215.1 ± 29.0 0–399	205.7 ± 28.3 30–378	196.8 ± 25.1 101–392	120.6 ± 19.1 0–244	210.6 ± 23.6 37–421	171.4 ± 17.7 36–325	145.8 ± 27.7 20–392
Crawl*	0.7 ± 0.5	1.1 ± 0.8	6.7 ± 4.7	1.5 ± 1.0	0.2 ± 0.2	0.7 ± 0.8	0.1 ± 0.1	0.8 ± 0.7
Walk	40.5 ± 8.7	29.0 ± 8.4	4.0 ± 1.4	10.0 ± 2.2	50.6 ± 20.5	13.9 ± 7.3	37.1 ± 20.8	45.9 ± 20.8
Climb out	104.2 ± 22.0	90.3 ± 18.4	96.2 ± 22.0	131.8 ± 24.5	55.5 ± 11.6	84.8 ± 13.4	95.2 ± 13.1	97.9 ± 10.8

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5 DISCUSSION AND CONCLUSIONS

In the frame of this dissertation, which consists of six published articles, we used experimental and field studies to investigate the competing potential between two lizard species and potential mechanisms involved in avoiding competition in syntopic populations.

5.1 (DIS)SIMILARITY IN ALTITUDINAL DISTRIBUTION AND HABITAT USE

In our first study (data collected in 2006-2008; article I) we surveyed the entire reptile community in the study area. Results showed that reptile community in the Kočevsko region is composed of ten species: four species from the family Lacertidae, one species from the family Anguidae, four species from the family Colubridae and one species from the family Viperidae (Article I). Both studied species, *P. muralis* and *I. horvathi*, were together with the green lizard (*L. viridis/bilineata*), the most abundant members of the reptile community in this area (highest number of finds, Article I).

In the period between 2009 and 2015 we gathered additional count data of *P. muralis* and *I. horvathi* at 12 new localities and re-sampled all localities from 2006-2008. This resulted in a dataset of 78 different localities, among which one or both species were present at 62 localities (Annexes 6 and 7). At these localities we conducted transect line visual surveys with counts in minimum one to maximum three replicates (Annex 6). Because species are very similar in morphology and colouration, we either came very close to the lizard or photographed it, to inspect the position of scales on the head or colouration of the throat region that serve as reliable taxonomical signs to distinguish between studied species (Tome, 1999; Arnold and Ovenden, 2004). We did not distinguish sex or age of individuals in this data set (Annex 6). Additionally to transect line surveys, we noted presence/absence data of the studied species in several years, at other occasions (i.e. to collect individuals for morphological or experimental study or other purposes) (Annex 6). To compare altitudinal distribution of the studied species in the study area, we calculated relative abundances in five altitudinal belts, each encompassing 200 m of elevation (Table 1 and Fig. 5). We used the maximum counts from transect surveys (see Annex 6) and relative abundances were expressed as the number of individuals per kilometre of the total distance of transects surveyed in each altitudinal belt (Table 1).

Table 1: Distribution of transects across five altitudinal belts surveyed in the period between 2006 and 2015 (see Annex 6), number of individuals (No. of ind.) calculated as sum of maximum counts per transect (see Annex 6 for details) and calculated relative abundances (the number of individuals per kilometre of surveyed transects) of *Iberolacerta horvathi* and *Podarcis muralis* in the study area.

Preglednica 1: Razporeditev transektov v petih višinskih razredih, ki so bili pregledani v obdobju med 2006 in 2015 (glej Prilogo 6), število osebkov izračunano kot vsota največjih štetij iz transektov (glej Prilogo 6) in izračunane relativne gostote (število osebkov na kilometer pregledanih transektov) za vrsti *Iberolacerta horvathi* in *Podarcis muralis* na območju raziskave.

ALTITUDINAL BELT (m a.s.l.)	Number of transects	Total distance of transects (m)	Average distance of transects (m)	*P. muralis* No. of. ind.	*P. muralis* Relative abundance (ind./km)	*I. horvathi* No. of. ind.	*I. horvathi* Relative abundance (ind./km)
100-299	20	5430	271	71	13.1	3	0.6
300-499	10	3960	402	52	14.4	1	0.3
500-699	16	5470	342	48	8.3	7	2.4
700-899	6	2720	472	22	9.8	12	7.2
900-1099	10	2910	297	12	3.7	48	16.5
SUM	62	20490					

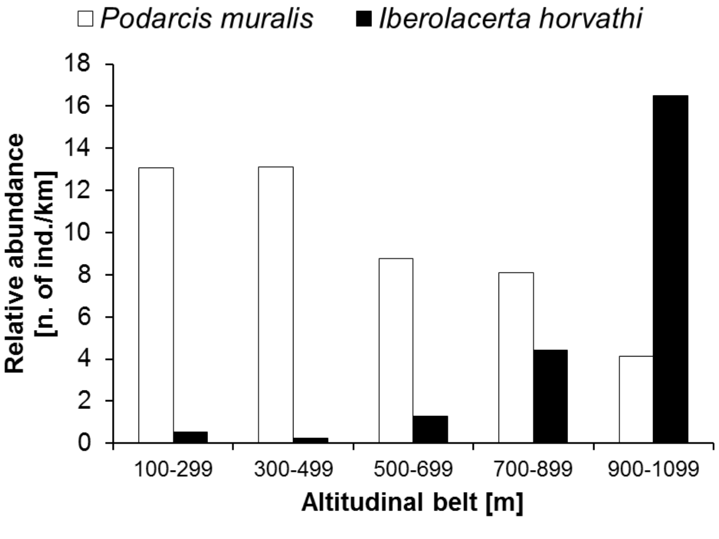

Figure 5: Relative abundances (number of individuals per kilometre of surveyed transects) of the studied species across five altitudinal belts.

Slika 5: Relativne gostote (število osebkov na kilometer pregledanih transektov) preučevanih vrst v petih razredih nadmorskih višin.

The highest relative abundance of *I. horvathi* was found at the highest altitudinal belt (900-1099 m a.s.l.) and relative abundances decreased with decreasing altitude (Fig. 5). Opposite pattern was observed for *P. muralis* with highest relative abundances at two lowest altitudinal belts (100-499 m a.s.l.) and relative abundances decreased with increasing altitude (Fig. 5). We used Chi square test to compare observed frequencies of lizards (number of individuals calculated as the sum of maximum counts per transect; Table 1) in five altitudinal belts with expected frequencies (if species were equally distributed across the altitudinal span in the study area according to the total distance of surveyed transects in each altitudinal belt). Results showed significant differences between expected and observed frequencies for both species (for *I. horvathi*: $\chi^2 = 180.10$, df = 4, P < 0.0001); for *P. muralis*: $\chi^2 = 20.87$, df = 4, P = 0.0003; Annex 8). Frequencies of *I. horvathi* were higher than expected in higher altitudes and lower than expected at lower altitudes and opposite was found for *P. muralis* (plots of observed vs. expected frequencies are in Annex 9). Altitudes of all finds were also statistically significantly different between species (N = 71, median = 948 m a.s.l. for *I. horvathi* and N = 205, median = 430 m a.s.l. for *P. muralis*; Mann-Whitney U tests: U = 1425, Z = 10.10, P < 0.0001). Thus, in our study area both species occurred across the entire altitudinal span but they exhibited an opposite pattern of relative abundances or frequencies, which increased with increasing altitude in *I. horvathi* and with decreasing altitude in *P. muralis* (Fig. 5).

A population was considered allotopic, when all visits on that location confirmed the presence of only one species and syntopic, when on the same visit both species were found at least once (i.e. both species were observed while counting on transect line surveys or noting the presence/absence of species). All surveyed localities fitted one of these criteria. From 62 localities, species were found in syntopic populations at 11 localities (18 %), *P. muralis* was found allotopic at 49 locations and *I. horvathi* at 9 locations (Annexes 7 and 8). Syntopic populations were found across the whole altitudinal span (Annex 6) and with the majority located at middle altitudes (mean = 630 m a.s.l., lower quartile range = 512 m a.s.l., upper quartile range = 813 m a.s.l.). The lowest syntopic population was found at the entrance to Bilpa cave at 200 m a.s.l. (Žagar, 2008b) and the highest at Kameni zid at 1061 m a.s.l (Annex 6). Previous studies reported that syntopic populations of *I. horvathi* and *P. muralis* occur in a limited zone of middle altitudes, while *I. horvathi* was found allotopic at higher altitudes and *P. muralis* at lower altitudes (De Luca, 1988; Lapini et al., 1993; Richard and Lapini, 1993; Lapini et al., 2004; Cabela et al., 2007; Rassati, 2010). So far this is the first observation of syntopic populations found across the entire altitudinal span of a study area. This may be due to the specific topography of our study area; in Kočevsko region altitudes do not exceed 1100 m a.s.l. (Perko and Orožen Adamič, 1998), whereas other study areas had higher altitude range (over 2000 m a.s.l in the Alps or up to 1757 m a.s.l. at Velebit). There *I. horvathi* was found up to highest peaks in Velebit or up to 2000 m a.s.l. in the Alps (e.g. De Luca, 1998), while at so high altitudies are likely unsuitable for *P. muralis*.

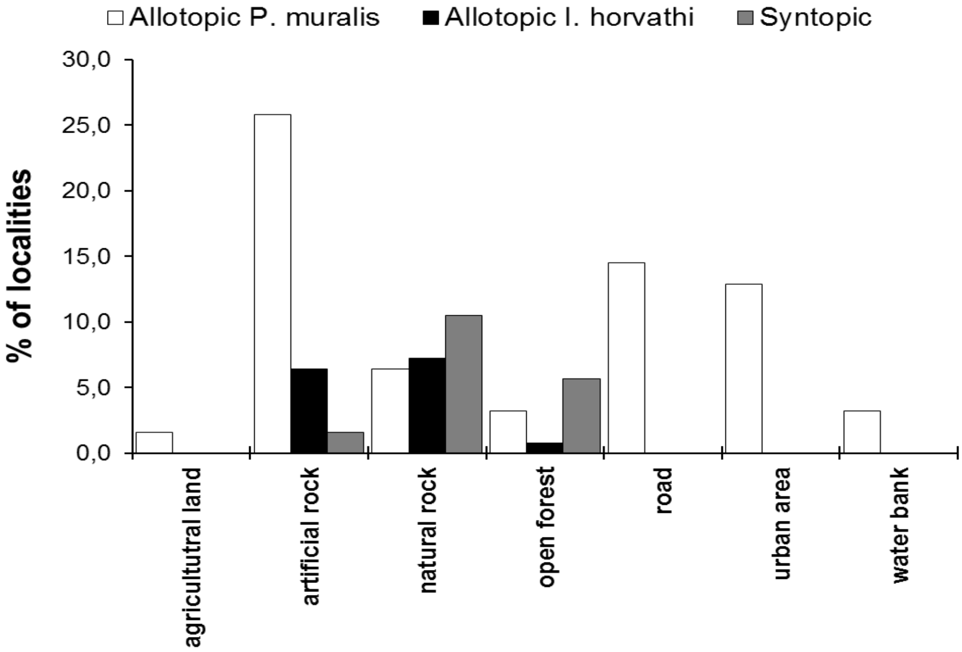

Figure 6: Relative proportion of allotopic and syntopic populations of *Podarcis muralis* and *Iberolacerta horvathi* calculated from all population (N = 62) in seven different habitat types in the study area of Kočevsko region.

Slika 6: Relativni delež alotopičnih in sintopičnih populacij vseh popisanih populacij (N = 62) vrst *Podarcis muralis* in *Iberolacerta horvathi* v sedmih habitatnih tipih na proučevanem območju na Kočevskem.

In the frame of the first study (article I) we described eight different habitat types in the study area occupied by different reptile species (see Supplementary material of Article I). Studied lizard species were found in seven different habitat types; *I. horvathi* occurred in three habitat types and *P. muralis* in seven habitat types (Article I). Extended data set from the period 2006-2015 was re-analysed and the same pattern persisted; *P. muralis* was found in a more diverse array of habitat types (seven) than *I. horvathi* (three; Annex 6 and Fig. 6). Using the entire data set, we calculated the relative proportion of allotopic and syntopic populations in each habitat type (Fig. 6). Syntopic populations occurred in all three habitat types, where we found *I. horvathi*: in natural and artificial rocky habitats and in open forests (Fig. 6). These three habitat types occurred throughout the altitudinal range (artificial rock: 203-1058 m n.m.v. (min-max), natural rock: 208-1055 m n.m.v. (min-max), open forest: 336-1118 m n.m.v. (min-max); Fig. 7). On the other hand, habitat types with only *P. muralis* (agricultural land, road, urban area, and water bank) were mostly limited to middle and lower altitudes (agricultural land: 588 m n.m.v. (one location), road: 204-612 m n.m.v. (min-max), urban area: 229-959 m n.m.v. (min-max), water bank: 204-274 m n.m.v. (min-max); Fig. 7). The difference in the range of habitat types used by both species and habitat types used only by *P. muralis* could have affected observed differences in the altitudinal distribution of the two species. Therefore, we repeated our analysis and compared the altitudinal distribution between studied species using only altitudes from the three habitat types that occurred throughout the altitudinal range and were used by both species (artificial and natural rocks and open forest). Results showed that also in these habitat types *I. horvathi* was found at significantly higher altitudes (N = 71, median = 948 m n.m.v.) than *P. muralis* (N = 113, median = 507 m n.m.v.; Mann-Whitney U tests: U = 815, Z = 9.09, P < 0.0001).

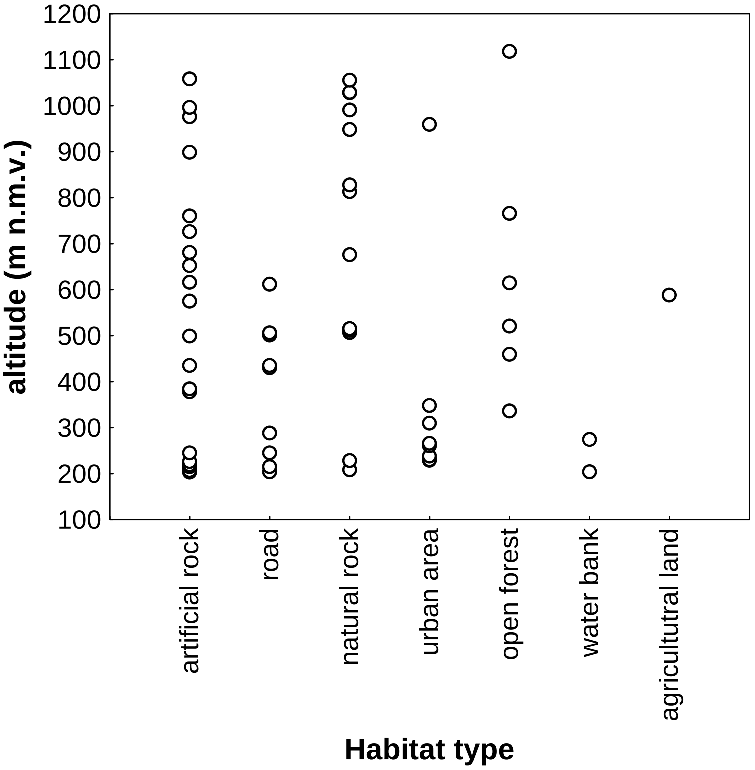

Figure 7: Altitudinal distribution of sampled locations (N = 62) according to the habitat type.

Slika 7: Razporeditev pregledanih transektov (N = 62) po nadmorskih višinah glede na habitatni tip.

In observed three habitat types (Fig. 6) species could potentially come in competition, if they do not segregate in habitat use at a finer spatial scale (microhabitat). In the scope of the anti-predator behaviour study (article VI), which was conducted in a syntopic population at Kuželjska stena in a natural rock habitat type, we collected data on the microhabitat use of both species (Table 2). Both species mainly occupied same microhabitats; i.e. small and large rocks with no or scarce vegetation (Table 2). Compared to *I. horvathi, P. muralis* occupied a wider variety of microhabitats and was found also on the ground with shrubs and grass (Table 2). Similarly was observed in other syntopic populations, where we did not systematically gather data, but noted that both species occurred together in rocky microhabitats and *P. muralis* was occasionally found also on the ground with vegetation, where *I. horvathi* was very rare (pers. observations). A high interspecific overlap in the microhabitat use in syntopic population in our opinion suggests that competition is very likely to occur between species, when they live in syntopic populations. Since *P. muralis* had a wider habitat and microhabitat use than *I. horvathi*, this suggests that *P. muralis* could to some extent avoid competition across the study area and in syntopic populations.

Table 2: Microhabitat use of adult *Iberolacerta horvathi* and *Podarcis muralis* in a syntopic population at Kuželjska stena, presented with the number of individuals and relative proportions in brackets (for details on data collection, see Article VI).

Preglednica 2: Mikrohabitata raba prostora odraslih osebkov vrst *Iberolacerta horvathi* in *Podarcis muralis* iz sintopične populacije na Kuželjski steni, predstavljena kot število popisanih osebkov in izračunan relativni delež za posamezno mikrohabitatno kategorijo (v oklepajih). Metoda zbiranja podatkov je predstavljena v članku VI.

Habitat type	*Iberolacerta horvathi*	*Podarcis muralis*
Ground with vegetation	-	3 (15.5 %)
Small rocks, scarce vegetation	25 (42 %)	3 (15.5 %)
Small rocks, no vegetation	20 (34 %)	7 (37 %)
Large rocks, no vegetation	14 (24 %)	6 (32 %)

In conclusion, opposite pattern in relative abundances across the altitudinal span between the two species and wider use of habitat and microhabitat of *P. muralis* suggest that the species to some extent segregate in their spatial niches and thus avoid competition. Opposite pattern of relative abundances over the altitudinal span suggest that *I. horvathi* are potentially competitively stronger at higher altitudes and *P. muralis* at lower altitudes. However, we have found a high altitudinal overlap in the distribution of studied species, relatively high proportion of syntopic populations (18 %), and overlap in three habitat types and in the microhabitat use on rocks. Together with similar food preferences, morphologic and ecologic similarity (see Introduction and our results for references) these results suggest that species also have a high potential to currently compete in syntopic populations. When species have a high potential for competition, various abiotic and biotic factors may modulate the out-come of competition (Lotka, 1910; Volterra, 1926; Tome, 2006) and cause temporal shifts between syntopic and allotopic populations. During our study period we did not observe major temporal changes in distribution patterns of the studied species in the Kočevsko region. However, additional studies will be needed to evaluate long-term temporal dynamic of observed patterns.

5.2 MORPHOLOGICAL (DIS)SIMILARITY

The morphology of animals is known to reflect long- and short-term evolutionary history, i.e. phylogeny and local adaptation, together with phenotypic plasticity (e.g. Kaliontzopoulou et al., 2012a). Morphological differences between species can also reveal current niche segregation in sympatry (Schoener, 1977). In our comparative morphological study we included individuals from a sympatric area of Kočevsko region, where we measured six biometric characters of body and head size (Article II). Results showed that the two species were similar in four measured characters, which described body length, pileus length, head length, and head width (Article II). Interspecific differences were found in the head height (*I. horvathi* had flatter heads than *P. muralis*) and body mass (*P. muralis* were heavier than *I. hrovathi*; Article II). Species also had similar pattern and magnitude of sexual dimorphism. Females had longer bodies, were lighter and had smaller heads than males in both species (Article II). Important to note is that sexual dimorphism was greater than interspecific differences in these biometric characters, except in the head height (Article II). Differences between sexes can result from avoiding intraspecific competition, as well as from sexual selection pressures for maximizing the reproductive output (e.g. Olsson et al., 2002). It is known that in lacertid lizards longer trunks or bodies of females are derived from selection pressures towards having larger body volume to hold eggs and may also influence their reproductive success (e.g. Olsson et al., 2002; Roitberg et al., 2013). The number of eggs carried by the female has been found to correlate with body/trunk length in both studied species (De Luca, 1992; Ji and Braña, 2000). Since females of both species had similar body lengths, this character is not expected to affect differences in reproductive output between the species.

According to the Lotka-Volterra model of interspecific competition, it is not possible to predict the outcome of competition, when interspecific competition is greater than intraspecific competition (Lotka, 1910; Volterra, 1926). The competitively stronger species will be the one with additional advantage, e.g. larger population, earlier colonization of given area, lower parasite load, etc. (Lotka, 1910; Volterra, 1926; Tome, 2006). Observed strong sexual dimorphism and high interspecific similarity in most measured biometric characters (except head height) suggest high potential for competition between males and between females of *P. muralis* and *I. horvathi* in the Kočevsko region. Consequently, we would expect that one species should out-compete the other (under different sets of conditions) and the two species should exhibit a segregating pattern to avoid competition (Begon et al., 2006). In our study area we found a partial segregation pattern of contrasting relative abundances along the altitudinal gradient with a relatively high proportion of syntopic populations (18 %), mostly at mid-altitudes and natural rock habitat types (see chapter 5.1). In such areas of overlap, found high resemblance in morphology suggests that females and males of both species will likely come into competition.

The only studied morphological character that differed between the species and could thus potentially promote their coexistence was head height. Head dimensions, and especially head height, have been shown to correlate with the volume and the power of jaw muscles (e.g. Herrel et al., 2001). Interspecific difference in bite force performance could have repercussions for dietary niche segregation, asymmetrical success in male-male combats and spatial segregation in the use of crevices. Some studies correlated bite-forces of lacertid lizards with their diet (e.g. in *Zootoca vivipara*: Herrel et al., 2008; but see Kaliontzopoulou et al., 2012b). For *I. horvathi* and *P. muralis,* previous studies showed that dietary niches in syntopic populations overlap to a large extent (e.g. De Luca, 1992; Richard and Lapini, 1993; Capizzi, 1999), which suggest that head height is not connected with diet niche segregation in this species pair. Richard and Lapini (1993) suggested that the high dietary overlap was likely due to the high degree of structural complexity of the habitat and consequently high diversity of preys available. Furthermore, the head height could potentially be a limiting factor for use of shelters; *I. horvathi* with a flatter head could potentially be able to occupy narrower crevices than *P. muralis*. This could give *I. horvathi* a potential advantage to escape common predators that prey lizards in their shelters (e.g. saurophagus snakes; Amo et al., 2004b). When the impact of common predators is asymmetric towards lizard prey species, this can indirectly impact lizards' competitive interaction (i.e. "apparent competition";Holt, 1977; see also chapter 5.5). However, the link between the head height and the use of crevices has not yet been fully established in lacertid lizards. Lack of such studies is connected to limited access to sites that small lacertid lizards use for shelters and because small body mass of these species does not allow the use of radio-tracking devices. With current knowledge it is therefore difficult to predict implications of observed interspecific difference in the head height of *P. muralis* and *I. horvathi* and further studies are needed, especially on their use of shelters.

Beside head height, also other adaptations (e.g. physiological and behavioural traits, or other morphological characters not studied here) or mechanisms (e.g. via common predators) could be involved in promoting coexistence between species (see paragraph 5.1). Thus, in further studies we used experimental approaches to compare several physiological and behavioural traits, and the potential effect of common predators (articles III, IV, V and VI) to further examine the potential for competition by realizing potential segregations on the level of species' physiology and behaviour. In most studies we followed established experimental methodologies for studying physiological and behavioural traits of lacertids (e.g. Carretero et al., 2005, 2006). Mostly we restricted our experiments to males (except in study of article III and VI), because physiology and behaviour of females can be effected by egg production (e.g. Bauwens and Thoen, 1981; Huey, 1982) and it was difficult to reliably determine the precise status of egg development inside collected females and account for egg development status in the analysis of observed traits. Males of lacertid lizards are also known to exhibit aggressiveness with other males thus were suitable for studying potential competition via agonistic social interactions (see article V ofr literature review and more information).

5.3 (DIS)SIMILARITY IN PHYSIOLOGY

Reptiles in general have distinct water physiology, which in most cases reflect climatic properties of their habitat (e.g. Hillman and Gorman, 1977; Mautz, 1982; García-Muñoz and Carretero, 2013; Guillon et al., 2014; Caldwell et al., 2015; Carneiro et al., 2015). We expected to find similar water-loss rates between *I. horvathi* and *P. muralis* since we compared populations from similar altitudes and relative humidity. Surprisingly, we found that *P. muralis* had higher mean instantaneous water loss rates and accumulated water loss when exposed to long dry periods. However, the interspecific differences in water-loss rates of studied species (approx. 0.1 % of instantaneous water-loss rate) were very small compared to values measured in other studies (e.g. García-Muñoz and Carretero, 2013;

Carneiro et al., 2015). Thus, the effect of interspecific dissimilarity in water-loss rates is likely weak. A broader study using multiple-species comparison is needed in order to assess the significance of differences in water physiologies detected with used metholodogy, which will improve understanding of their implications for interspecific interaction.

Higher body temperatures have been shown to directly correlate with lizards’ maximum performance (sprint speed, speed of digestion of food, e.g.: Angilletta, 2001; Angilletta et al., 2002), which affect a wide array of lizards’ life-important activities and processes (e.g. Husak et al., 2006; Sacchi et al., 2014) and thus the overall fitness of individuals. Both temperatures (Hertz et al., 1993) and environmental heterogeneity at the scale of an organism (Sears and Angilletta, 2015) are the most important factors determining effective thermoregulation of heliothermic lizards. In habitats with high spatial heterogeneity lizards have higher thermoreglatory precision with lower energetic costs (Sears and Angilletta, 2015). When species coexist in thermally restrictive environments (e.g. at higher altitude, shady places) with sufficient heterogeneity of space, higher precision of thermoregulation will potentially be an advantageous trait. Oppositely, in thermally non-restrictive (warmer) places, with similar heterogeneity of space, more precise thermoregulation could potentially be costly and less beneficial due to costs involved in thermoregulatory behaviour of heliothermic lizards (Huey, 1982).

Species had a similar mean temperature set point (mean Tp) but they significantly differed in the Tp range across seasons. Namely, *I. horvathi* thermoregulated to a higher set point in spring than *P. muralis*, while this interspecific difference disappeared in summer. Since available environmental temperatures are lower in spring than in summer (ARSO, 2015), these results suggest that *I. horvathi* is a more precise thermoregulator. Precise thermoregulation may be an advantage or a disadvantage, depending on the thermal properties of the environment (Hertz et al., 1993; Sears and Angilletta, 2015). Dissimilarity in thermal physiology between *I. horvathi* and *P. muralis* were in line with observed partial altitudinal segregation pattern in relative abundances of studied species, and could potentially explain found distribution patterns. If higher precision of thermoregulation is an advantageous physiological trait in thermally restrictive (colder) environments, it is in line that at higher altitudes we found lower relative abundances of *P. muralis* and higher relative abundances of *I. horvathi*. On the contrary, at lower altitudes we would expect to find both species. Surprisingly, *P. muralis* was found more frequently alone at lower altitudes, which suggests that other mechanisms of species interaction should play a role there.

Thermoregulation of lizards is expected to directly affect their rate of metabolism because temperature is one of the major factors influencing metabolic rates (Bennett and Dawson, 1976; Bennett, 1982; Huey, 1982; Gillooly et al., 2001). We have found that species were similar in measured metabolic rates (article IV). Moreover, we also determined the potential for metabolic activity (see Article IV), which was higher in *I. horvathi* than *P. muralis*. By integrating results of species'metabolic rates and their thermoregulatory strategies (higher precision of thermoregulation found in *I. horvathi*, article III), we might predict that *I. horvathi* has a physiologically advantageous predisposition for higher physiological performance in thermally more restrictive environments. Preciser thermoregulation likely enables *I. horvathi* to maintain their body temperatures in a narrower range of body temperatures than *P. muralis*, which directly affects their metabolic rates. Thus, under the same environmental conditions and with different thermoregulatory strategies that result in different body temperatures, the higher precision of thermoregulation found for *I. horvathi* would allow this species to realize its potential metabolic activity to a higher extent than *P. muralis*. This is another physiological trait that could potentially give *I. horvathi* a competitive advantage over *P. muralis* in thermally restrictive environments and is in line with found distributional patterns of studied species.

5.4 INTERFERENCE IN THERMOREGULATION

The studied species live in predominantly forested landscapes where access to sun-exposed areas and thermoregulation opportunity is limited. Consequently, we expected that potential for competition was higher in such habitats (e.g. Magnuson et al., 1979; Downes and Shine, 1998). In a test of interference competition in thermoregulation, *I. horvathi* obtained lower body temperatures than their optimal preferred body temperature due to high sensitivity in responses to agonistic social interactions. Lower body temperatures can be translated in poorer performance and fitness (Huey, 1982) thus represents disadvantage for *I. horvathi*. *P. muralis* did not change its body temperatures in interference trials. Result of the behavioural experimental study showed that interference occurred due to exhibited social agonistic behaviours by males that caused displacement of lizards approached/touched inside the thermal gradient. Consequently, this behavioural response had a negative effect on achieving the range of preferred body temperatures (the negative effect was found in *I. horvathi* but not in *P. muralis* (article V)). Found interference was assymetrical and should provide an advantageous position for *P. muralis,* which did not lower its Tp when in pair with a con- or hetero-specific lizard (article V). Thus, our results suggest that in situations when sun-exposed areas limit opportunities for thermoregulation in syntopic populations, interference in thermoregulation between species likely occurs and *P. muralis* is competitively stronger thus could potentially out-compete *I. horvathi*. This could potentially be the mechanism by which *P. muralis* excluded *I. horvathi* from majority of lowland populations, which are predominately allotopic *P. muralis* populations (paragraph 5.1).

5.5 INFLUENCE OF SHARED PREDATORS

Common predators may indirectly shape relationships between prey species in syntopic populations (Fig. 8; Holt, 1977; Tokeshi, 2009). The predation pressure in a population depends on the ability of predator to capture the prey, which is also modulated by preys' antipredator tactics. We assessed antipredator responses of studied species against two types of common predators: predators that attack lizards on ground (birds and mammals) and predators that prey on them inside refuges (snakes).

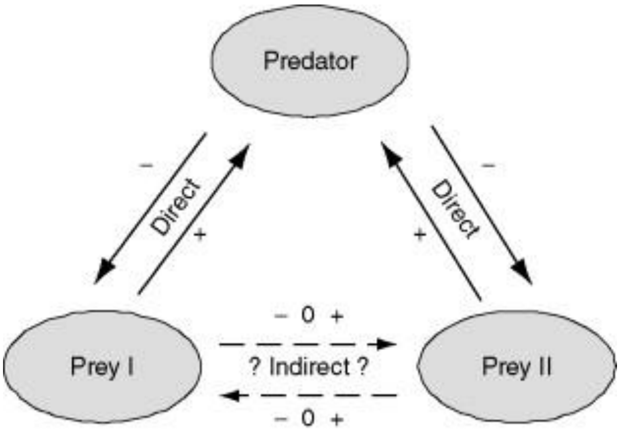

Figure 8: Schematic representation of apparent competition between two prey species that are attacked by a common predator. Indirect interactions are marked with dash arrows (adapted from Holt, 1977: 218).

Slika 8: Shema prikritega tekmovanja med dvema vrstama, ki imata skupnega plenilca. Posredne interakcije so označene s črtkanimi puščicami (prirejeno po Holt, 1977: 218).

Results of both studies showed interspecific differences in their antipredator responses. *I. horvathi* had a "shier" escape strategy than *P. muralis*; it escaped at a greater approach distance, stayed longer inside the refuge, and had a higher behavioural response to predator-snake scents. A direct benefit of the "shier" response is a higher success in escaping predators, and consequently a higher short-term survival rate (e.g. Martín and López, 1999). On the other hand, because refuge sites are cold they represent thermal costs for active lizards; *I. horvathi* must devote additional time for basking after emerging from a refuge. Thus, its "shier" antipredator response involves both energetic and time costs. Antipredator responses will be evoked by both, real predation attempts and fake predation attempts, which may or may not be caused by predators. In real predation attempts the "shier" species will have an advantage because of its higher chance of successful escape. On the contrary, in fake predation attempts the same response will entail unnecessary costs. Thus in case of high predation pressure *I. horvathi* will likely benefit from this behavioural response. Common predators will have a more negative effect on *P. muralis* than on *I. horvathi*, which indirectly influences their competitive interaction. In a situation when predation pressure is low and many predation attempts are fake, the situation may be the opposite, providing *P. muralis* with an advantage over *I. horvathi* by reacting less.

5.6 FUTURE RESEARCH PERSPECTIVES AND GENERAL CONCLUSION

Our results show that studied species can potentially compete in syntopic populations due to their high overlap found by comparing different dimensions of ecological niche. Both species overlap in habitat use of *I. horvathi*, while *P. muralis* uses also habitats with higher vegetation cover. They have similar morphology with the only difference in the height of the head. They are also similar in physiological traits. However, it seems that physiology of *I. horvathi* is more adapted to thermally more restrictive environments. Jointly, found similarities between the species on one hand suggest that species likely compete in areas of overlap (syntopic populations). On the other hand, observed dissimilarities probably promote segregations on different levels of the ecological niche and suggests that competition is thus avoided between species.

Arnold (1987) suggested that species from genus *Iberolacerta* become stricly saxicolous in syntopic populations with *Podarcis* sp. If the spatial niche of the species is wider in allotopic than in syntopic population, this suggest that displacement from a part of spatial niche of the species occurs due to competition in syntopic population (Tome, 2006). During our field work we have not observed any marked changes in the general habitat use between allotopic and syntopic populations of both species, but we have not systematically made observations to be able to test it. It is also possible that the scale of our observations was too coarse thus a more detailed microhabitat use study would provide better data to test the hypothesis of habitat displacement. Moreover, such a study should be done by collecting data from field observations from allotopic and syntopic populations (e.g. Tarkhnishvili et al., 2010). In such studies it is important to ensure similar abiotic and biotic factors of compared populations and in parallel collect data on variation in these factors to include them in the comparative analyses. Another possibility would be to observe microhabitat use under semi-natural conditions (mesocosmos) with controlled conditions (e.g. Monasterio et al., 2010).

The only morphological difference between species was in the head height; *I. horvathi* has flatter heads than *P. muralis*. There are several possibilities on how this morphological difference can translate into performance and have an effect on the competitive interaction in syntopic populations (see chapter 5.2). In the future functional morphology could be verified by measuring bite-force and experimentally testing outcomes of male-male combats, determining diet with advanced analysis, e.g. isotopic analysis of diet (e.g. Comas et al., 2014), and examining the link between head height and shelter use. Flatter head could potentially allow *I. horvathi* to use smaller rock crevices thus promote spatial segregation of shelter use between species. So far there is no study available to support the link between the flatness of the head and limit of the refuge use in lizards.

Results of found assymetric potential for interference competition in thermoregulation for both species and realized interspecific differences in antipredator responses call for attention that both mechanisms may play a role in observed pattern of species segregation and coexistence patterns in the study area. Thus any future studies in syntopic population of studied populations need to take into account the potential factors likely to affect both species and their interaction in a direct and indirect way: the quality of habitat for thermoregulation and ther presence and predation pressure of common predators.

This study was based on a prediction that *I. horvathi*, which has a range-restriced distribution at higher altitudes, could be threathened by lowland populations of *P. muralis* that will start moving to higher altitudes with rising environmental temperatures due to future climate change. Our results showed that *I. horvathi* has specific eco-physiological advantages to cope with thermally restrictive (cooler) environments, while *P. muralis* is adapted to less thermally restricted environments. This may probably be the mechanism that currently prevents *P. muralis* from spreading to higher altitudes. Predicted global temperature rise could in future lower the thermal restrictiveness at higher altitudes, thus promote *P. muralis* to spread higher-up. When *P. muralis* would come into new contact with *I. horvathi*, our results suggest that species may co-exist (suggested by already relatively frequent syntopic populations in the study area). High similarity between species suggests that the potential for interspecific competition in syntopic populations is high and we found evidence of interspecific interference competition in thermoregulation. But at the same time we found several dissimilarities between species that may act as mechanisms by which species will exhibit fine-scale niche segregations that promote their coexistence by avoiding competition.

Global climatic changes are representing one of the major threats for biodiversity loss in the future (e.g. Sala et al., 2000). Predictive models of the impacts of climate change are needed to direct conservation efforts towards most threatened species and ecosystems. Recent studies showed that climate change can impact various antagonistic and mutualistic interactions thus change the power of relationships in communities (e.g. Tylianakis et al., 2008; Gilman et al. 2010). Predicting the effects of climate change is dependent upon identifying those interactions between species that are key determinants of the structure and function of the community, such as competition (Bonsall and Hassell, 1997). To decrease the uncertainty of the models for a complex network of species in the community, mechanisms of interspecific interactions need to be first realized and understood. Results of this doctoral dissertation provide this type of information that will be useful for construction of predictive models in the future. Including known interspecific relationship between studied species in these predictions will improve the accuracy of such models (e.g. Gilman et al., 2010) and improve the effectiveness of their conservation.

6 SUMMARY

6.1 SUMMARY

Ecosystems are usually composed of multiple species organised in communities where they interact with each other. In communities where two or more members of the same ecological guild coexist and resources that they utilize are limited, they will either segregate in one or more dimensions of ecological niche to avoid interspecific interactions or they will interact. The main aim of this dissertation was to study interspecific competition between two species, which belong to the same ecological guild and have a sympatric distribution in the study area. We studied lizards that are small, active, diurnal and abundant: the Horvath's rock lizard (*Iberolacerta horvathi* [Méhely, 1904]) and the Common wall lizard (*Podarcis muralis* [Laurenti, 1768]) in the Northern Dinaric Mountains in Slovenia. We used a multidisciplinary approach including fields of morphometry, eco-physiology, behaviour and ecology. The studied species are ectotherms with limited dispersal ability thus are likely to be strongly impacted by rapid climate changes. Understanding species interactions and how they can be affected by future climate change is important for future planning of conservation activities of a potentially threatened species.

Firstly, we compared habitat use and spatial distribution pattern between species in our study area (article I and paragraph 5.1). Species had a partial segregation pattern along the altitudinal gradient; *P. muralis* was most abundant at low and *I. horvathi* at higher elevations. Syntopic populations were found across the altitudinal span but were most frequent at middle altitudes. In general, both species resembled in habitat use (most common on rocky substrate), while *P. muralis* had a broader distribution range and used more variable habitat types than *I. horvathi*. These results indicated that in the study area species coexist and occur in syntopic populations thus there is a high potential for interspecific competition. Secondly, we compared morphology of adult lizards from the area of sympatry (article II). Both species had similar body length, head width, length and pileus length. They differed in the head height; heads of *I. horvathi* were more flattened than those of *P. muralis*. Morphology can translate in performance and in the case of head

height found interspecific differences suggest that *P. muralis* have stronger bite-forces than *I. horvathi*. Performance traits for studied populations have not been studied yet. However, if bite-forces of *P. muralis* are bigger, this species could potentially exhibit competitive advantage in male-male agonistic social interactions or prey harder prey items. We also hypothesized that height of the head may influence the spatial use of refuge sites (*I. horvathi* could potentially enter smaller crevices due to flatter heads than *P. muralis*).

Furthermore, we have compared species' eco-physiological traits. Preferred body temperatures (Tp) and rates of evaporative water loss (EWL) are physiological characters that together with behavioural thermoregulation influence lizards' performance and fitness (article III). The means of Tp were similar in both species, but their seasonal dynamics differed, which indicated that thermal accuracy might be important. Species differed in seasonal (and daily) variation of Tp; variations were bigger in *P. muralis* than in *I. horvathi*. For water physiology, our results showed interspecific differences with higher values of water loss rates found in *P. muralis* than in *I. horvathi*. We concluded that physiology of *I. horvathi* could be competitively advantageous in thermally restrictive (cooler) environments. On the other hand, such precise thermoregulation is known to induce substantial time and energetic costs and could therefore be disadvantageous in thermally less-restrictive environments.

Since metabolism is highly dependent on body temperature in ectotherms, thermoregulation is expected to directly affect their metabolism. We compared metabolic rates of adult males of two species from an area of sympatry, which we measured under two temperature regimes (20°C and 28°C, article IV). Both species increased metabolic rates with temperature in a similar pattern. We also compared potential metabolic activity (enzymatic capacity) from tail tissues. *I. horvathi* attained higher values than *P. muralis*, which together with the ability to thermoregulate more precisely could again represent a higher competitive advantage over *P. muralis* in thermally more restrictive environments such as those at higher altitudes. Improved knowledge of differences in metabolism provided valuable information for understanding recent distributional patterns as well as species interactions.

In the next step, we were interested if the two species compete for limited resource - sun-exposed areas in a forested landscape - while taking into account the observed interspecific differences in thermoregulation (article V). In a social context with heterospecific or another conspecific male, *I. horvathi* achieved lower realized body temperatures compared to its preferred body temperature (Tp), while realized body temperatures of *P. muralis* did not vary among social contexts. Our results suggest that interference was a result of direct agonistic interactions, assessed by the frequency of approaches and touches. *I. horvathi* showed higher interference susceptibility than *P. muralis* indicating an asymmetric interaction between the two species. We have shown that sunlight (as a resource) might be an important factor influencing distribution patterns in assemblages of heliothermic ectotherms where sun-exposed basking sites are limited. Finally, we assessed the role of common predators as mediators influencing the interaction between the two lizard species (article VI). Results showed that *I. horvathi* has more pronounced anti-predator response than *P. muralis* in refuge-escape tactics. Additionally, while both species were able to recognize chemical cues of predator snakes, the behavioural responses were more frequent and variable in *I. horvathi* than in *P. muralis*. While this “more cautious” attitude of *I. horvathi* should provide higher short-term benefits (higher survival rates), this would hold true only in populations where predation pressure is high. Otherwise it carries substantial time and thermoregulatory costs.

Overall, results of present dissertation provide significant insights into the potential and possible mechanisms of interspecific competition between studied sympatric species. Strong assymetric direct interference competition effects were found that are pormoted via particularity of the environment – limited sun-exposed areas inside the forest landscape. At the same time our results show that the studied system is very complex. Several factors, abiotic and/or biotic play a role in the exhibited coexistence – segregation pattern: altitude, habitat type, microhabitat, common predators. At the same time studied species were found to avoid competition via developed differences in physiology and behaviour. Factors and species' specific traits affect the interspecific competition either straightforward or in connection with other factors and species specific traits.

6.2 POVZETEK

Raziskave medvrstnega tekmovanja so zapletene in zahtevajo uporabo različnih metodoloških pristopov, če želimo celostno razumeti mehanizem tekmovanja med preučevanima vrstama. Najprej je potrebno prepoznati potencial za tekmovanje med vrstama (ali vrsti sobivata, kako se prekrivata njuni fundamentalni niši, ali izrabljata vire na enak način, itd.). Če se fundamentalni niši dveh vrst ne prekrivata, potem je to lahko posledica tekmovanja v preteklosti, ki je privedlo do današnjega ločevanja niš na genotipski ravni. Če pa se vrsti prekrivata v (relativno velikem delu) funadmentalne niše, obstaja uetmeljen sum, da bo v sintopičnih populacijah prihajalo do medvrstnega tekmovanja. Ko opazimo, da se vrsti razlikujeta v eni ali več dimenzijah realizirane ekološke niše v simpatriji vendar ne v alopatriji (ta pojav imenujemo premik niše; angl. »niche shift« ali »niche differentiation«) in to je lahko posledica dejanskega tekmovanja med vrstama.

Glavni namen pričujoče doktorske disertacije je izboljšanje razumevanja mehanizma interakcij med ekološko podobnimi vrstami, ki živijo v simpatriji. Za takšne medvrstne interakcije se trenutno predvideva, da so globalno eden izmed najpomembnejših dejavnikov, ki vplivajo na strukturo živalskih združb. Obenem medvrstne interakcije v veliki meri vplivajo na razširjenost posamezne vrste. V okviru disertacije sem iz različnih vidikov raziskala mehanizem tekmovalnih interakcij med dvema vrstama kuščaric, kjer je medvrstno tekmovanje pričakovano, saj se vrsti prostorsko prekrivata (živita v simpatriji) na preučevanem območju in sta si zelo morfološko in ekološko podobni.

Kuščarice iz rodov skalnih kuščaric (*Podarcis*) in gorskih kuščaric (*Iberolacerta*) imajo zelo podobne habitatne zahteve in načine prehranjevanja ter spadajo v isti ekološki ceh. Kuščarice so predvsem plenilci členonožcev, ki lovijo z aktivnim iskanjem, le redko s plenjenjem iz zasede. V cehih so negativni medvrstni odnosi kot so tekmovanje ali znotrajcehovsko plenilstvo lahko še posebej močni, ker vrste na enak način izrabljajo skupne vire. Rod gorskih kuščaric združuje sedem vrst, ki imajo majhna območja razširjenosti v Pirenejih in osrednjem delu Iberskega polotoka, ena od vrst pa je razširjena v Vzhodnih Alpah in Dinaridih. Območje razširjenosti večine vrst tega rodu se vsaj delno prekriva z območjem razširjenosti ene ali več vrst iz rodu skalnih kuščaric, ki so široko razširjene v Evropi. V Sloveniji je znano takšno prekrivanje območij razširjenosti (simpatrija) med velebitsko kuščarico (*Iberolacerta horvathi* (Méhely, 1904)) in pozidno kuščarico (*Podarcis muralis* (Laurenti, 1768)) na več mestih v južni Sloveniji, kar omogoča podrobno preučevanje medvrstnih odnosov med tema ekološko podobnima vrstama. Na območjih simpatrije so pozidne kuščarice bolj številčne na nižjih nadmorskih višinah, velebitske kuščarice pa na višjih nadmorskih višinah, pogosto pa sobivata na območjih srednjih nadmorskih višin.

Glavne hipoteze doktorske dizertacije so bile:

- Na preučevanem območju obstaja visok potencial za medvrstno tekmovanje med pozidno kuščarico (*P. muralis*) in velebitsko kuščarico (*I. horvathi*), ker je njuna razširjenost simpatrična (z obstoječimi sintopičnimi populacijami) in se v rabi prostora njuni prostorski niši prekrivata (članek I, poglavje 5.1 in Priloge 7, 8 in 9)

- Fundamentalni ekološki niši obeh vrst sta zelo podobni:
    - vrsti sta morfološko podobni (članek II),
    - vrsti sta si podobni v fiziologiji termoregulacije in regulacije vode (članek III),
    - vrsti sta si podobni v značilnostih metabolizma (članek IV).

- Realizirani ekološki niši tekmujočih vrst se razlikujeta ob prisotnosti / odsotnosti druge vrste kot posledica realizacije večjega dela fundamentalne niše ob odsotnosti druge vrste (t.i. »kompeticijska sprostitev«):
    - prisotnost druge vrste vpliva na doseganje telesne temperature kuščaric; dejanske telesne temperature so drugačne od izbranih optimalnih telesnih temperatur posamezne vrste (članek V),
    - medvrstno tekmovanje se odraža prek neposrednih socialnih agonističnih interakcij med samci (članek V).

- Vrsti se razlikujeta v odzivih na skupne plenilce, ki igrajo vlogo mediatorja in lahko posredno vplivajo na interakcije med plenskimi vrstami (članek VI).

S pomočjo terenskih popisov s transektno metodo ter z začasnim odlovom posameznih osebkov kuščaric in poskusi v ujetništvu sem zbrala podatke o demografskih, morfoloških, fizioloških, vedenjskih in ekoloških značilnostih obeh preučevanih vrst na območju raziskovanja na jugu Slovenije (Kočevska).

V prvi raziskavi smo ocenili potencial za tekmovanje med vrstama z raziskavo razširjenosti na območju in s primerjavo njunih prostorskih niš (rabe prostora, članek I in poglavje 5.1). Za glavni dejavnik prostorskega ločevanja obeh vrst se je izkazala nadmorska višina; pozidna kuščarica je bila pogostejša (višje relativne gostote in frekvenca lokacij s prisotnostjo vrste) v nižinah in velebitska kuščarica je bila pogostejša na višjih nadmorskih višinah. Na območju naše raziskave sta bili obe vrsti najdeni v sintopiji v relativno velikem deležu vseh populacij (18 %) in preko celotnega višinskega gradienta (od 200 m n.m.v pred jamo Bilpa, do 1061 m n.m.v. na Kamenem zidu). Največ sintopičnih populacij smo našli na srednjih nadmorskih višinah. V splošnem sta bili obe vrsti zelo podobni v rabi prostora; obe vrsti najpogosteje živita na skalnatih ali kamnitih podlagah z malo ali nekaj rastja, s to razliko, da se pozidna kuščarica pojavlja tudi v drugih okoljih (ima širšo nišo kot velebitska kuščarica). Obstoj sintopičnih populacij na preučevanem območju in močno prekrivanje njunih prostorskih niš po našem mnenju nakazuje na to da, kjer vrsti sobivata (v sintopičnih populacijah), obstaja relativno visok potencial za medvrstno tekmovanje.

Vrsti sta kazali veliko podobnosti v morfoloških značilnostih (članek II). Odrasli osebki istega spola obeh kuščaric so enake telesne dolžine in mase ter imajo podobno dolžino in širino glave ter dolžino zgornjega dela glave s ploščicami (pileusa). Vrsti sta se razlikovali le v eni izmerjeni morfološki lastnosti - višini glave; velebitske kuščarice so imele bolj sploščeno (nižjo) glavo od pozidnih kuščaric. Pri kuščaricah je znano, da višja glava lahko (ne pa vedno) pomeni večjo moč ugriza, kar vpliva na velikost plena, ki ga lahko uplenijo. Močnejši ugriz po navadi določa premoč pri agonističnih spopadih med samci za teritorije in izboljšano sposobnost primeža samice med kopulacijo. Če razlike v višini glave med vrstama dejansko pomenijo razliko v moči ugriza, bi lahko pričakovali, da bosta vrsti ločeni v prehranski niši, saj bi lahko vrsta z močnejšim ugrizom uplenila trši plen kot vrsta s šibkejšim ugrizom. Obenem bi lahko bila vrsta z močnejšim ugrizom v tekmovalni prednosti pred vrsto s šibkejšim ugrizom v medvrstnih agonističnih interakcijah. Dosedanje objavljeni rezultati iz raziskav prehrane obeh preučevanih vrst navajajo, da se prehranski niši obeh vrst ne razlikujeta, prav tako ni bilo zabeleženega še nobenega primera spopada med samci različnih vrst. Višina glave bi lahko tudi omejevala dostop v nizke špranje, ki so tipične v kraškem okolju, kjer vrsti sobivata. Takšne špranje kuščarice uporabljajo za skrivališča, ko pobegnejo pred nevarnostjo zunaj ali v obdobjih neaktivnosti. Predvidevamo, da bi večja sploščenost glave velebitske kuščarice lahko potencialno omogočila prostorsko ločevanju v uporabi skrivališč med vrstama. Velebitska kuščarica bi lahko na primer uporabljala mesta, v katera pozidna kuščarica ne more dostopati, ker ima višjo glavo. Tak mehanizem bi lahko omogočal / pospeševal njuno sobivanje.

V tretji fazi smo primerjali fiziološke in vedenjske značilnosti obeh vrst. Raziskali smo sposobnost regulacije telesne temperature (določili smo območja preferenčnih telesnih temperatur in natančnosti termoregulacije) in zadrževanje vode ter značilnosti metabolizma (članka III in IV). Uporabili smo eksperimentalne labolatorijske poskuse po metodologijah, ki so splošno uporabljene in standarditzirane za razsikave kuščaric. Pri teh poskusih smo osebke iz narave zadržali v labolatorju za kratko obdobje in jih nato spustili nazaj v naravo. Večino raziskav smo bili primorani osredotočiti na samce, saj pri samicah lahko na fiziološke in vedenje procese vpliva njihov reprodukcijski status (gravidnost in stopnja razvitosti zarodka v njihovem telesu).

Vrsti sta imeli podobno povprečno izbrano telesno temperaturo izmerjeno v poskusu s termalnim gradientom. Opazili pa smo razlike v natančnosti termoregulacije, in sicer smo odkrili, da je velebitska kuščarica sposobna natančnejše termoregulacije, saj je svojo telesno temperaturo vzdrževala v ožjem območju temperatur spomladi in poleti, kot pozidna kuščarica. Na območju raziskave so za pomlad in poletje značilne različne okoljske temperature (spomladi je povprečna temperatura zraka nižja kot poleti) in zato višje izbrane telesne temperature spomladi pri velebitski kuščarici nakazujejo, da je le-ta sposobna učinkovitejše termoregulacije v obdobju leta, ko so okoljske temperature nižje.

To lahko nakazuje na višjo stopnjo prilagoditve na višje nadmorske višine, kjer so temperature nižje in je sezonsko obdobje aktivnosti krajše kot v nižinah. Na višjih nadmorskih višinah bi zato učinkovitejša termoregulacija lahko imela za kuščarice, ki imajo nestalno telesno temperaturo, določene prednosti. Doseganje višjih telesnih temperatur se neposredno odraža v višji aktivnosti kuščaric, ki vplivajo na višjo maksimalno delo (hitrost gibanja, hitrost presnove hrane, itd.) in tako vpliva na raznolik spekter za kuščarico življensko pomembnih procesov, ki vplivajo na fitnes osebka. Hkrati s prednostmi pa natančnejša termoregulacija spomladi, ko so okoljske temperature nižje, predstavljajo za velebitsko kuščarico višje stroške v smislu časa, ki ga porabijo za vedenjsko termoregulacijo, saj gre le-ta na račun časa, ki ga potrebujejo za ostale življenjsko pomembne funkcije (iskanje hrane, hranjenje, obramba teritorija pri samcih, iskanje parnerjev, parjenje itd.). Obenem daljši čas sončenja pomeni večjo izpostavljenost plenicem.

Pri primerjavi metabolizma med vrstama smo ugotovili, da je stopnja dihanja med vrstama podobna pri dveh različnih temperaturnih režimih: 20°C in 28°C (članek IV). Pri obeh vrstah se je stopnja dihanja povečala s povišano telesno temperaturo na enak način. Vrsti pa se razlikujeta v potencialu metabolizma, ki smo ga določili z biokemijsko metodo merjenja količine reduciranih encimov, ki so vključeni v celični metabolizem, izoliranih iz koščka repa. Velebitska kuščarica je imela višje izmerjene vrednosti maksimalnega potenciala za metabolizem kot pozidna kuščarica.

Ker so encimske reakcije in metabolizem na splošno temperaturno odvisni, pričakujemo, da ima termoregulacija kuščaric vpliv na njihov metabolizem. Ko povežemo naše rezultate o razlikah v termoregulaciji med vrstama (članek III) z rezultati o razlikah v metabolnem potencialu, lahko sklepamo, da bo velebitska kuščarica, ki termoregulira tako, da dosega višje in ožje območje telesnih temperatur, imela višjo stopnjo metabolizma in s tem potencialno prednostno predispozicijo za učinkovitejšo aktivnost spomladi in na višjih nadmorskih višinah, ko je okolje termalno bolj restriktivno (hladnejše). Te razlike v fiziologiji med vrstama kažejo na razlike v funadmentalnih nišah med vrstama, kar prispeva k sobivanju med vrstama, saj te razlike verjetno sproščajo tekmovalni pritisk v sintopičnih populacijah.

V naslednjem koraku nas je zanimalo, če med vrstama prihaja do tekmovanja za omejene vire sončne energije (mesta za sončenje), ki jo kuščarice izrabljajo za vedenjsko termoregulacijo (članek V). Kuščarice so živali z nestalno telesno temperaturo, ki jo vzdržujejo v območju preferenčnih telesnih temperatur s premikanjem med toplejšimi (soncu izpostavljenimi) in hladnejšimi mesti. Na Kočevskem kuščarici živita na soncu izpostavljenih skalnatih območjih, ki so obdana z gozdom, tako da so običajno takšna mesta omejena in zato omejujejo velikost populacije. V takšnih situacijah, ko je nek vir omejen, prihaja med osebki do tekmovanja, v tem primeru za sončna mesta. Predvidevali smo, da prihaja do tekmovanja med osebki za uporabo mest za sončenje. Naredili smo dva poskusa, kjer smo v prvem testirali, ali prisotnost dodatnega osebka iste ali druge vrste vpliva na doseganje preferenčnih telesnih temperatur. V drugem delu poskusa smo osebke snemali in opisali agonistične interakcije, do katerih je prihajalo med termoregulacijo. Rezultati so pokazali obstoj asimetričnega interferenčnega tekmovanja za toplotni vir. Posledice interferenčnega tekmovanja so se bolj odrazile pri samcih velebitskih kuščaric, saj so dosegali precej nižje temperature od preferenčnih telesnih temperatur, ko so bili v poskusu skupaj z osebkom iste ali druge vrste.

Nazadnje smo ovrednotili vpliv skupnih plenilcev (v našem primeru nekaterih vrst ptic, sesalcev ter kač) na medvrstno tekmovanje med kuščaricama na sintopičnem območju (članek VI). Izvedli smo dva poskusa, da bi ugotovili, kako kuščarice bežijo pred napadom plenilca na kopnem ali iz zraka ter kako kuščarice prepoznajo vonj kač, ki jih lovijo v njihovih skrivališčih in kako se na ta vonj odzivajo. Rezultati so pokazali, da se vrsti razlikujeta v protiplenilskih taktikah, in sicer je velebitska kuščarica bolj plašna kot pozidna kuščarica. V pobegu pred simuliranim napadom na tleh ali iu zraka je zbežala na daljši razdalji od napadalca in ostala v skrivališču dlje časa kot pozidna kuščarica. Prav tako je več osebkov velebitske kuščarice izražalo več različnih protiplenilskih vedenjskih vzorcev, ko je zaznala vonj plenilske kače v terariju kot pozidne kuščarice. Ti rezultati kažejo, da vrsti drugače reagirata na skupne plenilce in imajo skupni plenilci najverjetneje nanju različen vpliv, kar ima posredni vpliv na tekmovalni odnos med vrstama.

Poglobljeno razumevanje mehanizmov medvrstnih interakcij je pomembno, če želimo v prihodnje izboljšali naravovarstvene smernice za ogrožene vrste z upoštevanjem njihovih medvrstnih interakcij. Znanje o medvrstnih interakcijah bo omogočalo tudi, da se bo te interakcije vključilo v prostorska modeliranja o vplivih bodočih podnebnih in okoljskih sprememb na ogrožene živalske vrste. Podnebne spremembe namreč predstavljajo eno izmed pomembnejših bodočih groženj svetovni biotski pestrosti. Razvoj učinkovitih ukrepov za omiljevanje posledic podnebnih sprememb je ključen za ustavitev šestega vala izumiranj, ki ga trenutno povzroča človek in ki je verjetno ena izmed najresnejših dolgoročnih groženj človeštvu. Dosedanji naravovarstveni ukrepi za omiljevanje posledic segrevanja ozračja so se osredotočali predvsem na spremembe abiotskih dejavnikov, ki jih prinašajo podnebne spremembe. Pri tem pa se pogosto zanemari njihov vpliv na medvrstne odnose v živalskih združbah, ki so ključni za delovanje ekosistemov. Izboljšano znanje o medvrstnih interakcijah, ki izhaja iz rezultatov pričujoče disertacije, bo uporabno za razumevanje posrednih učinkov podnebnih sprememb na ekosistemske procese (v našem primeru medvrstne interakcije) ter upam, da bo obenem vzpodbudilo nadaljni razvoj raziskav na tem področju.

Konkretno na primeru preučevanih vrst se zaradi omejene prostorske razširjenosti na višjih nadmorskih višinah predvideva, da je velebitska kuščarica dodatno ogrožena zaradi tekmovanja s pozidno kuščarico, ki jo izriva v višje lege. Ta proces izrivanja bi lahko pospešile bodoče podnebne spremembe, ki predvidevajo, da se z leti zvišuje povprečna temperatura ozračja in ravno povišana temperatura v povezavi z opaženimi razlikami v termoregulacijski natančnosti bi lahko bil eden od glavnih dejavnikov, ki bo med vrstama določal tekmovalno prednost v prihodnosti. Izboljšano poznavanja fundamentalnih morfoloških, fizioloških, vedenjskih in ekoloških lastnosti vrst potrjuje predvidevanja, da bo višanje temperature (trend bodočih podnebnih sprememb) potencialno povzročil, da se bo pozidna kuščarica lahko pomikala na višje nadmorske višine, saj naši rezultati nakazujejo, da je sedanja odsotnost te vrste v višjih nadmorskih višinah najverjetneje posledica fiziološko-vedenjskih prilagoditev na termalno manj restriktivna okolja. Naše raziskave so pokazale, da je velebitska kuščarica natančnejši termoregulator, kar je ugodna prilagoditev na okolja z nižjo temperaturo in predvidevamo, da jo bodo zato bodoče višje temperature še bolj ogrozile, če bodo pospešile širjenje pozidne kuščarice, ki na takšna okolja ni toliko prilagojena. Hkrati je velebitska kuščarica bolj prilagojena na termalno omejujoča okolja, kjer je tekmovalno uspešnješa od pozidne kuščarice in ji zato pomikanje v še višje nadmorske višine verjetno ne bo povzročalo težav, razen na mestih, kjer se ne bo uspela pomakniti višje, ker že zaseda najvišje lege. Prav tako je velebitska kuščarica vedenjsko bolj previdna in verjetno lahko zaradi bolj sploščene glave zaseda manjše špranje; vse to pa so značilnosti, v katerih se vrsti delno že razlikujeta in najverjetnejp pripomorejo k temu, da se tekmovanju v sintopičnih izogibata in lahko zato ne prihaja do dejanskega izključevanja, vendar sobivanja, v katerem imajo najverjetneje pomembno vlogo tudi skupni plenilci.

Pomanjkanje zanesljivih in natančnih podatkov o ekologiji in bologiji preučevanih vrst kuščaric, ki sta zaščiteni tako z nacionalno kot mednarodno zakonodajo, do sedaj ni omogočalo zasnove realnih naravovarstvenih ukrepov za obe vrsti pri nas. Na splošno so plazilci namreč med najslabše raziskanimi skupinami vretenčarjev v Sloveniji. Rezultati naših raziskav imajo uporabno vrednost za pripravo naravovarstvenih smernic za dolgoročnejšo ohranitev teh vrst in so lahko osnova tudi za ostale vrste skalnih kuščaric.

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ANNEXES

ANNEX 1

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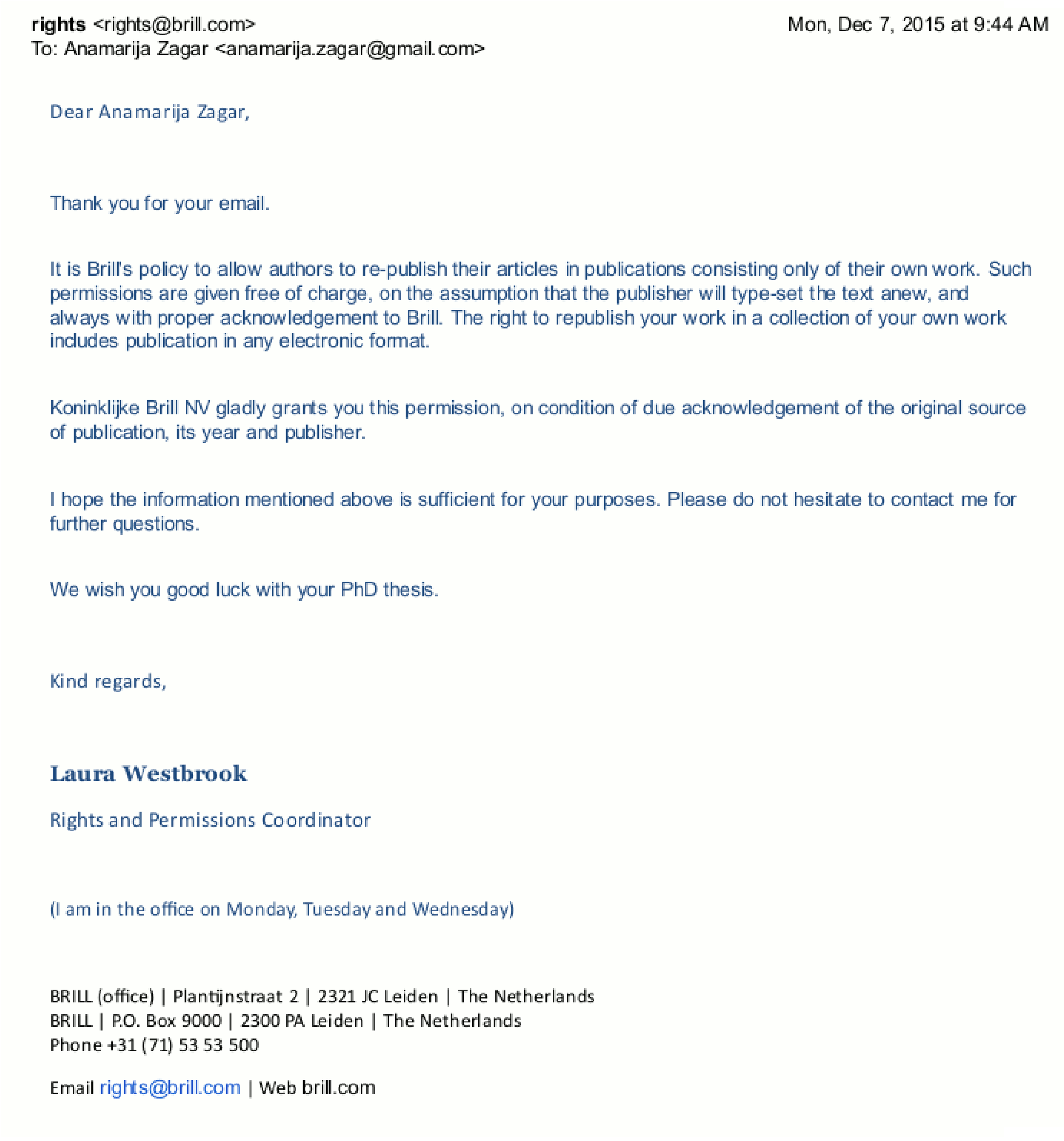

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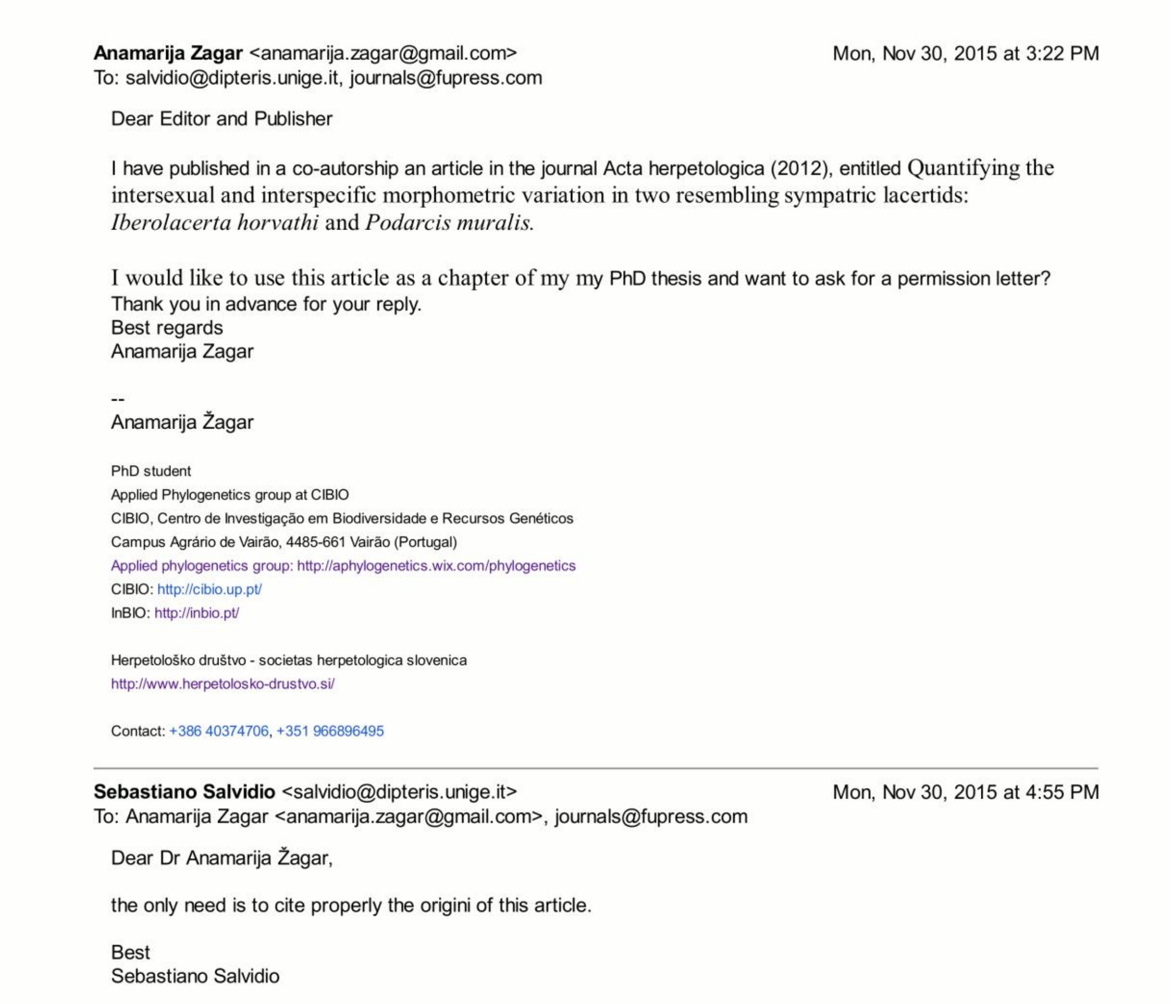

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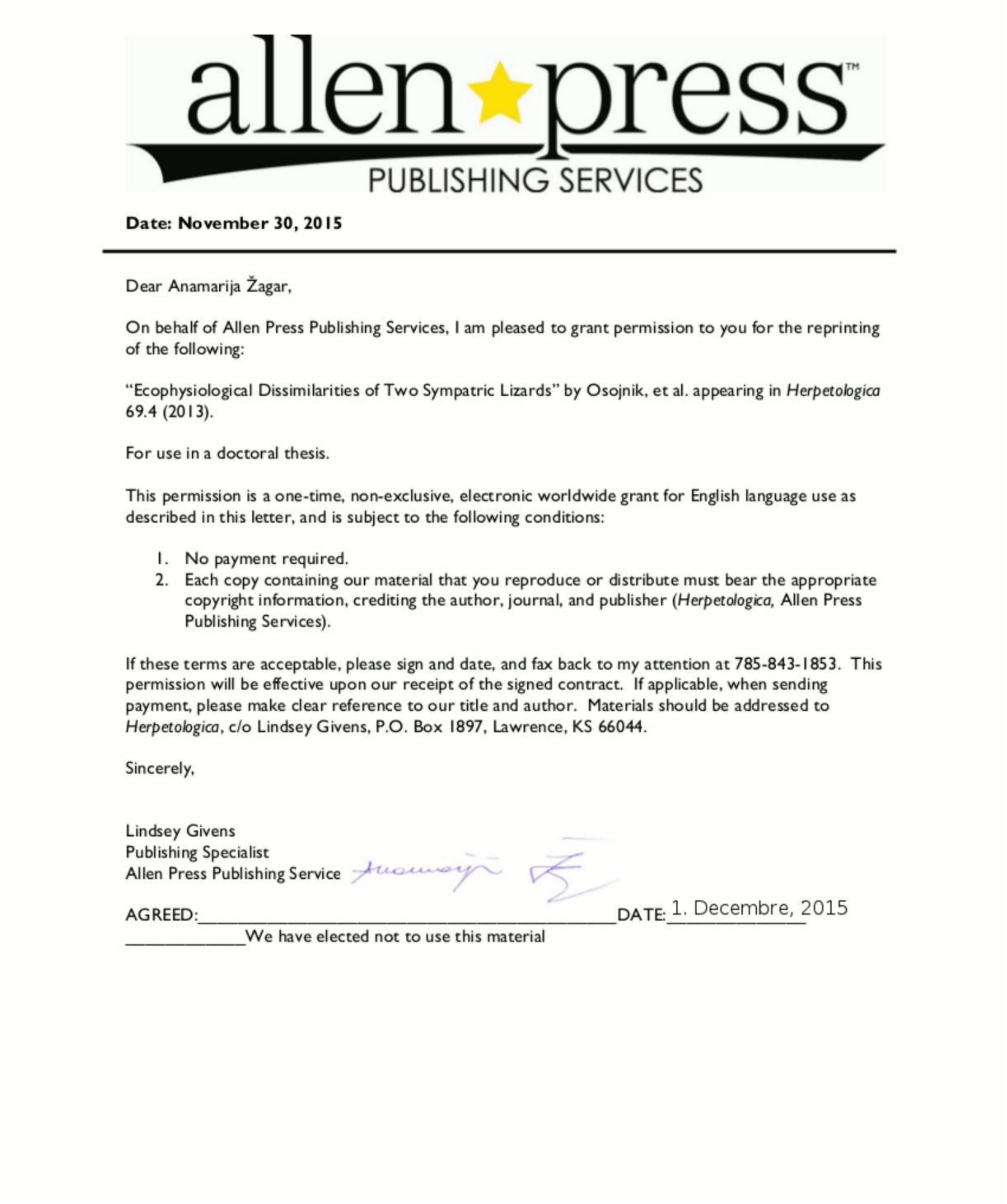

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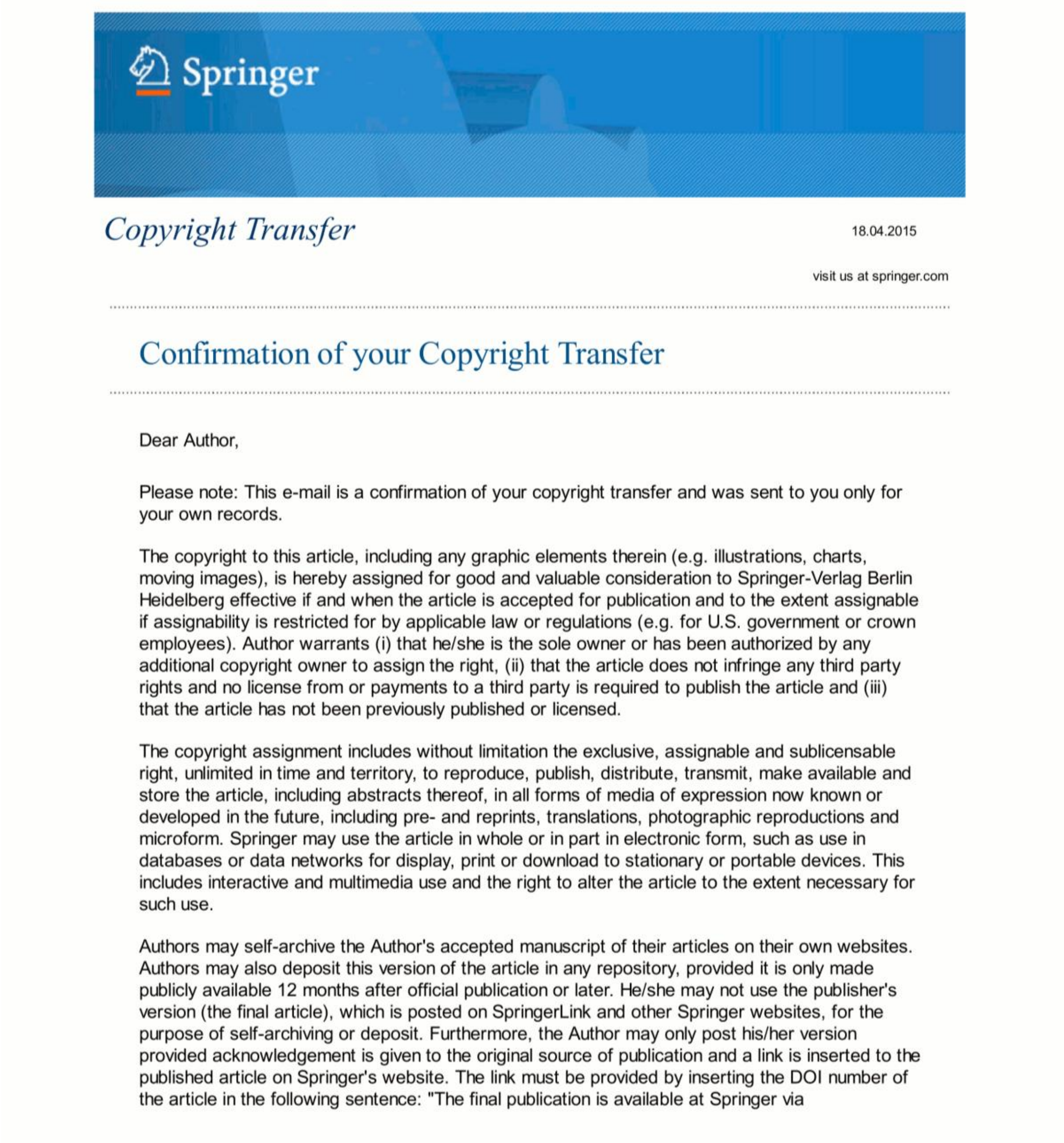

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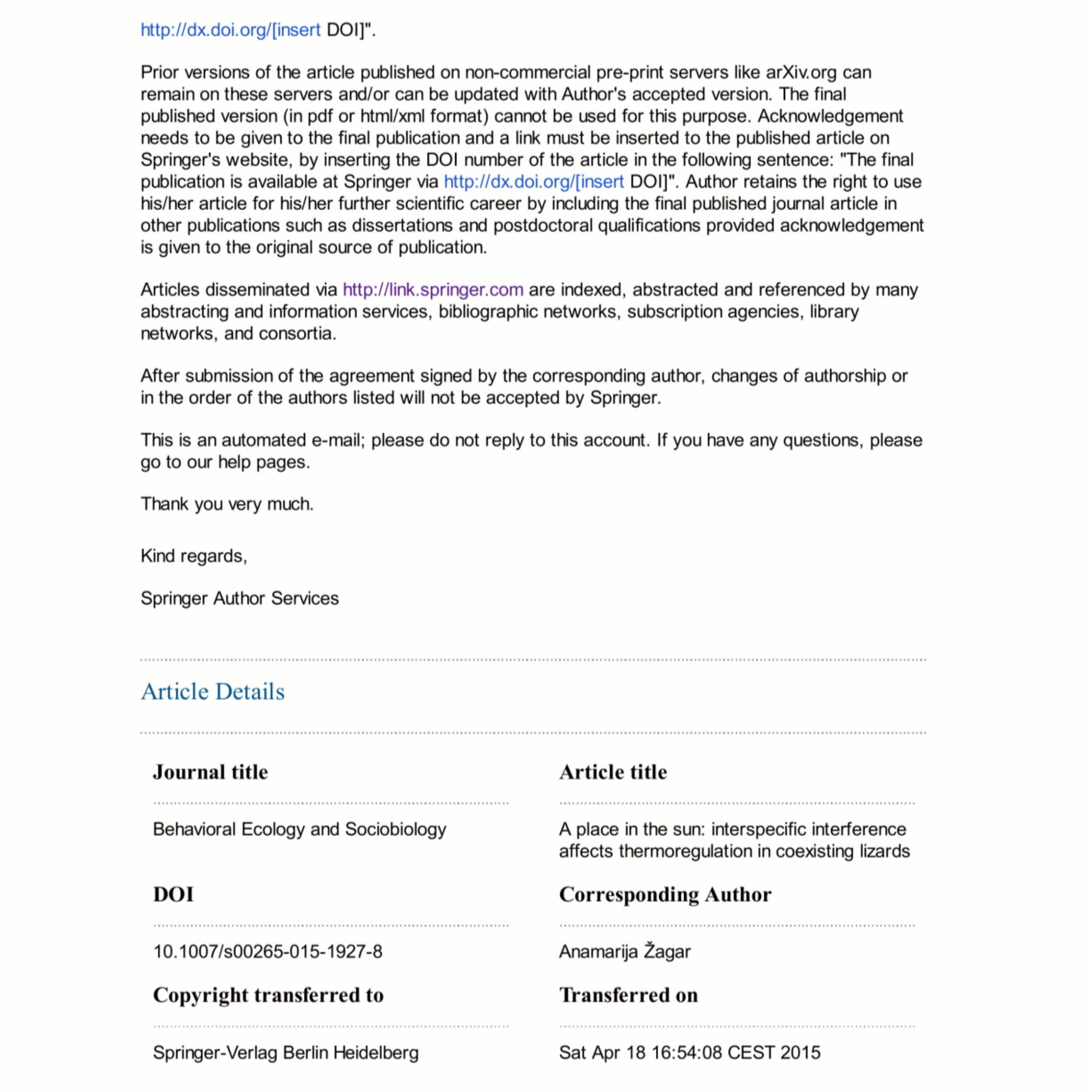

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ANNEX 6

Locations of all transects surveyed in (2006-2015) in Kočevsko region sorted by altitude. At each visit we conducted either transect line surveys with counts or we only noted presence (P) or absence (/) of the studied species at the location. Location was considered to be “Allotopic” if all visits confirmed the presence of only one species and “Syntopic” if in the same visit both species were found. Maximum numbers of individuals counted with transect line surveys are in bold and were used for calculating relative abundances (paragraph 5.1). In cases when the maximum number of individuals was found more than once per location, only the first count is in bold. Legend for habitat type description is available in the Supplemetary material of Article I. Aver. alt. = average altitude of the transect. GKY and GKX = Y and X coordinates of the Gauss Krüger coordinate system. T. length = transect length. *P.m.* = *Podarcis muralis*. *I.h.* = *Iberolacerta horvathi*. (1) and (2) = correspond to the first half (until 30th June) and the second half of the calendar year.

Location description	**Species presence**	**Aver. alt. (m)**	**Habitat type**	**GKY**	**GKX**	**T. lenght (m)**	***P.m.* 2006 (1)**	***I.h.* 2006 (1)**	***P.m.* 2007 (1)**	***I.h.* 2007 (1)**	***P.m.* 2007 (2)**	***I.h.* 2007 (2)**	***P.m.* 2008 (1)**	***I.h.* 2008 (1)**	***P.m.* 2008 (2)**	***I.h.* 2008 (2)**	***P.m.* 2010 (1)**	***I.h.* 2010 (1)**	***P.m.* 2011 (1)**	***I.h.* 2011 (1)**	***P.m.* 2011 (2)**	***I.h.* 2011 (2)**	***P.m.* 2012 (1)**	***I.h.* 2012 (1)**	***P.m.* 2012 (2)**	***I.h.* 2012 (2)**	***P.m.* 2013 (1)**	***I.h.* 2013 (1)**	***P.m.* 2013 (2)**	***I.h.* 2013 (2)**	***P.m.* 2014 (1)**	***I.h.* 2014 (1)**	***P.m.* 2014 (2)**	***I.h.* 2014 (2)**	***P.m.* 2015 (1)**	***I.h.* 2015 (1)**
pri Žlebih	NO FINDS	200	water bank	495330	42607	200	0	0			0	0	0	0																						
med Žlebi in Grgeljem	Allotopic *P. muralis*	203	artificial rock	495705	42336	330	**5**	**0**			0	0	5	0																						
pri Gorenji Žagi	NO FINDS	203	water bank	493501	41499	450	0	0			0	0	0	0																						
med Bilpo in Lazami	Allotopic *P. muralis*	204	road	497228	41041	100																	**12**	**0**							P	/			P	/
pri Žlebih	Allotopic *P. muralis*	204	water bank	494406	42644	270	0	0			**1**	**0**	0	0																						
pri Gorenji Žagi	Allotopic *P. muralis*	207	artificial rock	493685	41801	160	**4**	**0**			0	0	3	0																					P	/
Bilpa	Syntopic	208	natural rock	497441	40858	60																	**6**	**3**							P	P	P	P	P	P

med Gorenjo Žago in Žlebi	Allotopic *P. muralis*	215	road	493751	41851	60			**1**	**0**	0	0	1	0									0	0												
pri Gorenji Žagi	Allotopic *P. muralis*	215	artificial rock	493920	41899	140			**8**	**0**	5	0	3	0																					P	/
Žlebi	Allotopic *P. muralis*	215	artificial rock	494412	42675	180			1	0	1	0	**2**	**0**									P	/												
med Kobilno jamo in Gorenjo Žago	Allotopic *P. muralis*	219	artificial rock	494125	42501	140	1	0			0	0	**2**	**0**																					P	/
med Vasjo pri Fari in Pirčami	NO FINDS	220	agricultural land	490419	36368	1620	0	0			0	0	0	0																						
med Faro in Gorenjo Žago	NO FINDS	220	water bank	491450	36947	460	0	0					0	0	0	0																				
med Sapnikom in Brsnikom	Allotopic *P. muralis*	226	artificial rock	493567	38681	110	2	0			1	0	**4**	**0**																					P	/
med Lobičem in Žlebi	Allotopic *P. muralis*	228	natural rock	494419	42673	250	2	0			0	0	**5**	**0**																					P	/
Maverc	Allotopic *P. muralis*	229	urban area	493728	40033	440					**2**	**0**	2	0	2	0																			P	/
Sapnik	Allotopic *P. muralis*	230	urban area	493652	38810	200	0	0			0	0	**2**	**0**																						
pri Grivacu	NO FINDS	234	water bank	487536	35329	130	0	0			0	0	0	0																						
pokopališče v Fari	Allotopic *P. muralis*	238	urban area	491217	37083	510	3	0			3	0	**6**	**0**									P	/											P	/
pri Gladloki	NO FINDS	240	agricultural land	486087	35266	770	0	0			0	0	0	0																						

med Grivacom in Gladloko	Allotopic *P. muralis*	245	road	486880	35251	180					0	0	**1**	**0**	0	0																				
med Grivacom in Gladloko	Allotopic *P. muralis*	245	artificial rock	486880	35251	100	**1**	**0**			1	0	1	0																						
Mirtoviči	Allotopic *P. muralis*	260	urban area	483050	40666	340					1	0	**2**	**0**	1	0																				
Srobotnik	Allotopic *P. muralis*	266	urban area	484664	39915	340	**1**	**0**					1	0	0	0																				
Mirtoviški potok	Allotopic *P. muralis*	274	water bank	482871	41106	850					0	0	**3**	**0**	2	0																				
med Sv. Štefanom in Faro	NO FINDS	283	closed forest	491408	37284	260			0	0	0	0	0	0																					P	/
nad cerkvijo v Fari	Allotopic *P. muralis*	288	road	491251	37067	670			**3**	**0**	2	0	0	0																						
pokopališče Sv. Štefan	Allotopic *P. muralis*	310	urban area	491452	37337	210			**12**	**0**	8	0	1	0					P	/															P	/
pri Srobotniku	Allotopic *P. muralis*	336	open forest	484894	39571	730			0	0			2	0	**3**	**0**																			P	/
Kostel	Allotopic *P. muralis*	348	urban area	492939	40372	630	0	0			**4**	**0**	1	0									P	/												
nad vasjo Planina zapuščen kamnolom	Allotopic *P. muralis*	378	artificial rock	489201	37430	140	2	0			3	0	**4**	**0**																						
kamnolom v Podstenah	Allotopic *P. muralis*	384	artificial rock	491440	42191	140	1	0			2	0	**5**	**0**																					P	/

pri Srobotniku	NO FINDS	391	closed forest	484697	39777	290	0	0					0	0	0	0																				
od Planine na Planinsko steno	Allotopic *P. muralis*	430	road	489253	37450	620	10	0			3	0	**11**	**0**																						
med Friškovo grabo in Dolenjim Potokom	Allotopic *P. muralis*	435	road	489983	42358	120	0	0			1	0	**6**	**0**																						
med Friškovo grabo in Dolenjim Potokom	Allotopic *P. muralis*	435	artificial rock	490044	42240	160	0	0			0	0	**1**	**0**																						
nad Srobotnikom	NO FINDS	445	open forest	485388	39428	290	0	0					0	0	0	0																				
pot na Krempo	Allotopic *P. muralis*	459	open forest	482701	41016	870			0	0			**5**	**0**	1	0																				
nad Srobotnikom	NO FINDS	478	closed forest	485570	39372	110			0	0			0	0	0	0																				
od vasi Podstene do sten	Syntopic	499	artificial rock	492289	42271	340	0	0			0	0	**1**	**1**																						
pod Podstenami	Allotopic *P. muralis*	501	road	490457	43051	410			0	0	0	0	**5**	**0**									P	/											P	/
nad Podstenami	NO FINDS	502	closed forest	490511	43082	970			0	0			0	0	0	0																				
od Planine na Planinsko steno	Allotopic *P. muralis*	506	road	489309	37690	440	**6**	**0**			0	0	0	0																						
pri Srobotniku	Allotopic *P. muralis*	507	natural rock	485700	39266	220	2	0					**4**	**0**	3	0																				

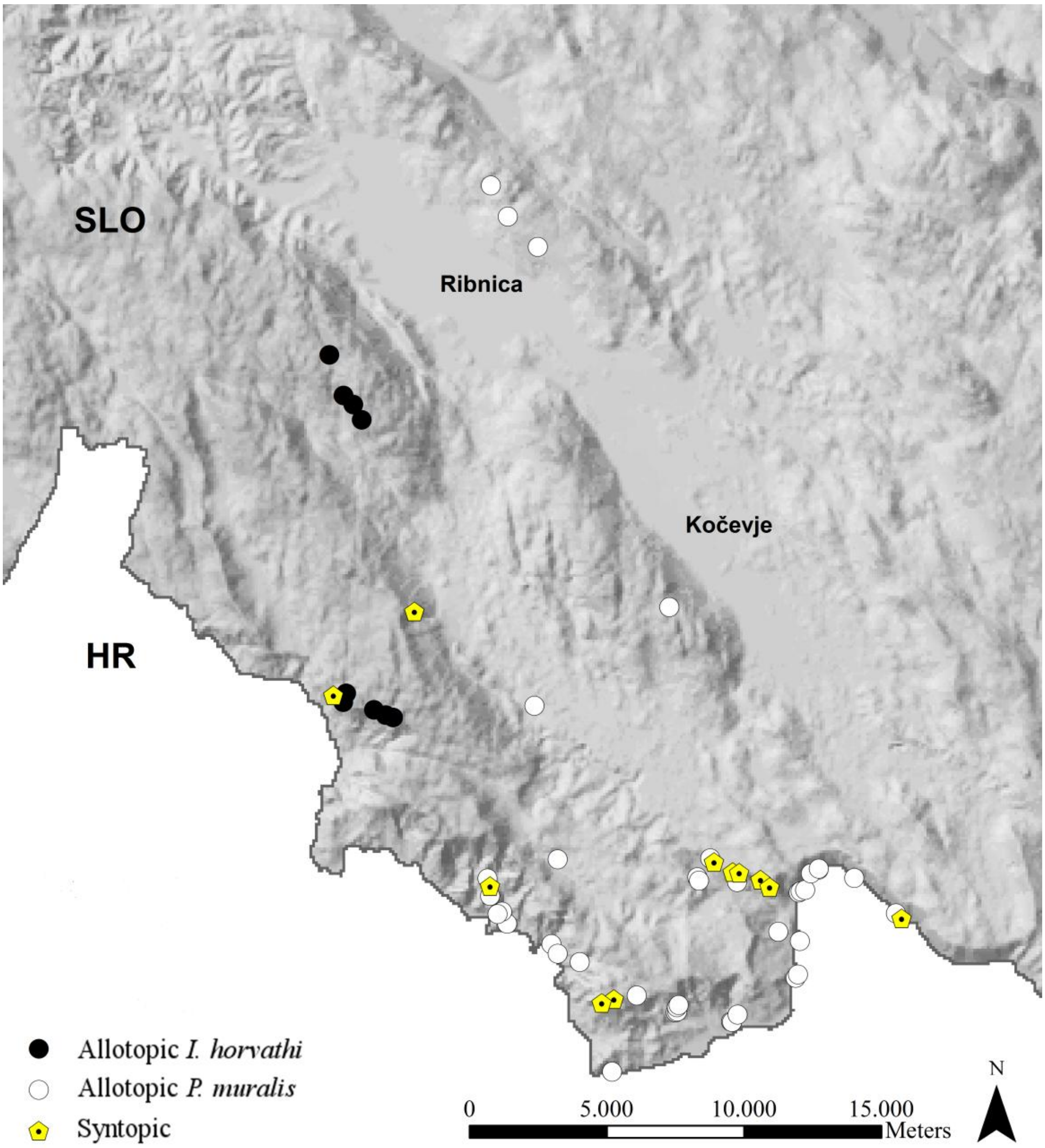
Podstene	Syntopic	512	natural rock	490601	42918	490	1	1			0	0	**2**	**4**																					P	P
pod Planinsko steno	Allotopic *P. muralis*	513	natural rock	489248	37615	160	1	0			1	0	**3**	**0**																						
Podstene	Syntopic	515	natural rock	492625	42002	630	0	1			**3**	**1**	0	1																						
Podstene	Syntopic	515	natural rock	491281	42557	130	0	1			**1**	**1**	0	0																					P	P
Kočevska Reka	NO FINDS	518	water bank	484366	47478	360	0	0			0	0	0	0																						
Kočevska Reka	NO FINDS	520	water bank	483862	48287	130	0	0			0	0	0	0																						
od vasi Podstene do sten	Syntopic	521	open forest	491514	42527	380	0	0			0	0	**2**	**1**																						
Kočevska Reka	NO FINDS	534	agricultutral land	484046	47942	550			0	0	0	0	0	0																						
Kočevska Reka	NO FINDS	539	agricultutral land	484422	48389	470			0	0	0	0	0	0																						
kamnolom pri Kočevski Reki	Allotopic *P. muralis*	575	artificial rock	484048	48638	180			0	0	2	0	**5**	**0**									P	/											P	/
pot na Krempo	Allotopic *P. muralis*	588	agricultutral land	482433	41682	330			0	0			**1**	**0**	0	0																				
od Planine na Planinsko steno	Allotopic *P. muralis*	612	road	489309	37690	1010			**3**	**0**	2	0	3	0																						
pot na Krempo	Syntopic	615	open forest	482433	42036	290	**3**	**0**					1	0	0	0																				

med Gornjo Brigo in Borovcem pri Kočevski Reki	Allotopic *P. muralis*	616	artificial rock	484898	43018	360	0	0			**1**	**0**	1	0																						
Planinska stena	Allotopic *P. muralis*	652	artificial rock	487781	38035	180																	**3**	**0**							P	/			P	/
pot na Krempo	Allotopic *P. muralis*	676	natural rock	482339	42317	140	0	0					**2**	**0**	0	0																				
Mala gora	Allotopic *P. muralis*	681	artificial rock	484171	65412	120													P	/			**4**	**0**									P	/	P	/
Mala gora	Allotopic *P. muralis*	726	artificial rock	482454	67654	450													**11**	**0**	P	0	P	/	P	/	P	/	P	/	P	/			P	/
Mala gora	Allotopic *P. muralis*	760	artificial rock	483079	66525	130													P	/			**4**	**0**									P	/	P	/
pod Kuželjsko steno	Syntopic	766	open forest	486949	37909	870	0	0			0	0	**1**	**1**																						
Kuželjska stena	Syntopic	813	natural rock	486505	37768	760	0	2			1	1							**2**	**4**			P	P	P	P			P	P	P	P				
Žurgarska stena	Syntopic	828	natural rock	476722	49022	150	0	1					5	0	**4**	**1**			P	P																
pri Žurgarski steni	NO FINDS	892	closed forest	476722	49022	430	0	0					0	0	0	0																				
pred Žugarsko steno	Allotopic *I. horvathi*	899	artificial rock	477181	49089	360	0	3					**0**	**6**	0	0			/	P																
Žurgarska stena	Allotopic *I. horvathi*	948	natural rock	477075	48768	690	0	1					0	3	**0**	**13**					/	P									/	P				
Fridrikštajn	Allotopic *P. muralis*	959	urban area	488966	52243	60													P	/			**10**	**0**							P	/				

Male Bele stene	Allotopic *I. horvathi*	976	artificial rock	476572	61464	250											**0**	**5**	/	P			/	P							/	P			/	P
Taborska stena	Allotopic *I. horvathi*	991	natural rock	478628	48293	170	**0**	**1**					0	0	0	0																				
Velike Bele stene	Allotopic *I. horvathi*	996	artificial rock	477087	59976	250											/	P	**0**	**9**	/	P	/	P	/	P	0	8	/	P	/	P	/	P	/	P
Kameni zid	Syntopic	1028	natural rock and open forest	479672	52082	160													**2**	**3**	/	P	2	2							P	P			P	P
Taborska stena	Allotopic *I. horvathi*	1029	natural rock	478193	48482	440	0	3					**0**	**4**	0	1																				
Taborska stena	Allotopic *I. horvathi*	1055	natural rock	478891	48207	400	**0**	**1**					0	1	0	0																				
Velike Bele stene	Allotopic *I. horvathi*	1058	artificial rock	477753	59090	340													/	P			**0**	**8**							/	P	/	P	/	P
Velike Bele stene rob sten	Allotopic *I. horvathi*	1118	natural rock and open forest	477442	59648	150																	**0**	**4**							/	P				

ANNEX 7

Map of the Kočevsko region with localities where one or both studied species, *Iberolacerta horvathi* and *Podarcis muralis*, were found (N = 62) during field work conducted in the period between 2006 and 2015 (see Annex 7 for detailed information).



ANNEX 8

Observed frequencies (number of individuals calculated as sum of maximum counts per transect, see Annex 7 for details) of *Iberolacerta horvathi* (IHOR (N)) and *Podarcis muralis* (PMUR (N)) across five altitudinal belts and expected frequencies (IHOR expected and PMUR expected), if species were equally distributed across the altitudinal span in the study area according to the total distance of surveyed transects in each altitudinal belt. Results of Chi square tests showed significant differences between expected and observed frequencies for both species (for *I. horvathi*: $\chi^2 = 180.10$, df = 4, $P < 0.0001$); for *P. muralis*: $\chi^2 = 20.87$, df = 4, $P = 0.0003$).