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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.

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):

$$\delta_{ar} = \frac{|T_a - T_r|}{T_a + T_r}; \quad \delta_{sr} = \frac{|T_s - T_r|}{T_s + T_r}$$

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

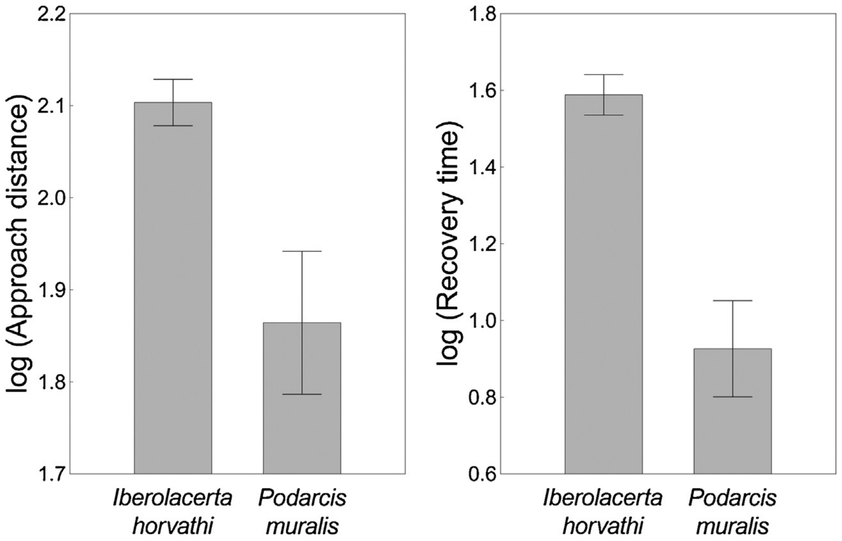

Fig. 1. Variation in approach distances (m) and recovery time (s) of adult *Iberolacerta horvathi* and *Podarcis muralis* in the study area. Both variables showed significant interspecific variation (see Table 2). Boxes represent means and whiskers standard errors.

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

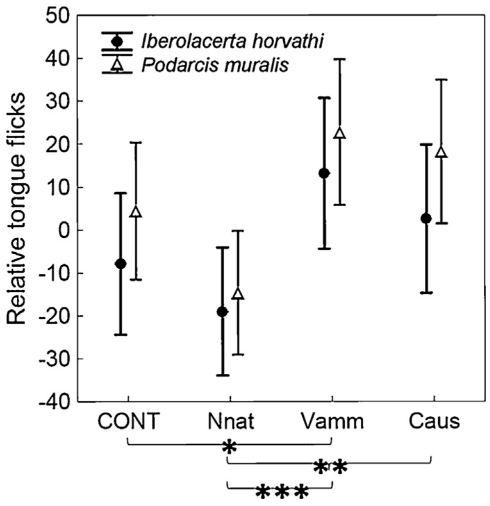

Fig. 2. Relative tongue flicks of *Iberolacerta horvathi* and *Podarcis muralis* in terraria with four scents. *X* axis shows the residuals of regression of the total number of tongue flicks on total time lizards were active to control for time being active. Symbols denote the mean value and vertical 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

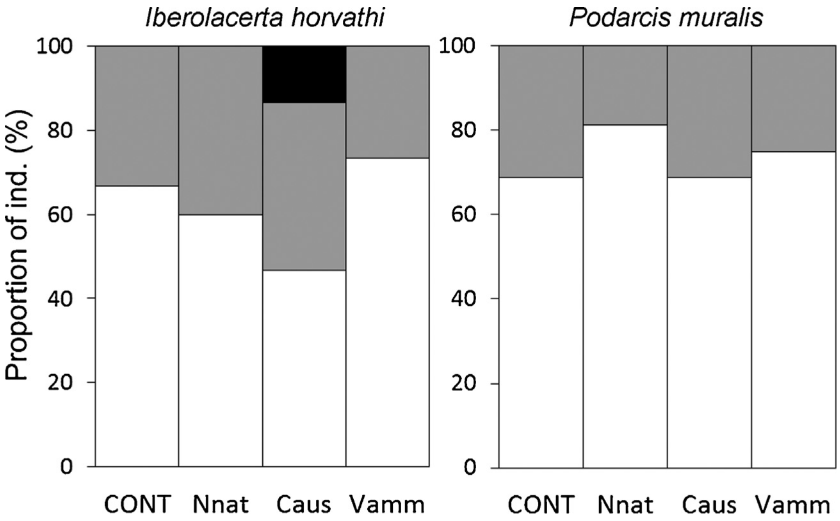

Fig. 3. Behavioral responses to chemical cues of *Iberolacerta horvathi* and *Podarcis muralis*. Presented are proportions of individuals that exhibited none (Zero response, in white), one or two different types (Medium response, in gray) or more than three different types (High response, in black) of 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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