



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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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

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