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Urbanization affects refuge use and habituation to predators in a polymorphic lizard

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Prey–predator interactions are plastic behaviours shown by both players, which constantly modify their decisions depending on physiological conditions and ecological context. We investigated whether the behavioural response to repeated simulated predatory attacks varied between adult males of the common wall lizard, *Podarcis muralis*, inhabiting environments characterized by different degrees of human presence. Our aim was to detect possible effects of urbanization on antipredator responses, in terms of activity, time spent hidden in refuges and habituation. Moreover, since this lizard species exhibits intrapopulation colour polymorphism, we looked for the occurrence of possible correlations between antipredator strategy and individual ventral coloration. We found that urban lizards spent less time in their refuge after predatory attacks and decreased successive hiding times faster than rural lizards, suggesting different wariness towards a potential predator. Irrespective of population, yellow lizards gradually spent less time in the refuge before appearing and emerging outside than the other two morphs. Conversely, red lizards showed progressively longer appearance and emergence times after successive tests, suggesting a growing sensitization to the potential threat of a predatory attack. In conclusion, our study showed the occurrence of different levels of behavioural plasticity in common wall lizard's antipredator response: the population level, depending on ecological context, here different degrees of exposure to human disturbance, and the individual level, which suggests the occurrence of morph-specific antipredator strategies. Thus, using a lizard species as a model, we shed light on two key points of evolutionary ecology concerning both the antipredator response and the factors driving the maintenance of intraspecific polymorphism.
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Prey–predator interactions and alternative antipredator strategies have primarily been investigated by behavioural ecologists and evolutionary biologists (see Abrams, 2000; Barbosa & Castellanos, 2005; Dawkins & Krebs, 1979 for reviews). The ability of prey to modify individual responses to repeated predatory attacks requires the evolution of behavioural plasticity, so that reactions are constantly subject to short-term adjustments, optimizing the cost–benefit trade-off (Lima, 1998; Lima & Dill, 1990). One of the most common strategies adopted by prey to avoid a predatory attack is to escape and hide inside a refuge. However, this behaviour could be costly in terms of time lost from other activities such as foraging or mating, and may have detrimental physiological consequences such as hypothermia or hypoxia in unfavourable refuge conditions (Amo, López, & Martín, 2007; Martín, 2001; Sih, 1997; Weatherhead & Robertson, 1992; reviewed in Martín & López, 2015). Thus, the use of refuges and the time spent inside them should be tuned to the predation risk, to limit the waste of resources (Cooper & Frederick, 2007; Martín, López, & Cooper, 2003a; Polo, López, & Martín, 2011, 2005). Another effect of behavioural plasticity is habituation to potential or inefficient predators, whereby a prey reduces its response to a predatory stimulus after repeated nonthreatening exposures to it (Hemmi & Merkle, 2009; Shettleworth, 2010). Although intrapopulation differences in habituation ability between individuals in relation to age and sex have been detected (Ellenberg, Mattern, & Seddon, 2009; Rodríguez-Prieto, Fernandez-Juricic, Martín, & Regis, 2009; Rodríguez-Prieto, Martín, & Fernandez-Juricic, 2011),

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several other factors that could similarly influence the habituation response to predatory pressure are far from being understood.

Some features typically related to antipredator behaviour, such as flight initial distance, hiding times or habituation indices, have frequently been associated with different factors such as sex, age, social individual status or even environmental conditions (Hawlena, Pérez-Mellado, & Cooper, 2009; Ortega, Martín, & López, 2014; Schulte, Losos, Cruz, & Nunez, 2004). The latter may play a key role in interindividual, specifically prey–predator, interactions (Kjernsmo & Merilaita, 2012; Larimer, Powell, & Parmerlee, 2006; Martín & López, 1995). For populations inhabiting different environments and therefore exposed to different predatory pressures, the ability of individuals to modify their behavioural response is critical for their survival. Habitats can differ in many aspects such as type of predators, climate or vegetation cover, and prey should react differently to attacks, by modifying their antipredator strategy or behavioural responses, depending on the level of local risk (e.g. by varying hiding times or vigilance behaviour, Cooper & Wilson, 2007; López & Martín, 2013). Lastly, prey behaviour could be affected by factors not directly related to predatory pressure. This is particularly evident in habitats affected by the anthropic footprint, such as agricultural landscapes or urban areas. In these scenarios, considering the not negligible influence that humans have on wild species, along urban gradients (where human presence increases), individuals of the same species are expected to show substantial variation in their antipredator response. Recently, wildlife tolerance induced by human disturbance has received much attention, particularly in mammals, birds and lizards, in which disturbed populations were more tolerant of humans than less disturbed ones (reviewed in Samia, Nakagawa, Nomura, Rangel, & Blumstein, 2015).

A growing number of studies dealing with antipredator responses and refuge use have been performed on lizards (see review in Cooper, 2015), as they represent a suitable model to investigate all the above-mentioned topics, often being found at high densities in many environments (including anthropized habitats) and being relatively easy to observe in the field or manipulate in the laboratory. Moreover, a vast literature states that lizards frequently show ecological interindividual differences within populations (Huey, Pianka, & Schoener, 1983; Huyghe, Vanhooydonck, Herrel, Tadic, & Van Damme, 2007; Pérez i de Lanuza, Carazo, & Font, 2014; Pianka & Vitt, 2006; Sinervo & Zamudio, 2001).

A case in point is the common wall lizard, *Podarcis muralis*, a small lacertid (52–73 mm snout-to-vent length, SVL), widespread from western to central and southern Europe. In Italy, populations occur in many different habitats across northern and central regions, being less abundant in the south and on islands (Bellati et al., 2011; Biaggini, Bombi, Capula, & Corti, 2011). Notably, dense populations of this species often occur in environments characterized by high human presence, and apparently even thrive in cities, where they benefit from greater food availability and higher temperatures (Biaggini, Berti, & Corti, 2009).

In northern Italy, populations of the common wall lizard show one of the most attractive aspects of its biology, colour polymorphism, with white, yellow or red coloration of the belly in both sexes within the same population (Calsbeek, Bonvini, & Cox, 2010; Cheylan, 1988; Sacchi et al., 2013; Sacchi, Scali et al., 2007; see Fig. 1 in Galeotti et al., 2010 for ventral coloration). Differences between morphs have been found in male immune response (Calsbeek et al., 2010; Sacchi, Rubolini et al., 2007), stress and haematological profiles (Galeotti et al., 2010), female reproductive strategies (Galeotti et al., 2013; Pérez i de Lanuza, Font, & Carazo, 2013) and chemical composition of male femoral gland secretions (Pellitteri-Rosa et al., 2014). Although the nature and adaptive significance of this colour polymorphism are currently debated, as well as the mechanisms governing its maintenance (e.g. Calsbeek et al., 2010; Pérez i de Lanuza & Font, 2015), the occurrence of morph-specific strategies, mainly related to physiological variation, suggests that other ecological or behavioural differences similarly related to this polymorphism still need to be disclosed.

At present, only two studies have investigated the relationships between escape behaviour and predator pressure: these were on two Spanish populations of *P. muralis*, and tested variation in responses between sites that differed in both the environment and degree of human disturbance (Diego-Rasilla, 2003b, 2003a). The results showed differences between populations in wariness (i.e. in terms of distance to a safe refuge and flight initial distance), suggesting interpopulation variation in predation pressure. Although previous field surveys showed that common wall lizards can track short-term changes in risk level through time and modify their antipredator hiding responses accordingly (Amo, López, & Martín, 2003; Martín & López, 2005), the effect of colour morphs has never been considered before.

Therefore, by using the common wall lizard as a model to test antipredator response variation in relation to predator pressure, human disturbance and colour polymorphism, we aimed to investigate whether antipredator responses to repeated simulated predatory attacks varied between two populations inhabiting completely different environments with different degrees of human presence (i.e. rural versus urban sites). Our main goal was to detect a possible effect of urbanization on antipredator responses, in terms of activity indices, time spent hiding inside a refuge and habituation to predators after repeated attacks. Similarly, since colour polymorphism undoubtedly plays a key role in the behaviour of this species, we also considered individual colour morph in our trials. Finally, as other possible factors may further influence antipredator response, we considered morphological characteristics, which have been demonstrated to play important roles in life history and antipredator behaviour contexts in lizards (e.g. relative size and number of lateral blue spots, Cabido, Galán, López, & Martín, 2009; Huyghe, Vanhooydonck, Scheers, Molina-Borja, & Van Damme, 2005; López, Martín, & Cuadrado, 2004; Salvador & Veiga, 2008). Our study allowed us to address two fundamental questions in behavioural and evolutionary ecology: whether different habitats could affect behavioural traits, and whether predator pressure could lead to different antipredator strategies that may help to maintain the colour polymorphism within a given population.

METHODS

Sampling and Housing

During spring 2014 (April–May, corresponding to the species' mating season in Italy) we captured sexually mature male lizards at two sites located in different habitats. The 'urban' site was located within a small town near Pavia, Lombardy (45°14′03.75″N, 9°10′41.67″E). Lizards were captured on concrete or wood structures within anthropic environments, in microhabitats such as boundary walls of houses, orchards, gardens, walls along roads, wood and tool sheds. The 'rural' site was located 30 km northwest of the 'urban' site (45°28′05.27″N, 8°58′31.47″E), in an agricultural landscape with woods, tree rows, waterways, fields and farms. Here, lizards were collected in microhabitats such as trees, edges of the fields, concrete walls along waterways and woodpiles, where human disturbance was absent or very low. We sampled only adult males to reduce possible variation due to age and sex differences (Martín & López, 2003; Martín, López, & Cooper, 2003b). Males were clearly distinguishable by both hemipenis eversion and their larger body and head than females. In addition, males have well-

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