



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 (Hawlana, 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-

developed femoral pores, which in females are only vestigial structures lacking secretion (Martín, Amo, & López, 2008). For each site, we noosed 24 male lizards equally distributed among the three colour morphs (eight each of white, yellow and red). Each was easily assigned to the correct colour morph by visual inspection. Indeed, recent spectrophotometry analysis showed that colour morphs are discrete and can be easily recognized by eye (Sacchi et al., 2013). Individuals were measured using a digital calliper (accuracy ± 0.1 mm) for SVL and head size (height, width and length), weighed (accuracy ± 0.1 g), photographed for counting blue spots, and transferred to our laboratory within 2 h from capture. Lateral blue spots are known to play a role in intrasexual social relationships between males in lizards, functioning as a long-distance signal enhancing body size of larger, older and dominant males (Font, Pérez i de Lanuza, & Sampedro, 2009; López et al., 2004). Thus, males with fewer spots should be more submissive in social contexts, and this attitude could be exhibited towards potential predators as well. Overall, we housed 48 adult male lizards indoors under a natural light–dark cycle in transparent plastic jars (20 \times 30 cm and 20 cm high) provided with paper sheets as substratum, a water tank and a shelter; they were fed daily with three mealworms, *Tenebrio molitor*. Jars were placed under a UV-B lamp (18 W) to provide the daily UV requirements for vitamin D production and calcium fixation, and an incandescent lamp (25 W) for heating that allowed lizards to attain their preferred body temperatures. UV lamps were switched on for 3 h per day (from 1000 to 1300), and incandescent lamps were lit for 6 h per day (from 1100 to 1700). Prior to testing, lizards were housed for at least 1 week to familiarize them with the novel cage environment.

Experimental Design

Before starting the experiment, we placed each jar containing a lizard in an open and sunny location outside the laboratory for 1 h, to allow the animals to acclimate to the new environment and thermal conditions. Each jar was provided with a brick refuge that allowed partial shade. We tested lizards during May between 1630 and 1800, when all individuals were active. Jars were placed separately from each other, so that the approach to a jar did not influence the other lizards. The experimental design followed the same procedure adopted by Lopez, Hawlena, Polo, Amo, and Martín (2005), Polo et al. (2011) and Rodríguez-Prieto et al. (2011). Each trial was performed by the same experimenter (D.P.-R.), who simulated many consecutive attacks to each lizard. The position of the lizard relative to the refuge was recorded before each attack as follows: hiding (body and head inside the refuge), leaning out (the lizard's body inside the refuge, but its head sticking out) or outside (at least half of the body and entire head outside the refuge). The experimenter first crawled slowly on the ground to avoid being noticed by the lizards in the other cages. Then, he suddenly raised himself above the cage and tapped the lizard close to its tail with a little paint-brush, thus simulating a predatory attack. This approach made the lizard escape into its refuge. If the lizard was already hidden in the refuge, the experimenter tapped the refuge entrance with the paint-brush. Humans as simulated predators have been used in many other studies and the responses of lizards are like those observed to natural predators (Cooper & Blumstein, 2015; Martín & López, 2015). For each lizard, we simulated nine attacks in a day (one attack every 10 min within 1 h and 30 min period). During the trial, three observers placed out of sight from the lizards checked the activity of eight lizards each, using binoculars from a vantage point. We noted the starting position of each lizard before each attack and recorded the exact times at which lizards emerged from the refuge. We tested 24 lizards at each experimental session with three observers to detect more accurately their activity times

in response to consecutive attacks; therefore, we tested all lizards on 2 consecutive days with the same weather conditions and during the same hours. Each lizard was tested in two replicates of the experiment and the order of participation was randomized with respect to the site of capture and the colour morph (12 lizards for each site and eight for each morph each day). The interval between tests was 7 days for each lizard, and the order of participation within each test session was changed to avoid possible influence of the previous position.

The total number of times that a lizard was inside, outside or leaning out of the refuge after the previous attacks was calculated by using the observations of initial positions of lizards taken every 10 min immediately before the new attack. We considered these measurements as indices of general activity level after predatory attacks, from 0 (lizard hidden in the refuge in all observations) to 9 (lizard always outside the refuge). Moreover, by recording the exact hiding times of each lizard, we calculated three different time variables: (1) time spent hidden in the refuge after each attack until the lizard leant out of the refuge and looked outside with the snout outside or closer than 1 cm to the exit of the refuge ('appearance time'); (2) time spent after each attack hidden in the refuge until at least the head and half of the body of the lizard was outside the refuge ('emergence time'); (3) time spent leaning out of the refuge and looking outside between appearance and emergence ('monitoring time'). From the 18 observations per individual, we calculated the average appearance, emergence and monitoring times for each lizard, to be used in the statistical analyses.

Statistical Analyses

Given the high correlation between morphological measurements, we used principal component analysis (PCA) to reduce the six morphological variables to two independent components with eigenvalues greater than one, which accounted for 80.8% of the variance (Table 1). These components represented the absolute body size (MPC-1) and the number of blue spots (MPC-2). The initial factorial solutions were rotated by the Varimax procedure (Sokal & Rohlf, 1995). We used the factor scores of each MPC for further analyses.

Table 1
Morphological principal components analysis (MPC) of common wall lizards

	MPC-1	MPC-2
SVL	0.93	0.01
Weight	0.92	0.03
Head length	0.92	0.10
Head width	0.77	0.24
Head height	0.81	−0.04
Blue spots	0.05	0.99
Eigenvalue	3.85	1.00
% Variance	64.1	16.7

Correlations of variables with the principal components greater than 0.60 are shown in bold.

From the observations of antipredator behavioural responses, we computed nine different average variables for each individual from each day: number of times inside the refuge, number of times leaning out, number of times outside the refuge, appearance time, emergence time, monitoring time, and the habituation indices for appearance, emergence and monitoring times. These indices were related to the temporal sequence of repeated attacks in each test, calculated as the slope of the regression lines of the successive different times over time with lower slopes indicating a higher habituation (Rodríguez-Prieto et al., 2011).

We tested individual variation in antipredator behaviour between the 2 days by using repeatability analysis (Lessells & Boag, 1987) of the values calculated for each of the antipredator variables, as assessed on two replicates of the same trial. Some variables showed a significant repeatability (appearance time: $r = 0.56$, $F_{47,48} = 2.28$, $P = 0.003$; appearance habituation index: $r = 0.41$, $F_{47,48} = 1.69$, $P = 0.035$; monitoring time: $r = 0.35$, $F_{47,48} = 1.55$, $P = 0.05$), while other variables were not significant, thus suggesting that some lizards showed different behavioural responses during the 2 days in which the experiment was run. Thus, for each variable, we used the mean of the values obtained in the two replicates (see Table 2).

Table 2
Antipredator behaviour variables of male common wall lizards

	Mean±SE	Minimum	Maximum	CV
Inside refuge (No. times)	2.6±0.3	0.5	8.0	69.1
Leaning out refuge (No. times)	2.3±0.2	0.0	8.0	67.3
Outside refuge (No. times)	5.1±0.3	0.5	9.5	42.0
Appearance time (s)	327.5±15.9	97.9	551.3	33.6
Emergence time (s)	442.9±14.6	173.8	600.0	22.9
Monitoring time (s)	115.4±10.4	9.9	324.8	62.5
Habituation appearance (index)	-7.7±3.1	-57.7	27.6	273.9
Habituation emergence (index)	-8.9±2.8	-59.0	45.4	218.7
Habituation monitoring (index)	-1.2±1.8	-23.6	35.2	1116.1

Mean ± SE, minimum and maximum values and coefficient of variation (CV in %) are shown.

All variables were checked for normality, and the numbers of times counted for the position of the lizard with respect to the refuge were square root transformed. A PCA on these nine antipredator variables (see Results) was then calculated and its PC scores were used for further analysis. Then, we ran separated backward stepwise general regression models (GRMs) with each of the PC scores of the antipredator PCA ('APC scores') as the dependent variable, with colour morph and site of origin and its interaction (both as potential fixed predictors) and the four MPC scores of the PCA for morphology (as potential continuous predictors). Final GRM models retained only those predictor variables that were significant. Similar forward stepwise GRMs yielded similar results in all cases.

We also used a mixed general linear model (GLM) to test whether variation in hiding time (dependent variable) through successive trials (within factor) depended on colour morph and site of origin (between factors), including the interactions in the model.

Ethical Note

The procedure we adopted to collect lizards (noosing) is commonly used since it is known to be very effective and does not harm the animals. In our study, all animals were maintained in indoor conditions as much as possible like natural ones. During the trials, lizards did not show any sign of stress, and at the end of the experiments were returned to their capture sites. All of them

Table 3
Antipredator responses of common wall lizards from two sites (urban and rural) and three colour morphs (white, yellow, red)

	Urban (N=24)	Rural (N=24)	White (N=16)	Yellow (N=16)	Red (N=16)
Inside refuge (No. times)	1.9±0.3 (66.8)	3.3±0.4 (59.7)	2.6±0.5 (80.0)	2.1±0.3 (62.5)	3.1±0.5 (59.7)
Leaning out refuge (No. times)	2.2±0.3 (62.0)	2.4±0.4 (72.7)	1.9±0.3 (71.8)	2.8±0.5 (69.9)	2.2±0.3 (52.7)
Outside refuge (No. times)	5.9±0.4 (31.0)	4.3±0.4 (50.5)	5.5±0.6 (46.8)	5.1±0.5 (41.2)	4.7±0.4 (36.7)
Appearance time (s)	274.8±17.6 (31.4)	380.2±21.9 (28.3)	315.8±28.5 (36.1)	286.9±17.8 (24.9)	379.7±30.8 (32.4)
Emergence time (s)	399.3±19.8 (24.3)	486.5±17.9 (18.0)	414.1±29.4 (28.4)	431.2±25.1 (23.3)	483.3±18.75 (15.5)
Monitoring time (s)	124.5±13.1 (51.6)	106.3±16.2 (74.8)	98.3±15.2 (62.0)	144.3±19.4 (53.9)	103.7±18.0 (69.3)
Habituation appearance (index)	-16.7±3.9 (115.9)	1.2±3.9 (1576.1)	-8.9±5.5 (246.9)	-18.7±5.1 (110.0)	4.36±3.70 (333.5)
Habituation emergence (index)	-15.0±3.7 (119.2)	-2.7±3.9 (702.5)	-10.6±5.8 (219.2)	-15.9±4.6 (116.7)	-0.14±3.18 (9245.7)
Habituation monitoring (index)	1.68±2.8 (825.8)	-3.98±2.3 (280.3)	-1.74±3.7 (850.5)	2.8±3.2 (453.8)	-4.50±2.56 (227.6)

Mean ± SE and coefficient of variation (in parentheses; in %) are shown.

maintained their original body mass throughout the experiment. The Italian Ministero dell'Ambiente e della Tutela del Territorio e del Mare provided the permission (Prot. no. 0022746/PNM 10/11/2014) to capture, handle and measure lizards.

RESULTS

Overall, lizards were observed outside the refuge before an attack significantly more often than they were observed inside it (repeated measures ANOVA: $F_{1,47} = 22.41$, $P < 0.0001$) and leaning out ($F_{1,47} = 30.88$, $P < 0.0001$). Lizards hid in the refuge when subjected to the simulated attack; after that they usually first appeared from the refuge, monitored the outdoor environment for some time and finally emerged entirely. The habituation indices related to appearance and emergence generally showed a slight trend to progressive habituation to simulated predatory attacks (i.e. the successive different appearance and emergence times within a trial tended to be shorter leading to negative slopes; see below). However, these antipredator variables varied in relation to site of origin and colour morph (Table 3).

The PCA for antipredator measures produced three components that together accounted for 85.6% of the variance (Table 4). The first antipredator PC (APC-1) was positively correlated with variables describing longer appearance and emergence times from the refuge after a predatory attack, and more times that the lizards were observed hidden inside the refuge (or fewer times seen outside refuges) during the trials. Thus, APC-1 described a gradient from individuals that spent shorter times in the refuge after predatory attacks to lizards with longer hiding times. The second PC (APC-2) was positively correlated with variables describing longer monitoring times, more times that the lizards were leaning out of the refuge and slower habituation related to monitoring time (i.e. greater slopes of the regression line relating the successive monitoring times over time). Thus, APC-2 described a gradient of lizards that had longer monitoring times and habituated more slowly, as

Table 4
Principal components analysis (antipredator principal components, APC) for the antipredator responses of lizards

	APC-1	APC-2	APC-3
Inside refuge	0.93	-0.23	0.06
Leaning out of refuge	0.22	0.87	0.19
Outside refuge	-0.82	-0.42	-0.16
Appearance time	0.91	-0.23	0.23
Emergence time	0.81	0.38	0.35
Monitoring time	-0.25	0.90	0.14
Habituation appearance	0.20	-0.14	0.97
Habituation emergence	0.24	0.25	0.82
Habituation monitoring	0.02	0.62	-0.36
Eigenvalue	3.92	2.41	1.36
% Variance	43.58	26.80	15.17

Bold type indicates correlations of variables with the principal components greater than 0.60.

suggested by the slower decrease in the successive monitoring times. The third PC (APC-3) was positively correlated with variables describing slower habituation (i.e. greater slopes) related to appearance and emergence times. Thus, APC-3 described a gradient from lizards that habituated quickly, i.e. that decreased their hiding time across successive tests more quickly, to lizards that habituated slowly.

The correlation between morphological MPC scores and the behavioural APC scores was not significant (Pearson correlation: $-0.21 < r < 0.25$, $P > 0.09$) except for one significant relation between MPC-2 and APC-1 ($r = -0.32$, $F_{1,46} = 5.21$, $P = 0.027$); lizards with fewer blue spots spent more time hidden after a predatory attack. However, this relationship might be confounded by the difference in the number of blue spots between lizards from different sites, which was highly significant (GLM: site: $F_{1,42} = 11.32$, $P = 0.002$) but did not vary between colour morphs (morph: $F_{2,42} = 0.02$, $P = 0.98$; site*morph: $F_{2,42} = 2.20$, $P = 0.12$).

A stepwise GRM model ($R^2 = 0.17$, $F_{1,46} = 9.38$, $P = 0.004$) indicated that the APC-1 scores varied significantly between sites ($\beta = -0.41$, $t = -3.06$, $P = 0.004$) but not between morphs, and the interaction was not significant, independently of differences in morphology (i.e. none of the two MPCs were included in the final model; Fig. 1). Thus, lizards from the urban site had shorter hiding times after a predatory attack and spent more time outside the refuge, independently of their colour morph and morphological traits.

A further stepwise GRM with the APC-2 scores as the dependent variable did not include any of the predictor variables in the final model. Thus, monitoring times did not vary significantly between sites or morphs and were independent of morphology (Fig. 1).

The APC-3 scores varied significantly between sites ($\beta = -0.34$, $t = -2.67$, $P = 0.01$) and morphs ($\beta = -0.36$, $t = -2.46$, $P = 0.018$) and the interaction between site and morph was not significant, independently of morphology (model $R^2 = 0.28$, $F_{3,44} = 5.65$,

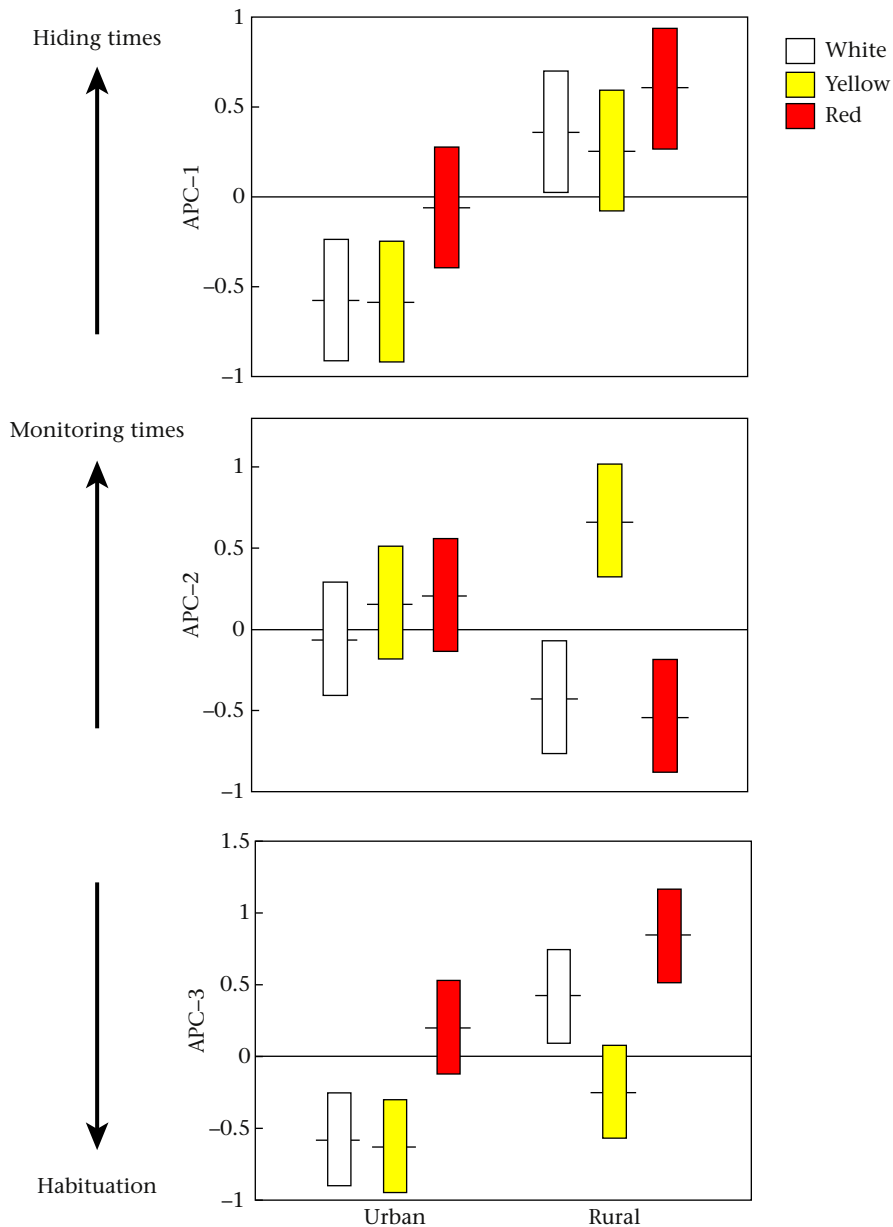


Figure 1. Mean \pm SE factor scores of the three components from a PCA of antipredator behaviour variables (APC) in relation to the site of origin and the colour morph in common wall lizards.

$P = 0.002$; Fig. 1). This suggests that lizards from the urban site habituated more quickly to successive simulated attacks, decreasing their successive hiding times quicker than lizards from the rural population. In addition, within each population, lizards of the yellow morph habituated quicker to successive attacks, decreasing their successive hiding times quicker, with respect to the other two morphs, particularly the red ones, which conversely seemed to become more susceptible after repeated attacks.

Regarding habituation, an additional GLM test showed that hiding times varied significantly through successive trials (GLM, successive trials, within factor: $F_{8,336} = 3.59$, $P < 0.001$), but that this variation depended on the site of origin (site: $F_{1,42} = 15.57$, $P < 0.001$; site*trial: $F_{8,336} = 4.02$, $P = 0.0001$) and on the morph (morph: $F_{2,42} = 4.21$, $P = 0.022$; morph*trial: $F_{16,336} = 2.41$, $P = 0.002$), with other interactions being not significant (site*morph: $F_{2,42} = 0.33$, $P = 0.72$; trial*site*morph: $F_{16,336} = 0.82$, $P = 0.66$). Thus, lizards from the urban site habituated quickly by decreasing successive hiding times whereas lizards from the rural site seemed to maintain their hiding times in successive trials (Fig. 2a). Also, yellow and white morph lizards seemed to habituate more quickly than red morph lizards, which did not show habituation (Fig. 2b).

DISCUSSION

In the present study, we found that various factors, related to both environmental conditions and ventral colour polymorphism, might affect antipredator responses in male common wall lizards. First, habitat could affect antipredator responses, principally in relation to human disturbance. We are aware that our study has the limitation that we examined only one population for each habitat

due to logistical difficulties in using many animals from multiple sites. For this reason, we cannot ensure that differences are due to a site effect rather than to an urbanization effect, and therefore we prefer to be cautious in interpreting our results. Future studies should examine antipredator responses in several different populations within each of the rural and urban habitats in comparison with several populations within the other habitat. Nevertheless, we found many significant differences in behavioural variables between sites, while the only apparent difference between sites is that they have completely different microhabitats. In particular, all microhabitats where lizards were captured differed between urban and rural sites, while other factors not related to urbanization such as climate or lizards' population density did not differ between sites. We are thus confident that urbanization is very likely to be the main factor affecting our results.

Lizards tested in our experiments showed different behavioural responses to simulated repeated attacks. Our experimental design, previously tested in other studies (López et al., 2005; Polo et al., 2011; Rodríguez-Prieto et al., 2011), allowed us to detect significant variation between lizards from urban and rural sites. In detail, urban lizards spent less time hidden in their refuge after predatory attacks and decreased their hiding time faster than rural lizards, thus suggesting a different wariness level towards a potential predator. Lizards from the rural site seemed to be shyer and more diffident, hiding longer in a refuge, while the bolder urban lizards seemed to habituate faster to disturbance, as suggested by the difference in appearance and emergence times after repeated attacks. Lizards are known to adjust their risk assessment and thus modulate their level of wariness in relation to variation in environmental conditions and predatory pressure (Delibes & Blazquez, 1998; Polo et al., 2011). However, the possible effects of anthropic environments on antipredator responses in lizards has rarely been explored (Diego-Rasilla, 2003b, 2003a). Local variation in human presence could lead to differences in escape and hiding behaviour, as recently revealed for many species of birds (Møller & Tryjanowski, 2014), which differ significantly in flight initiation distance (FID) between urban and rural habitats. The outcomes could be either an increased wariness at a high level of anthropic disturbance (Burger & Gochfeld, 1993), or conversely habituation to people where they are not a possible danger (Burger, Gochfeld, & Murray, 1991). Our results seem to converge on this second hypothesis, since lizards inhabiting human-dominated habitats showed greater confidence to simulated attacks than those from rural and more natural sites. In terms of potential predation, humans may be considered as low-risk attackers, since they generally do not actively prey on lizards. Thus, an ability to habituate to human presence could provide benefits in terms of time and costs saved for other activities such as foraging or mating. Martín and López (1999a, 1999b) detected costs of antipredator refuge use: lizards suffering an increase in the frequency of simulated predatory attacks spent more time hidden, and consequently had significantly lower body mass than control individuals (see Martín & López, 1999b, 2015).

Our findings are consistent with a previous study carried out in Spanish populations showing that common wall lizards inhabiting a touristic site are less wary, and have shorter approach distances, than lizards from a nearby site not accessible to people (Diego-Rasilla, 2003a). This seems to confirm that lizards inhabiting rural areas, with limited human presence, tend to consider people as a real predatory threat and consequently show much more caution, as found in other vertebrates (Berger, Wikelski, Romero, Kalko, & Roedl, 2007; Mainini, Neuhaus, & Ingold, 1993; Nowak, le Roux, Richards, Scheijen, & Hill, 2014; Recarte, Vincent, & Hewison, 1998). Therefore, lizards may become habituated to stable and predictable human activities and could thrive in anthropic

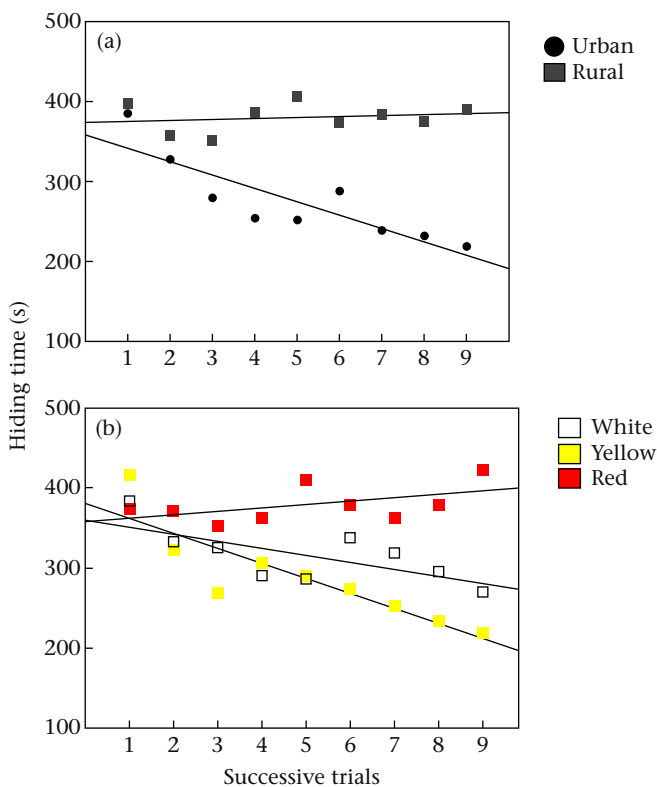


Figure 2. Differences in habituation (mean hiding times in successive trials) in relation to (a) the site of origin and (b) the colour morph in common wall lizards. Regression lines for each site and colour morph are shown.

environments where the presence of other more effective predators such as birds, snakes or mammals is restricted. In this scenario, urban contexts, typically characterized by more abundant resources of food and shelters, and by fewer predators, represent more beneficial habitats for many species compared to their rural counterparts (Evans, Chamberlain, Hatchwell, Gregory, & Gaston, 2011; Francis & Chadwick, 2012; Luniak, 2004; Valcarcel & Fernández-Juricic, 2009). Colonization of human-dominated landscapes could be further facilitated for those individuals with greater propensity to take risk and ability to quickly habituate to new potential threats (Lowry, Lill, & Wong, 2013).

Differences in antipredator response might also be related to variation in morphology, body condition or health (López et al., 2005). In our study, we considered body and head measurements and the number of lateral blue spots, the latter appearing to be the only variable associated with antipredator responses. Lizards with fewer blue spots showed longer hiding times and were more often inside the refuge after repeated attacks. However, we also found a strong relationship between site of origin and number of blue spots, and, thus, we cannot exclude that these results were mainly due to a population effect. Interestingly, lizards from the rural site had fewer lateral blue spots than urban ones, suggesting that habitat conditions could affect some morphological traits. Specifically, as being more conspicuous would mean greater exposure to predatory attacks, the cost associated with having more blue spots should be counter-balanced by social benefits and greater survival rate in urban lizards (Cabido et al., 2009). Recently, Lazić, Kaliontzopoulou, Carretero, and Crnobrnja-Isailović (2013) pointed out that urban *P. muralis* are more asymmetrical, suggesting variation in predatory pressure between urban and rural areas (i.e. the latter being more threatening in terms of number and type of predators) as the factor affecting their findings. Similarly, urban contexts where threats are limited might allow male lizards to have more lateral blue spots, without incurring an increased risk of being preyed upon.

A further interesting result of our study is related to the possible effects of colour polymorphism on the behavioural response of *P. muralis* males towards potential predators. Our current results indicated that, irrespective of the site of origin, yellow lizards spent gradually less time in the refuge before appearing and emerging outside than the other two morphs. Conversely, red lizards showed progressively higher appearance and emergence times after successive tests, suggesting a growing sensitization to the potential threat of the predatory attack. The common wall lizard has recently been studied in relation to alternative colour morph-specific strategies, concerning morphophysiological, life history or ecological traits. In males, significant variation has been detected for immune response (Calsbeek et al., 2010; Sacchi, Rubolini et al., 2007), haematological profiles (Galeotti et al., 2010) and chemical composition of male femoral gland secretions (Pellitteri-Rosa et al., 2014). Predation may similarly play a key role in maintaining polymorphism among lizards, although its effects have been mainly investigated in species with alternative dorsal coloration (Calsbeek & Cox, 2012). Common wall lizards are polymorphic only on the throat and belly, ventral surfaces not easily detectable by predators such as birds or mammals, but visible by ground predators such as snakes. In our study areas, the main snakes are dice and grass snakes, *Natrix tessellata* and *Natrix natrix*, and the Aesculapian and western whip snakes, *Zamenis longissimus* and *Hierophis viridiflavus*. The latter two are active saurophagous foragers that use vision to detect prey and thus can perceive the lateral ornamentation and parts of the ventral coloration of lizards (Sinclair, 1985). Pérez i de Lanuza and Font (2015) recently found that alternative colours of ventral surfaces of a Pyrenean population of *P. muralis* generate different levels of conspicuousness, the red being the most visible compared to the yellow and white morphs. Red individuals

should thus be more detectable by competitors, predators or prey, paying an increased detection risk by predators to gain higher efficacy of social signalling (Godin & McDonough, 2003; Husak, Macedonia, Fox, & Saucedo, 2006; Pérez i de Lanuza & Font, 2015; Stuart-Fox, Moussalli, Marshall, & Owens, 2003). The ventral coloration of Pyrenean and northern Italian populations of common wall lizards are similar (Pérez i de Lanuza, Bellati, Pellitteri-Rosa, Carretero, Fasola, 2014), the red morph being the most chromatically conspicuous to conspecifics and predators, whereas the white morph is the least detectable. Thus, red lizards could adopt a more cautionary strategy towards a potential predator than the yellow and white morphs, gradually evolving to be more sensitive to persistent threats.

Variation in morph-specific antipredator responses could reflect the existence of evolutionary strategies involving physiological conditions, life history traits or microhabitat selection. Yellow males have a lower immune response than both red and white lizards (Sacchi, Rubolini et al., 2007), thus suggesting possible higher levels of circulating testosterone and hence greater aggressiveness, as reported for other lizards (Belluire, Meyland, & Clobert, 2004; Mills et al., 2008). Higher aggressiveness should be associated with behavioural traits like boldness, determination and self-confidence and this could explain the greater ability of yellow lizards to habituate faster to repeated predatory attacks than the other two morphs. An alternative explanation is that intermorph differences in temporal changes in antipredator behaviour might be due to changes over time in physiological demands that might differ between morphs rather than differences in habituation. In a previous study, we found that in larger yellow males the heterophil:lymphocyte (H:L) ratio, a sensitive measure of immunodepression and long-term stress, is significantly lower than in the other morphs, while higher blood parasite loads occur in larger red individuals, thus indicating a generally better physiological condition of yellow lizards with respect to red ones (Galeotti et al., 2010).

In conclusion, our experiment has highlighted two key points of the evolutionary ecology of antipredator behaviour, using a lizard species as a model. First, we detected different levels of behavioural plasticity in antipredator responses depending on different habitats and thus predatory pressure, including the effects of human disturbance. Second, we had evidence of different antipredator strategies between common wall lizard colour morphs, thus shedding light on an additional factor driving the maintenance of colour polymorphism in this species.

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