

Biological correlates of two dorsal color pattern types in the Common Wall Lizard, *Podarcis muralis* (LAURENTI, 1768) (Squamata: Sauria: Lacertidae)

Biologische Entsprechungen zweier Rückenzeichnungstypen
bei *Podarcis muralis* (LAURENTI, 1768)
(Squamata: Sauria: Lacertidae)

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KURZFASSUNG

Bei der Mauereidechse *Podarcis muralis* (LAURENTI, 1768) treten mehrere Farbmuster-Typen der Rückenzeichnung auf: (i) eine mehr oder weniger durchgehende Rückenmittellinie auf einem hellen Rückenband ohne weitere Musterung, (ii) ein dunkles Netzmuster ohne Vertebrallinie und (iii) eine Zwischenform, bei der das dunkle Netzmuster eine mehr oder weniger durchgehende Rückenmittellinie bildet. Diese Farbmuster-Typen repräsentieren unterschiedliche Melaninverteilungen auf dem Rücken und könnten Thermoregulation, Mimikry und Sexualverhalten beeinflussen. Die Autoren untersuchten die Häufigkeitsverteilung dieser Farbmuster-Typen im Hinblick auf Geschlecht, Kopf-Rumpf-Länge und Fundorthöhe (submontan und planar).

Eine Rückenmittellinie war bei der submontanen Mauereidechsen-Population häufiger als in der Population der Ebene, und bei Weibchen häufiger als bei Männchen ausgebildet. Darüber hinaus trat sie in der submontanen Population bei großen Tieren häufiger auf als bei kleinen, während für die Tieflandpopulation das Gegenteil festgestellt wurde. Die in Bezug auf Geschlecht, Körpergröße und vertikale Verbreitung beobachteten Unterschiede in der Häufigkeit der Farbmuster-Morphen könnten mit unterschiedlicher Temperatur- und Mikrohabitatwahl in Zusammenhang stehen.

ABSTRACT

Common Wall Lizards, *Podarcis muralis* (LAURENTI, 1768), show a polymorphic dorsal color pattern including (i) a single, more or less continuous dark vertebral stripe on a dorsal band lacking further markings, (ii) dark dorsal reticulation without any vertebral stripe, and (iii) an intermediate pattern in which the dorsal reticulation forms a more or less continuous dark vertebral stripe. These patterns correlate with different distributions of the melanin in the back, and potentially can affect thermoregulation, mimesis and sexual behavior. The authors analyzed the frequencies of these pattern types in relation to sex and size, in both a submontane and lowland population.

A vertebral stripe occurred more frequently in the submontane than the lowland population, and more frequently in females than in males. In addition, in the submontane population, the vertebral stripe pattern occurred more frequently in large lizards than in small ones, whereas the opposite was observed in the lowland population. The interpopulation differences in the color pattern morphs' frequencies in relation to sex, size and altitude may be associated with differences in temperature and microhabitat selection.

KEY WORDS

Reptilia: Squamata: Sauria: Lacertidae, *Podarcis muralis*, Common Wall Lizard, dorsal color pattern polymorphism; thermoregulation, crypsis, thermal ecology, behavior

INTRODUCTION

Polymorphism is defined as the coexistence within a single interbreeding population of two or more distinct and genetically determined morphs, the rarest of which being too frequent to be solely due to recurrent mutation (FORD 1945; HUXLEY 1955). It is commonly attributed to a balance between opposing selective pressures

favoring different morphs such as frequency dependent selection, correlated response to selection, heterozygous advantage, and random processes such as founder effects and genetic drift (HEDRICK et al. 1976; JONES et al. 1977; ROSE 1985; HEDRICK 1986; ENDLER 1990; MCKINNON & PIEROTTI 2010).

Dorsal color polymorphisms are common in reptiles, and particularly in snakes (see e. g., ANDRÉN & NILSON 1981; CAPULA & LUISELLI 1994; FORSMAN & SHINE 1995; FORSMAN 1995a, 1995b) and lizards (see e. g., GREEN 1988; STUART-FOX & ORD 2004; STUART-FOX et al. 2004; CARRETERO et al. 2006; CAPULA et al. 2009; LEPETZ et al. 2009). Several hypotheses have been proposed to explain the occurrence of dorsal color polymorphism in these two taxa, including thermoregulatory advantages in different microclimatic conditions (e.g. GIBSON & FALLS 1979; SHERBROOKE et al. 1994; FORSMAN & SHINE 1995; FORSMAN 1995a, 1995b; LEPETZ et al. 2009), mimesis when different habitats favor different morphs (e.g., SCHOENER & SCHOENER 1976; KING 1987; BRODIE 1992; STUART-FOX et al. 2004; ROSENBLUM 2006; CAPULA et al. 2009), protection from ultraviolet radiation (PORTER 1968), and sexual selection (e.g., TORR & SHINE 1994; STUART-FOX & ORD 2004).

The Common Wall Lizard, *Podarcis muralis* (LAURENTI, 1768), is a European, small to medium sized species, that shows a polymorphic dorsal coloration with three main types of ornamentation including: (i) a single, more or less continuous dark verte-

bral stripe on a bright dorsal band without further markings, (ii) dorsal reticulation without any vertebral stripe, and (iii) an intermediate pattern in which the dorsal reticulation forms a more or less continuous dark vertebral stripe (Fig. 1). These patterns reflect differences in the quantity or distribution of melanin on the back, which could lead to differences in thermoregulation, mimesis, and sexual signalling. We regarded the linear pattern to have more melanin than the reticulated one, since the pigment concentration in large dark patches is more effective in capturing solar radiation (LEPETZ et al. 2009). The possible adaptive significance of the different dorsal patterns in this species has not yet been investigated. Therefore, to evaluate alternative hypotheses potentially explaining the occurrence and maintenance of dorsal color polymorphism in Common Wall Lizards, we analyzed the morph frequencies in two populations under different environmental conditions (i.e., submontane and lowland environments). In particular, our aims were to assess if the frequency of the two extreme pattern types of dorsal ornamentation (vertebral stripe only versus reticulation only) differed according to body size, sex or altitude.

MATERIALS AND METHODS

Study area

This study was conducted in two sites of Lombardy (Northern Italy), located northwest to Pavia (i.e., the lowland site, 45°14'45"N, 9°13'30"E) and near the village of Lemna in the Province of Como (i.e., the submontane site, 45°51'21"N, 9°9'46"E), respectively.

The lowland site is the typical farmhouse arrangement of the Po river plain, characterized by many buildings such as stables, barns, warehouses, farms and manor houses; the walls of the buildings being old, with many cracks and fissures, forming suitable habitats for lizards. In the open spaces among buildings, there were piles of stones or stacks of wood which also provided ideal micro-habitats. Mean annual temperature and rainfall were 13.0 °C and 941 mm, respectively, and the altitude was 80 m a.s.l.

In contrast, the submontane site (570 m a.s.l.) included several dry-stone walls delimiting stable meadows and tracks among some isolated houses. The meadows were bordered by forests, which also covered small portions of the tracks. Mean annual temperature and rainfall were 11.1 °C and 1256 mm, respectively.

Individual collection and dorsal coloration measure

Adult Common Wall Lizards (snout-vent length, SVL > 54 mm, BARBAULT & MOU 1986, 1988) were collected by noosing between 25th March and 16th June 2009. Overall, we caught 280 lizards including 220 in the lowland site (110 males and 110 females) and 62 in the submontane site (31 males and 31 females). Multiple captures of the same individual were avoided by photo-

graphic identification (SACCHI et al. 2010). After capture, each lizard was measured (SVL) using a calliper (accuracy: 0.2 mm) and photographed to assess the dorsal ornamentation using Nikon Coolpix 4300 (resolution 2272 × 1704 pixels). All individuals were released thereafter, at the point of capture.

The dorsal coloration pattern of each individual was scored with 0 to 1 from photographs in agreement with increasing linear pattern. According to this scale, individuals with a completely reticulated pattern without any hint of a vertebral stripe were scored with 0 (Fig. 1a), whereas individuals showing the striped design without any reticulation were scored with 1 (Fig. 1c). Individuals showing an intermediate pattern were considered as intermediates (Fig. 1b) and scored with 0.5.

The ornamentation varied slightly between the anterior and posterior portions

of the back within individuals (Wilcoxon signed-rank test, $Z = 4.922$, $n = 282$, $P < 0001$). To cope with this nonhomogeneity, we assigned two independent scores to each lizard, one for the anterior and another one for the posterior back, and computed a mean score from their average. These three dorsal scores were highly repeatable, as we checked on a sample of 23 individuals (12 males and 11 females) scored twice at one day interval (frontal portion: $r = 0.93$, $F_{22, 23} = 13.91$; $P < 0001$; rear portion: $r = 0.91$, $F_{22, 23} = 11.45$, $P < 0001$; mean score: $r = 0.93$, $F_{22, 23} = 13.86$, $P < 0001$).

Statistical analyses

We used a chi squared test (χ^2) to check if the frequency of the three dorsal colorations varied among populations or between sexes. Then, in order to check if

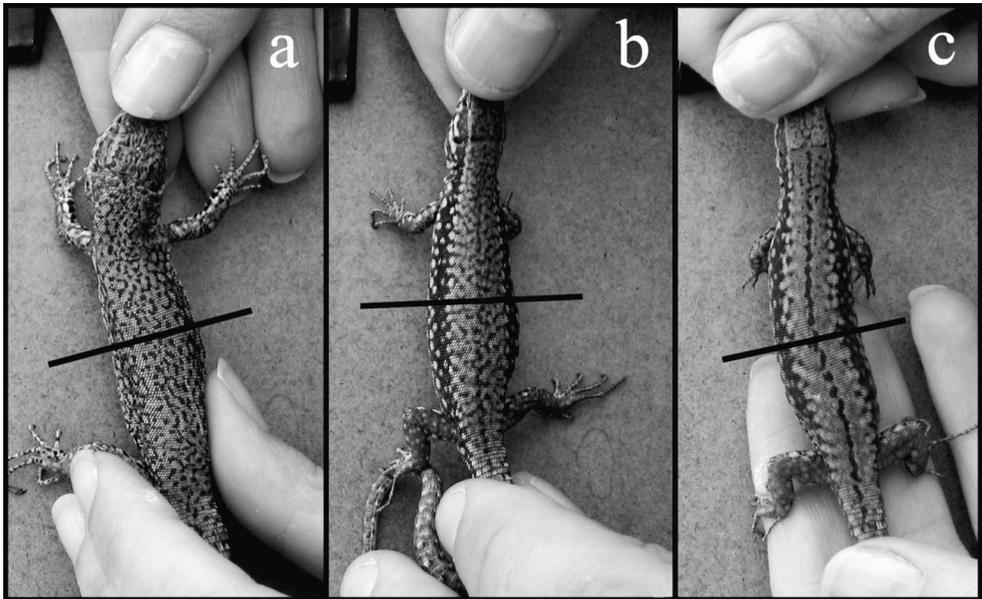


Fig. 1: Representative pictures of the three types of dorsal pattern of the Common Wall Lizard, *Podarcis muralis* (LAURENTI, 1768): a) reticulated individual without melanic vertebral stripe, b) intermediate individual, and c) individual with melanic vertebral stripe, but without reticulation. The black lines separate the front and rear portions of the dorsal pattern, which received independent scores (see Methods for details).

Abb. 1: Repräsentative Abbildungen von drei Typen der Rückenzeichnung bei der Mauereidechse *Podarcis muralis* (LAURENTI, 1768): a – retikuliert ohne dunkle Rückenmittellinie, b – intermediär, c – mit dunkler Rückenmittellinie, ohne Netzmuster. Die dunklen Linien trennen die unterschiedlich bewerteten vorderen und hinteren Rückenregionen.

sex, size and altitude (submontane environment vs. lowland) affected the dorsal ornamentation, we conducted a logistic regression analysis using the mean scores as dependent variable and the sex, size and population as independent predictors. The three predictors entered the initial model as three-way interaction; then we proceeded to

a model simplification (using the Likelihood-ratio χ^2) by removing all non-significant terms ($P > 0.05$) until the minimum model containing only statistically significant terms was obtained (FARAWAY 2006). All analyses were performed using the software R 2.12.1 (R DEVELOPMENT CORE TEAM 2010).

RESULTS

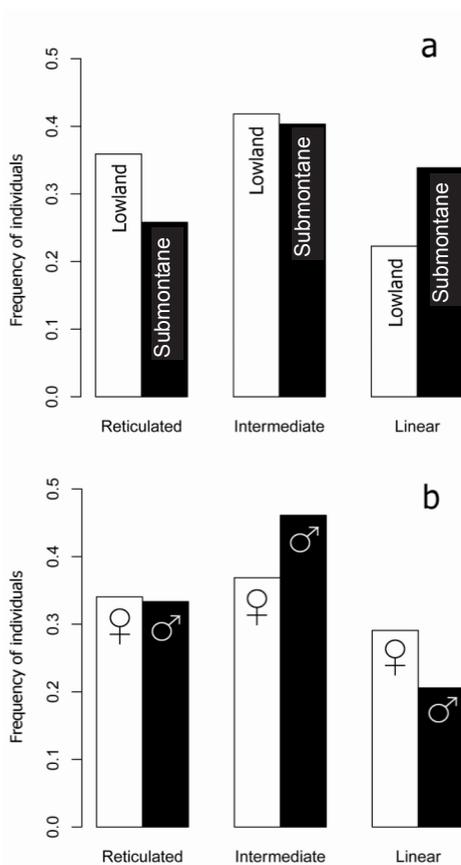


Fig. 2: Frequencies of the three dorsal patterns of the Common Wall Lizard, *Podarcis muralis* (LAURENTI, 1768), according to altitude (a) and sex (b).

Abb. 2: Häufigkeiten von drei Typen der Rückenzeichnung bei der Mauereidechse *Podarcis muralis* (LAURENTI, 1768), in Abhängigkeit von Seehöhe (a - Ebene und submontane Stufe) und Geschlecht (b).

In both populations nearly half of the individuals showed the intermediate pattern (lowland: 41.8%; submontane location: 40.3%), but the linear pattern prevailed in the submontane site (33.9% vs. 22.3%), whereas the reticulated one prevailed in the lowland location (25.8% vs. 35.9%, Fig. 2a). Nevertheless, these differences were not significant ($\chi^2 = 4.11$, $df = 2$, $P = 0.13$).

Also between sexes, the frequencies of dorsal color pattern morphs did not vary significantly ($\chi^2 = 3.51$, $df = 2$, $P = 0.17$, Fig. 2b), although in both males and females the intermediate pattern was the most frequent (males: 46.1%; females: 36.9%). Although not significant, females showed the striped pattern more frequently than males (males: 20.6%; females: 29.1%), whereas no difference was found between sexes in the occurrence of the reticulated pattern type (males: 33.3%; females: 34.0%).

The minimum significant logistic model contained all the two-way interactions as significant terms, even though the P -value after removal of the three-way interaction term 'sex \times population \times SVL' was not significant ($LR\text{-}\chi^2 = 3.733$, $df = 1$, $P = 0.053$). Thus, the final model indicated that the linear pattern occurred more frequently in females than males, particularly in the submontane population (sex \times population interaction: $LR\text{-}\chi^2 = 7.035$, $df = 1$, $P = 0.008$, Fig. 3); in addition, the large individuals in the lowland site were more reticulated than the small ones, while the opposite was observed in the submontane population (SVL \times population interaction: $LR\text{-}\chi^2 = 95.510$, $df = 1$, $P < 0.001$, Fig. 3). The effect of size was more pronounced in males than in females (sex \times SVL interaction: $LR\text{-}\chi^2 = 9.025$, $df = 1$, $P = 0.003$, Fig. 3).

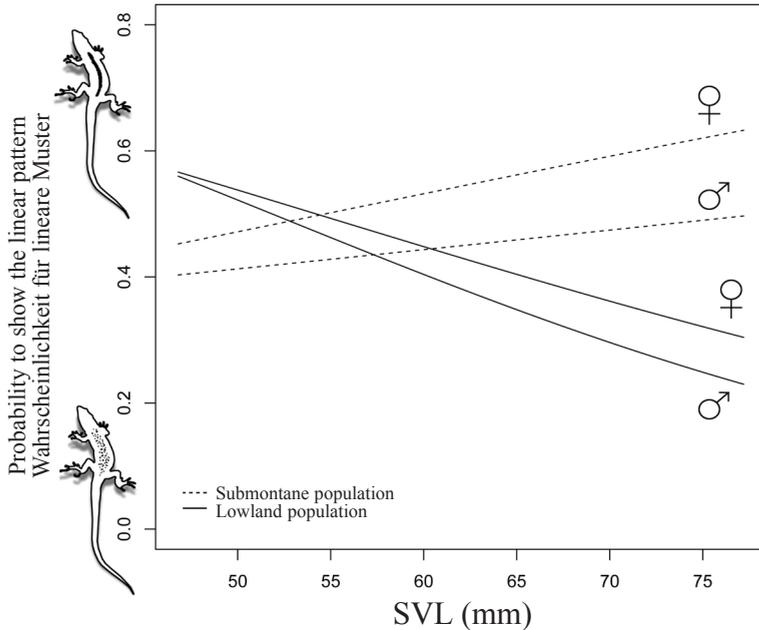


Fig. 3: Probability of showing a melanized linear pattern according to size (SVL), sex and altitude (submontane environment vs. lowland) in Common Wall Lizards, *Podarcis muralis* (LAURENTI, 1768).

Abb. 3: Die Wahrscheinlichkeit des Auftretens eines dunklen, linearen Zeichnungsmusters in Abhängigkeit von Größe (Kopf-Rumpf-Länge, SVL), Geschlecht und Seehöhe (submontane Höhenstufe gegenüber Ebene) bei der Mauereidechse *Podarcis muralis* (LAURENTI, 1768).

DISCUSSION

Before this study, the available information on the characteristics and the adaptive significance of dorsal coloration of Common Wall Lizards was extremely limited and mostly anecdotal (CORTI & LO CASCIO 1999; CAPULA et al. 2009). Thus, the results obtained here provide a first understanding of individual correlates of the dorsal coloration in Common Wall Lizards, allowing the formulation of hypotheses regarding the selective pressures controlling expression of dorsal color pattern polymorphism in this species. The results revealed a complex association between dorsal ornamentation, body size and altitude of the location, which can be summarized as follows: (i) females showed the linear pattern

more frequently than males, (ii) the dorsal ornamentation pattern varied according to individual size, and (iii) both these relationships varied differently according to the altitude. They did so in that females exhibited the linear pattern more frequently in the submontane than lowland environment, and large individuals were more frequently reticulated than small ones under lowland conditions, while the opposite was true in the submontane site, irrespective of sex.

In reptiles, the dorsal color pattern is known to be of major importance in mimicry, temperature regulation and, less frequently, sexual selection (e.g., SCHOENER & SCHOENER 1976; GIBSON & FALLS 1979; KING 1987; BRODIE 1992;

FORSMAN & SHINE 1995; FORSMAN 1995a, 1995b; CAPULA et al. 2009; LEPETZ et al. 2009). According to ENDLER (1978, 1983) and CLUSELLA TRULLAS et al. (2007) for example, differences in ornamentation between species and populations or between sexes and age classes are the result of subtle differences in the balance between opposite environmental and sexual pressures.

Our finding that the effects of sex and size differed according to population (altitude) can be interpreted in the light of both environmental and climatic differences between the two studied sites, reflecting different thermoregulatory or mimesis-related adaptive responses. On one hand, the melanized linear pattern might reflect a thermoregulatory response to low temperatures, as predicted by the thermal melanism hypothesis (LUSIS 1961; NORRIS 1967; WATT 1968; KETTLEWELL 1973; LUKE 1989). This hypothesis states that darker individuals heat up faster and reach higher equilibrium temperature than lighter ones under the same solar radiation conditions (LUSIS 1961; NORRIS 1967; WATT 1968; KETTLEWELL 1973; GATES 1980; LUKE 1989). Accordingly, LEPETZ et al. (2009) found that the linear pattern is more effective in capturing solar radiation than the reticulated one in Common Lizards.

Under low temperature conditions, individuals showing a concentration of melanin in a broad vertebral stripe should be advantaged because they become active earlier and for longer periods relative to the lighter ones, thus obtaining better fitness. LEPETZ et al. (2009) attributed the increased incidence of individuals showing the linear pattern under cold climate conditions, to their higher efficiency in thermoregulation. This is probably due to the higher quantity of pigment deposited in the skin by this morph or the larger size of black patches, which are more effective in capturing solar radiation. In addition, a vertebral stripe could also heat the spinal cord more efficiently. Actually, previous studies highlighted that melanism should be more frequent in populations located in cooler rather than warmer areas (CAPULA & LUISELLI 1994; FORSMAN 1995a; CLUSELLA TRULLAS et al. 2007). The dorsal ornamentation of the Common Wall Lizard fits this pattern,

since the linear pattern occurred more frequently in the submontane population than in the lowland environment, which is characterized by higher mean temperatures, lower humidity and a substrate prevalently consisting of bare soil, stone and brick walls. Overall, this is a more open and sunny exposed environment compared to the submontane habitat, in which the mean temperature is lower, the air humidity is higher, while the substrate mainly consists of stable meadows interspersed by dry-stone walls. The prevalence of the linear pattern in submontane populations could reflect a higher efficiency in thermoregulation in analogy with previous results on the Common Lizard *Zootoca vivipara* (JACQUIN, 1787) (LEPETZ et al. 2009). The concentration of the melanin along a vertebral stripe might confer lizards a more efficient absorption of solar radiation (perhaps just the spinal cord is heated), resulting in a thermoregulatory advantage against the reticulated individuals when the mean temperature is low. At the opposite, the dispersed distribution of melanin could allow the reticulated lizards to reduce heat absorption in sunny environments. This pattern of pigmentation may be actually more efficient in environments dominated by high temperatures and lacking vegetation, where lizards need to avoid the overheating (LEPETZ et al. 2009). However, new studies are needed to verify if the proportion of black pigment is higher in the linear than the reticulated pattern also in Common Wall Lizards, and if this difference affects the ability of capturing solar radiation.

The thermoregulatory hypothesis predicts that melanism is at higher advantage for females, which may reduce the time of gestation, having additional time to replenish the energy reserves spent in egg production (ANDRÉN & NILSON 1981; CAPULA & LUISELLI 1994; FORSMAN 1995a). Our results agree with this prediction, as females expressed the linear pattern more frequently than males, and this difference was particularly evident among larger individuals. Our assumption is consistent with previous studies on adders (FORSMAN 1995b; LUISELLI 1992), which reported higher survival rates for melanistic females as compared to brighter, zigzag patterned females.

The different forming of dorsal coloration relative to individual size in the two populations may be explained through the non-consistent direction for the effects of size on thermoregulatory efficiency under different climatic regimes (CLUSELLA TRULLAS et al. 2007). Under cold conditions, melanism is expected to provide an advantage to large individuals rather than small ones, because large organisms have higher thermal inertia, thus preserving the equilibrium temperature over longer time compared to the smaller ones (GATES 1980; STEVENSON 1985; BAKKEN 1992). In warm climate conditions, melanism should provide an advantage to the smaller individuals relative to the larger ones because of their numerically higher surface-mass ratio, which allows them to dissipate heat more quickly, thus avoiding overheating (PORTER & GATES 1969). Our data are consistent with both these predictions. Indeed, we did not find any significant effect of SVL on the occurrence of dorsal ornamentations, but rather a strong significant effect depending on the population site. In the submontane population, the linear pattern occurred more frequently in large than in small individuals, according to the more pronounced effect of thermal inertia on larger individuals in low temperature conditions (STEVENSON 1985; SHINE & KEARNY 2001). By contrast, in the lowland population, the linear pattern occurred more frequently in small rather than large lizards, maybe reflecting their need to decrease heat loads and to avoid overheating under high temperature conditions (PORTER & GATES 1969).

An alternative explanation to the thermoregulation hypothesis is crypsis. In snakes showing dorsal color pattern polymorphism, the ornamentation is frequently composed of longitudinal stripes in the prairies or in any environment with grass cover, since striped patterns confer a more effective camouflage in the presence of linear shadows (PORTER 1972). Several studies have confirmed that snakes with longitudinal stripes in grasslands incur lower predation rates than the other morphs (KLAUBER 1931; JACKSON et al. 1976).

Dorsal color patterns associated with microhabitat selection are common also among lizards (VAN DER WINDEN et al.

1995; STUART-FOX & ORD 2004; ROSENBLUM 2006), and have been related to anti-predator behaviors (CARRETERO et al. 2006). When facing a predator, lizards may choose between two alternative strategies: escape or crypsis (GREEN 1988). A trade-off between risk of capture and costs of fleeing exists (MARTIN & LOPEZ 1999a, 1999b) and optimal strategy models predict that lizards should stay immobile adopting a mimic posture, unless predators pose a serious threat to survivorship and the costs of fleeing are acceptable (MARTIN & LOPEZ 1999a, 1999b). In this scenario, the dorsal patterns may correlate with behaviors, as what makes a lizard cryptic when immobile, may expose it upon flight and vice versa (CARRETERO et al. 2006). In a study on the escape behavior of *Scelarcis perspicillata* (DUMÉRIL & BIBRON, 1839), the spotted form showed longer approach distances and took more time to abandon shelter than the striped one, suggesting that the dorsal pattern and antipredatory behavior had coevolved in this species (CARRETERO et al. 2006). Our results are consistent with the hypothesis that the dorsal patterns of the Common Wall Lizards correlate with habitat features in order to improve mimesis. Indeed, the striped pattern prevailed in lizards of the submontane environment with a dominant grass cover, as opposed to the predominantly sunny habitats with reduced herbaceous cover of the lowland site. Under a mimesis hypothesis, results are more difficult to interpret, and may reflect differential microhabitat selection between adults and subadults at least within the lowland population.

Finally, we cannot exclude the possibility that the dorsal ornamentation in Common Wall Lizards could be used for sexual recognition or sexual selection, but we find this hypothesis very unlikely, because it leaves open the question of why the mountain and lowland populations should display different patterns.

In conclusion our study suggests that both thermal regulation and mimesis hypotheses are consistent with our observed data, and the adaptive advantages of dorsal colorations probably vary geographically and sexually.

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