Evolutionary history drives the geographical distribution of dorsal patterns in the common wall lizard (*Podarcis muralis*)

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Abstract. Melanin-based dorsal pattern polymorphisms are common in reptiles and generally evolve under the interaction between opposite selective pressures, notably thermal advantage in cold environments and background matching to avoid predation. When those pressures change over space and time, the relative frequencies of morphs can vary across the species range. However, no previous study has analysed the spatial patterns of variation of morphs under a phylogenetic perspective in addition to the adaptive responses to natural selection. In this study, we focused on the distributional patterns of the three dorsal morphs of *Podarcis muralis* at wide-range scale to assess how they associate with geography, climate, microhabitat, phylogeny and sexual dimorphism. By using open access data from iNaturalist, we assembled a dataset of 4096 georeferenced points with information on sex and morph. Data were analysed through Bayesian GLMs, and four alternative models were formulated depending on the specific factors affecting morphs' frequency. The dorsal morphs are not randomly distributed in Europe, but follow clear geographic patterns, vary with altitude and habitats, show sex-specific trends, and correlate with the phylogenetic history of the species. When comparing models, the phylogenetic model always obtained the best performance, and no overlap with other models occurred, thus best explaining the distributional patterns of dorsal morphs. The evolutionary processes, in addition to present environmental pressures, can significantly affect local-scale microevolutionary adaptations, influencing the current distribution of dorsal phenotypes across the species range. More generally, results point out the importance of considering the evolutionary processes when analysing distributional patterns of polymorphisms.

Keywords: citizen science, crypsis, geographic distribution, melanin-dorsal polymorphism, phylogeny, thermoregulation.

Introduction

The broad variety of animal species that exhibit dorsal ornamentations (e.g., spots and stripes) that might enhance thermoregulatory efficiency, protection from ultraviolet radiation, sexual selection and camouflage is the evidence of how colour patterns can play a major role in animal fitness and adaptation (Endler, 1983; Forsman, 1995; Stuart-Fox and Ord, 2004; Rosenblum, 2006; Lepetz et al., 2009; Pizzatto and Dubey, 2012). Dorsal colourations often show intraspecific patterns of variation, both at geographic and population scale (Lattanzio and Miles, 2014; Ortega et al., 2015; While et al., 2015), as well as between sexes (Sacchi et al., 2012; Johnson, Jordan Price and Pruett-Jones, 2013; Medina, Losos and Mahler, 2017). Those patterns arise in response to spatial, temporal or intersexual variability of natural and sexual selective pressures, which in turn may favour one specific pattern among others (Butler and Losos,

2002; Stuart-Fox and Ord, 2004; Medina, Losos and Mahler, 2017). Sexually dimorphic populations can manifest higher variability because they can adapt to a wider range of conditions, and thus respond more effectively to environmental changes, increasing their resilience to local extinction events (Forsman and Åberg, 2008a, b; Roulin, Burri and Antoniazza, 2011).

The adaptive role of dorsal polymorphisms has been long debated in ectotherms because body temperature directly affects basal physiological functions, and thus some crucial traits of the life history such as performance, feeding or growth (Clusella-Trullas, Van Wyk and Spotila, 2009). Dorsal polymorphisms are widespread among reptiles, particularly in lizards (Stuart-Fox and Ord, 2004; Capula, Rugiero and Luiselli, 2009; Lepetz et al., 2009; Ortega et al., 2015) and snakes (Andrén and Nilson, 1981; Forsman and Shine, 1995; Martínez-Freiría et al., 2017; Pizzigalli et al., 2020). As for other species, the different explanatory hypotheses that have been proposed include: i) thermoregulatory advantages under different microclimatic conditions (Gibson and Falls, 1979; Forsman and Shine, 1995; Clusella-Trullas, van Wyk and Spotila, 2007; Lepetz et al., 2009; Muri et al., 2015; Bolton, Rollins and Griffith, 2016), ii) protection against ultraviolet radiation to minimise oxidative stress (Reguera, Zamora-Camacho and Moreno-Rueda, 2014), iii) sexual selection in sexually dimorphic species (Forsman, 1995; Stuart-Fox and Ord, 2004; Bolton, Rollins and Griffith, 2016), iv) camouflage when different habitats favour different morphs (Rosenblum, 2006; Capula, Rugiero and Luiselli, 2009; Sacchi et al., 2012), and v) the evolutionary history of species (Corl et al., 2010).

Thermoregulatory advantages of dorsal colourations in ectotherms are the core of the thermal melanism hypothesis (Clusella-Trullas, van Wyk and Spotila, 2007), which states that darker individuals have a fitness advantage at lower temperatures because they heat up faster. Several studies have found that thermal advantage of darker individuals results in higher growth rates, larger body sizes, better body conditions and higher reproductive success (Andrén and Nilson, 1981; Luiselli, 1995). Consequently, darker individuals tend to become more frequent with increasing latitude or elevation (Vidal, Ortiz and Labra, 2007; Leaché, Helmer and Moritz, 2010; Sacchi et al., 2012; Castella et al., 2013; Reguera, Zamora-Camacho and Moreno-Rueda, 2014; González-Morales et al., 2021). However, thermal advantage from darker colourations in smaller species, which also rely upon air temperature in addition to solar radiation as heat sources (Fraser and Grigg, 1984; Tosini, Lanza and Bacci, 1992; Bittner, King and Kerfin, 2002; Lorioux et al., 2008) has been demonstrated only in few cases (González-Morales et al., 2021) and therefore cannot be taken as a common phenomenon.

The "protection against UV radiation" hypothesis (Cope et al., 2001; Reguera, Zamora-Camacho and Moreno-Rueda, 2014) is an alternative, non-exclusive, hypothesis explaining higher frequencies of darker colourations at higher altitudes. It states that dorsal darkness is favoured with respect to normal colourations at higher elevation because melanin protects individuals by absorbing the UV radiation (Cope et al., 2001). As the latter increases with altitude (Blumthaler, Ambach and Ellinger, 1997), individuals will probably tend to be darker with increasing elevation. There is little evidence supporting this hypothesis (Reguera, Zamora-Camacho and Moreno-Rueda, 2014), mainly because the effects of UV radiation can be difficult to discern from those of thermal advantage. Nevertheless, some evidence for this hypothesis has been found in *Psammodromus algirus* in Southern Spain (Reguera, Zamora-Camacho and Moreno-Rueda, 2014).

The occurrence of geographic patterns of variability in the distribution of dorsal polymorphisms can be interpreted also from the ecological point of view, taking into consideration the role of dorsal cryptic colourations and disruptive pattern to enhance predator avoidance

reducing predation risks. Camouflage results from reduced contrast of the animal's body against the background (Endler, 1978), and ultimately depends upon the interaction between the visual properties of the predators and the efficiency of body colourations to reduce the signal-to-noise ratio (Endler, 1978; Michalis et al., 2017). Consequently, habitat patchiness will promote dorsal polymorphisms whenever patterns match some backgrounds at the expense of others, so that the frequencies of morphs in a given population are affected by their ability to match available habitats (Chapple et al., 2008). In this scenario, darker individuals may suffer higher predation rates because of a reduced camouflage compared to coloured ones (Andrén and Nilson, 1981), due to lower background matching and/or less disruptive patterns when the dominant background is not dark (Castella et al., 2013).

Finally, even the species' evolutionary history *per se* can influence the variability in dorsal colourations by noticeably affecting the spatial distribution of the different morphs (Corl et al., 2010). Indeed, processes such as the expansion of a species range to colonize new areas (Corl et al., 2010) or the cyclical alternation of glacial and interglacial periods (Provan and Bennett, 2008) can cause random fluctuations in morph frequencies within populations. When populations are small, fluctuations can determine the occurrence of bottleneck events leading to genetic drift. Therefore, the prevalence of one phenotype with respect to others at geographic scale might be the outcome of past processes of genetic drift rather than or along with a current response to selective pressures.

A melanin-based dorsal pattern polymorphism occurs in the common wall lizard (*Podarcis muralis*), a small lacertid lizard distributed throughout Europe, from the Iberian Peninsula to Turkey, and from Southern Italy and Greece to Northern France (Sillero et al., 2014). The species shows three main types of dorsal ornamentation (Sacchi et al., 2012), including a single, more or less continuous dark vertebral stripe (linear morph), a dorsal reticulation without any vertebral stripe (reticulated morph), and an intermediate pattern in which the reticulation forms a more or less continuous dark vertebral stripe (intermediate morph) (fig. 1). The linear morph has been found to occur more frequently in sub-montane than in lowland populations and in females than in males (Sacchi et al., 2012). However, information about morph frequencies at a wider geographic scale or over altitudinal clines is still scarce. Common wall lizard populations spread over a wide altitudinal range and face remarkable temperature gradients, thus providing a good opportunity to study the evolution of body colourations and its relationship with thermoregulation, habitat structure and evolutionary history of the species.

Therefore, in this study, we analysed the spatial pattern of distribution of the three dorsal phenotypes of common wall lizards all over its distribution range in order to assess whether the geographic patterns observed in phenotype distribution are associated with thermoregulation, habitat type (i.e., camouflage), sex or phylogeny. First, we looked for geographic patterns by searching for latitudinal, longitudinal or altitudinal clines of morph frequencies in both sexes. Secondly, we tested whether those patterns correlated with the temperatures and habitats of the sampling localities to estimate to what extent thermoregulation and camouflage may have driven such geographic patterns. Finally, we analysed the correlation between the recently detected genetic lineages of the target species (Yang et al., 2022) and the geographic patterns of dorsal morphs.

Materials and methods

Data collection

Data were acquired from the online database iNaturalist (https://www.inaturalist.org). From this source, we retrieved 9352 georeferenced points of the target species, of which 9169 (98%) were associated with a digital image. The photos were taken across 38 years, from 1983 to 2021. More than 92% was from 2019-2022 and only 1.5% was before 2010. We carefully checked the images of 4606 randomly
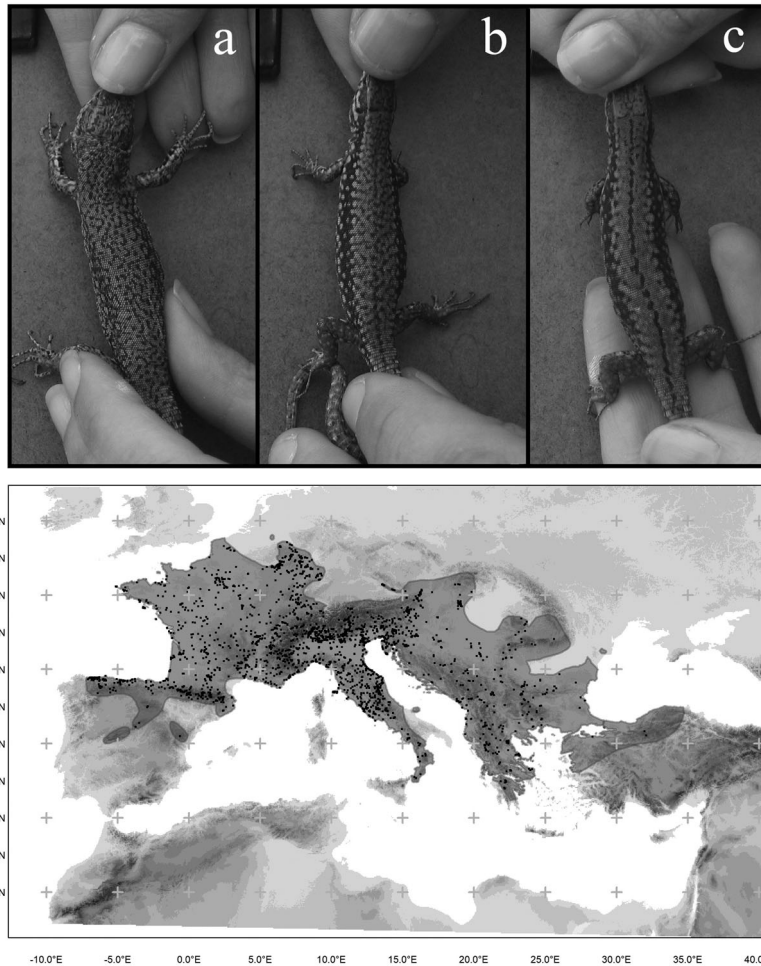
Figure 1. Representative pictures of the three dorsal morphs of the common wall lizard a) reticulated, b) intermediate, and c) linear phenotypes (Sacchi et al., 2012). The map represents the distribution of the 4096 georeferenced points with complete information about sex and dorsal phenotype used for the analyses. The dark grey area corresponds to the species distribution.

selected points (50.2%) in order to (i) confirm the species identification, and (ii) assess sex and phenotype (i.e., linear, reticulated or intermediate). Points associated with low quality images (sex and/or phenotype uncertain) were discarded (n = 510, 11.1%). By doing so, we assembled a sample of 4096 georeferenced points with complete information about sex and dorsal phenotype. We regarded this sample as representative of the spatial pattern of distribution of dorsal phenotypes. Given the very high number of different observers (more than 3000), we believe very unlikely that a directional pattern of preference toward one specific phenotype on a regional basis would have significantly bias the observed frequencies with respect to the actual ones.

Ecological and zoogeographical information for each point were extracted from high resolution digital maps available on the web using the package 'raster' (Hijmans, 2019) in R 3.6.3 (R Core Team, 2018). Altitude was extracted from the SRTM digital elevation maps (available at: https://www.

usgs.gov) with 1 arc-second resolution. Climatic information was obtained from the bioclimatic maps (1 km resolution) available at the WorldClim data website (https://worldclim.org). Variables were correlated one another, and we selected the two variables more informative on thermal ecology of the target species with the lowest correlation (Pearson correlation coefficient: $r_p = -0.19$) i.e., annual mean temperature (BIO1), and temperature seasonality (BIO4). Information about habitat was retrieved from the Corine Land Cover maps (CLC, available at: https://land.copernicus.eu), with 0.25 km resolution. We computed the percentage coverage of three target habitats over a circular buffer with 500 m of radius, centred on the coordinates of the species occurrence points. The three target habitats were grassland (CLC habitat codes: 18 pastures, 26 natural grasslands, and 27 moors and heathland), woodland (CLC habitat codes: 23 broad-leaved forest, 24 coniferous forest, and 25 mixed forest), and not vegetated habitat (CLC

habitat codes: 30 beaches-dunes-sands, 31 bare rocks, and 32 sparsely vegetated areas). We selected these three main habitats in relation with the shape of shading projected on the ground, which can directly affect the effectiveness of dorsal patterns to disrupt the outline of the body and reduce the risk of detection by predators (Díaz et al., 2017). Under this perspective, the linear pattern should be favoured in grasslands or woods, which project mainly linear or spotted shading, while reticulated morphs should prevail in open not vegetated habitats, where the background keeps irregular or absent shading (Jackson, Ingram, and Campbell, 1976). The three variables were not correlated one another ($|r_p| < 0.08$). Finally, each record was assigned to one of the six main clades (i.e., WE, Western Europe; SA, Southern Alps; CI, Central Italy; SI, Southern Italy; SB, Southern Balkans; NB, Northern Balkans, see supplementary fig. S1 (Yang et al., 2022), according to the geographic positions. In summary, our final dataset consisted of 4059 complete records (fig. 1), since 37 (0.9%) out of the 4096 georeferenced points were discarded because they lacked at least one ecological or zoogeographical covariate.

Statistical analyses

To analyse the geographic distribution of dorsal patterns occurring in both sexes, we modelled the probability to observe a given dorsal phenotype through a Generalized Linear Model (GLM) with binomial error distribution, where latitude, longitude, elevation, and sex were fit in the model as predictors. We also added the latitude × sex, longitude × sex, and elevation × sex two-way interactions in order to account for sexual differences in geographic patterns of morphs. Latitude, longitude and altitude were standardized to have zero mean and standard deviation equal to one in order to remove the effects of variables being measured at different scales. One different and independent model was performed for each morph (*Geographic model*). Then, we used the same approach to analyse the effect of the temperature on the probability of observing a given dorsal phenotype. In this case, the predictors implemented in the model were annual temperature, seasonality in temperature and sex. As in the previous model, all the two-way interactions with sex were also added to the predictors and variables were standardized to have equal range and/or variance (*Climatic model*). The effects of habitat variables on the probability of observing a given dorsal phenotype were modelled using grassland, wood, open habitat and sex and all the two-way interactions with sex as predictors (*Habitat model*). Finally, the effect of the clade was also analysed through a GLM in which the clade, sex, and the s ex × clade interactions were used as predictors (*Phylogenetic model*).

Models were fit in a Bayesian analytical framework available through the R (v. 3.6.3) package 'R2jags' (Su and Yajima, 2015), which uses the samplers implemented in JAGS 4.3.0. Uninformative normal priors ($\mu = 0$ and $\sigma = 0.001$) were used for model's coefficients, and gamma prior (a = 0.001 and b = 0.001 corresponding to $\mu = 1$ and $\sigma = 1000$) was used for the error term (σ). Three chains were run using randomly selected initial values for each parameter within a reasonable interval, and conventional convergence criteria were checked. The number of iterations was selected for each run to obtain at least 10 000 valid values for each chain after convergence and thinning. Model selection was based on the leave-one-out information criterion (LOOIC) (Vehtari, Gelman and Gabry, 2017; Tiberti, Mangiacotti and Bennati, 2021). For each model we calculated the mean LOOIC and its standard error (SE) using the package loo (Vehtari, Gelman and Gabry, 2017), and two models were regarded as different when their mean ± 1 SE LOOIC intervals did not overlap, the preferred model being the one with the lower LOOIC. Results from the posterior distribution are reported as the half sample mode (HSM; Bickel and Frühwirth, 2006) with 95% and 50% highest density intervals (HDI$_{95}$ and HDI$_{50}$; Meredith and Kruschke, 2018).

Results

Phenotypic frequencies

The majority of the analysed lizards, 2924 out of 4059 (72%), showed the linear dorsal pattern, while only 285 (7.1%) showed the reticulated one, and 850 individuals (20.9%) had the intermediate phenotype. However, relative phenotype occurrence varied significantly between sexes: the linear phenotype largely prevailed among females (84.2%), while slightly exceeding half in males (57.4%). By contrast, the reticulated morph was nearly six times more common in males than females (12.6% vs 2.3%) and the intermediate morph was more than double in males compared to females (30.0% vs 13.4%).

Spatial pattern of distribution in males and females (Geographic model)

The GLM based on spatial predictors clearly confirmed that the linear pattern occurred more frequently in females than males ($P_{(♀ > ♂)} > 0.999$; table 1), and showed a clinal variation both at geographic scale (table 1) and according with altitude (table 1). In detail, the probability of observing the linear phenotype increases with latitude (from South to North, $P_{(\beta > 0)} = 0.998$; fig. 2), longitude (from West to East, $P_{(\beta > 0)} > 0.999$; fig. 2), and altitude ($P_{(\beta > 0)} > 0.999$; fig. 2). Furthermore, these patterns were slightly different between sexes (fig. 2), in a way that the effect of latitude and altitude was

Table 1. Posterior distributions of the response variables for geographic, thermal, habitat and phylogenetic hypotheses as estimated by the corresponding GLMs. HSM and HDI$_{95}$ estimates are shown.

Model	Linear		Intermediate		Reticulated	
	Females	Males	Females	Males	Females	Males
Geographic model						
Sex	**1.759** (1.635 – 1.880)	**0.312** (0.217 – 0.406)	**−1.918** (−2.047 − −1.789)	**−0.862** (−0.965 − −0.765)	**−4.504** (−5.010 − −4.024)	**−2.045** (−2.202 − −1.899)
Quote	**0.595** (0.431-0.772)	**0.382** (0.279-0.491)	**−0.410** (−0.586 − −0.241)	**−0.243** (−0.357 − −0.125)	**−1.654** (−2.278 − −1.078)	**−0.394** (−0.560 − −0.237)
Latitude	**0.212** (0.089 – 0.339)	**0.152** (0.047 – 0.258)	−0.059 (−0.194 – 0.075)	0.063 (−0.049 – 0.178)	−0.930 (−1.292 − −0.593)	−0.451 (−0.621 − −0.291)
Longitude	0.009 (−0.106 – 0.119)	**0.208** (0.107 – 0.309)	−0.009 (−0.131 – 0.116)	−0.098 (−0.209 – 0.005)	**−0.004** (−0.245 – 0.246)	**−0.246** (−0.389 − −0.111)
Climatic model						
Sex	**1.693** (1.574 – 1.806)	**0.272** (0.175 – 0.370)	**−1.880** (−2.009 − −1.760)	**−0.851** (−0.950 − −0.750)	**−3.789** (−4.084 − −3.509)	**−1.943** (−2.082 − −1.806)
Mean annual temp.	−0.022 (−0.107 – 0.076)	−0.596 (−1.096 − −0.191)	0.032 (−0.070 – 0.118)	0.095 (−0.024 – 0.233)	−0.206 (−0.875 – 0.130)	0.098 (−0.024 – 0.224)
Seasonality	**0.214** (0.092 – 0.336)	0.066 (−0.034 – 0.169)	**−0.189** (−0.317 − −0.056)	−0.073 (−0.181 – 0.035)	**−0.303** (−0.600 − −0.007)	−0.062 (−0.208 – 0.086)
Habitat model						
Sex	**1.743** (1.616 – 1.866)	**0.303** (0.210 – 0.396)	**−1.921** (−2.055 − −1.792)	**−0.863** (−0.965 − −0.762)	**−5.238** (−7.257 − −3.974)	**−1.957** (−2.102 − −1.821)
Grassland	**0.134** (0.007 – 0.262)	0.050 (−0.044 – 0.148)	−0.070 (−0.199 – 0.056)	0.018 (−0.082 – 0.119)	**−1.077** (−2.190 − −0.259)	**−0.166** (−0.342 − −0.006)
Wood	**0.464** (0.182 – 0.801)	**0.138** (0.035 – 0.251)	**−0.404** (−0.740 − −0.136)	**−0.153** (−0.286 − −0.026)	**−6.049** (−15.32 − −0.269)	−0.051 (−0.218 – 0.101)
Open environment	**0.178** (0.057 – 0.301)	**0.251** (0.159 – 0.346)	**−0.162** (−0.296 − −0.035)	**−0.237** (−0.341 − −0.134)	−0.197 (−0.497 – 0.085)	−0.115 (−0.254 – 0.023)

Table 1. (Continued.)

| Model	Linear		Intermediate		Reticulated	
	Females	Males	Females	Males	Females	Males
Phylogenetic model						
Western Europe	**1.784** (1.608 – 1.958)	**0.274** (0.134 – 0.422)	**−1.888** (−2.072 – −1.710)	**−0.726** (−0.884 – −0.579)	**−4.412** (−4.990 – −3.886)	**−2.139** (−2.378 – −1.909)
Southern Alps	**1.352** (1.091 – 1.632)	−0.023 (−0.232 – 0.191)	**−1.468** (−1.758 – −1.197)	**−0.609** (−0.834 – −0.394)	**−4.027** (−4.903 – −3.240)	**−1.714** (−2.012 – −1.431)
Central Italy	**0.458** (0.174 – 0.742)	**−0.745** (−1.001 – −0.499)	**−1.134** (−1.460 – −0.819)	**−0.631** (−0.883 – −0.388)	**−1.788** (−2.193 – −1.399)	**−0.711** (−0.973 – −0.468)
Southern Italy	**48.99** (2.410 – 120.5)	0.557 (−0.995 – 2.117)	**46.14** (−101.7 – −2.703)	−0.556 (−2.131 – 0.951)	**−84.69** (−210.5 – −2.325)	**−116.5** (−294.5 – −1.845)
Northern Balkans	**2.309** (1.970 – 2.661)	**1.103** (0.830 – 1.377)	**−2.442** (−2.802 – −2.081)	**−1.225** (−1.507 – −0.942)	**−4.669** (−5.754 – −3.708)	**−3.839** (−4.717 – −3.059)
Southern Balkans	**2.344** (1.862 – 2.87)	**1.384** (0.974 – 1.795)	**−2.349** (−2.871 – −1.853)	**−1.57** (−2.009 – −1.140)	**−55.23** (−112.7 – −5.110)	**−3.65** (−4.769 – −2.691)
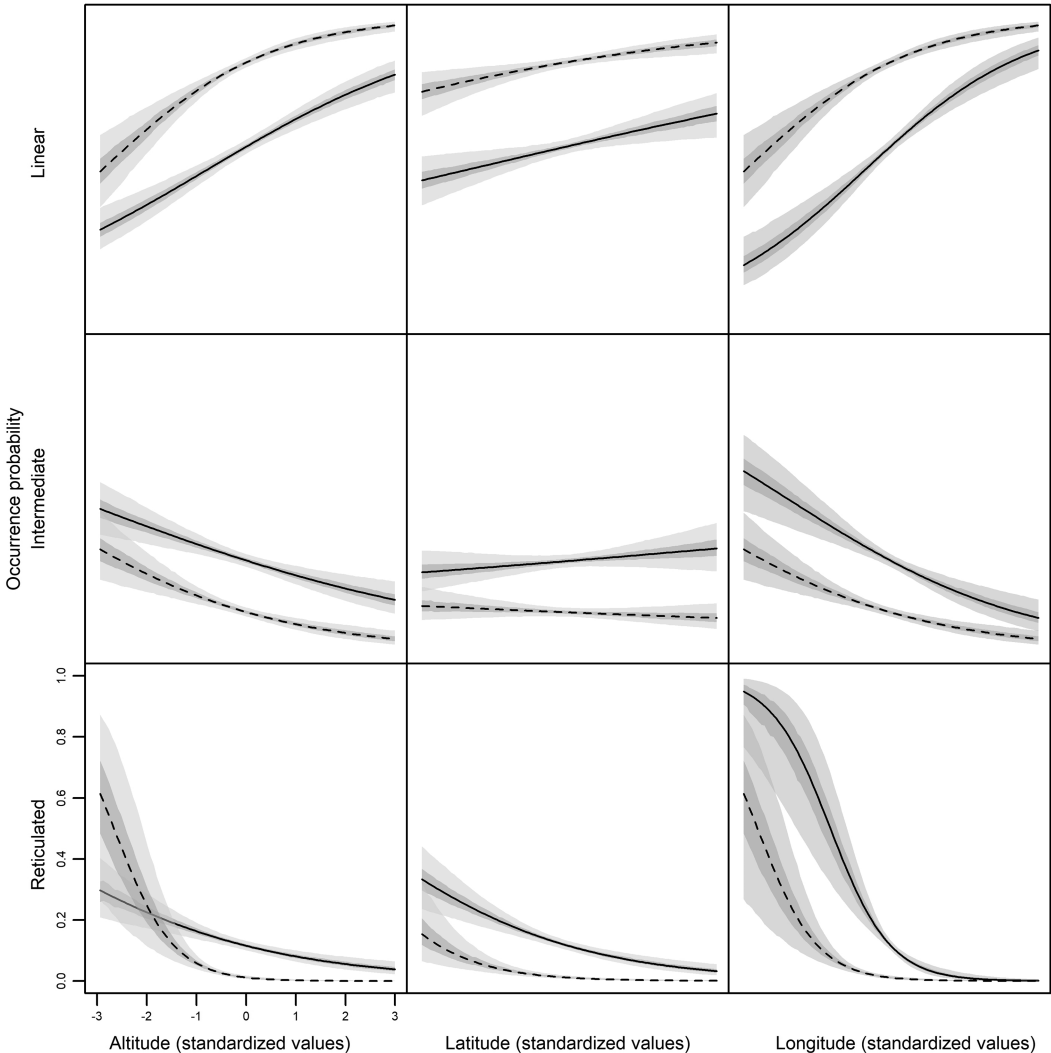
Figure 2. Variability of morph occurrence in response to the altitude, latitude and longitude as predicted by the geographic model. Lines indicate HSM (solid lines: males, dashed lines: females), and dark and light grey areas represent HDI_{50} and HDI_{95}, respectively.

more pronounced in females ($P_{(♀ > ♂)} = 0.759$, and $P_{(♀ > ♂)} = 0.983$ respectively), whereas the effect of longitude was more marked in males ($P_{(♀ > ♂)} = 0.004$).

The GLM model for the intermediate morph produced a pattern of response ultimately opposed to that of the linear morph (table 1, fig. 2). The intermediate pattern occurred more frequently in males than females ($P_{(♀ > ♂)} <$ 0.001), and the probability of observing it decreased with elevation ($P_{(β > 0)} < 0.001$;

table 1, fig. 2), following a stronger effect in females than males ($P_{(♀ > ♂)} = 0.057$). The longitudinal effect was weak, and the frequency of the intermediate morph decreased from West to East (fig. 2) in males only (females: $P_{(β > 0)} = 0.438$, males: $P_{(β > 0)} = 0.036$; table 1), whereas the latitudinal effect was negligible in both sexes (table 1).

The geographic pattern of the reticulated morph was comparable to that of the intermediate, but with much stronger effects (table 1).

The pattern was much more frequent in males than females ($P_{(♀ > ♂)} < 0.001$), and seemed to become significantly less frequent with increasing latitude ($P_{(β > 0)} < 0.001$; table 1, fig. 2) or altitude ($P_{(β > 0)} < 0.001$; table 1, fig. 2). Both effects were more pronounced in females than males ($P_{(♀ > ♂)} < 0.001$, and $P_{(♀ > ♂)} < 0.006$, respectively).

The probability of observing the reticulated morphs was lower with increasing longitude only in males (females: $P_{(β > 0)} = 0.485$; males $P_{(β > 0)} < 0.001$, $P_{(♀ > ♂)} = 0.954$; table 1, fig. 2).

Dorsal morphs frequencies and temperatures (Climatic model)

As expected, the GLM aimed to detect possible correlations between the frequency of dorsal phenotypes and the temperatures of the localities where they had been detected, and confirmed all the sex-based differences highlighted by the geographic model, for all the three morphs (table 1). The effects of the annual mean temperature (BIO1) on the occurrence of the three morphs in females were weak or negligible (fig. 3), as shown by the low probability of the beta coefficients (table 1) to deviate from zero (linear: $P_{(β > 0)} = 0.319$; intermediate: $P_{(β > 0)} = 0.747$; reticulated: $P_{(β > 0)} = 0.125$). By contrast, a relevant effect emerged for males (fig. 3, table 1). The probability of observing the linear morph in males decreased with increasing temperature ($P_{(β > 0)} < 0.001$), whereas the opposite trend was observed for intermediate ($P_{(β > 0)} = 0.950$) and reticulated ($P_{(β > 0)} = 0.946$) male morphs, even if the effect was less marked than in the linear one (fig. 3).

A weak effect on morphs occurrence also appeared for thermal seasonality (BIO4), in both sexes (table 1, fig. 3). The probability to observe the linear morph increases with increasing seasonality in both sexes (females: $P_{(β > 0)} > 0.999$; males: $P_{(β > 0)} = 0.897$), but the effect was stronger in females ($P_{(♀ > ♂)} > 0.999$; fig. 3). The other two morphs showed the opposite trend in both sexes (table 1, fig. 3).

The occurrence probability of the intermediate morph clearly decreased with increasing seasonality in both sexes (females: $P_{(β > 0)} = 0.002$; males: $P_{(β > 0)} = 0.091$), with a more pronounced effect in males ($P_{(♀ > ♂)} = 0.090$; fig. 3). The reticulated morph showed the same trend of response (females: $P_{(β > 0)} = 0.020$; males: $P_{(β > 0)} = 0.206$) as the intermediate one (table 1, fig. 3), and the effect was still more pronounced in males $P_{(♀ > ♂)} = 0.075$.

Dorsal morphs frequencies and habitat (Habitat model)

The "habitat model" supported the same intersexual differences within each phenotypic class that were detected with both previous models (table 1). The occurrence probability of the linear phenotype in females increased with higher relative abundance of each of three habitats we selected for the analysis (grassland: $P_{(β > 0)} = 0.984$; open habitat: $P_{(β > 0)} > 0.999$; wood: $P_{(β > 0)} = 0.998$; fig. 4). The opposite trend occurred in females of both the intermediate (grassland: $P_{(β > 0)} = 0.163$; open habitat: $P_{(β > 0)} = 0.001$; wood: $P_{(β > 0)} = 0.007$) and reticulated morphs (grassland: $P_{(β > 0)} < 0.001$; open habitat: $P_{(β > 0)} = 0.001$; wood: $P_{(β > 0)} = 0.087$; fig. 4). Both morphs became less frequent with increasing amounts of the habitats (fig. 4). Males showed the same pattern of response as females (table 1), but in a much less evident way (fig. 4). Indeed, in all habitats, the probability of observing the linear pattern increased (grassland: $P_{(β > 0)} = 0.847$; open habitat: $P_{(β > 0)} = 0.996$; wood: $P_{(β > 0)} > 0.999$), whereas it decreased for the reticulated one (grassland: $P_{(β > 0)} = 0.019$; open habitat: $P_{(β > 0)} = 0.253$; wood: $P_{(β > 0)} = 0.050$). However, the occurrence probability of the intermediate morphs in males was not affected by the amount of grassland ($P_{(β > 0)} = 0.635$), but negatively affected by that of open habitats ($P_{(β > 0)} = 0.005$) and woods ($P_{(β > 0)} < 0.001$; fig. 4).
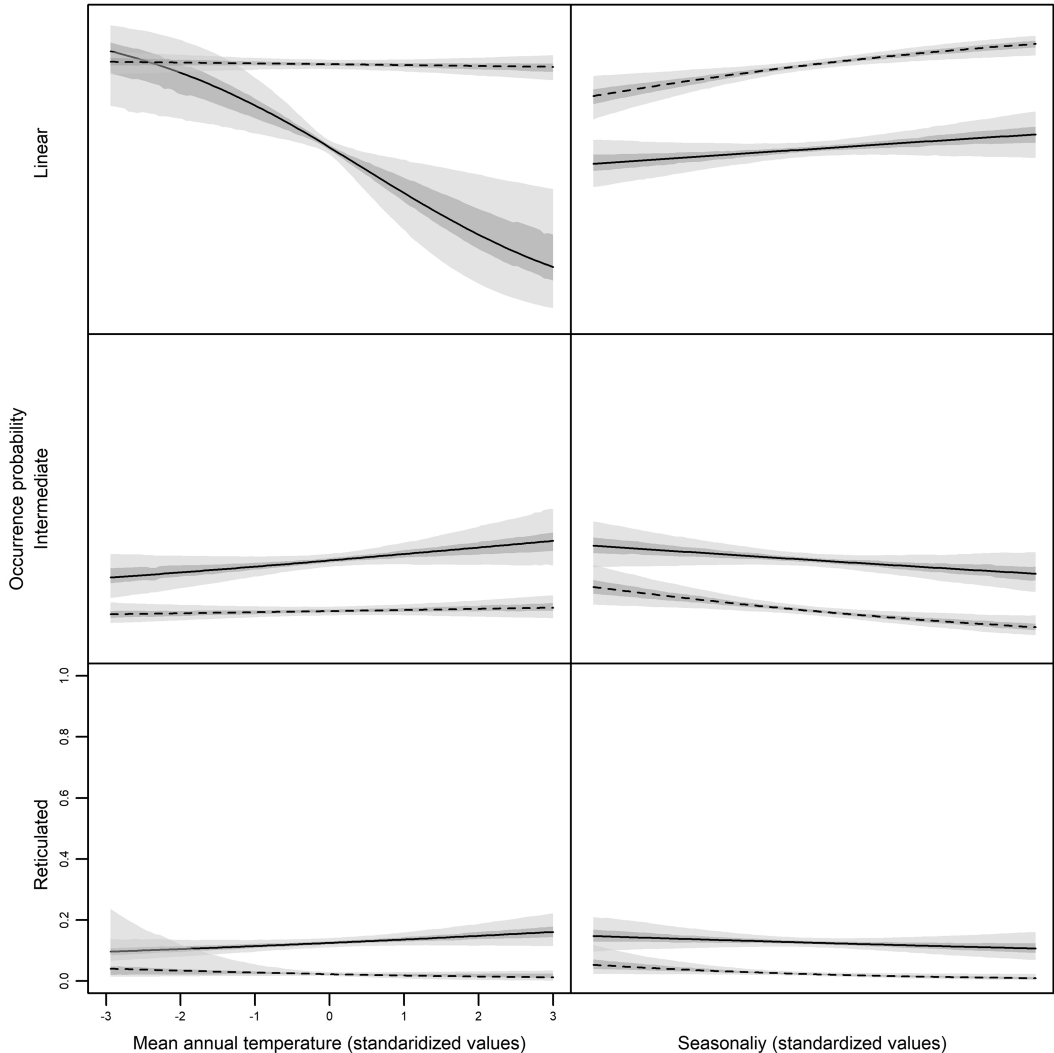
Figure 3. Variability of morph occurrence in response to the mean annual temperature (BIO1) and temperature seasonality (BIO4) as predicted by the thermal model. Lines indicate HSM (solid lines: males, dashed lines: females), and dark and light grey areas represent HDI_{50} and HDI_{95}, respectively.

Dorsal morphs frequencies and clades (Phylogenetic model)

The effect of sex detected by the GLM with the clade as a main predictor was fully consistent with that obtained in all the three previous models for each of the three morphs (table 1). In all clades, the linear morph was more frequent in females than males, while the opposite occurred for the intermediate and reticulated morphs (table 1, fig. 5). However,

the occurrence probability of each morph differed among clades, irrespective of sex (table 1, fig. 5). Indeed, the linear morph was more frequent in eastern (North and South Balkans) and southern clades (Southern Italy), whereas it was the least frequent in the Central Italy clade, for both sexes (table 1, fig. 5, see supplementary table S1 for details on pairwise comparisons). The intermediate phenotype occurred more frequently in Western Europe, Southern Alps and Italy, even if in males only for Southern Italy
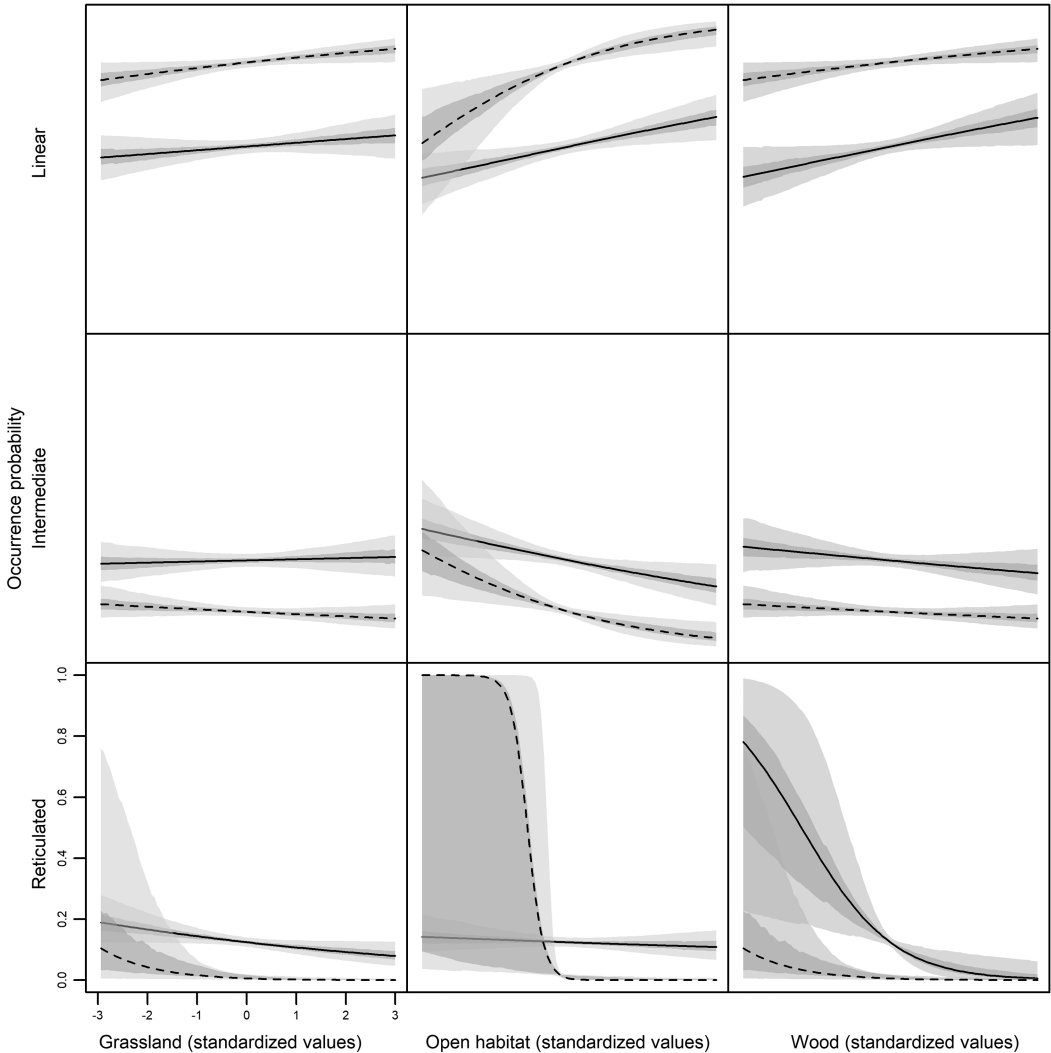
Figure 4. Variability of morph occurrence in response to the availability of grasslands, open habitats and woods annual as predicted by the habitat model. Lines indicate HSM (solid lines: males, dashed lines: females), and dark and light grey areas represent HDI_{50} and HDI_{95}, respectively.

(fig. 5, supplementary table S1). The intermediate morph was very rare in the two Balkan clades and in females of the Southern Italy clade (table 1, fig. 5). The reticulated phenotype occurred more frequently in both sexes of the Central Italy clade than in any other clade (fig. 5, table 1, supplementary table S1). It was still present in males of the Western Europe and Southern Alps clades (fig. 5), but with frequencies almost halved compared to the Central Italy one (fig. 5, supplementary table S1). In females of these last two clades, as well as in both sexes of North and South Balkans and Southern Italy, the reticulated phenotype was the rarest morph (fig. 5, table 1). Consequently, the Central Italy clade was the only one in which the three morphs occurred with similar frequencies, while in all other clade morph frequencies were biased toward the linear morph, especially in the eastern clades (fig. 5).
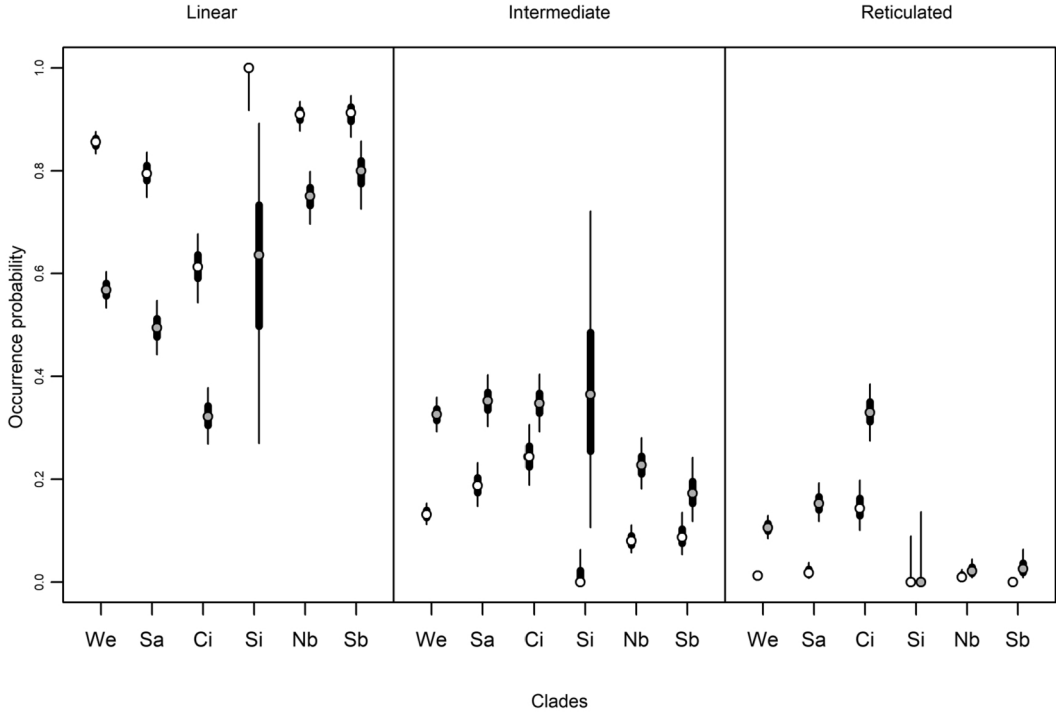
Figure 5. Variability of morph occurrence in relation to the phylogenetic lineages. Circles indicate HSM (grey: males, white: females), and thick and thin lines represent HDI_{50} and HDI_{95}, respectively.

Table 2. LOOIC values for the four GLM models explaining the occurrence of the three dorsal morphs of the common wall lizards according to the geographic distribution, temperature, habitats and phylogeny of the species. See methods for the definition of the structure of the competing models. The minimum values correspond to the best models.

	Linear		Intermediate		Reticulated	
	LOOIC	SE	LOOIC	SE	LOOIC	SE
Geographic model	−8.45	1.05	−7.60	0.97	−7.41	1.73
Thermal model	−5.81	1.06	−5.75	0.96	−5.77	1.35
Habitat model	−8.30	1.05	−7.55	0.98	−7.77	2.11
Phylogenetic model	−12.41	1.95	−11.21	1.86	−10.07	2.54

Model comparison

When comparing models within dorsal morph (table 2), the phylogenetic model always obtained the lowest LOOIC, and no overlap unless one SE with other models occurred. Therefore, the phylogenetic model was tangibly the best one explaining the distribution patterns of dorsal morphs. However, the habitat model showed very similar LOOIC values to the geographic model, as values were well inside the respective mean + SE intervals. Finally, the climatic model showed the worst performance as it absolutely gave the higher LOOIC values, with only a marginal overlap with the geographic and habitat models for the GLMs referring to the reticulated morphs.

Discussion

Geographic pattern and sexual dimorphism

In order to evaluate the relative importance of the possible ecological factors underlying the

variability of the dorsal patterns of the common wall lizard, in this paper we analysed the geographic pattern of morph frequencies across its range and in relation to ecological conditions such as climate and habitat. We showed that the phenotypes are not randomly distributed in Europe, but rather they occur following a clear geographic pattern. Indeed, the occurrence of the linear morph increases with altitude, from South to North as well as from West to East. A clear effect of sexual dimorphism emerged through the geographic model, as the linear phenotype is largely more frequent in females than males, whereas the opposite is true for the reticulated morph. The geographic and sexual patterns only slightly interacted with one another, and the intensity of sexual dimorphism (i.e., the difference between sexes for the probability of showing a given phenotype) remained substantially constant all over the species range. However, some deviations occurred in Southern Europe, notably in the Central and Southern Italy clades, where dimorphism was less marked if compared with the northernmost regions, probably because of the higher frequency of the intermediate and reticulated morphs here than anywhere else.

Sexual dimorphism in dorsal patterns has been reported in some species of reptiles (Forsman, 1995; Forsman and Shine, 1995; Gvoždík, 1999; Sacchi et al., 2012; Medina, Losos and Mahler, 2017). Although sexual selection is often well accepted for explaining sexual dimorphism, natural selection may also play a central role in promoting dimorphism (Slatkin, 1984). Under natural selection, sexual dimorphism arises when the dorsal patterns differently affect the survival rates of males and females (Forsman and Shine, 1995). For example, melanic females may have an advantage with respect to non-melanic ones in terms of thermal efficiency and thus reproductive output, despite being more susceptible to predators than males (Andrén and Nilson, 1981; Capula and Luiselli, 1994). Sexual dimorphism in dorsal patterns can also evolve in response

to natural selection through opposite microhabitat use by sexes as well as in response to climatic variation (Forsman and Shine, 1995; Thorpe and Stenson, 2003). We found that the effects of the ecological conditions, namely temperatures and microhabitats, affected the occurrence probability of dorsal phenotypes differentially in males and females, supporting the hypothesis that sexual dimorphism in dorsal pattern of this species might be linked to sex-specific responses to ecological trade-offs (e.g., thermoregulation vs camouflage) controlled by natural selection. Sexual selection, whether it is mate choice or male-male competition, is unlikely to be involved in the promotion and maintenance of these patterns, for two main reasons. Firstly, sexual selection generally favours conspicuous ornamentations and brilliant colourations, which function as male quality signals within the intraspecific communication system. The three dorsal phenotypes are poorly contrasted against the background and dully coloured, which are not typical features of sexual signals. Secondly, both inter- and intra-sexual selections, with some exceptions involving females (Cuervo and Belliure, 2013; Moreno-Rueda et al., 2021), tend to promote more prominent colourations in males. Neither of them is the case for *Podarcis muralis*, where the difference between sexes concerns the relative frequency of dorsal phenotypes, and not dorsal patterns, which are similar between males and females in each of the three morphs. However, it is necessary to point out that, given that we did not investigate colour variability in terms of detectability and background matching, bold conclusions cannot be drawn. Therefore, it appears essential for future research to address this matter to provide a broader perspective on the adaptive role of dorsal colourations and patterns in the model species.

By analysing the geographic distribution of the three dorsal phenotypes at the largest possible scale (i.e., the areal-wide scale), we achieved for the first time in this species a

high detailed comprehension of the interactions and the relative strength of the main factors (i.e., thermoregulation, camouflage and evolutionary history) potentially affecting the expression of the three phenotypes at population level. Indeed, a morph can be strongly advantaged in selection with respect to the others under certain environmental conditions or in a specific habitat, whereas it can be penalized in other circumstances. Consequently, different phenotypes may represent alternative strategies achieving similar fitness (Galeotti et al., 2003; Gasparini et al., 2009), and morphs' frequencies may not be stable through space when habitats and environmental conditions vary at geographic scale (Roulin, Burri and Antoniazza, 2011).

Climatic correlates

The climatic model provides low support for the hypothesis that thermoregulation could explain the geographic patterns of dorsal morphs, even if some effects consistent with the thermal advantage hypothesis for ectotherms (Clusella-Trullas et al., 2007) were detected in males. The effect of the average annual temperature was, in fact, negligible in the presence of any of the three morphs in females, whereas the probability of observing the linear dorsal pattern in males increased (while it decreased for the reticulated and intermediate ones) with decreasing temperatures. This pattern of response by males fits the predictions of the thermal advantage hypothesis, since the linear one should be the most advantaged pattern in colder climates, because it concentrates the melanised scales in few, large (linear) spots along the spine, thus allowing a greater efficiency to assimilate solar radiation (Lepetz et al., 2009). Though weak, an effect occurred for the seasonality of temperature, with the linear phenotype being more frequent under higher values of seasonality in both sexes, especially in females. Temperature seasonality is more pronounced in Northern than Southern Europe, leading populations at high latitudes to face a wider temperature range. As

for the mean annual temperature, the linear phenotype should be the most advantaged under sharp temperature variation because of the ability to heat up more rapidly thanks to lower skin reflectance (Clusella-Trullas et al., 2009). Even if this has not been experimentally assured, the linear morph might achieve and maintain optimal body temperatures more easily than reticulated or intermediate ones. This should confer to the linear morph an adaptive advantage in terms of time spent for food collection and assimilation, growth and reproduction (Clusella-Trullas et al., 2009). In accordance with the geographic model, going North and rising in altitude the probability of finding individuals (males) bearing the linear pattern increases, supporting the hypothesis that it could be promoted by natural selection for higher thermal efficiency in colder environments (Castella et al., 2013).

However, two main points raise some questions when we assume the thermoregulatory function as the main driver of phenotypes' geographic variability in common wall lizards. Firstly, temperature affected phenotype occurrence in males but not in females, which are generally more frequently and significantly affected by temperature variations in reptiles. For example, in snakes, melanic individuals grow faster and are larger than non-melanic ones, leading females to produce larger litters (Andrén and Nilson, 1981; Capula and Luiselli, 1994; Luiselli, 1995). There is general evidence that thermal advantages are similar in the two sexes and, even if females may be melanic more frequently than males, there are not marked (i.e., statistically significant) intersexual differences in melanism occurrence within population (Luiselli, 1995; Castella et al., 2013).

Secondly, thermal advantages of darker colourations are generally lower or absent in small-sized species, or alternatively the difference between darker and lighter phenotypes is too small to be ecologically relevant (Gvoždík, 1999; Bittner, King and Kerfin, 2002; Lorioux et al., 2008). For example, in small and

medium-sized garter snakes (*Thamnophis sirtalis*) no difference in heating rate or equilibrium temperature between morphs was found (Bittner, King and Kerfin, 2002), and the thermal advantage in two species of sea-kraits (*Laticauda* spp.) did not reliably account for the occurrence of darker phenotypes (Lorioux et al., 2008). Similarly, Gvoždík (1999) did not find any thermal benefit in darker compared to lighter individuals in *Zootoca vivipara*, which is a small lizard, with similar size to *P. muralis*. Accordingly, some support for the common wall lizard not having substantial thermal benefit from darker colourations has been provided by Tosini et al. (1992), who found a very low difference in skin reflectance between darker and lighter individuals, supporting the lack of thermal advantage for the former. However, this study involved only six individuals, so further studies are needed before concluding that melanism is not related to thermoregulatory functions in this species. Nonetheless, thermal advantages of dark-coloured lizards in terms of heating rate and net heat gain were recently demonstrated for *Sceloporus grammicus* (González-Morales et al., 2021). As a matter of fact, there is contrasting evidence across the literature regarding the thermal advantage hypothesis for melanism. Therefore, we believe that this matter should be addressed mildly and considered case by case because a multitude of biotic and abiotic factors can influence heat gain in lizards, such as size, elevation and behaviour (Carrascal et al., 1992; Plasman et al., 2020).

Habitat correlates

Our analyses showed that the probability of phenotype occurrence varied similarly (the linear phenotype increases whereas the intermediate and reticulated ones decreased) in response to the increased availability of the three habitats considered, regardless of their structure (i.e., the extent of the vegetation cover). This result is only partially in accordance with what expected under the hypothesis that camouflage was one of the main drivers of geographic variability in phenotypes occurrence at areal-wide scale. Indeed, more complex and conspicuous patterns are more easily detectable in prairies, whereas linear ones are more successful in avoiding spotting by blending better with the background (Jackson, Ingram and Campbell, 1976). Indeed, linear patterns are likely favoured in prairies because they resemble closely the shadows cast by filiform herbs as shown for some snakes where longitudinal stripes reduce predation rates in a prairie environment (Sacchi et al., 2012; Díaz et al., 2017).

The positive relationship between linear phenotype occurrence and the abundance of grassland suggests an adaptation of the animal's body colouration for background matching to conceal themselves. On the other hand, darker colourations have been shown to be disadvantageous in open environments lacking vegetation cover, thus exposing individuals to greater risk of predation than less dark ones because they are easier to detect, unless background is permanently dark (Gibson and Falls, 1979; Andrén and Nilson, 1981). The positive relation between linear phenotype occurrence and the abundance of open habitats can be interpreted as an adaptation of the animal's body colouration for background matching, as spotted individuals should match better a rocky background. Additionally, the positive relationship between linear phenotype occurrence and the abundance of woods is not easy to explain in terms of background matching. As a matter of fact, there is some evidence that darker individuals might be advantaged in forest habitat in the absence of sunny gaps, since they may heat faster and reach slightly higher body temperatures (Forsman, 1995; Clusella-Trullas et al., 2009; Castella et al., 2013). Furthermore, the lack of predators such as raptors could enhance the thermoregulatory advantage of being darker in cool and shady areas (Tanaka, 2007).

If, on the one hand, it can be difficult to assess from the habitat perspective why the linear phenotype becomes more frequent with increasing

latitude and longitude, on the other hand for altitude, a possible explanation can be formulated: at higher altitudes woodlands, prairies and bare rocks are predominant; hence linear phenotypes are expected to be more abundant as well.

Phylogenetic correlates

The most interesting result of this study was the large effect of the clade, which strongly correlated with the geographic distribution of dorsal phenotypes. Indeed, the most recent common ancestor of extant *P. muralis* probably appeared in the central Italian Peninsula and experienced an expansion in Southern Italy and northward in Europe following the Messinian salinity crisis (Yang et al., 2022). The dispersion out of Italy resulted in the differentiation of the six extant lineages on the Iberian (through France), Italian, and Balkan Peninsulas (Yang et al., 2022). Accordingly, the Central Italian clade was the only one in which the frequencies of the three dorsal phenotypes were equally distributed, while in all others European lineages the linear morph tends to prevail, especially in the eastern clades. Furthermore, the presence of a gradient can be detected from the Central Italy clade westwards, with a progressive increase of the linear phenotypes across the Southern Alps clade to the Western Europe clade. This pattern supported the hypothesis that the species, during the out-of-Italy colonization following the Messinian crisis, has undergone stochastic processes of selection, such as genetic drift, that caused linear-biased frequencies of the dorsal phenotypes.

An overall view

Classical theory predicts that the presence of multiple phenotypes evolves when promoting the ecological success of species, because it broadens the spectrum of environmental conditions to which individuals can adapt by establishing reproductive populations (Forsman et al., 2008; Pizzatto and Dubey, 2012). Indeed,

different morphs are able to survive under certain specific conditions or habitats, but not in others, so that each morph represents an alternative and equally fit strategy (Sinervo and Lively, 1996; Galeotti et al., 2003). Consequently, the frequency of phenotypes varies in space according to geographic patterns of environmental features by advantaging or disadvantaging specific morphs (Castella et al., 2013). This theory well applies to melanin-based polymorphisms in ectotherms, as body colour directly affects thermoregulation and predation risk with opposite effects by boosting thermal efficiency and reducing camouflage effectiveness (Andrén and Nilson, 1981; Forsman, 1995; Castella et al., 2013). Consequently, until now, all the studies performed on ectotherms with the aim of explaining the causes for morphs' frequency variability through time and space were ultimately based upon the trade-off between contrasting selective pressures related to thermal benefits or predator-prey interactions (i.e., camouflage, aposematism or mimicry; e.g., Roulin, 2004; Leaché et al., 2010; Rosenblum et al., 2010; Sacchi et al., 2012; Castella et al., 2013; Chen et al., 2013; Reguera et al., 2014; Medina et al., 2017). Nonetheless, in recent years there is increasing interest in studies on ectotherms from different taxa to address phenotypic variation at large spatial scale including information on phylogeny (e.g., Pincheira-Donoso et al., 2008; Aragón and Fitze, 2014; Pizzigalli et al., 2020). In this study we showed that geographic morphs' frequency variability in the common wall lizard also depends marginally, though significantly, upon thermal benefits or predator-prey interactions. However, the main factor explaining morphs' frequency variability through space at areal-wide extent is the genetic structure of the populations, namely the evolutionary history of the species and the spreading patterns that determined the current distribution of the species itself. Indeed, when comparing the effects on the morphs' geographic patterns, the phylogenetic one largely overcomes the two ecological ones (i.e., thermoregulation

and background matching). In other words, we cannot explain thoroughly the geographic pattern of dorsal phenotypes occurrence in the model species according only to present-day selective processes (e.g., the thermal and habitat models). Instead, the evolutionary history of the species must be taken into account, with respect to stochastic processes such as genetic drift in spreading out from a refuge area (Yang et al., 2022) as well as the long series of climatic and environmental events that the populations have faced in time and that have led to the present-day situation.

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Evolutionary history drives the geographical distribution of dorsal patterns in the common wall lizard (*Podarcis muralis*)

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Supplementary material

Table S1. Pairwise comparisons ($P_{row<column}$) of dorsal morph occurrence among clades within sex as estimates by the phylogenetic GLM.

Females **Males**

Linear

	Si	Nb	Sa	Sb	We		Si	Nb	Sa	Sb	We
Ci	<0.001	0.001	<0.001	0.001	<0.001	**Ci**	0.043	0.755	0.221	0.844	0.354
Si		>0.999	>0.999	>0.999	>0.999	**Si**		>0.999	>0.999	>0.999	>0.999
Nb			<0.001	0.546	0.003	**Nb**			<0.001	0.872	<0.001
Sa				>0.999	0.995	**Sa**				>0.999	0.988
Sb					0.014	**Sb**					<0.001

Intermediate

	Si	Nb	Sa	Sb	We		Si	Nb	Sa	Sb	We
Ci	>0.999	0.998	>0.999	0.999	>0.999	**Ci**	0.461	0.196	0.473	0.109	0.414
Si		<0.001	0.064	<0.001	<0.001	**Si**		0.001	0.552	<0.001	0.261
Nb			>0.999	0.614	0.997	**Nb**			>0.999	0.093	0.999
Sa				0.001	0.008	**Sa**				<0.001	0.197
Sb					0.960	**Sb**					>0.999

Reticulated

	Si	Nb	Sa	Sb	We		Si	Nb	Sa	Sb	We
Ci	>0.999	0.991	0.994	0.678	0.993	**Ci**	>0.999	0.994	>0.999	0.995	0.999
Si		<0.001	<0.001	<0.001	<0.001	**Si**		<0.001	<0.001	<0.001	<0.001
Nb			0.836	0.001	0.672	**Nb**			>0.999	0.614	>0.999

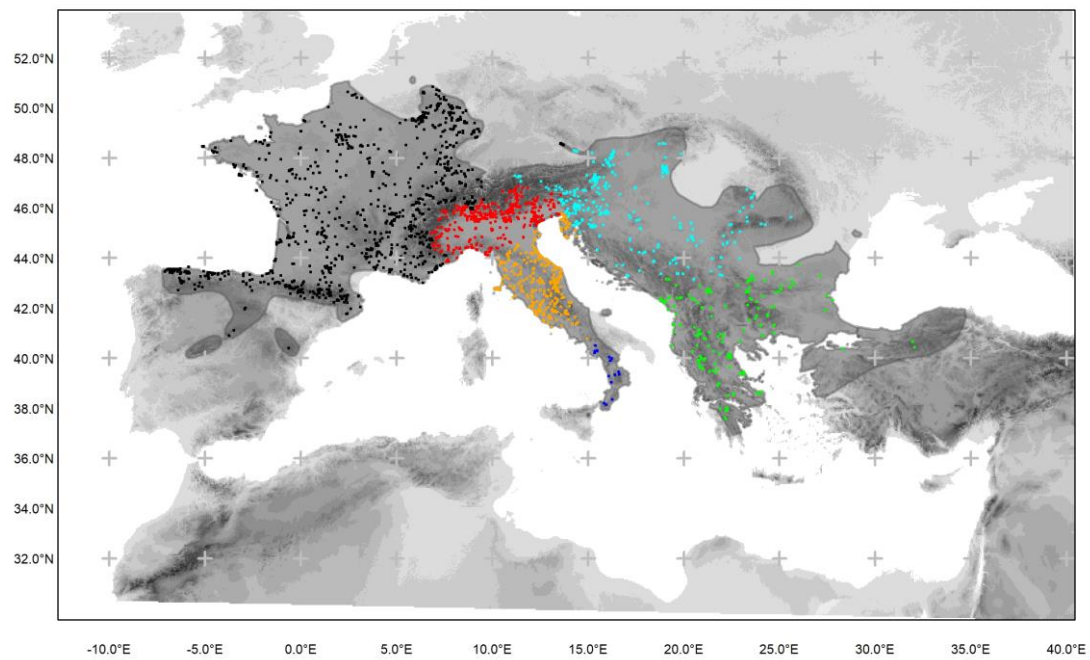|						
Sa			<0.001	0.223	**Sa**				<0.001	0.013
Sb				**>0.999**	**Sb**					**>0.999**

Figure S1. Classification of the the 4096 georeferenced points with complete information about sex and dorsal phenotype according to the genomic clades defined by Yang et al. (2022): black dots: Western Europe (WE); red dots: Southern Alps (SA); orange dots: Central Italy (CI); blue dots: Southern Italy (SI); green dots: Southern Balkans (SB); cyan dots: Northern Balkans (NB).