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Population dependent behavioral responses among color morphs of Common wall lizard (*Podarcis muralis*)?[§]

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Abstract. Color polymorphisms are common across reptile species and are frequently correlated with variation in behavior and other functional traits. Here, we tested whether the ventral color morphs (yellow, orange and white pure morphs, as well as yellow-orange and white-orange mosaic morphs) of Common wall lizards *(Podarcis muralis)* exhibit differential temporal changes in their reaction to exposure to a novel environment. We conducted 15 min long trials of a novel environment test (open field test) in a set of populations from the eastern Pyrenees. Locomotion, boldness and freezing behavior changed over time, in agreement with a previous study carried out in central Pyrenees, but without highlighting a clear behavioral difference among color morphs. Only yellow-orange lizards showed a distinct correlation pattern between locomotion and body size compared to the other morphs. Carefully standardized studies involving more populations are needed to unravel the complex interactions between morphological and behavioral traits among lizard color morphs.

Keywords. Behavior, color polymorphism, locomotion, open field test, Common wall lizard, *Podarcis muralis*, selection.

INTRODUCTION

Coexistence of multiple categorical color phenotypes within a single population (color polymorphism) has been reported throughout the animal kingdom, including lizards (Sinervo and Lively, 1996; Svensson, 2017). Maintenance of alternative genetically determined color phenotypes (i.e., color morphs) is often explained by complex evolutionary processes involving multiple selective forces (Sinervo and Lively, 1996; Svensson, 2017). Such morphs should be either characterized by equal fitness, or if fitness differences exist, rare morphs should be promoted by selection (Sinervo and Lively, 1996). This is usually explained as a consequence of the co-variation between color and other phenotypic traits, which results in development of alternative strategies involving complex combinations of behavioral, physiological, morphological or life history characteristics (Coladonato et al., 2020; Galeotti et al., 2013; Sacchi et al., 2007; Sinervo and Lively, 1996; Svensson et al., 2001; Thompson et al., 2023). In

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reptiles, variation in color within populations (including those that may be polymorphic) is often interpreted as an adaptive compromise between conflicting selective pressures exerted by social, antipredator, and thermoregulatory functions (Cooper and Greenberg, 1992).

Functional traits that sometimes covary with color, such as locomotor behavior, can influence the fitness of alternative color morphs and play a major role in regulating selective processes (Grant and Liebgold, 2017; Sreelatha et al., 2021). Animals with more active locomotion may be more exposed to predators and, hence, suffer increased risk of mortality (Werner and Anholt, 2015). However, high locomotor activity can be advantageous for finding resources (foraging or basking spots) as well as for social, and reproductive interactions (Arnold and Bennett, 1988; Boratyński, 2020; Huyghe et al., 2007; Pačuta et al., 2018; Sinervo et al., 2000). Animals with high level of boldness (prone to undertake risky behaviors) and low level of neophobia may explore an unfamiliar space (novel environment) more likely and faster (Damas-Moreira et al., 2020; White et al., 2013). On the contrary, reluctant to explore a novel environment (freezing), shy animals may avoid exploring unfamiliar space, reducing probability to forage under high predation risk (Evans et al., 2019). Consequently, some individuals can familiarize with novelty much faster than the others on exposure to a new environment and over short time intervals, differing in their locomotion and freezing behaviors (Pačuta et al., 2018; Sreelatha et al., 2021). Even though the locomotion of lizards is strongly dependent on environmental temperature (Braña, 1991; Paladino, 1985), they may develop alternative strategies corresponding to these behaviors. An interplay between the alternative behavioral strategies and morphological, physiological and life history traits might eventually affect the variable fitness optima of color morphs (Pérez i de Lanuza and Font, 2015; Sacchi et al., 2017, 2018; Sinervo and Svensson, 2002).

The Common wall lizard, *Podarcis muralis* (Laurenti, 1768), exhibits ventral color polymorphism characterized by three pure color morphs (yellow, white, orange) and two intermediate (i.e., mosaic) morphs (yellow-orange and white-orange; Aguilar et al., 2022; Pérez i de Lanuza et al., 2013, 2018; Scali et al., 2013). Previous studies have identified cases where these color morphs use alternative resources, optimizing their fitness to local adaptive optima (Abalos et al., 2016; Coladonato et al., 2020). In the Eastern Pyrenees region, the local frequencies of yellow and yellow-orange morphs seem to be constrained by climatic factors, whereas white, orange and white-orange morphs are widely distributed over species range (Pérez i de Lanuza et al., 2018). At smaller spatial scales, orange animals prefer more humid microhabitats than other morphs (Pérez i de Lanuza and Carretero, 2018; Scali et al., 2016). The local diversity of the morphs can also depend on the intensity of sexual selection (i.e., sex-ratio, emerging rare yellow and yellow-orange morphs in male-biased populations; Pérez i de Lanuza et al., 2017). Thus, the color polymorphism within populations of *P. muralis* appears to be locally maintained by a combination of environmentally dependent and sexual selections, showing a great geographical dependence (Calsbeek et al., 2010; Galeotti et al., 2013; Pérez i de Lanuza et al., 2013, 2018; Pérez i de Lanuza and Carretero, 2018; Sacchi et al., 2007).

In a previous study, focused on the behavioral strategies of the three pure morphs of *P. muralis* from Val d'Aran (central Pyrenees), we found that the morphs differed in locomotion and freezing behavior, and showed significant changes throughout a 15-minute experimental trial (Sreelatha et al., 2021). Yellow animals showed a risk sensitive strategy, by exploring the novel environment quickly and gradually decreasing the locomotion over time, moving to potentially safe areas. Orange and white lizards showed a risk aversive strategy, with the opposite pattern. Such variation in locomotion was repeatable over consecutive experimental trials (Sreelatha et al., 2021). Here, we extend our approach by testing if *P. muralis* color morphs differ in behavioral strategies in populations from an independent, more anthropized area within the same region. We quantified behavioral traits of the several morphs by exposing them to a novel environment. By doing so, we aimed at generalizing our previous findings, which suggested behavioral differences among morphs. Additionally, we also explore eventual maladaptive behaviors in the mixed morphs, which are often less frequent in natural populations than expected, assuming random pairing (Pérez i de Lanuza et al., 2013).

MATERIALS AND METHODS

Sampling was conducted in small towns of the Cerdanya plateau (Fig. S1), eastern Pyrenees, about 90 km eastwards the area of the previous study (Val d'Aran; Fig. S1), during the breeding season in June 2019. We captured 94 adult male lizards, including both pure (orange: N = 24, white: N = 24, yellow lizards: N = 26) and mosaic (white-orange: N = 9 and yellow-orange: N = 11) color morphs. After capture, lizards were acclimatized to the laboratory conditions for at least 24h (with water *ad libitum*) before the experimental trials (Pačuta et al., 2018). The snout-vent length (SVL; ± 0.01 mm) was recorded as a measure of lizard size. We restricted the analysis only to adult lizards (i.e., SVL ≥ 56 mm; Pérez i de Lanuza et al., 2013).

We measured the behavioral responses to the novel environment using an open field arena (1×1 m, walls: 0.25 m, white in color) in a temperature-controlled room (30 ± 1.5 °C, around the preferred body temperature of the animal; Braña, 1991) that was unfamiliar to the lizards (Montiglio et al., 2010; Sreelatha et al., 2021). A video camera (Casio EXILIM EX-F1, filming at 50 frames per second) was placed directly above the open field for recording the experimental trials. The trials were started by gently placing the animal in the middle of the open field arena, covered by an opaque plastic cup placed upside down. For minimizing the disturbance to the animal, nobody was present in the trial room during the experimental trials. After 2 minutes of acclimatization time, the cup was gently removed, and the animal was allowed to explore the open field arena. The activity of the animal was recorded with the video camera for another 15 minutes. At the end of each trial, the animal was removed from the arena and the arena was thoroughly cleaned with 70% ethanol. Two arenas were used in rotation. All the animals were subjected to the trials no later than 48h from their time of capture, and then released to their exact point of capture.

Using the Ethovision XT 14 software (Noldus, The Netherlands), animals were automatically tracked from the videos to record their movement and duration spent in the different parts of the arena (center: 0.6 × 0.6 m; border zone excluding corners: 0.6 × 0.2 m; corners: 0.2 × 0.2 m; Sreelatha et al. 2021). We measured 14 behavioral variables (Table S1); total distance moved in the arena, distance moved in center, corners and border zone (cm), duration of time lizards spent in the center, corners and border zone (s), number of visits to the center, corners and border zone, duration of the mobility (s), number of times the mobility was initiated, mean and maximum velocity (cm/s; Noldus et al., 2001; Sreelatha et al., 2021). To evaluate the short-term responses of the morphs in the measured locomotor and behavioral traits on exposure to a novel environment, the 15-minute duration was divided into 2.5 minutes intervals (six time intervals, Sreelatha et al., 2021). An alternative analysis with 5 min interval duration was also conducted producing comparable results (Table S2). All the measured traits in different scales were standardized by scaling and centering prior to the analysis. To summarize the data, the 14 correlated behavioral traits were reduced to a few uncorrelated components using principal component analysis (PCA) with varimax rotation on data combining information from six-time intervals for each animal. The first four rotated principal components (RCs), each explaining > 5% of the variance in the data with eigenvalues > 1, were considered for further analyses (Table S1, Fig. 1).

In order to determine if the behavioral traits change during the trial duration and vary among the color morphs, we conducted linear mixed model analyses fitted with the function "lmer" in the "lme4" (Bates et al., 2015) package in R v.3.5.0 (R Core Team, 2018). We used four different models with each of the four principal components as dependent variable. Morph (five levels) and time (six-time intervals, ordered categorical variable) were included as factorial predictors while SVL (scaled and centered) was included as a continuous predictor. Two-way interactions between morph and SVL, as well as morph and time, were tested. To reduce the complexity of the model we used a stepwise backward elimination of non-significant interactions (P > 0.05). Individual ID was encoded as a random factor.

RESULTS

The first four rotated-principal components explained 85% of variance observed in the data. The first rotated-principal component (RC1: Table S1; Fig. 1) explained 44% of the variance and was positively correlated with variables representing locomotion, such as total distance moved, distance moved in the corners and border zone, number of visits to the corners and borders,

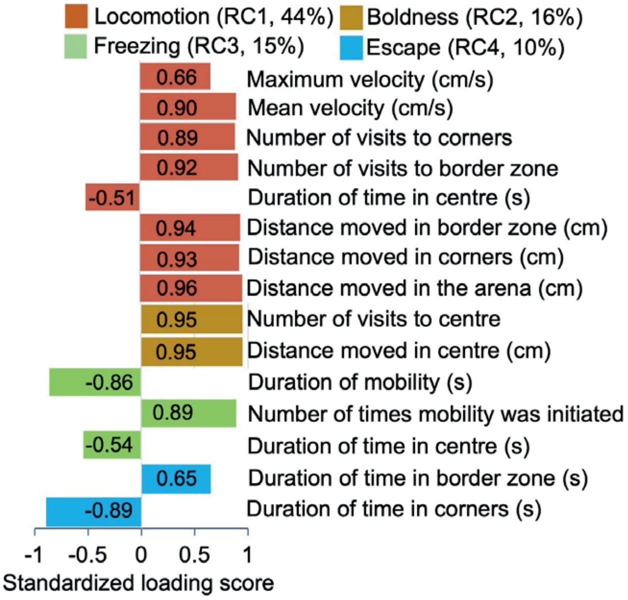

Fig. 1. Results from principal component analysis on behavioral variables obtained after tracking *Podarcis muralis* lizards in an open field arena. The analysis was conducted on 15-minute-long trials, divided into 2.5 minute intervals.

Table 1. Differences in behavioral traits (rotated principal components) among the five color morphs (orange, white, yellow, yellow-orange and white-orange) of *Podarcis muralis*. The analysis was conducted on 15 min long trials, divided to 2.5 min intervals. Models included individual ID as random factor. MS refers to mean square, and $F_{n,d}$ to F statistic with degrees of freedom for numerator and denominator.

Dependent variables	Predictors	MS	$F_{n, d}$	P
Locomotion (RC1)	Morph	0.27	$0.78_{4, 84}$	0.54
	Time	6.77	$19.57_{5, 465}$	<0.001
	SVL	0.00	$0.01_{1, 84}$	0.97
	SVL: Morph	1.12	$3.23_{4,84}$	0.02
Boldness (RC2)	Morph	1.44	$1.75_{4, 58.54}$	0.15
	Time	0.98	$1.19_{5, 465}$	0.31
	SVL	0.99	$1.20_{1, 86.88}$	0.28
Freezing (RC3)	Morph	0.08	$0.80_{4,88}$	0.53
	Time	92.84	$968.88_{5, 465}$	<0.001
	SVL	0.11	$1.16_{1, 88}$	0.28
Escape (RC4)	Morph	0.64	$0.81_{4, 88}$	0.52
	Time	0.15	$0.19_{5, 465}$	0.97
	SVL	0.63	$0.80_{1, 88}$	0.37

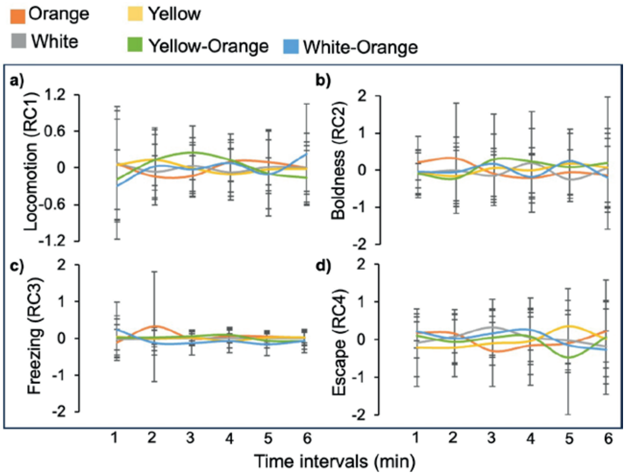

Fig. 2. Changes over time of the behavioral traits among color morphs (orange, white, yellow, white-orange and yellow-orange) of *Podarcis muralis* lizards. The residual scores of behaviors are averaged (± SD) within morph and time interval. The 15-minute trials were divided to 2.5-minute time intervals during the analyses: (1) 0.0–2.5 min; (2) 2.5–5.0 min; (3) 5.0–7.5 min; (4) 7.5–10.0 min; (5) 10.0–12.5 min; (6) 12.5–15.0 min. In order to obtain the residual scores of locomotion, we adapted a mixed model including the scores of principal components as dependent variables, morphs and time as predictors and individual ID as random factor.

number of times the mobility was re-initiated, and mean and maximum velocity of mobility. The second rotated-principal component (RC2: Table S1; Fig. 1) explained 16% of the variance and was positively correlated with variables representing boldness, notably distance moved in the center and number of visits in the center. The third rotated-principal component (RC3: Table S1; Fig. 1) represented 15% of the variance and was positively correlated with variables linked to freezing, i.e., number of times the mobility was re-initiated, and negatively correlated with the duration of mobility. The fourth rotated-principal component (RC4: Table S1; Fig. 1) explained 10% of the variance and correlated with variables signifying the effort of animals to escape from the arena, i.e., duration of the time spent near borders, and negatively correlated with the time spent in corners.

Locomotion changed significantly over time (RC1: $F_{5,465}$ =19.57; P < 0.001; Table 1), decreasing significantly from the fourth time interval till the sixth (Table S3), irrespectively of the color morph (morph by time interaction: $F_{20,445}$ =1.07; P = 0.38; Fig. 2). There was correlation between body size and locomotion of the different color morphs (SVL by morph interaction: $F_{4,84}$ =3.20; P = 0.016; Tables 1, S3; Fig. S2). However, only in the yellow-orange animals locomotion decreased significantly with body size ($F_{1,22}$ = 5.52; P = 0.040; Table S4; Fig. S2). Analysis showed that boldness did not change over the trial duration (RC2: $F_{5, 465}$ = 1.19; P = 0.31; Table 1; Fig. 2) while freezing behavior was positively correlated with trial duration (RC3: $F_{5, 465}$ = 968.88, P < 0.001, Table 1, Table S5, Fig. 2). The levels of escape behavior remained similar during the trial ($F_{5, 465}$ = 0.19, P = 0.97; Table 1; Fig. 2). The responses for boldness (RC2: $F_{4, 58.54}$ = 1.75; P = 0.15; Table 1), freezing (RC3: $F_{4, 88}$ = 0.80; P = 0.53; Table 1) and escape behaviors (RC4: $F_{4, 88}$ = 0.81; P = 0.52; Table 1) did not depend on morph types. Analysis after excluding mosaic morphs from the data showed similar results (Table S6).

DISCUSSION

Our results indicate that males of *Podarcis muralis* shifted locomotion and freezing behaviors with time on exposure to a novel environment, but without marked differences among the morphs. The only significant difference detected is in the correlation between locomotion and body length, where the yellow-orange mosaic morph showed a different (negative) relation compared to the other morphs. Pure and mosaic color morphs shifted freezing behavior similarly with time on exposure to a novel environment. The efficiency of locomotion might be dependent on the body size of animals (Lindstedt, 1987). Thus, the significant interaction between morph and body size perhaps suggest that growing individuals may change their behavioral strategies with age (Makai et al., 2020). This also suggests that investigating behavioral mechanisms behind color polymorphism can be very complex, requiring much higher sample size than in this and many other studies. Meanwhile, negative results should be treated with caution.

In our previous study we showed behavioral differences among pure morphs of *P. muralis* from Val d'Aran, particularly in locomotion, freezing and escape behaviors. Yellow lizards were expressing a risk sensitive strategy, while white and orange lizards follow risk aversive strategy (Sreelatha et al., 2021). Results from the same lizard species but from another population (Cerdanya plateau) presented here suggest differential behavioral responses, indicating that these morph specific behavioral patterns are not consistent between the two populations. The substantial difference in the levels of anthropization and human disturbance, as well as other unmeasured parameters between the study areas could account for these different outcomes. The environmental context of such behavioral differences should be investigated with a wider population dataset. Previous studies indicate that higher disturbance implies shier behavior towards predator-simulated attacks, but also suggest that such behaviors are modulated by habitat (Carretero et al., 2013). Open and more disturbed habitats in Cerdanya area may be shifting behavior of the lizards towards shyness and, hence, masking any differences among morphs. This advises for caution while generalizing the results of the color morphs of *P. muralis* (Labra and Leonard, 1999). To confirm these hypotheses, further studies are needed comparing populations or eventually manipulating human disturbance and predation pressure.

Finally, mosaic morphs in Cerdanya area apparently follow the same behavioral patterns as pure morphs in locomotion, boldness, freezing, and escape behavior, discarding eventual negative selection. Our field observations indicate that *P. muralis* populations from Val d'Aran and Cerdanya differ in the proportion of yellow animals, relatively common in Cerdanya but rare in Val d'Aran. This may lead to reconsideration of the role of alternative strategies and local adaptation in maintaining color polymorphism, incorporating the processes overlooked heretofore. To provide firm conclusions further experiments are needed where standardized conditions are carefully maintained for individuals originating from variable populations and localities. Sample sizes of hundreds of individuals from variable habitats and morphs are needed for carefully designed tests targeting specific behaviors. Finally, extensive investigation with multiple populations and species from variable habitats is needed for generalizing any conclusions.

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SUPPLEMENTARY MATERIAL

Supplementary material associated with this article can be found at <http://www.unipv.it/webshi/appendix> Manuscript number 14610.

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