

Original Article

Color-assortative mating in a color-polymorphic lacertid lizard

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Color polymorphisms are common in lizards, which provide an excellent model system to study their evolution and adaptive function. The lacertid genus *Podarcis* is particularly interesting because it comprises several polymorphic species. Previous studies with lacertid lizards have tried to explain the maintenance of color polymorphisms by correlational selection between color morphs and several phenotypic traits. Particular attention has been paid to their putative role as signals reflecting alternative reproductive strategies under frequency-dependent selection, but the relationship between mating patterns and color polymorphism has not been previously considered. In this study, we use longitudinal behavioral data obtained during six consecutive breeding seasons (2006–2011) in a free-ranging polymorphic population of *Podarcis muralis* lizards to examine the hypothesis that lizards mate assortatively by color. We provide spectrophotometric data that confirm the existence of discrete color morphs and show that morphs are ontogenetically stable once they develop fully in sexually mature individuals. We also present data on the year-to-year variation of relative morph frequencies. Finally, we provide evidence that, over a 6-year period, homomorphic male–female pairs in the wild were significantly more common than heteromorphic pairs. Taken together, our results suggest that color assortative mating may be involved in the maintenance of discrete color morphs in this and other lacertid species. **Key words:** alternative reproductive strategies, assortative mating, color variation, polymorphism. [*Behav Ecol*]

INTRODUCTION

A major challenge in evolutionary biology is to understand the genetic mechanisms and evolutionary processes involved in the maintenance of phenotypic variation, including color polymorphisms (Roulin 2004; Chunco et al. 2007; Pryke and Griffith 2007; McKinnon and Pierotti 2010). Studies with lizards have contributed importantly to this endeavor and suggest that the lizard model is an ideal one in which to test hypotheses and predictions about the evolution and maintenance of color polymorphisms (Sinervo and Lively 1996; Zamudio and Sinervo 2000; Vercken et al. 2007). Color polymorphisms are common in lacertids (Arnold and Oveden 2002) and typically consist of lizards exhibiting either white or orange ventral colorations (i.e., throat and/or belly), although some populations feature an additional yellow morph as well as several rare intermediate phenotypes. Polymorphic populations of lizards seem to be particularly abundant in the lacertid genus *Podarcis* (*Podarcis melisellenis*, Huyghe et al. 2007, 2009a,b, 2010a,b; *Podarcis muralis*, Cheylan 1988; Sacchi et al. 2007a,b, 2009; Calsbeek et al. 2010; Galeotti et al. 2010; Font et al. 2010; *Podarcis gaigeae*, Runemark et al. 2010; *Podarcis vaucheri* and *Podarcis liolepis*, Pérez i de Lanuza G, unpublished data), which makes it an excellent system to study the evolution, maintenance, and adaptive function of genetic color polymorphisms.

Although different evolutionary processes may underlie color polymorphisms (Roulin 2004; Bond 2007; Gray and McKinnon 2007; Roulin and Bize 2007), work on lizards has mainly focused on the search for phenotypic syndromes associated with discrete color polymorphisms (e.g., Sinervo and Calsbeek 2006; Calsbeek et al. 2010). Several studies have explored potential differences across color morphs in a number of life history, behavioral, performance, morphological, ecological, and physiological traits. In particular, much attention has been paid to the possibility that lacertid color polymorphisms reflect the existence of alternative reproductive strategies that would be maintained by frequency-dependent selection (Sinervo and Lively 1996; Sinervo et al. 2007). In *P. melisellenis*, males of different color morphs have been found to differ in several phenotypic traits (i.e., morphology, fighting ability, corticosterone levels, hemoparasite infection levels, immune response) that hint at the existence of alternative reproductive strategies (Huyghe et al. 2007, 2009b, 2010a). In the wall lizard (*P. muralis*), male morphs do not differ in aggressive levels or fighting success, although immune response and susceptibility to stress in captivity appear to covary with color morphs (Sacchi et al. 2007a, 2009; Galeotti et al. 2010). Calsbeek et al. (2010) recently reported differences among *P. muralis* morphs in hemoparasite infection rate, intensity, and probability of survival. These authors proposed that *P. muralis* morphs experience different multivariate selection pressures and suggested that such correlational selection may have favored the evolution of alternative optimal morph-specific phenotypes (Lande and Arnold 1983; Forsman et al. 2008). However, the fact that multiple phenotypic optima may underlie alternative behavioral strategies does not explain why each strategy should be associated with a different ventral coloration (Roulin 2004); indeed, there is no experimental confirmation of the presumed signaling role of ventral colorations or of the information they

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make available to potential receivers. In conclusion, we are still far from identifying the genetic and evolutionary processes underlying the maintenance of color polymorphisms in lacertid lizards.

Mate choice has been put forward as one of the evolutionary mechanisms that can contribute to maintaining color polymorphisms (Roulin 2004; Pryke and Griffith 2007; Puebla et al. 2007; Reynolds and Fitzpatrick 2007; Elmer et al. 2009). Although the evolution of monotonic directional preferences is predicted for condition-dependent color traits, in polymorphic systems, color-based mate choice decisions may be morph-specific. This will happen when the reproductive fitness of mating with a given morph is dependent on the morph of both sexes (Roulin 2004; Pryke and Griffith 2009) and will be reflected by the existence of nonrandom assortative or disassortative mating between different color morphs (Lank 2002; Galeotti et al. 2003; Roulin 2004; Gray and McKinnon 2007; Pryke and Griffith 2007; Roulin and Bize 2007).

Here, we address the possibility that mate choice patterns (i.e., mate recognition/assessment sensu Johansson and Jones 2007) may be nonrandom with respect to color morph. To this end, we used data collected over six consecutive breeding seasons in a free-ranging polymorphic population of *P. muralis*: 1) to objectively evaluate (i.e., using spectrophotometric methods) the existence of discrete color morphs, 2) to assess the ontogenetic stability of color morphs, 3) to study interseasonal variation in relative morph frequencies, and 4) to analyze the existence of assortative color-based mating between different morphs.

MATERIALS AND METHODS

Study population

We studied a white–yellow–orange polymorphic population of *P. muralis* from the Cerdanya valley in the south-eastern Pyrenees. In this population, males and females typically exhibit three alternative pure-color morphs (white, W; yellow, Y; orange, O), although some individuals show intermediate phenotypes consisting of a mosaic of white and orange scales (WO) or a mosaic of yellow and orange scales (YO). Despite extensive sampling, we did not find lizards with an intermediate white and yellow phenotype as described by Calsbeek et al. (2010). Whereas in males ventral colorations extend over the throat and belly, in females yellow and orange colorations are restricted to the throat (i.e., the belly is always white). All the lizards included in this study came from a homogeneous, continuous population, so our estimates of morph frequency are not confounded by interpopulation differences in morph frequencies, which seem common in this species (Cheylan 1988; Sacchi et al. 2007b; Pérez i de Lanuza G, unpublished results).

Color morph characterization, color morph development, and polymorphism stability

Our main study area was a 2.1 Ha continuous patch of abandoned cultivated terraces with artificial stonewalls and sparse vegetation mainly consisting of ashes, rosebushes, hawthorns, and blackthorns. Each spring between 2006 and 2011, we performed field surveys in this area during 4–5 weeks from late May to early July. Overall, we captured 770 animals for which we determined color morph (eye-based assignment), sex, and age (i.e., juvenile, subadult, or adult). We measured body size (as snout-vent length, SVL), body mass, and head width in all the lizards, and throat coloration in a subsample of adult males and females. To obtain objective measurements of throat coloration, we used a USB2000 portable spectrometer with a PX-2 Xenon strobe lamp (Ocean Optics Inc.,

Dunedin, FL) and standard spectrophotometric techniques (for details see Font et al. 2009; Pérez i de Lanuza and Font 2011). We restricted color analyses to the 300–700 nm range, which encompasses the visual spectrum of diurnal lizards (Fleishman et al. 1993, 1997; Loew et al. 2002). We measured brightness (Q) and hue (H) according to Endler's Segment Classification method (Endler 1990). Additionally, we calculated medium wavelength chroma (MC) as $R_{400-600}/R_{300-700}$, where $R_{400-600}$ and $R_{300-700}$ are the sums of the percent reflectance between 400 and 600 nm and between 300 and 700 nm, respectively. We chose this chroma variable because chromatic differences among color morphs are due mainly to variation in reflectance between 400 and 600 nm (see Figure 1). We also calculated the spectral location of the median reflectance (R_{50} , i.e., the difference between maximum and minimum reflectance divided by two; Marshall et al. 2003).

Spectral data were analyzed by fitting a two-way analysis of variance (ANOVA) model with morph and sex as fixed factors. In those cases in which we could not assume data to be normally distributed, we used the Scheirer–Ray–Hare test (Sokal and Rohlf 2009). Finally, we used one-way ANOVA or Kruskal–Wallis (i.e., when heteroscedasticity and/or normality could not be safely assumed) tests to look for intermorph

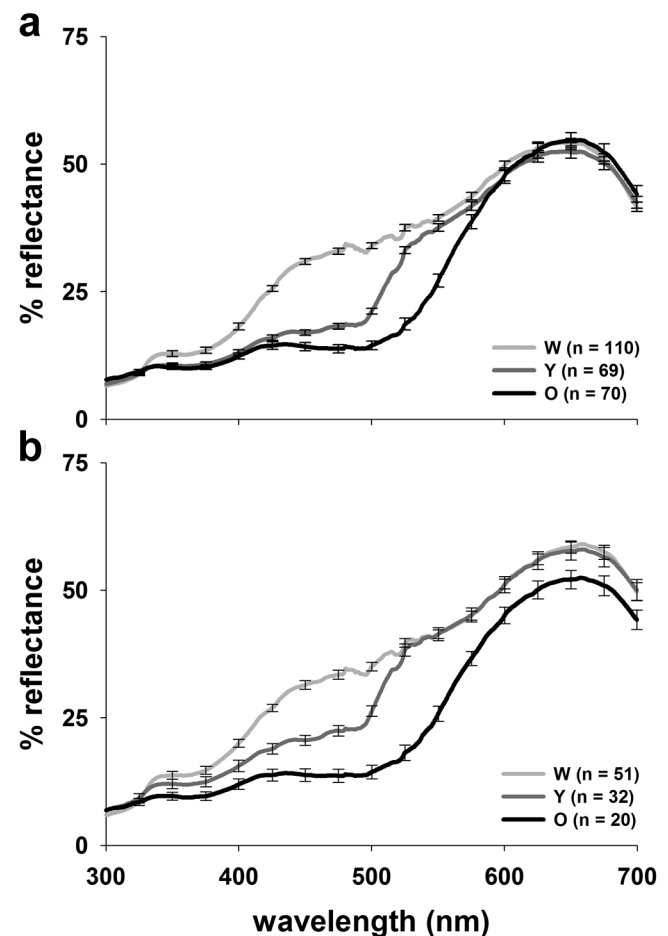


Figure 1

Throat reflectance spectra from pure *P. muralis* adult male (a) and female (b) morphs. W, Y, and O represent white, yellow, and orange morphs, respectively. Spectra from white, yellow, and orange scales from intermediate white–orange and yellow–orange morphs are similar to those depicted here (see Figure S1 in Supplementary Material). Vertical lines: error bars (± 1 standard error of mean).

morphometric differences in SVL and body condition. Body condition index (BCI) was calculated as the body mass residuals after regressing body mass against SVL (Green 2001). We restricted this analysis to adult lizards with fully developed coloration (i.e., SVL > 56 mm; see results).

Before releasing lizards back at their capture locations, all the individuals were marked by toe-clipping for subsequent identification. We used toe-clipping because this is the most adequate and ethically sound method for durable marking in lizards of this size range (for full details see Perry et al. 2011). Briefly, we clipped toes by cutting their distal two-thirds with a pair of sharp surgical scissors. We clipped a maximum of two toes and always tried to select small digits that did not usually draw blood. Injuries that drew blood were cleaned with alcohol and treated with antibiotic to avoid infection. Lizards that presented natural toe loss were not toe clipped. Repeated annual surveys enabled us to quantify yearly frequencies of each color morph, whereas lizard recaptures during consecutive seasons allowed us to assess ontogenetic variation in ventral coloration.

Mating system and assortative pairing

Podarcis muralis exhibits a polygynandrous mating system in which adult territorial males patrol and aggressively defend against intruding males an area that typically overlaps the home range of one or more females (Boag 1973; Barbault and Mou 1988; Edsman 1990; Oppliger et al. 2007; our own unpublished observations). As a result, during the breeding season males mate repeatedly with females within their territory, and most copulations occur between members of established pairs that associate in time and space (e.g., basking together, sharing refuges). These observations are consistent with reports of male mate guarding in other lacertid species (e.g., Olsson 1993a; Marco and Pérez-Mellado 1999; Martín and López 1999) and suggest that consistent spatiotemporal male–female associations during the breeding season can be used as an indicator of mating pattern.

To examine the existence of assortative pairing, we conducted field surveys using two complementary sampling procedures. First, we used data on male–female spatial association obtained from individually identified, marked adult animals during systematic field observations conducted during the first 5 years at our main study site. For these individuals, spatiotemporal association and interactions (e.g., copulations) among males and females were well documented. Second, in 2010 and 2011, we supplemented longitudinal data by sampling pairs of unmarked lizards observed during independent transects in areas adjacent (>500 m) to our main study site. In this second type of surveys, we used a conservative criterion to record male–female pairs based on previous observations of individually identified animals: 1) we only recorded pairs in which both lizards could be unambiguously assigned to a morph, 2) pairs involving sub-adult individuals or young adults were discarded (to avoid the inclusion of lizards without a fully developed coloration; see results), and 3) pairs in which lizards were farther than 1 m apart were also discarded. To avoid pseudoreplication, transects involving unmarked individuals were conducted only once during the whole sampling period (2010–2011). To test for nonrandom pairing, we performed a Fisher's Exact test on the total pooled data set. To specifically test for assortative pairing, we used a binomial test comparing the proportion of homomorphic and heteromorphic pairs. Finally, we performed a Spearman correlation analysis with male and female SVL measurements from pairs of marked lizards to test the hypothesis that the pairing system is driven by size-assortative mating.

RESULTS

Objective color morph characterization

We obtained reflectance spectra from a total of 249 adult males and 103 females with pure-morph phenotypes (W, Y, O). Intermediate morphs (WO and YO) were discarded for spectrophotometric measurements because the patches of their throat mosaic were often too small to allow consistent measuring (see also Calsbeek et al. 2010). Measurement of a subsample of intermediate individuals exhibiting several adjacent scales of the same color (and thus large enough to allow consistent measurement) confirmed that the colors present in intermediate morphs had the same spectral properties as those of uniformly colored animals (see Figure S1 in Supplementary Material).

Reflectance spectra from the throats of pure white, yellow, and orange adult males and females indicate that coloration does not vary continuously (Figure 1), which supports our eye-based classification into three discrete color morphs. Differences among ventral colorations are explained by variation in chroma between 400 and 600 nm, which gives rise to three discrete spectral steps (see error bars associated with spectra in this range in Figure 1 and distribution of MC among morphs in Figure 2). We found color morphs to differ

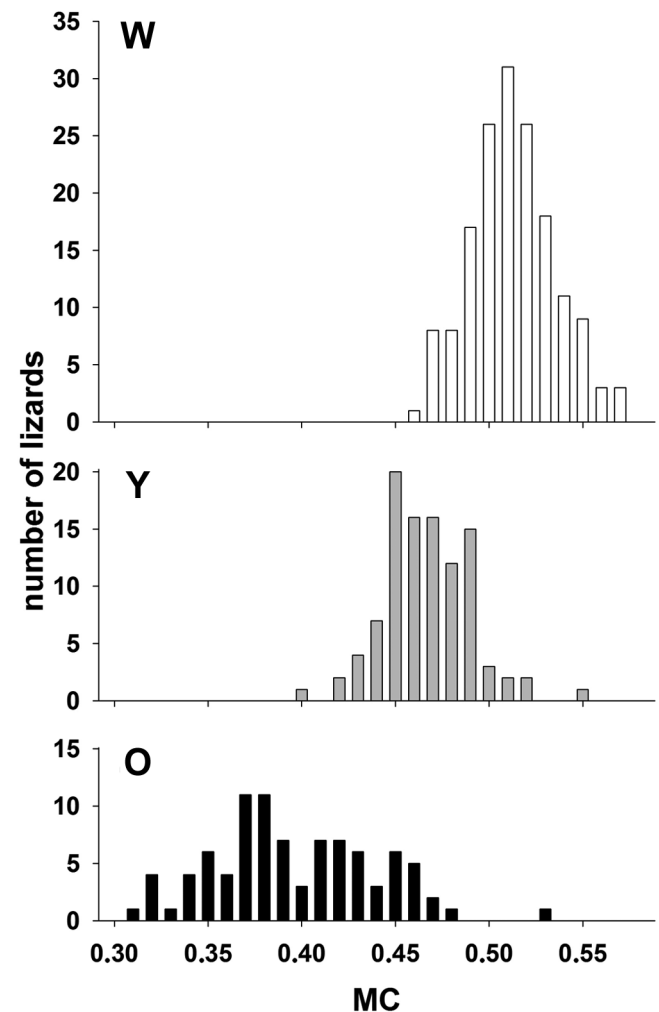


Figure 2
Distribution of medium wavelength chroma (MC) measurements (males and females considered together) from each pure morph. W, Y, and O represent white, yellow, and orange morphs, respectively.

in color variables, but sex and the interaction between morph and sex were not significant (Table 1 summarizes Q, MC, H, and R_{50} values for the three pure morphs). Finally, we found no differences among morphs in BCI and only males differed slightly in SVL (Table 2). Using post-hoc analyses, we found O males to be larger than W males ($P = 0.026$), but we did not find significant differences between W and Y and O and Y males ($P = 0.44$ and $P = 0.61$, respectively).

Color morph development and polymorphism stability

Data obtained from lizards recaptured during 2–3 consecutive reproductive seasons (i.e., 28 females and 44 males) indicate that lizards develop their full adult color by the time they reach a size of 56-mm SVL, which we used as a criterion to exclude individuals without a fully developed adult coloration. All juveniles sampled were white ventrally. As they grew, some juveniles retained their white coloration as adults, whereas others developed light yellow pigmentation or a series of isolated orange scales. Subsequently, light yellow individuals acquired an intense yellow coloration and, in some cases, developed some orange scales (YO intermediate morph). In turn, individuals with orange scales either remained white and orange (WO intermediate morph), changed their white scales to yellow scales (YO) or, more often, developed an overall orange coloration (Figure 3). No individuals examined more

than once as adults underwent a color change, suggesting that color morphs are stable through adulthood ($N = 30$). At the population level, the polymorphism remained stable over time with only minor fluctuations in the relative frequency of the different morphs (Figure 4).

Assortative pairing

Figure 5 shows the frequency of scored pairs sorted by color (40 independent pairs of marked lizards and 77 pairs of unmarked lizards). From the subset of individually identified lizards, 26 males were observed in association with females in more than one occasion. Of these, 17 males paired with a single female. In all the remaining cases, males were seen repeatedly with the same female and only sporadically with other females. In these cases, we considered the female with which the male paired consistently as his mate. Pairs observed repeatedly were tallied only once.

Pairing was not random with respect to male and female color morphs (Fisher's test, $P < 0.001$), pure-morph homo-morphic pairs of lizards being significantly more common than heteromorphic pairs (Binomial test, $N = 94$, $k = 69$, $P < 0.001$). Due to small sample sizes ($N = 23$), pairings involving intermediate morphs were not included in the analysis (see Table S1 in Supplementary Material for raw data). Although SVL measurements were only available for a subset of individually identified lizards, the correlation between male and female SVL within mated pairs was not significant ($N = 17$, $\rho = 0.10$, $P = 0.69$).

DISCUSSION

To our knowledge, no study to date has examined color-polymorphic assortative mating in *Podarcis* or in other lizards, although a recent study by Huyghe et al. (2010a) found indirect evidence that hinted at the existence of nonrandom mating in populations of *P. melisellensis* with three pure morphs. Here, we provide behavioral evidence of color-assortative pairing in a wild population of *P. muralis*, which is strongly suggestive of assortative mating in this species. Size-assortative mating cannot explain the pattern reported in this study because we did not find size differences between female morphs (and only a marginal size difference between orange and white-morph males), or a significant correlation between male and female SVL in mated pairs (Olsson 1993b; Cooper and Vitt 1997; Shine et al. 2001). Similarly, spatial data for this population (not shown) reveal that home ranges of lizards from different morphs overlap as often as those of lizards from the same morph. Thus, morphs are not in any way spatially segregated and interact with each other on a daily basis so there are ample opportunities for intermorph associations (Font et al. 2012; Pérez i de Lanuza G, Font E. and Carazo P, unpublished data).

The results presented here suggest that mate choice patterns may be involved in the maintenance of color polymorphisms in *P. muralis* (Roulin and Bize 2007). In polymorphic systems driven by mate choice, disassortative mating is the mechanism that best explains the durability of rare phenotypes (Pryke and Griffith 2007). In contrast, positive assortative mating will normally promote the reduction of gene flow among morphs and, consequently, induce incipient reproductive isolation (Pryke and Griffith 2007; Huyghe et al. 2010a). Theoretical arguments, mathematical models, and recent empirical evidence all suggest that the processes generating and maintaining color polymorphism tend to promote speciation (e.g. Gray and McKinnon 2007; Otto et al. 2008; Huggall and Stuart-Fox 2012). However, the existence

Table 1

Descriptive statistics and results of statistical analyses for color variables: brightness (Q), medium wavelength chroma (MC), hue (H, in degrees), and spectral location of middle point (R_{50} , in nm) for each morph and sex

	Q	MC	H	R_{50}
Males				
W	38 926±650	0.52±0.00	49.50±0.65	416.54±2.50
Y	33 500±726	0.46±0.00	37.83±0.60	496.10±3.17
O	30 790±1079	0.40±0.01	25.56±0.82	532.39±5.40
Females				
W	41 174±875	0.50±0.00	46.38±0.01	427.07±4.55
Y	38 955±1380	0.47±0.00	39.06±0.74	488.54±5.32
O	30 237±1546	0.40±0.01	26.00±1.15	536.29±6.58
Morph	$H = 14.70^*$	$H = 39.82^*$	$H = 38.6^*$	$F_{1,346} = 329^*$
Sex	$H = 0.01$	$H = 0.01$	$H = 0.02$	$F_{1,346} = 0.57$
Interaction	$H = 1.43$	$H = 0.66$	$H = 0.77$	$F_{1,346} = 0.12$

W, Y, and O represent the white, yellow, and orange morphs, respectively.

* $P < 0.001$ in all cases.

See sample sizes in Figure 1.

Table 2

Mean values of morphometric variables SVL and BCI, and results of comparisons among morphs

	SVL (mm)		BCI	
	Females	Males	Females	Males
W	61.78±0.73	62.57±0.51	-0.16±0.10	0.21±0.06
Y	63.56±0.77	63.63±0.51	-0.28±0.15	0.18±0.08
O	63.38±0.75	64.77±0.57	-0.49±0.17	0.02±0.11
	$F_{2,65} = 1.71$	$F_{2,168} = 3.58$	$F_{2,65} = 1.071$	$\chi^2 = 2.58$
	$P = 0.19$	$P = 0.03$	$P = 0.35$	$P = 0.28$

Values were log-transformed prior to the analyses.

W, Y, and O represent the white, yellow, and orange morphs, respectively.

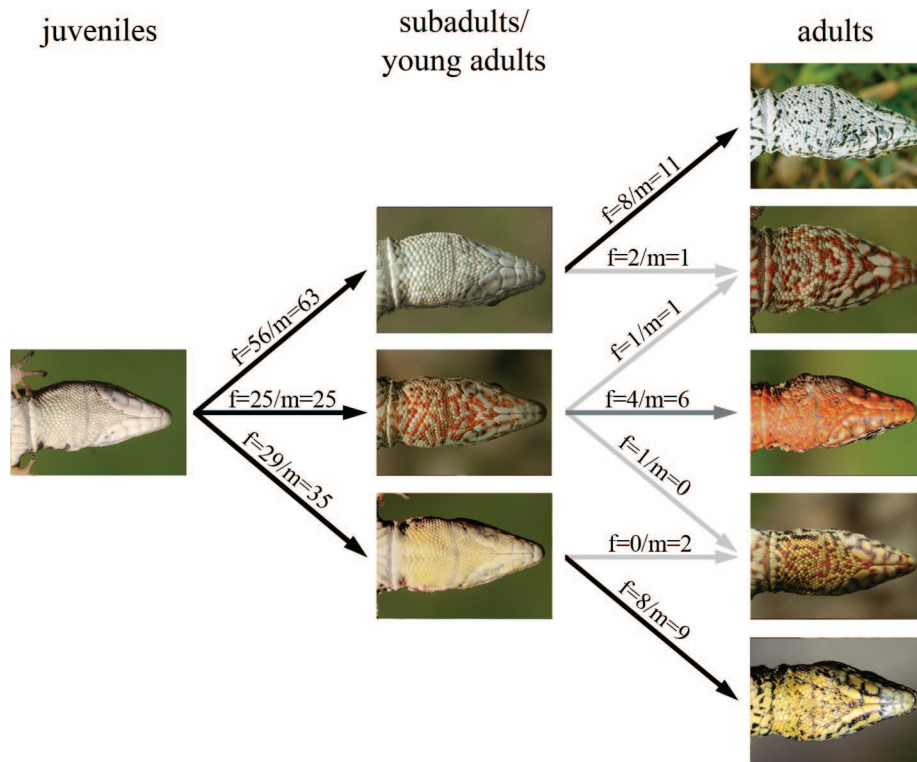


Figure 3

Developmental trajectories of color morphs in *P. muralis* reconstructed from recapture data. Arrows indicate direction of possible changes in coloration over time. Black arrows represent most frequent transitions and numbers over the arrows indicate the number of observed individuals for each transition in the population (f = females; m = males). Counts in transitions from juveniles to subadults/young adults consider 1-year-old animals with SVL < 56 mm (which always develop their ventral coloration from white juveniles). Transitions from subadults/young adults to adults were calculated considering only individuals captured for the first time with SVL < 56 mm and recaptured during the following spring as adults.

of social and ecological constraints on mate availability may curtail the divergence of color morphs into separate species despite strong assortative mate preferences, in which case assortative mating will contribute to the maintenance of the polymorphism (Pryke 2009).

Our own results reveal a complex situation in *P. muralis*, with obvious morph-assortative pairing but also a considerable proportion of heteromorphic pairs (38.5%) that could reflect the existence of costs and/or constraints of assortative mating (Pryke 2009), or other processes such as condition-dependent variation in mate choice (Bleay and Sinervo 2007). We hence suggest that positive assortative mating could contribute to the maintenance of color polymorphisms in this species even though it is unlikely that this is the only evolutionary process involved (Pryke 2009). As a matter of fact, color polymorphisms are widespread in the genus *Podarcis*, which suggest that other selective processes, such as negative frequency-dependent selection (Sinervo and Lively 1996), are probably also involved in the maintenance of color polymorphisms.

The findings reported here also contribute to our understanding of the form and development of lacertid color polymorphisms. First, our data show that there is no sexual dimorphism in the spectral characteristics of male and female morphs; the only observable sexual differences are in the distribution of ventral colorations (i.e., throat and belly in males, only throat in females). Second, spectrophotometric data confirm the existence of discrete color morphs in both males and females. Available data on the visual system of lacertids (Wagner 1933; Swiezawska 1950; Svoboda 1969; Dürcker and Rensch 1973; Pérez i de Lanuza G, Font E, in

preparation) and other diurnal lizards (Fleishman et al. 1997, 2011; Loew et al. 2002; Bowmaker et al. 2005) suggest that *Podarcis* lizards most likely perceive these color morphs as discrete phenotypes. Therefore, and given that morph differences are explained by variation within the human visible range (i.e., 400–700 nm), an eye-based classification seems to be an adequate procedure for discriminating color morphs in this species (for a discussion of the pros and cons of eye-based classifications of ventral colorations in lacertids, see Vercken et al. 2007, 2008; Cote et al. 2008). Our results also show that color morphs in adult *P. muralis* appear to be ontogenetically stable. All developmental changes observed in throat and belly coloration affected subadult and/or young adult lizards (i.e., SVL < 56 mm), so criteria used to identify adult, stable morphs should be taken into account in comparisons among morphs. For example, Sacchi et al. (2007a, 2009) classified individuals with SVL larger than 50 mm as adults, which could have led to overestimating the proportion of white morph lizards in Italian populations of *P. muralis* (Sacchi et al. 2007b; see also Calsbeek et al. 2010).

A host of interesting questions remain to be examined in more detail by future studies. In particular, it is often assumed that color polymorphisms in lacertids are, as in other polymorphic lizards, genetically determined (Sacchi et al. 2007a,b; Calsbeek et al. 2010; Runemark et al. 2010), but controlled matings have not been conducted to confirm the heritability of color morphs. Therefore, a crucial goal of future research should be to decipher the genetic basis underlying color polymorphism in this and in other polymorphic species of lacertid lizards.

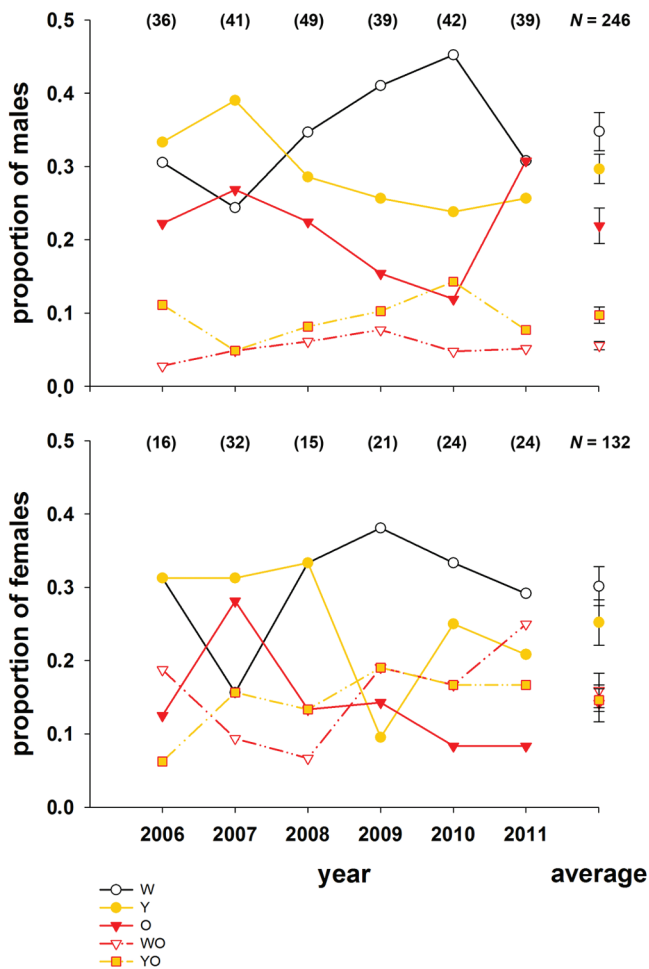


Figure 4
Changes in color morph frequencies during a 6-year period. Sample sizes for each sex and year are provided in brackets. N represents the total sample size across the 6 years.

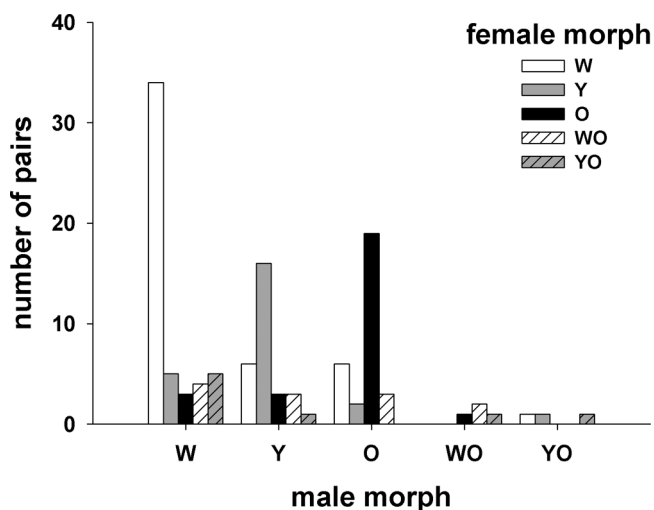


Figure 5
Number of male-female pairs classified by color morph from a total of 117 pairs.

SUPPLEMENTARY MATERIAL

Supplementary material can be found at <http://www.behco.oxfordjournals.org/>.

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