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ORIGINAL PAPER

Colour assortative pairing in a colour polymorphic lizard is independent of population morph diversity

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Abstract Previous work with a colour polymorphic population of *Podarcis muralis* (Lacertidae) revealed that lizards pair by ventral colour, favouring the same colour (i.e. homomorphic) pairs. Such assortative pairing, which probably results in colour assortative mating, can have consequences for the genetic structure of the population and potentially promote speciation. The population previously studied, located in the Pyrenees, encompasses white, yellow and orange animals, as well as intermediate white–orange and yellow–orange morphs. However, other Pyrenean populations of *P. muralis* have less ventral colour morphs. Our aim in this study is to test the generality of the assortative colour pairing system, extending our previous analyses to populations with different morph compositions and frequencies. The results show that the assortative pattern of pairing is similar in all the populations analysed and, hence, independent of morph composition and not restricted to pentamorphic populations. This suggests that assortative pairing by colour is a general phenomenon for colour polymorphic populations of *P. muralis*.

Keywords Assortative mating · Colour polymorphism · Population morph complexity

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Introduction

The processes generating and maintaining colour polymorphisms in animal populations are currently attracting much attention, and studies with lizards have led to significant progress in our understanding of this phenomenon (e.g. Roulin 2004; Chunco et al. 2007; Pryke and Griffith 2007; Roulin and Bize 2007; McKinnon and Pierotti 2010; Hugall and Stuart-Fox 2012; Wellenreuther et al. 2014). Following the description of the rock-paper-scissors game in populations of *Uta stansburiana* with three discrete throat colour morphs (Sinervo and Lively 1996; Sinervo and Zamudio 2001), several studies with iguanid, agamid and lacertid lizards have sought to establish links between the different colour morphs and alternative reproductive or life-history strategies (e.g. Lattanzio et al. 2014; McLean et al. 2015; Rankin and Stuart-Fox 2015).

Work with lacertid lizards has provided important insights into the evolution of colour polymorphisms (e.g. Huyghe et al. 2007; Runemark et al. 2010; Fitze et al. 2014). Several studies have been conducted with the European common wall lizard, *Podarcis muralis* (Laurenti 1768), which often shows complex population colour polymorphisms affecting both sexes (e.g. Cheylan 1988; Sacchi et al. 2007b, 2009; Calsbeek et al. 2010; Pérez i de Lanuza et al. 2014; Pérez i de Lanuza and Font 2015; Pérez i de Lanuza et al. 2016). However, most attempts to identify clear alternative strategies linked to colour morphs have produced inconsistent results (Sacchi et al. 2007a, b, 2009, 2015; Calsbeek et al. 2010; Pérez i de Lanuza et al. 2014; Scali et al. 2013, 2016; Pellitteri-Rosa et al. 2014; but see Galeotti et al. 2013).

In the course of a study of communication and social behaviour in a Pyrenean polymorphic population of *P. muralis*, we found that males and females associate non-randomly by ventral colour, favouring homomorphic pairs (Pérez i de Lanuza et al. 2013). This suggests a positive assortative mating in which lizards mate preferentially with individuals of the same colour as themselves. This mating pattern may, in combination with other evolutionary forces, contribute to the maintenance of the colour polymorphism (Wellenreuther et al. 2014).

The population in which colour assortative pairing was originally described is pentamorphic, encompassing white, yellow and orange pure morphs as well as white–orange and yellow–orange intermediate morphs (Pérez i de Lanuza et al. 2013, 2014, 2016; Pérez i de Lanuza and Font 2015). Given its prevalence in populations of *P. muralis* from western and eastern European lineages (and also in other *Podarcis* species; Gruschwitz and Böhme 1986; Arnold and Ovenden 2002), it is likely that the ventral colour polymorphism is plesiomorphic for this species. However, most polymorphic populations are trimorphic rather than pentamorphic, with only white, orange and white–orange morphs (Gruschwitz and Böhme 1986; Schulte 2008; Schulte and Beninde 2013). Therefore, to understand the relevance of assortative mating for the evolution of colour polymorphism, it is necessary to assess whether mating is also assortative in populations differing in the number of morphs.

Assortative pairing could be strictly local or a phenomenon that evolves only in highly complex (i.e. pentamorphic) populations. Populations with a reduced number of morphs could show differences in the mating pattern or in the intensity (i.e. the frequency of homomorphic pairs) of the assortative pairing. With the aim to assess the nature of the assortative pairing system, here we test if colour positive assortative pairing is present in populations with different morph compositions and morph frequencies and, ultimately, whether this phenomenon could be general, at least for the Pyrenean *P. muralis*. Thus, we applied our previous methodology to areas of the Eastern Pyrenees inhabited by populations showing morph compositions different from that of the population in which assortative pairing was originally reported (i.e. with few or no yellow and yellow–orange animals).

Materials and methods

We focused on populations geographically close to our original population but showing different morph compositions (and morph frequencies) to avoid possible confounding effects of sampling different phylogenetic lineages. Our study included populations from the Cerdanya valley, in the southern face of the Pyrenees, as well as northern populations from the Arièja valley (Fig. 1). In particular, we studied populations from three different geographic areas: (1) trimorphic populations without yellow and yellow–orange animals from the top of the Fontviva valley (a subsidiary valley of the main Cerdanya valley), which is continuous with the previously studied population but probably with some ecological barriers that reduce morph flow between populations; (2) populations from the northern face of the Pyrenees (Arièja valley), with low frequencies of the yellow and yellow–orange morphs at some localities; and (3) pentamorphic populations located in the central part of the main Cerdanya valley and surrounding areas of the Capcir valley, adjacent to the previously studied locality and showing the same type of polymorphism (i.e. pentamorphic).

We followed the sampling methodology used in the previous study, which assumes that consistent spatio-temporal male–female associations can be used as an index of mating pattern (Pérez i de Lanuza et al. 2013). During the reproductive season, wall lizards are rarely found in close proximity to conspecifics, the main exception being the male–female pairings that we used to assess patterns of colour assortative mating (Fig. 2). Most adult males defend exclusive territories that overlap the home ranges of one or more reproductively active females (Edsman 1990). In the course of their daily territorial patrols, males encounter and interact with the females residing in their territory. During these intersexual interactions, the male typically moves around the female, tongue-flicking at her body (particularly around the base of the tail) and at the substrate, while both perform stereotyped, sex-specific foot shake displays (type II foot shakes; Font et al. 2012). Occasionally, the interaction leads to copulation, but more often, the male and the female settle down and spend several minutes basking or perching together, often in physical contact with each other (Fig. 2). Repeated sightings of marked lizards in the field confirm that most of the observed pairs represent consistent social associations durable in time (Pérez i de Lanuza et al. 2013). The male–female pairings have recently been interpreted as mate-guarding behaviour in experiments conducted in mesocosm enclosures (Heathcote et al. 2016), which further supports the idea that the pairing observed in the field is not independent of mating patterns. Counts of male–female lizard pairs were made opportunistically in the course of transect surveys through the study area, avoiding any disturbance to the lizards. Morphs were visually identified by throat colouration (Pérez i de Lanuza et al. 2013), as in previous studies with *P. muralis* and other *Podarcis* species (e.g. Sacchi et al. 2007a, b, 2009, 2015; Huyghe et al. 2007; Calsbeek et al. 2010; Runemark et al. 2010). Sex was determined by head and body proportions and dorsal colour pattern (Pérez i de Lanuza et al. 2013). Since correct identification of sex and ventral colour morph is crucial for the validity of our conclusions, observations were done at a very close range (ca. 1 m) using short focus binoculars (Papilio 8.6 × 21, Pentax, Tokyo, Japan). To test the reliability of our sampling protocol, during 2016, we captured 96 adult lizards whose sex and ventral colour morph had previously been assessed using binoculars. Sex determination was correct in all cases, while ventral colour was correctly identified in 95.8 % of the lizards. Therefore, we assume that

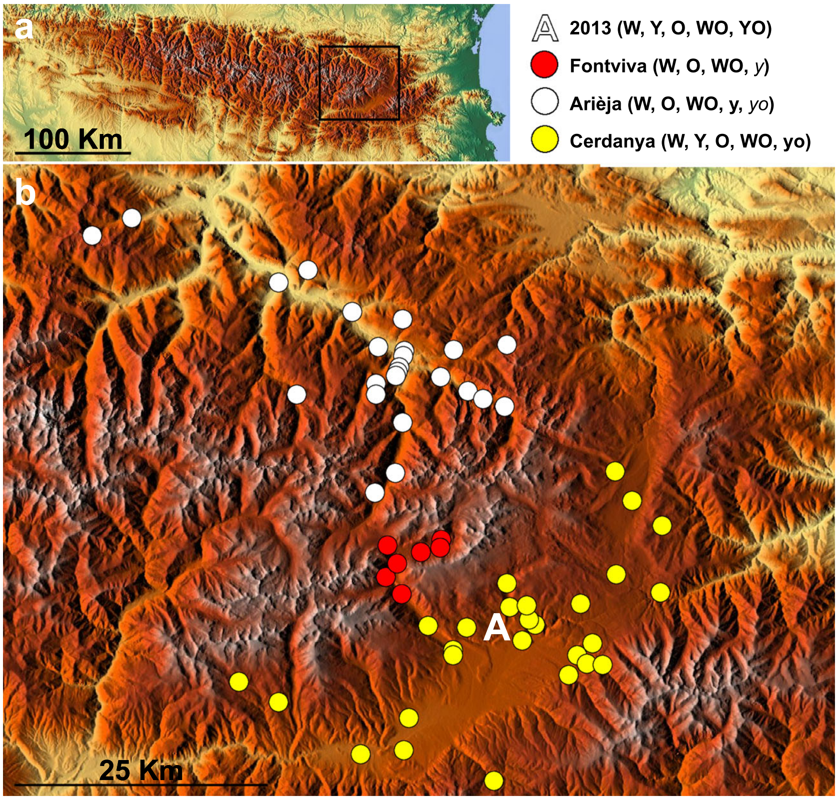

Fig. 1 Location of the sampling sites. **a** A map of the Pyrenees showing the general area where this study was conducted (enclosed in a *square*). **b** Detail of the area enclosed in a *square* in **a** showing the localities where lizards were sampled in the three study areas. The location of the population previously studied in the central Cerdanya is indicated with *A* (Pérez i de Lanuza et al. 2013). The *circles* indicate the location of sampling localities in the central Cerdanya (*yellow*), in Fontviva (*red*) and in Arièja (*white*). Morph codes in *parentheses* (*W* = white, *Y* = yellow, *O* = orange, *WO* = white–orange, *YO* = yellow–orange) indicate the morph composition per area. Codes in *uppercase* denote that the respective morphs are abundant; codes in *lowercase* denote that the morphs have a low frequency and may not be present in all the sampled localities; codes in *italics* denote that the morphs are found only occasionally

potential biases in sex and ventral colour classification are negligible or have little effect on the overall sample.

To avoid pseudoreplication, counts were made in independent line transects covering several localities (i.e. a single transect per locality) in each of the three study areas. We only counted pairs in which adult males and females were found close to each other (i.e. <1 m) showing natural undisturbed behaviours (i.e. basking, perching or socially interacting). In addition, we also counted all the adult lizards observed during surveys to obtain an estimate of morph frequency for each locality. These counts were then pooled to obtain pair counts and morph frequencies for the three study areas. Most transects were conducted during the breeding season (from April 25th to August 30th) in 2014 and 2015.

Fig. 2 An adult male (*below*) and an adult female (*above*) of *Podarcis muralis* sharing time and space in the field

Analyses were performed considering the three areas and using the corresponding pooled datasets. As the sample size for some morph combinations was very small or even zero, we used Fisher's exact tests to determine if males and females were paired randomly and binomial tests to check if homomorphic pairs were favoured (Pérez i de Lanuza et al. 2013). We performed independent tests in each area considering all the morphs and, in a second analysis, excluding the rare and/or intermediate morphs to prevent distortions caused by very infrequent pair combinations. Thus, we first considered the white, orange and white–orange morphs in the Fontviva area and then re-analysed the data excluding the white–orange

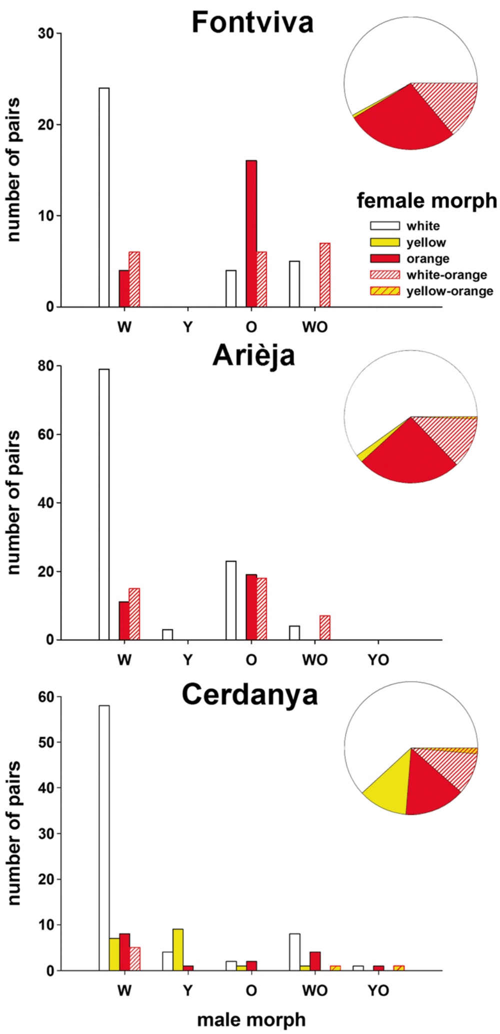

Fig. 3 Frequencies of each male–female pair type for each study area. Codes for male morphs are the following: *W* = white, *Y* = yellow, *O* = orange, *WO* = white–orange and *YO* = yellow–orange. Pie charts show the relative abundance of the different colour morphs found in the different study areas (counts correspond to the total number of adult males and females encountered in a single transect, not only to paired animals; $N_{\text{Fontviva}} = 300$, $N_{\text{Arièja}} = 1152$, $N_{\text{Cerdanya}} = 1196$; GPL, unpublished results)

morph. We considered the white, yellow, orange and white–orange morphs in the Arièja area, but we also repeated the analysis first excluding the yellow morph and then also excluding the white–orange morph. Finally, we considered the white, yellow, orange, white–orange and yellow–orange morphs in the central Cerdanya, but we also performed the analysis excluding the white–orange and the yellow–orange morphs as in our previous study (Pérez i de Lanuza et al. 2013).

Results

A total of 59 localities were surveyed (7 in Fontviva, 24 in Arièja and 28 in the central Cerdanya). Figure 3 summarizes the frequencies of each male–female pair type and the average morph frequencies for the three study areas. Morph frequency varied widely among the sampled localities. White morph individuals were the most abundant in the three study areas. The yellow morph was present in all localities from central Cerdanya but was extremely rare in localities from the Fontviva and Arièja areas. Morph frequencies for each study area are given in Table 1.

We counted 72 male–female pairs in Fontviva (2–40 pairs per locality), 179 in Arièja (1–22 pairs per locality) and 114 in central Cerdanya (1–20 pairs per locality) accounting for 20.7, 28.8 and 19.1 % of all observed individuals, respectively. In the three areas, the composition of the pairs deviated from random, and homomorphic pairs were more common than expected by chance, both considering all the morphs present in each area and excluding the rare morphs (Table 2). The proportion of homomorphic pairs was high (>74 % considering only the pure morphs) and differences among areas smaller than 10 %. The proportion of homomorphic pairs decreased when intermediate and rare morphs were included in analyses, and the reduction was similar in the three study areas (14–18 %). Although we used morph frequencies from paired lizards for analyses, these frequencies did not significantly differ from the overall frequencies calculated considering all the adult lizards observed during transects (G-test of goodness of fit $G < 0.042$, $df = 4$, $P > 0.99$ for the three study areas).

Discussion

The frequency and composition of colour polymorphic populations often show geographic variation (McLean and

Table 1 Average morph frequencies in each study area (range in parentheses)

	White	Yellow	Orange	White–orange	Yellow–orange
Fontviva	0.56 (0.43–0.69), 100 %	0.01 (0.00–0.03), 14.3 %	0.28 (0.09–0.44), 100 %	0.15 (0.09–0.27), 100 %	0.00, 0 %
Arièja	0.61 (0.27–0.77), 100 %	0.01 (0.00–0.06), 41.7 %	0.25 (0.14–0.45), 100 %	0.12 (0.02–0.24), 100 %	0.01 (0.00–0.04), 12.5 %
Cerdanya	0.62 (0.49–0.84), 100 %	0.11 (0.03–0.21), 100 %	0.15 (0.00–0.38), 96.4 %	0.10 (0.00–0.24), 96.4 %	0.02 (0.00–0.13), 50 %

The percentages indicate the percentage of localities in which each morph was found. The numbers of the sampled localities were 7 (Fontviva), 24 (Arièja) and 28 (Cerdanya)

Table 2 Statistics of Fisher's exact test and binomial test for the three study areas considering only the main pure morphs or all the morphs present in each study area

Study area	Morphs	*N*	% homomorphic	Fisher's exact test (*P*)	Binomial test (*k*, *P*)
Fontviva	W, O	48	83.33	<0.0001	40, <0.0001
	W, O, WO	72	65.28	<0.0001	47, 0.013
Arièja	W, O	132	74.24	<0.0001	98, <0.0001
	W, O, WO	176	59.66	<0.0001	105, 0.013
	W, Y, O, WO	179	58.66	<0.0001	105, 0.025
Cerdanya	W, Y, O	92	75.00	<0.0001	69, <0.0001
	W, Y, O, WO, YO	114	61.40	<0.0001	70, 0.019

W white, *Y* yellow, *O* orange, *WO* white–orange, *YO* yellow–orange

Stuart-Fox 2014; McLean et al. 2015). The finding of microgeographic variation in morph frequencies of *P. muralis* from the Pyrenees agrees with reports from other populations (Italian populations, Sacchi et al. 2007b; other Pyrenean populations, F. Aubret, personal communication). The loss or gain of a morph has the potential to affect intra- and interspecific interactions and may constrain the evolution of colour polymorphisms (Corl et al. 2010; McLean and Stuart-Fox 2014), but this issue has not been examined in any lacertid.

Our results confirm and extend previous reports of colour assortative pairing in *P. muralis*, reinforcing the hypothesis that mating patterns may contribute to maintaining population polymorphism. It could be argued that the colour assortative pairing observed in *P. muralis* results from different microhabitat selection by individuals of a given morph, irrespective of their sex and their mate preferences. However, detailed observations of spatial behaviour in a pentamorphic population from central Cerdanya indicate that the home ranges of lizards showing different morphs often overlap. This refutes microhabitat segregation as the reason why lizards pair assortatively and suggests instead that heteromorphic associations should be, in the absence of assortative pairing, as likely as those of lizards from the same morph (Pérez i de Lanuza G, Font E. and Carazo P, unpublished data). Therefore, the pairing pattern reflects, at least in part, the mating pattern of colour polymorphic *P. muralis*.

Colour polymorphisms appear to be relatively common in lizards. However, assortative mating by colour is not a universal characteristic of polymorphic lizards (Olsson et al. 2013). For example, in the side-blotched lizard, *U. stansburiana*, strong male–male competition overrides female preferences for the same coloured males (Bleay and Sinervo 2007). Most colour polymorphisms are probably maintained by some form of balancing selection (i.e. heterozygote advantage or negative frequency-dependent natural or sexual selection; Wellenreuther et al. 2014). In *U. stansburiana* male–male competition drives negative frequency-dependent selection which is responsible for maintaining the polymorphism. Assortative mating cannot itself maintain heritable colour polymorphisms, but it can alter genotype frequencies (Wellenreuther et al. 2014). When females mate with the same coloured males, the frequency of homozygotes increases in the population at the expense of heterozygotes. This may explain the low frequencies of intermediate (mixed) morph individuals in *P. muralis* populations. In fact, population genetics analyses performed with polymorphic Italian populations show reduced gene flow between colour morphs in syntopy (Bellati 2011).

Our results demonstrate that colour assortative pairing is prevalent in polymorphic *P. muralis* regardless of morph frequency and composition, at least in populations belonging to the Eastern Pyrenean lineage. In fact, we found evidence of colour assortative pairing in populations with white, orange and white–orange animals, which are the most common across the distribution range of *P. muralis* (Schulte 2008). Moreover, we found a roughly similar proportion of homomorphic pairs in trimorphic and pentamorphic populations. Differences in the proportion of homomorphic pairs among the three study areas (<10 %) may be related to the different numbers of morphs present in each area. Remarkably, the Fontviva population, with the smallest number of morphs, shows the largest frequency of homomorphic pairs. This suggests that an increase in the number of morphs may reduce the frequency of homomorphic pairs. The presence of rare morphs (i.e. with low population frequencies), in which males and females have very low probabilities to find a homomorphic mate, may also reduce the proportion of homomorphic pairs. In fact, in the three areas, the relative increase in homomorphic pairs is similar when rare morphs are excluded from the analyses. Alternatively, rare morphs could pair in a different way than the common morphs, but no data suggest this hypothesis.

Interestingly, the proportion of homomorphic pairs in the central Cerdanya (75 % considering only the three pure morphs, 61.40 % considering the five morphs) is very similar to that obtained in the previous study (73.4 % considering only the three pure morphs, 61.53 % considering all five morphs; Pérez i de Lanuza et al. 2013). Thus, the proportion of homomorphic pairs seems stable over time and across different localities within a homogenous eco-geographic area, at least for this study area.

A recent study by Sacchi et al. (2015) found no evidence for an active female choice of males of different morphs in *P. muralis* from Italy. However, as the authors acknowledge, this negative result does not rule out the possibility that *P. muralis* mates assortatively by colour. While Sacchi et al. (2015) specifically tested for female preference, assortative pairing in the field may be the result of both male and female behaviour (Pryke and Griffith 2007). It is also possible that the restricted laboratory setting in which these choice experiments were conducted prevented the expression of female mating preferences.

As the results presented here suggest, assortative pairing in *P. muralis* is not a local phenomenon, and a study of the spatio-temporal association of males and females in the field may shed light on the mating patterns of Italian populations. Furthermore, comparative analyses including other colour polymorphic species of *Podarcis* may be useful to clarify if assortative pairing is exclusive of *P. muralis* or is general in this chromatically variable genus of lizards.

Finally, as *P. muralis* has a large distribution range across Europe, from the Iberian Peninsula to Anatolia, and a complex phylogeography including many lineages (Salvi et al. 2013), an interesting new avenue for research would be to assess the extent of assortative pairing in other colour polymorphic lineages, considering morph gains and losses across lineages. Although more data on morph distribution are needed, it seems that complex polymorphisms including yellow and yellow–orange individuals are restricted to the western and central European clades, while eastern clades show only white, orange and white–orange animals.

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