



Partial divergence in microhabitat use suggests environmental-dependent selection on a colour polymorphic lizard

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Abstract

The study of polymorphic organisms in which sexual selection strongly drives the maintenance of the polymorphism often ignores the environmental context. However, natural selection is also crucial, often interacting with sexual selection. While most evidence suggests that sexual selection underlies the maintenance of the colour polymorphism shown by the common wall lizard, *Podarcis muralis*, involving up to five sympatric morphs (white -W-, yellow -Y-, orange -O-, white-orange -WO- and yellow-orange -YO), recent results using realised niche models suggest morph distribution at a geographical scale is constrained by climate. The Y and YO morphs occupy a narrow space within the niche of the other morphs, and local frequencies of W, WO and O morphs are environmentally dependent, with O and WO showing higher local frequencies in the most humid habitats. We hypothesised that morphs may behaviourally compensate for these differences at a microhabitat scale. Here, we tested this hypothesis collecting field microhabitat data from representative natural populations. Results highlighted that O lizards are partially segregated in microhabitat relative to the other morphs, tending to occupy more humid (vegetated, close to water) sites, and suggesting a physiological constraint. In contrast, the other morphs do not differ in microhabitat use, suggesting that the ecological restriction of Y and YO morphs derives from an indirect relationship between climate and population parameters (sex ratio, density) crucial for social selection, eventually involving alternative behavioural strategies.

Significance statement

The maintenance of different colour phenotypes (morphs) in a single population occurs in complex evolutionary scenarios where several selective forces interact. Common wall lizards may be white, orange, yellow, white-orange or yellow-orange ventrally. This polymorphism is most likely driven by sexual selection, but climate probably constraints the environmental distribution of morphs, driving local morph diversity. Here, we explore if geographical differences in morph distribution result in microhabitat segregation. Our results show that orange lizards appear more frequently in humid habitats than the other morphs, suggesting a direct relationship between ecophysiology and habitat use. Although yellow and yellow-orange morphs present a narrow distribution at a geographical scale, they do not differ from the white and white-orange morphs in microhabitat, suggesting that their restricted distribution is indirectly caused by some source of environmental dependence on social selection instead of a direct physiological constraint.

Keywords Colour polymorphism · Ecology · Environmental-dependent selection · Microhabitat · *Podarcis muralis*

Introduction

Stable local polymorphisms, in which several phenotypes co-exist in space and time, represent an exciting challenge to

evolutionary biologists. Colour polymorphisms are of particular interest to study the emergence and maintenance of polymorphisms because the different phenotypes show alternative colour morphs easily identifiable by observers (Roulin 2004; McKinnon and Pierotti 2010; Wellenreuther et al. 2014; Svensson 2017). Several evolutionary scenarios have been proposed to maintain polymorphisms over time, often involving complex interactions between complementary or even antagonistic selective forces (Svensson 2017). Sexual selection is often invoked as a main factor explaining the evolution of polymorphisms. For example, the existence of alternative reproductive strategies linked to different colour morphs

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combined with a frequency-dependent selection system underlies the renowned case of the lizards *Uta stansburiana* (Sinervo and Lively 1996; Sinervo et al. 2001). Sexual selection also underlies other well-known cases of striking colour polymorphisms in, for example, many fish, birds and insects (reviewed in Wellenreuther et al. 2014).

Other inevitable source of selection promoting polymorphisms is natural (e.g. environmental-dependent) selection. Obviously, natural selection underlies the coexistence of different colour morphs in dorsal coloration mainly driven by predation avoidance (e.g. Farallo and Forstner 2012; Santos et al. 2017). However, even in polymorphisms involving colour signals, the effect of a variety of selective forces not (directly) related to sexual selection is crucial (e.g. Gosden et al. 2011; Karlsson et al. 2013). Unfortunately, in many well-studied colour polymorphic organisms, this kind of selection has been vastly underestimated in comparison to the influence of sexual selection (Svensson and Waller 2013; Miller and Svensson 2014), such that there now exists a push to incorporate the impact of ecology on these systems (Svensson 2017). However, in particular cases, the relevance of environmental-dependent selection is supported by suggestive evidence. For example, population morph frequencies are associated to local bioclimatic factors in the beetle *Hygrotylus impressopunctatus*, morphologically polymorphic in its elytral structure (Green et al. 2014), or the colour polymorphic lizard *Ctenophorus decresii* (McLean et al. 2015). In *U. stansburiana*, recent evidence highlighted that the frequency-dependent selection interacts with climate, local morph composition fluctuating over time depending on climatic variation (Friedman et al. 2017).

The common wall lizard, *Podarcis muralis* (Lacertidae), is a colour polymorphic species that has been attracted much attention recently. In this species, the polymorphism is genetically determined (Andrade et al. 2017), involving up to five alternative colour morphs (i.e. white -W-, yellow -Y-, orange -O- pure morphs, as well as white-orange -WO- and yellow-orange -YO- intermediate mosaic morphs; sensu Pérez i de Lanuza et al., 2013; but see Sacchi et al. 2007; Calsbeek et al. 2010). This colour polymorphism seems closely sustained by sexual selection. In fact, females and males often pair assortatively by colour (58–65% of pairs are homomorphic, Pérez i de Lanuza et al., 2013, 2016a), offspring size and number depend on both the mother's and father's morphs (Galeotti et al. 2013), and the outcome of experimental male contests depends on the morphs of the opponents (Ábalos et al. 2016). In addition, there exists a positive relationship between local male morph diversity (i.e. morph richness) and sex ratio (i.e. male-biased populations tend to present more male morphs), suggesting that the intensity of male intrasexual-selection may be underlying the local complexity of the polymorphism (Pérez i de Lanuza et al. 2017).

Recently, we found biogeographic evidence that environmental-dependent selection probably constraints the local diversity of morphs (i.e. morph richness – 3 to 5 morphs- and frequencies) in *P. muralis*, where the rare morphs (Y, YO) are more constrained by climate than common morphs (W, O, WO; Pérez i de Lanuza, G., Sillero N. and Carretero, M. A. unpublished). In that study, covering a surface of 5800 km² (see also Pérez i de Lanuza et al. 2017), we found a relationship at a geographic scale between the presence of each morph and some climate variables. Particularly, the rare morphs present a more restricted niche than the other morphs, only occupying those areas with higher temperature seasonality (i.e. temperature standard deviation × 100: higher temperature changes over time) and relatively higher total precipitation than in the remaining studied area. In contrast, the common morphs are widely distributed across the whole distribution area of the species in the region, encompassing a wide range of environmental conditions and shared almost all locations. Nevertheless, results obtained interpolating local morph frequencies, suggested differences also between common morphs, with the WO morph and especially the O morph more locally abundant at higher altitudes in the bottom of secondary valleys, whereas the W morph is more frequent at lower altitudes.

This relationship between climate and the differential presence and frequency of each morph may be explained by a direct morph-dependent survival across different habitats (e.g. due ecophysiological morph differences; e.g. McLean et al. 2015; Friedman et al. 2017). Alternatively, the relationship between climate and morph diversity may be indirectly caused by some source of environmental dependence on sexual (or social) selection (Miller and Svensson 2014). At present, we are not able to disentangle these effects on this relationship in *P. muralis*. However, if the geographic variation in morph composition is environmentally dependent through temperature and/or water availability as our previous biogeographic results suggested, we could expect that the alternative morphs within a given population compensate their differences in thermoregulation and/or water loss by occupying, for example, different microhabitats. Indeed, finding differences at a reduced spatial scale may serve to elucidate the mechanisms underlying the environmental dependence of local morph composition (e.g. Merilaita and Jormalainen 1997).

Microhabitats may simply mirror geographic variation in the presence of morphs at a smaller scale. Thus, due to the narrow niche of the rare morphs, we expected differences in microhabitat use between the rare morphs and the common morphs, but likely falling within those of the common morphs because of differences in morph frequencies between different habitats (GPL et al. unpublished). However, as males and females often paired assortatively by morph (Pérez i de Lanuza et al. 2013, 2016b), we expect little variation in

microhabitat use between sexes. To test these hypotheses, we performed a set of independent transects covering an environmentally heterogeneous area in which the five morphs of *P. muralis* coexist, with the aim of determining the environmental context in which each morph preferably appears.

Materials and methods

Study area

We visited 14 different but close localities in the centre of the Cerdanya valley (Eastern Pyrenees, 42°37' N, 1°56' E; see details of the study area in Pérez i de Lanuza and Font 2015; Pérez i de Lanuza et al. 2014, 2016a, b), where *P. muralis* is found in abundance across an area of 13,200 ha. Sampling localities present different orientations and ranged between 1200 and 1750 m a.s.l. These localities mainly present granite or schist lithologies. The vegetation is composed by forests (mainly dominated by *Fraxinus excelsior* or *Pinus uncinata*), shrubbery (frequently including *Crataegus monogyna* and *Rosa* sp.) and dry meadows with sparse vegetation. These habitats often include dry-stone walls and isolated boulders. Some of these localities present rivers, irrigation ditches and/or small water ponds. Regardless of the habitat, lizards often use rock walls and boulders to bask, perch, feed and socially interact (in Pérez i de Lanuza et al. (2016a), >90% of lizards were observed in rocky substrates). These localities correspond to an area where the environmental and social conditions apparently promote the coexistence of the five morphs (i.e. high temperature seasonality and relatively high precipitation, GPL et al. unpublished; male-biased local sex ratio, Pérez i de Lanuza et al. 2017; see also Fig. 1 in Pérez i de Lanuza et al. 2016b, in which: many of the central yellow dots correspond to localities explored in the present study).

Field observations

Field observations were randomly performed from 3rd to 31st July 2017, during the hours of lizard activity (9–15:30 hours local time, sampling duration between 0:51 and 3:41 hours). Observations were made in independent unidirectional transects performed at a constant speed, avoiding visiting any location twice. In this way, we ensured that lizards were observed at different times of the day and therefore capture the individual variability in habitat use while preventing repeated observations of the same individual. We used short focus binoculars (Papilio 8.6 × 21, Pentax, Tokyo, Japan) to determine the colour morph, sex (determined based on head and body proportions, and colour pattern), and age (i.e. size class) of lizards (see a full detailed description of methods in Pérez i de Lanuza et al. 2013, 2016a, b, 2017). As juveniles and subadult lizards do not show a completely developed

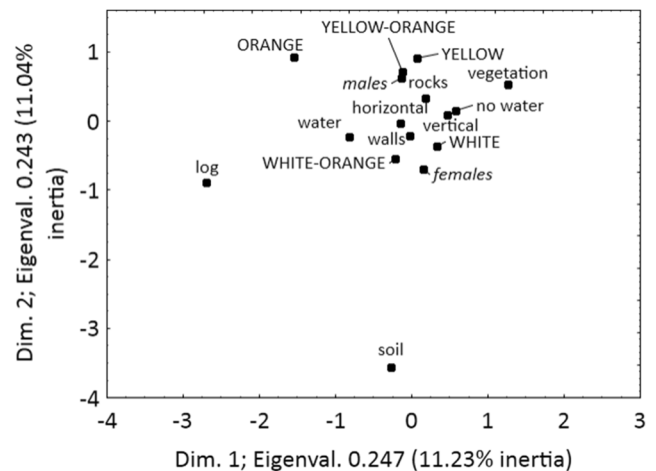


Fig. 1 Plot of colour morphs of *P. muralis* and habitat variable states associated with the observations by means of the multiple correspondence analysis using the first two axes. See “Materials and methods” for the definitions of the habitat variables

coloration, we only considered adult lizards (ca. SVL > 55 mm; presenting fully developed coloration and body proportions; Pérez i de Lanuza et al. 2013). Observations were made on individual lizards not involved in social interactions, and focal lizards were not selected by morph or sex. It was not possible to record data blind because our methodology involved focal animals in the field.

Habitat use variables

For a total of 1031 adult lizards, we quantified microhabitat and general habitat adapting the protocol by Gomes et al. (2016). In the exact site of each lizard observation, we recorded the height from the ground at the point of observation (HGR), inclination angle between the surface where the lizard was observed and the horizontal plane (INC; horizontal vs vertical), the type of substrate (SUBS: classified as either soil, vegetation, rocks, wall or log), and the proximity to water (WATER: classified as either closer or farther to 5 m from a water source). We also considered habitat in the 2-m diameter area surrounding the point of observation by visually estimating the percentage of bare soil, vegetation, rocks, walls and logs. Before subsequent statistical analyses, height from the ground and inclination were transformed as $y = \log_{10}(x + 0.5)$, and all percentages were arcsine-transformed. Observations were always made by the same observer (GPL).

Data analyses

Due to the categorical nature of most dependent variables, we first used multiple correspondence analysis (MCA, Lebart et al. 1984) to simultaneously represent lizard groups (morphs, sexes, microhabitats) and their respective variable states. After this first exploration, a log-linear model (Jobson 1992) was

Table 1 Eigenvalues and score coefficients associated to each factor in the multiple correspondence analysis

	Factor					
	1	2	3	4	5	6
Eigenvalue	1.905	1.460	1.016	0.979	0.585	0.055
% Total variance	31.753	24.331	16.932	16.314	9.756	0.913
Cumulative %	31.753	56.085	73.016	89.331	99.087	100
Score coefficients						
Height	-0.023	0.289	-0.024	0.892	-0.407	-0.062
Soil	-0.313	-0.453	-0.003	-0.012	-0.762	-1.786
Vegetation	0.241	0.468	-0.152	-0.398	-0.635	-1.680
Rocks	0.435	-0.285	-0.049	0.257	0.399	-2.565
Walls	-0.423	0.295	-0.106	-0.003	0.631	-2.287
Log	0.012	0.097	0.973	-0.028	-0.022	-0.647

fitted to infer any synergic effects of morph and sex on the frequency of each habitat use. Additionally, for all continuous microhabitat (e.g. HGR, INC) and habitat variables (% of bare soil, vegetation, rocks, walls and logs), we performed permutation ANOVAs using species, sex and their interaction as predictor variables, to evaluate differences between morph \times sex groups. Because multiple comparisons were evaluated simultaneously, we implemented the false discovery rate (FDR, Benjamini and Hochberg 1995) procedure to adjust the α -values of statistical tests.

Table 2 Results from the fitted log-linear model considering main factors and interactions between them. Significant results in bold

	df	Partial association		Marginal association	
		χ^2	<i>P</i>	χ^2	<i>P</i>
Sex	1	3.19	0.07		
Morph	4	720.37	<0.00001		
Inclination	1	261.15	<0.00001		
Microhabitat	4	1138.80	<0.00001		
Water	1	30.15	<0.00001		
Sex \times morph	4	20.86	0.0003	19.75	0.0006
Sex \times inclination	1	2.38	0.12	2.18	0.14
Sex \times microhabitat	4	4.37	0.36	5.28	0.26
Sex \times water	1	2.57	0.11	1.62	0.20
Morph \times inclination	4	2.22	0.70	2.33	0.68
Morph \times microhabitat	16	14.30	0.58	16.30	0.43
Morph \times water	4	20.43	0.0004	20.28	0.0004
Inclination \times microhabitat	4	2.56	0.63	2.66	0.62
Inclination \times water	1	0.01	0.93	0.03	0.86
Microhabitat \times water	4	20.84	0.0003	22.64	0.0001

Data availability The datasets analysed during the current study available from the corresponding author on reasonable request.

Results

The final sample included 1031 observations of adult lizards: 290 W, 55 WO, 80 O, 103 Y and 19 YO males, and 300 W, 67 WO, 34 O, 69 Y and 14 YO females. The average duration of transects (mean \pm SEM) was 144.3 ± 13.6 min (range 51–221), and the average amount of scored adult lizards per transect (mean \pm SEM) was 73.6 ± 9.1 (range 24–158).

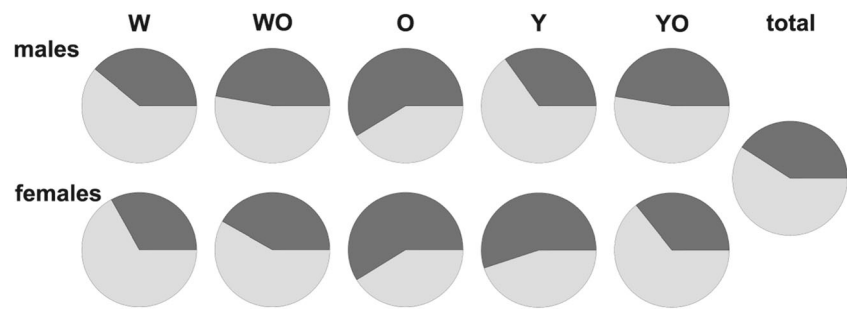
Results from the multiple correspondence analysis are shown in Table 1, being the O morph the most segregated in the multivariate space (Fig. 1). The fitted log-linear model (max likelihood $\chi^2 = 6.17$, $df = 4$, $P = 0.19$) highlighted that interactions between sex and morph, morph and water presence, and microhabitat and water presence are significant (Table 2). In particular, the O morph appears more frequently than the others in habitats close to water (Fig. 2). The Y females apparently tend to appear in places near to water bodies more frequently than Y males (Fig. 2), but this is not supported but the log-linear models (Table 2).

Results from the multivariate test for continuous variables were significant for morph ($F_{24,3546} = 1.88$, $P = 0.006$), and for the interaction between sex and morph ($F_{24,3546} = 1.79$, $P = 0.01$), but not for sex alone ($F_{6,1016} = 1.24$, $P = 0.28$). The subsequent univariate tests were significant for morph and the morphs and sex interaction focusing on soil proportion, for morph focusing on vegetation proportion, and for sex and morph interaction focusing on log proportion (Table 3; Fig. 3). Remarkably, while morphs did not much differ in the use of rocks and walls, the O morph tended to be found surrounded by more vegetations and less bare soil than the other morphs (Fig. 3).

Discussion

Our results indicate that there exists a differential habitat use by the alternative colour morphs of *P. muralis*. In general, sex did not have major effect on microhabitat selection, with males and females generally displaying similar trends in habitat use. The main difference involves the O morph in comparison to the other morphs. O lizards occupy, on average, more humid and vegetated localities than the rest of morphs. Therefore, the niche occupied by the O morph is partially biased from those of the other morphs. This suggests some source of environmental-dependent selection, probably constraining morph success or survival. Surprisingly, we did not find differences in microhabitat use between the rare morphs, i.e. Y and YO, and the W and WO common morphs.

Fig. 2 Proportions of observations made near a water body (dark grey) or away from the water (light grey) classified by sex and morph (W white, WO white-orange, O orange, Y yellow, YO yellow-orange)



Present results, however, allow us to discard a hypothesis of full spatial segregation between morphs, even considering the O morph. Quite the opposite, all morphs often appear in strict syntopy and interact with each other, even allowing the existence of inter-morph male-female pairs (39.3% of pairs; 20.6% involving a pure orange male or female; Pérez i de Lanuza et al. 2013, 2016b). In fact, all morphs share most microhabitat elements, especially rocks and walls, used as refuge as well as for thermoregulation and social interaction. In addition, the W, WO and O morphs coexist at population scale in most of the studied localities (> 88%; Pérez i de Lanuza et al. 2017). Interestingly, here, we detect differences in microhabitat use between morphs despite the fact that these microhabitat differences are subordinate to a main difference at an intermediate scale (i.e. habitat). Further to this, it is worth

noting that results analysing the geographical patterns of morph abundance by interpolating absolute and relative frequencies of morph presence suggested that the O morph is more frequent in relatively humid areas (i.e. at a relatively high altitude in secondary Pyrenean valleys; GPL et al. unpublished). Thus, in localities in which humidity is higher, there exist a greater number of water bodies, and vegetation is denser, the proportion of O lizards will be higher than in drier environments, humidity being relevant for the orange morph at a geographic scale instead on its spatial segregation within localities.

On the other hand, although ecological niche models showed that the Y and YO morphs are restricted to habitats presenting high-temperature seasonality and relatively high precipitation (GPL et al. unpublished), we have not found differences in microhabitat between these morphs and the W and WO common morphs. All these morphs do not seem directly affected by humidity in the same way as the O morph, or by other habitat variables described here. At a geographic scale, the distribution of the intermediate WO morph is similar to that shown by the O morph (GPL et al. unpublished). However, the microhabitat use of this morph is more similar to that of the W morph and differs from that of the O lizards.

Although plots suggest an apparent interaction between sex and morph exclusively affecting the Y morph, the Y females occupying microhabitats close to water more frequently than Y males, in fact, this was not statistically supported. This could be simply due to low sample size since Y morph is minority, but eventual sexual differences are to be considered with caution (e.g. the ecophysiological data are not currently available for females). If real, this partial mal-adjustment may be underlying, at least in part, the geographical distribution of rare morphs (i.e. Y, YO; Pérez i de Lanuza et al. 2016b, 2017).

In our biogeographic study, we discussed whether the environmental-dependence has a direct (i.e. physiological) cause or by some indirect relationship mediated by interaction between environment and social selection (GPL et al. unpublished). Present results suggest that the environmental dependence may be of a different nature for different morphs. Indeed, a direct relationship between environment and morph

Table 3 Results from the univariate tests of quantitative microhabitat variables, considering sex and morph as factors, as well as their interaction. Significant results in bold

Univariate tests		SS	df	MS	F	P
Height	Sex	0.06	1	0.06	1.06	0.30
	Morph	0.32	4	0.08	1.49	0.20
	Sex × morph	0.29	4	0.07	1.33	0.26
Habitat						
Soil	Sex	0.09	1	0.09	1.55	0.21
	Morph	0.93	4	0.23	4.07	0.003
	Sex × morph	0.82	4	0.21	3.57	0.007
Vegetation	Sex	0.01	1	0.01	0.13	0.72
	Morph	0.74	4	0.19	5.31	0.0003
	Sex × morph	0.34	4	0.09	2.43	0.046
Rocks	Sex	0.08	1	0.08	0.76	0.38
	Morph	0.41	4	0.10	10.46	0.38
	Sex × morph	0.07	4	0.02	0.17	0.95
Wall	Sex	0.06	1	0.06	0.65	0.42
	Morph	0.52	4	0.13	14.21	0.23
	Sex × morph	0.35	4	0.09	0.97	0.42
Log	Sex	0.05	1	0.05	270.20	0.10
	Morph	0.04	4	0.01	0.57	0.69
	Sex × morph	0.23	4	0.06	306.37	0.015

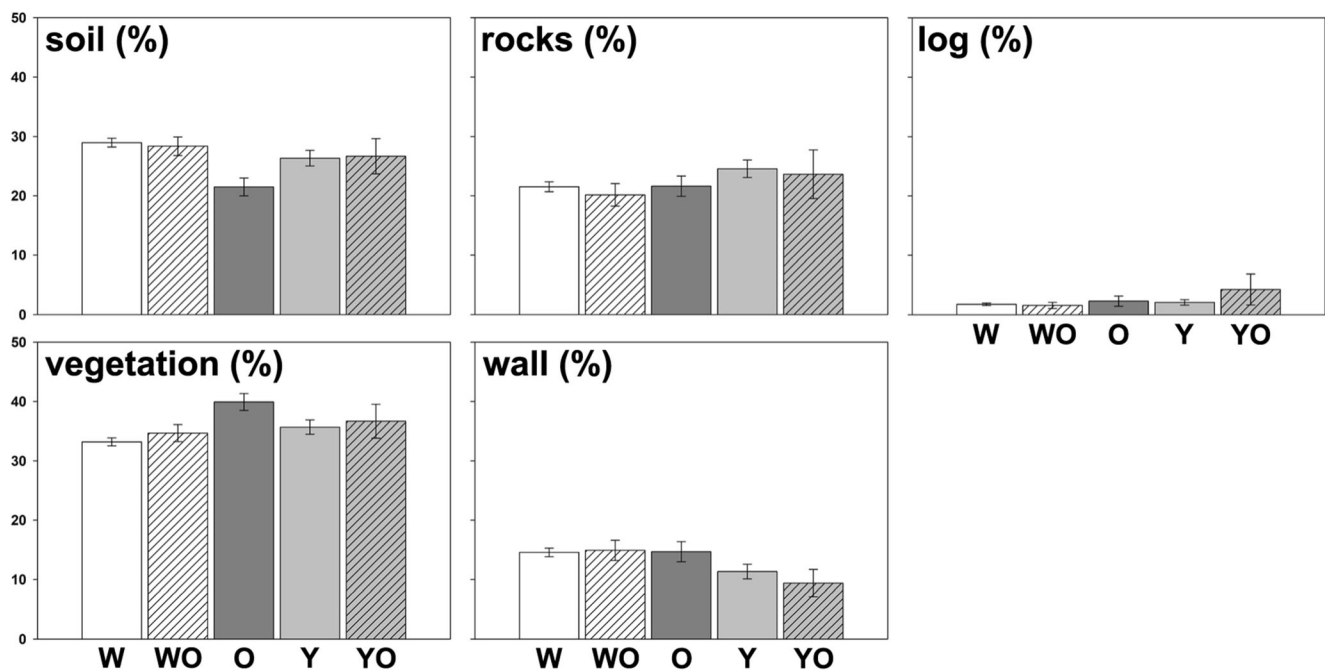


Fig. 3 Mean \pm SEM of each habitat type classified by morph (W white, WO white-orange, O orange, Y yellow, YO yellow-orange) pooling males and females

presence seems plausible for the O morph. Our own unpublished ecophysiological data suggest that the O morph differs from the other pure morphs in the fundamental niche, as the water loss rate of O males is higher than those of W and Y males (MAC et al. unpublished). This is coincident with results presented here, suggesting that some direct environmental dependence in morph fitness exists, at least for the O morph. Contrarily, such type of direct environmental dependence is more unlikely for the other morphs, especially because the W and the Y morphs do not differ either in microhabitat use or in ecophysiology. Thus, we could expect that environmental dependence acting on rare morphs is mediated by a relationship between environment and factors relevant for social selection, i.e. the environment affecting demography and sex ratio (Le Galliard et al. 2005; Donald 2007; Wapstra et al. 2009; Romero-Díaz et al. 2017), and then, the intensity of sexual and social selection). Interestingly, the rare morphs, Y and YO, emerge in those localities in which sex ratio is male-biased (Pérez i de Lanuza et al. 2017), but a detailed analysis of the interactions between sex ratio, environment and morph composition is needed.

Given these results, we may expect temporal variation in local morph frequencies to shifts either in activity (short-term) or in survival (long-term; Friedman et al. 2017). Regarding the second, in a context of climate change with variation in precipitation regimes (longer summer drought and Mediterraneanization, see Blondel et al. 2010), one would expect the O morph to decrease in activity/frequency, as it becomes further restricted by the presence of water sources and humid microhabitats. Seemingly, the removal of vegetation, as in the

case of forest fires (Ferreira et al. 2016), or the desiccation of water bodies should be more detrimental for the O morph. These predictions should be tested with field data and further experimental work.

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Compliance with ethical standards

Conflict of interest The authors declare that they have no conflict of interest.

Ethical approval Binocular observations allowed minimising lizard disturbance (at worst, lizards avoided the observer by moving away). No lizards were captured or manipulated during the observations. The habitat was not altered in any way. This research complied with the ASAB/ABS Guidelines for the Use of Animals in Research. Permits for working in our study area were provided by the Préfecture des Pyrénées Orientales (Arrêté no. 2016-2-09).

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