

RESEARCH ARTICLE

Through the eye of a lizard: hue discrimination in a lizard with ventral polymorphic coloration

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ABSTRACT

Colour polymorphisms are thought to be maintained by complex evolutionary processes, some of which require that the colours of the alternative morphs function as chromatic signals to conspecifics. Unfortunately, a key aspect of this hypothesis has rarely been studied: whether the study species perceives its own colour variation as discrete rather than continuous. The European common wall lizard (*Podarcis muralis*) presents a striking colour polymorphism: the ventral surface of adults of both sexes may be coloured orange, white, yellow or with a mosaic of scales combining two colours (orange–white, orange–yellow). Here, we used a discrimination learning paradigm to test whether *P. muralis* is capable of discriminating colour stimuli designed to match the ventral colours of conspecifics. We trained 20 lizards to eat from colour-coded wells bored in wooden blocks. Blocks had four colour-coded wells (orange, white, yellow and an achromatic control), but only one contained food (mealworm larvae). After six trials, the lizards performed significantly better than expected by chance, showing a decrease in both the number of wells explored and the latency to finding the food. Using visual modelling techniques, we found that, based on their spectral properties and the lizards' cone sensitivities, the ventral colours of *P. muralis* correspond to discrete rather than continuous colour categories, and that colour discriminability (i.e. distance in perceptual space) varies depending on the morphs compared, which may have implications for signal detection and discrimination. These results suggest that *P. muralis* can discriminate hue differences matching their own ventral colour variation.

KEY WORDS: Colour discrimination, Colour polymorphism, Colour vision, Learning experiment, Visual modelling

INTRODUCTION

Understanding the processes responsible for the evolution of population polymorphisms is one of the most exciting challenges facing evolutionary biology. Colour polymorphic species such as the peppered moth, *Biston betularia*, have been extensively used as models to test important evolutionary hypotheses about the origins and maintenance of phenotypic variation (Majerus, 1998; Gray and McKinnon, 2006; Oliveira et al., 2008; Svensson et al., 2009; McKinnon and Pierotti, 2010; Wellenreuther et al., 2014; Svensson, 2017). However, assessing colour variants and their functional

significance in colour polymorphic species is not straightforward. Colour variation is often described from the perspective of a human viewer but should instead be judged from the perspective of the appropriate receivers (Bennett et al., 1994; Eaton, 2005), which requires the use of modern instrumentation and methods for objective colour characterization (e.g. reflectance spectrophotometry and visual modelling). Also, the widely held assumption that the colours of the different morphs act as chromatic signals and that conspecifics use colour variation to identify alternative phenotypes (e.g. related to age, sex, individual quality or reproductive strategies) and adjust their behaviour accordingly has rarely been tested.

Recent work with pollinating insects and birds and with cichlid fish underscores the importance of considering perceptual mechanisms in the study of colour polymorphisms (Chittka and Raine, 2006; Muchhala et al., 2014; Thairu and Brunet, 2015). Cichlids show striking and hypervariable interpopulation and intrapopulation colour polymorphisms, and abundant evidence has demonstrated that colour discrimination, visual ecology and sensory drive play a critical role in the evolution of this interesting polymorphic clade (e.g. Seehausen et al., 2008). However, there is no information on morph discrimination for most colour polymorphic species, including lizards (but see Teasdale et al., 2013; Merckling et al., 2016).

The European common wall lizard *Podarcis muralis* (Laurenti 1768) (family Lacertidae) has attracted much interest in studies of colour polymorphism (e.g. Calsbeek et al., 2010; Galeotti et al., 2013; Pérez i de Lanuza et al., 2013, 2017). To the human eye, this species may show up to five discrete ventral colour morphs that are fixed at sexual maturity: white, yellow and orange pure-colour morphs, as well as white–orange and yellow–orange mixed phenotypes that display a mosaic of scales of two different colours (sensu Pérez i de Lanuza et al., 2013; Pérez i de Lanuza and Font, 2015). These colours extend over the throat and the belly in males but, at least in some populations, are restricted to the throat in females (females in these populations have a white belly). Much effort has been devoted to the identification of consistent behavioural, morphological, physiological or ecological correlates of the colour variation, but the results are so far inconclusive (Sacchi et al., 2007; Calsbeek et al., 2010; Galeotti et al., 2013; Pérez i de Lanuza et al., 2014).

While it is often assumed that the ventral colours in *P. muralis* function as social signals, the evidence in this regard is very scant. It is possible that the ventral coloration, while correlated with other phenotypic traits, has no effect on receiver behaviour and is therefore not a chromatic signal to conspecifics. Rather, a link between polymorphic coloration and alternative phenotypes could result from pleiotropic effects of whatever genes are responsible for the polymorphism. However, there are some indications that lizards assess each other's ventral colours and adjust their behaviour based on their own colour relative to that of others with which they

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interact. For example, although morphs are not spatially segregated, males and females pair assortatively by ventral colour (Pérez i de Lanuza et al., 2013, 2016). Also, male ventral colour seems to be important in the resolution of lab-staged fights (Ábalos et al., 2016). Further, it has been suggested that females may adjust their breeding strategy according to their own and their mate's colour morph (Galeotti et al., 2013).

A necessary condition for the colour of alternative morphs to function as social signals is that the animals themselves can perceive them as different stimuli, which ultimately depends on their visual perception, not ours (Teasdale et al., 2013; Pérez i de Lanuza and Font, 2014). Research on colour polymorphic *P. muralis* rests on the reasonable assumption that lizards perceive their own chromatic variation as categorically distinct phenotypes (i.e. morphs), much as humans do. However, nobody has formally tested this assumption. Given the known differences between the visual systems of lizards and humans, establishing the existence of discrete colour morphs from the lizards' perspective is essential for many current hypotheses about the genetic underpinnings of the polymorphism and the evolutionary processes generating and maintaining it (e.g. Cote et al., 2008; Paterson and Blouin-Demers, 2017).

Although the human visual system has little trouble identifying discrete colour morphs in *P. muralis*, lizards could perceive their own colour variation in a different way. *Podarcis muralis* has, in common with other diurnal lizards, a sophisticated colour vision system with four types of single cones that are sensitive to light in the wavelength range between 320 and 700 nm (Pérez i de Lanuza and Font, 2014; Martin et al., 2015). Their retinas also contain large numbers of long-wavelength sensitive double cones that are thought to be responsible for luminance (i.e. brightness) perception (Loew et al., 2002; Olsson et al., 2013). As the ventral colours differ both in spectral shape and in luminance (Pérez i de Lanuza et al., 2013; Pérez i de Lanuza and Font, 2015), discrimination of the alternative morphs could be based on either of these variables.

Discrimination experiments are a useful tool to confirm animal colour vision and the perception of colour differences (Kelber et al., 2003; Kelber and Osorio, 2010). There is no shortage of papers testing the ability of lizards to visually discriminate between stimuli of different size, shape, pattern, luminance or colour (i.e. hue). In his comprehensive review of learning processes in reptiles, Burghardt (1977) listed 12 such studies, of which half involved some type of hue discrimination, and more have been published in the ensuing decades. These studies have shown that lizards can discriminate between stimuli differing only in hue (e.g. Wagner, 1933; Swiezawska, 1949; Rensch and Adrian-Hinsberg, 1963; Elinor and Benes, 1969; Dücker and Rensch, 1973) or in luminance (e.g. Vance et al., 1965; Garzanit and Richardson, 1974; Peterson, 1976; Hodgkinson and Still, 1980). Unfortunately, few studies have used standard colour stimuli with known reflectance properties (e.g. Ostwald, Munsell) and many do not include luminance controls (i.e. greys). Luminance controls may be of little relevance if the focus of the study is learning per se rather than colour discrimination (e.g. Leal and Powell, 2012). But if the goal is to establish that colour vision is present, luminance controls are essential to ensure that the animals respond differentially to hue-independent stimuli (Kelber et al., 2003). Also, most studies using colours as discriminanda make no attempt to use colours that resemble natural stimuli that the animals might encounter in the field, such as colours of prey or conspecifics (but see Hews and Dickhaut, 1989).

Here, we used a behavioural experiment adapted from previously used experimental designs (Leal and Powell, 2012; see also Clark

et al., 2014) to test whether *P. muralis* can discriminate the ventral colour variation shown by this species. Additionally, we reanalysed spectral data collected in previous studies (Pérez i de Lanuza et al., 2013, 2014; Pérez i de Lanuza and Font, 2015) and used visual modelling techniques based on the receptor noise model (Vorobyev and Osorio, 1998) to assess the colour variation and quantify the degree of discriminability among colour morphs from a lizard's visual perspective.

MATERIALS AND METHODS

We captured 20 lizards (10 males and 10 females) by noosing (i.e. using a pole with a slipknot that tightens around the neck of the lizard) on 8 July 2015 in Angostrina (Eastern Pyrenees, France). The lizards were individually held in cloth bags and transferred by car to the Ethology lab at the University of Valencia (470 km) on the day following their capture. In the laboratory, lizards were housed in individual terraria (20×40 cm and 26 cm high) provided with water, a shelter, and a brick over which an incandescent reflector lamp (40 W; Parabolica RP50 Radium, Wipperfurth, Germany) was suspended. Terraria were housed in an animal room with temperature and light cycle mimicking average field conditions at the capture site (thermal gradient of 24–40°C inside the terraria during the day; 12.5 h light:11.5 h dark). In addition, ultraviolet (UV)-rich fluorescent tubes (Reptistar 5.0, Sylvania, Danvers, MA, USA; colour temperature 6500 K) suspended above the terraria were switched on for 1.5 h (12:00 h–13:30 h) three times per week. During the colour discrimination experiments (11 July to 27 August 2015), lizards had access to food only during the experimental trials, but individuals failing to eat in five consecutive trials were discarded from the experiment and fed 3–4 times per week. After the experiments were completed, all lizards were released back at their capture location on 31 August 2015. Lizards were captured under research permit number 2013095-0001 from the Préfecture des Pyrénées-Orientales (France). This research complied with the ASAB/ABS Guidelines for the Use of Animals in Research and all applicable local, national and European legislation.

Colour discrimination experiment

For the colour discrimination experiment, we trained lizards to eat mealworm larvae (*Tenebrio molitor*; ca. 2 cm long and 150 mg) dusted with vitamins (Exo Terra, Montreal, QC, Canada) from a well in a wooden block. The block had four evenly spaced circular wells (2 cm diameter, 1.5 cm deep) and each well was associated with a different colour by means of two coloured paper stickers: a ring-shaped sticker surrounding the well's entrance and a rectangular sticker marking its position on the lateral side of the block (Fig. 1). In total, we used 10 wooden blocks, each of which was used by only two lizards. Each block had three wells fitted with orange, white and yellow stickers resembling the ventral colours of *P. muralis*, and a fourth grey-coloured sticker having the same luminance as the training colour (see 'Experimental stimulus design', below). To prevent the lizards from locating prey using chemical cues, we placed two live mealworm larvae inside all wells for 2 weeks before the start of the experiment, and two nights per week during the experiment (Monday and Thursday; 19:30 h–09:30 h).

We trained half the animals (five males and five females) to eat from the orange well, and the other half to eat from the yellow well (Fig. S1). To begin a trial, we introduced two larvae into the orange or yellow well, and positioned the wooden block inside the terrarium of the animal to be tested (4 cm from the shelter's entrance; see Fig. 1). A trial ended when the lizard located and ate

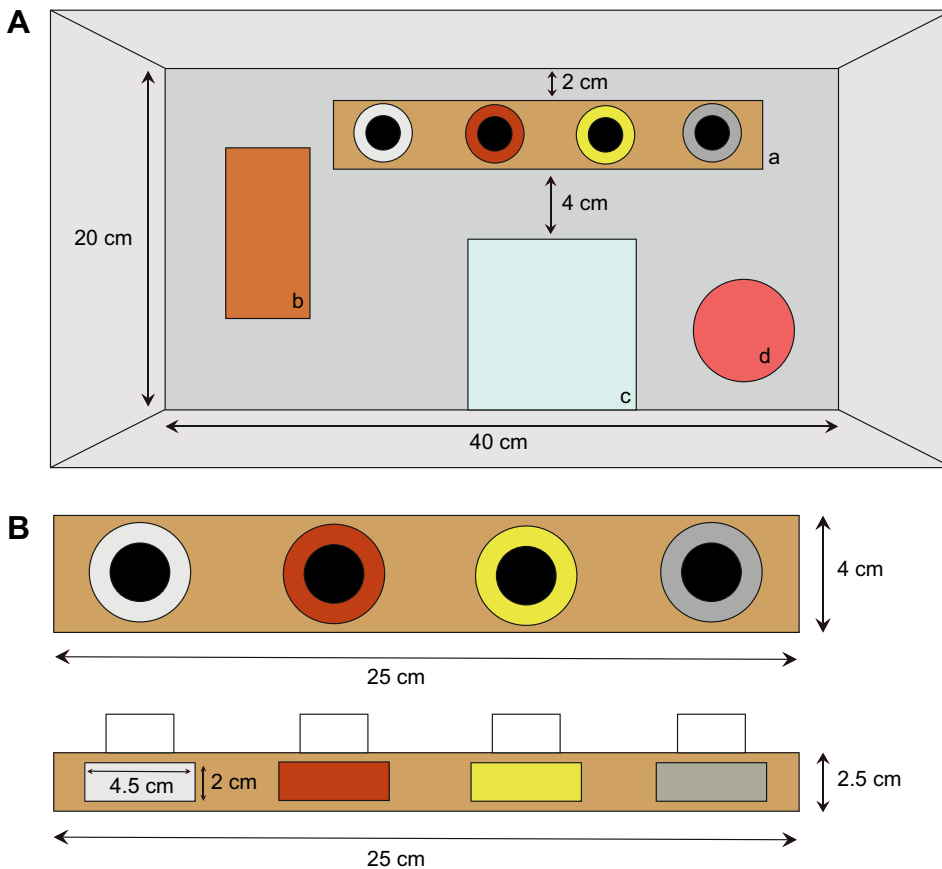


Fig. 1. Experimental terraria. (A) Location of elements within the individual terraria: (a) wooden block (only inside the terraria during experiments); (b) basking brick; (c) shelter; (d) water dish. (B) Schematic view of the experimental wooden block as seen from above (top, lids removed) and from the side facing the shelter (bottom, lids on wells).

the prey or after 25 min had elapsed. We tested each lizard on alternate days to ensure motivation toward the food reward (one trial per day). Prior to each trial, the position of the coloured stickers was determined using a random number generator, discarding combinations in which the larvae would remain in the same position as in the previous trial. During trials, both the UV-rich fluorescent tube and the incandescent lamp were on, providing a continuous light spectrum across the entire visual range of *P. muralis* (see irradiance spectrum in Fig. S2). We conducted trials during the lizards' natural daily period of activity (10:00 h–13:30 h and 16:00 h–19:00 h local time).

The experiment comprised a training phase and a testing phase. Training consisted of six trials (12 days) during which the mealworm larvae were in the orange or yellow well and we gradually reduced their visibility by partially covering the well with a white plastic lid weighing 8.5 g (i.e. covering 50% of the opening in trials 1 and 2, 75% in trials 3 and 4, 95% in trials 5 and 6). During the testing phase (18 trials, 36 days), we presented the wooden block with all four wells completely covered and videorecorded every trial using a photographic camera (Canon[®] EOS 60D, Tokyo, Japan) mounted on a tripod. We played back each filmed trial and one researcher (J.A.) recorded whether or not the animal found and consumed the prey, the number of incorrect lids lifted (errors), and the time elapsed from when it left the refuge until it lifted the correct lid (latency).

Experimental stimulus design

Experimental stimuli were designed to resemble the natural colour variation found in *P. muralis* ventral coloration. We prepared a palette of whites, yellows and oranges in Adobe Illustrator and printed them on five types of paper differing in whiteness,

brightness and shade (resulting in 790 stimuli). These stimuli were measured with a portable spectrometer (see details below) and differences from natural lizard reflectance spectra (averaged over at least 164 spectra per morph; Fig. 2) were explored graphically, comparing colour variables (i.e. hue, chroma and brightness), and calculating chromatic and achromatic distances between any two colours using visual modelling (see details below). We chose the three chromatic stimuli that best matched natural colours (orange: CMYK=0%, 99%, 91%, 0%, Couché mate 130 g m⁻²; white: CMYK=6%, 10%, 21%, 2%, Color copy 250 g m⁻²; yellow: CMYK=0%, 23%, 86%, Couché mate 130 g m⁻²; Fig. 2; Fig. S3).

By presenting an achromatic control with the same luminance as the training colour, we controlled the possibility that lizards base their discrimination on luminance differences among the colour stimuli. We designed two achromatic controls that were isoluminant with the chromatic yellow and orange experimental stimuli. Unfortunately, no evidence regarding how lizards judge luminance differences is available. Therefore, we conservatively designed the achromatic stimuli to show an absolute luminance (i.e. the integral of the spectral curve) similar to that of the chromatic stimuli (orange–achromatic: CMYK=0%, 0%, 0%, 82%, Couché mate 130 g m⁻²; yellow–achromatic: CMYK=0%, 0%, 0%, 67%, Couché mate 130 g m⁻²; Fig. 2; Fig. S3). However, as it has been hypothesized that luminance is perceived by a sensory channel involving the long-wavelength sensitive cones (as single cones: Fleishman et al., 1997; Fleishman and Persons, 2001; or as the main component of double cones: Osorio and Vorobyev, 2005), we also compared luminance between the chromatic stimuli and their corresponding achromatic stimuli using visual models assuming that luminance is processed by the long-wavelength sensitive cones (see methodological details in 'Visual modelling', below).

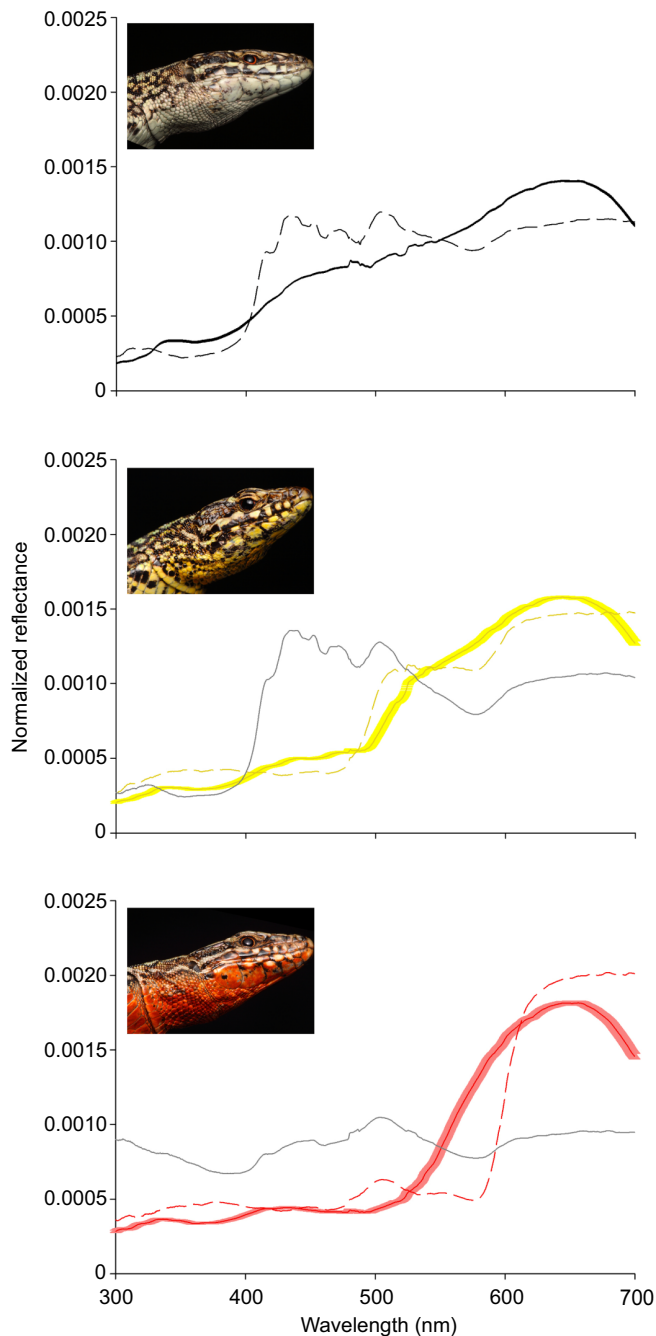


Fig. 2. Reflectance spectra. Lines represent spectra from natural *Podarcis muralis* throats (solid lines and shaded area represent means \pm 1 s.e.m.) and the corresponding artificial stimuli (long-dashed lines represent the chromatic stimuli; grey lines for yellow and orange morphs represent the corresponding achromatic stimuli). For clarity, the spectra have been normalized by dividing the reflectance at each wavelength by the entire reflectance under the curve (i.e. luminance). See sample sizes for natural spectra in Materials and methods.

Statistical analyses

In order to account for inter- and intra-individual variability within trials, we grouped experimental trials in blocks of three, hence defining six blocks where the number of errors and mean latency were calculated. We then compared the mean number of errors per individual in each block with the average expected by chance (Baldwin, 1979; Margules and Gallistel, 1988; Brannon and Terrace, 1998). With four options to choose, the maximum

number of errors is three. If choosing randomly, lizards are equally likely to make 0, 1, 2 or 3 errors. By multiplying each number of errors by its probability (1/4) we obtain the mean number of errors expected by chance ($\bar{X}_{\text{errors}} = 0 \times 1/4 + 1 \times 1/4 + 2 \times 1/4 + 3 \times 1/4 = 6/4 = 1.5$). We established better-than-chance performance in a block of trials as the criterion for successful learning.

To check for a decrease in both the mean number of errors and the mean latency with time, we ran two generalized linear mixed models (GLMMs) with errors (Poisson distribution) and latency (Gaussian distribution) as dependent variables, block and sex as fixed factors, and animal identity, training colour and (only in the model with number of errors) whether or not the animal located the prey as random factors. We checked graphically that both the number of errors and latency followed non-normal distributions (qqplots in R; <http://www.R-project.org/>). We power-transformed latency to follow a normal distribution by calculating the fourth root of each value (Shapiro–Wilk test for normality: $W=0.99$, $P=0.14$). We did not transform the number of errors as transforming count data is not recommended (O’Hara and Kotze, 2010), and adjusted a GLMM following a Poisson distribution after checking the mean and the variance of this variable had similar values ($\bar{X}=1.12$, $S^2=0.98$).

In addition, as a more conservative test of discrimination learning, we coded the performance of each individual lizard in each trial as either 1 (if the lizard’s first choice was correct) or 0 (if the lizard made any number of errors). Then, we fitted a logistic mixed model with the lizard’s performance as dependent variable, trial and sex as fixed effects, and animal identity, training colour and whether or not the animal located the prey as random factors. We plotted the fitted model with confidence intervals against time (i.e. trial) to check for a significant increase in the probability of correct first choice from chance levels (0.25).

Model fitting and model selection were conducted using backward single-term deletions ($P \leq 0.05$) of the saturated model followed by model comparisons via likelihood ratio tests (lme4 package in R: Bates et al., 2015; <http://www.R-project.org/>). We did not find a problem of over-dispersion in the Poisson model ($\phi=1.002$). We explored graphically that residuals from both models conformed to normality and homoscedasticity assumptions by plotting them against the logarithm of the fitted values.

Visual modelling

To determine quantitatively the discriminability between pairs of ventral colours (i.e. white against yellow, white against orange, and yellow against orange) we used Vorobyev and Osorio’s (1998) receptor noise model. Calculations were performed in R 3.3.2 (<http://www.R-project.org/>) using the package PAVO (Maia et al., 2013). We assumed a cone abundance ratio of 1:1:1:4 (corresponding to the UV-, short-, middle- and long-wavelength sensitive cones; J. F. Le Galliard, personal communication based on results from Martin et al., 2015), and a Weber fraction of 0.05 for the long-wavelength sensitive cone (Siddiqi et al., 2004; previously used in other studies with lacertids: Marshall and Stevens, 2014; Martin et al., 2015). Cone absorbance spectra of *P. muralis* were obtained from the literature (Martin et al., 2015). As the illuminant, we used the irradiance spectrum inside the experimental terraria resulting from the combination of the light provided by the incandescent lamp and the UV-rich fluorescent tube (Fig. S2). The discriminability between morphs was expressed as just noticeable differences (JND). A value of 1 JND is traditionally assumed as the threshold of discrimination between two colour patches, i.e. pairs of colours giving values < 1 JND are not discriminable, values between

1 and 3 JND represent colours that are discriminable under good illumination conditions, and values above 3 JND represent easily discriminable colours (Siddiqi et al., 2004; Marshall and Stevens, 2014). However, as behavioural data to confirm this assumption in *P. muralis* are completely lacking, these thresholds have to be interpreted with caution. Therefore, we conservatively adopted a threshold of 3 JND to declare that two colours were discriminable to the lizards.

To determine quantitatively whether our experimental stimuli resembled the lizards' ventral coloration, we also used Vorobyev and Osorio's (1998) receptor noise model to calculate chromatic and achromatic distances between natural spectra and the spectra obtained from the artificial stimuli. Based on these analyses, we chose for behavioural experiments those artificial chromatic stimuli that minimize the chromatic distance when compared with natural spectra (see below), and those artificial achromatic stimuli that minimize the achromatic distance when compared with artificial chromatic stimuli.

For visual modelling, we used reflectance spectra of throat coloration in the same Pyrenean population of *P. muralis* from which experimental animals were obtained (Angostrina, Eastern Pyrenees, France). Spectra were compiled from previously published studies (Pérez i de Lanuza et al., 2013, 2014; Pérez i de Lanuza and Font, 2015; raw data are available from the corresponding author on request), resulting in a dataset of 643 adult lizards showing pure morphs (199 white males, 88 white females, 135 yellow males, 57 yellow females, 131 orange males and 33 orange females). Reflectance spectra were obtained with a USB-2000 portable spectrometer and a PX-2 xenon strobe light source (Ocean Optics Inc., Dunedin, FL, USA), calibrated with a Spectralon white diffuse reflectance standard (Labsphere) (for more details, see Font et al., 2009; Pérez i de Lanuza et al., 2013, 2014; Badiane et al., 2017). Irradiance inside the experimental terraria was measured with a second USB-2000 spectrometer calibrated by means of a LS1-CAL calibration light source (Ocean Optics), using a cosine-corrected irradiance probe (Ocean Optics CC-3-UV). To assess differences in discriminability (i.e. chromatic distances) between the different pairs of ventral colours, we used a generalized linear model including the paired colour combinations (i.e. white–yellow, white–orange and yellow–orange) and sex as factors, as well as their interaction.

As parameters used to run visual models (i.e. cone proportion: 1:1:1:4; Weber fraction=0.05) are not supported by any empirical data in *P. muralis*, and because small variations in visual parameters can affect the results of visual modelling (Lind and Kelber, 2009; Bitton et al., 2017; Olsson et al., 2017), we repeated the analyses to assess whether our results are robust to variations in these parameters. Therefore, we also ran models with cone proportions of 1:1:1:1, 1:1:1:8 and 2:3:3:11 (i.e. the original count presented by Martin et al., 2015), and Weber fraction values of 0.03 and 0.07.

RESULTS

Colour discrimination experiment

Twelve lizards (seven males: three trained to eat from the orange well and four from the yellow well; and five females: three trained to eat from the orange well and two from the yellow well) completed the experiment. The remaining eight individuals failed to uncover a well in five consecutive trials and were discarded from the experiment.

The mean number of errors per block was significantly smaller than expected by chance (1.5) in all but the first two blocks of trials (Table 1, Fig. 3). Both the number of errors (Fig. 3) and latency (Fig. S4; Table 2) showed a significant reduction with time (Errors~Stage, $Z=-2.40$, standard coefficient±s.e.= -0.30 ± 0.13 ,

Table 1. Number of errors in colour discrimination experiment

Block	N	No. of errors		P
		Mean	CI	
1	32	1.34	0.35	0.158
2	34	1.29	0.41	0.153
3	32	1.19	0.36	0.049
4	36	1.08	0.36	0.013
5	35	1.09	0.30	0.008
6	33	0.73	0.27	$1.92e^{-5}$

Mean number of errors and 95% confidence interval (CI) in each of six consecutive blocks of trials (three trials per block) comprising the training phase and the experiment, and *P*-values for one-way Wilcoxon tests ($\mu<1.5$). *N*, number of trials per block (out of 36) in which all 12 trained lizards uncovered at least one well.

$P=0.016$; see Table S2; Latency~Stage, $t=-3.49$, standard coefficient±s.e.= -0.55 ± 0.16 , $P<0.0001$; see Table S1). Also, we found an effect of sex on the number of errors (Errors~Sex, $Z=2.58$, standard coefficient±s.e.= 0.34 ± 0.13 , $P=0.001$), with females committing fewer errors than males on average across blocks (mean±s.e.m., males: 1.24 ± 0.09 , females: 0.94 ± 0.10 ; Fig. 2). After finding violations of normality in the model with the number of errors, we ran a bootstrap analysis based on 10,000 simulations and compared the mean coefficients, their standard errors and *P*-values with those obtained before. This analysis confirmed our GLMM results showing similar coefficients but smaller standard errors and *P*-values (see details in Table S1).

Plotting the logistic mixed model fitted with confidence intervals against time showed that the probability of the lizards' first choice being correct nearly doubled during the experiment, from chance levels in the first trial ($P\pm CI=0.23\pm 0.08$) to even odds in the last trial ($P\pm CI=0.41\pm 0.04$; Fig. 4).

Throughout the experiment, no colour was overrepresented in the total record of errors (trained to orange, $\chi^2=3.15$, d.f.=2, $P=0.207$; trained to yellow, $\chi^2=0.703$, d.f.=2, $P=0.704$; Fig. 5). However, wrong first choices were biased towards yellow in lizards trained to orange more frequently than to white or to the achromatic grey control ($\chi^2=8.41$, d.f.=2, $P=0.015$), while lizards trained to yellow showed a marginally non-significant bias toward orange ($\chi^2=5$, d.f.=2, $P=0.08$; Fig. 5).

Visual modelling

The natural spectra from the three morphs are relatively segregated in colour space (Fig. 6). Assuming a discrimination threshold of 3 JND and the proposed cone proportions (i.e. 1:1:1:4) and Weber fraction (i.e. 0.05), the three colours are chromatically discriminable considering all paired combinations (Fig. 7). Similar results were found using models with alternative cone proportions and/or Weber fraction (see Materials and methods). The effect of considering other visual parameters is graphically illustrated in Fig. S6.

Discriminability varied with morph combination ($t=-5.66$, standard coefficient±s.e.= -0.13 ± 0.02 , $P<0.00001$), the white–orange combination being more discriminable than the white–yellow and the yellow–orange combinations ($P<0.00001$), and the white–yellow combination being more discriminable than the orange–yellow combination ($P<0.00001$). Male morphs were more discriminable than female morphs ($t=-4.27$, standard coefficient±s.e.= -0.07 ± 0.02 , $P=0.00002$), and the interaction between morph combination and sex was significant ($t=4.10$, standard coefficient±s.e.= 0.05 ± 0.01 , $P=0.00005$). The results remained significant using visual models with alternative visual parameters (Table S3).

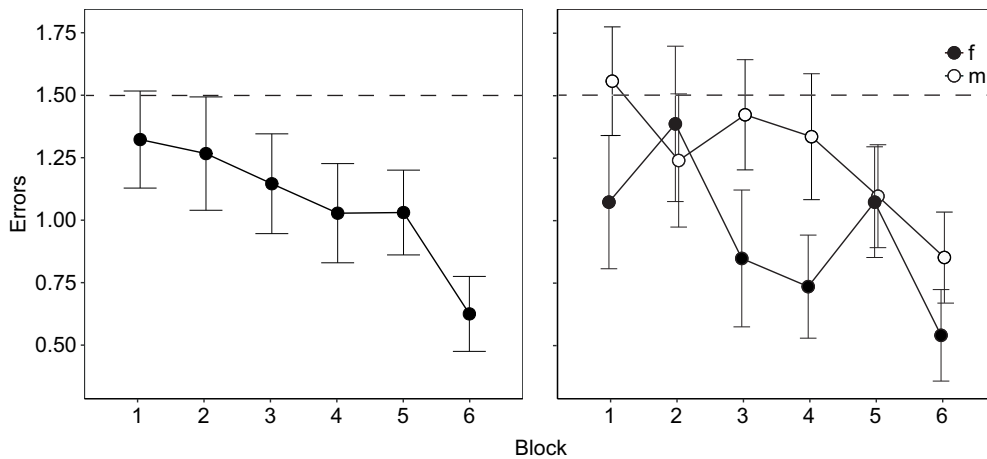


Fig. 3. Mean number of errors per block of trials. Left, mean number of errors, pooled from males and females (12 lizards, three trials per block). Right, mean number of errors per block of trials, grouped by sex (f, females; m, males). Each well of the wrong colour uncovered by a lizard in the allotted time (25 min) was considered an error (maximum of three errors). Error bars represent s.e.m. After two blocks of trials, the lizards responded to training by showing a significantly smaller number of errors than expected by chance (dashed line at 1.5).

DISCUSSION

Our results show that adult *P. muralis* learn to perform a procedural task (lifting the one lid among four giving access to prey in a colour-coded well), as shown by a significant reduction in both the number of errors and latency throughout the experiment. The fraction of lizards that successfully learned to perform the discrimination task (12 out of 20) is similar to that observed in experiments with other lizard species (e.g. Leal and Powell, 2012). The number of wrong choices was smaller than expected by chance after six trials (a week of testing) and the probability of correct first choice after 18 trials nearly doubled from initial chance levels. These results demonstrate that *P. muralis* is capable of discriminating experimental colour stimuli designed to match natural colours on the ventral surface of this species. Although the achromatic controls did not match perfectly the luminance of chromatic stimuli, as lizards did not choose the achromatic (grey) control incorrectly more often than the other available incorrect stimuli, we can reasonably assume that the discrimination was based on wavelength (i.e. hue) rather than luminance differences among stimuli. This evidence provides support for the idea that *P. muralis* is capable of discriminating its own ventral colour variation based on hue. Results of reflectance spectrophotometry and visual modelling reinforce this conclusion, showing that ventral colours of *P. muralis* correspond to discrete rather than continuous colour categories based on their spectral properties (independent of the human visual system) and lizard cone sensitivities. Interestingly, lizards were able to discriminate the two artificial stimuli showing the smallest perceptual distance (i.e. yellow versus orange), which is in the lower range of perceptual distances generated by the natural yellow and orange morphs (Fig. 7).

Our results bear out the assumption that the ventral polymorphism of *P. muralis* is discrete, encompassing several

Table 2. Latency in colour discrimination experiment

Block	N	Latency (s)		
		Mean	CI	s.e.m.
1	27	284.67	119.75	58.26
2	30	325.60	116.91	57.16
3	29	310.07	127.80	62.39
4	35	243.09	99.48	48.95
5	30	217.03	125.91	61.56
6	31	152.13	31.65	64.64

Mean latency, s.e.m. and 95% CI in each of six consecutive blocks of trials (three trials per block) comprising the training phase of the experiment. N, number of trials per block (out of 36) in which the trained lizards found the prey.

chromatically distinct morphs. On a practical note, our results also provide support for the use of a categorical classification of ventral colours in *P. muralis*, although perhaps not in other lacertid species. For example, in *Zootoca vivipara*, the assumption that the polymorphism is represented by categorically distinct colour morphs unleashed a heated controversy (Vercken et al., 2007, 2008; Cote et al., 2008). Unfortunately, although mate choice is involved in the maintenance of colour polymorphism in *Z. vivipara* (Sinervo et al., 2007; Fitze et al., 2014; San-José et al., 2014), colour discrimination among morphs was not tested and thus there is no conclusive evidence that lizards discriminate morphs visually, or that ventral colours in this species act as social signals.

Previous studies of the visual system of *P. muralis* demonstrated that ventral colours differ in conspicuousness when viewed against other body patches or against natural backgrounds (i.e. rocks, vegetation), which raises interesting questions regarding their potential role as social signals (Pérez i de Lanuza and Font, 2015). The results presented here indicate that colour discriminability varies according to the morphs being compared, white and orange being more discriminable than white and yellow, and yellow and orange ventral colours, and white and yellow being

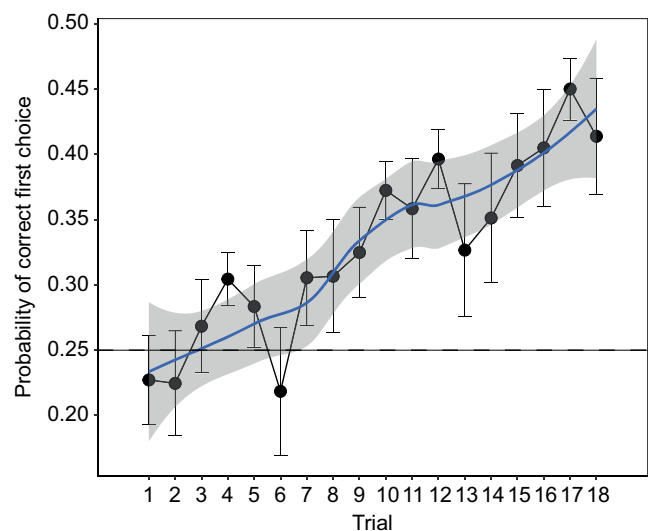


Fig. 4. Fitted logistic mixed model of the probability of correct first choice against time (i.e. trial). Circles and error bars represent mean probability with 95% confidence intervals in each trial. Blue line and shaded area are the smoothed tendency line with its confidence interval. The learning curve shows that the probability of correct first choice nearly doubled during the experiment.

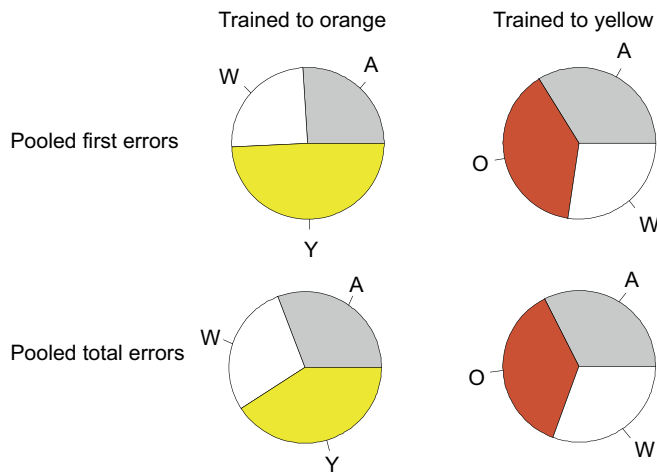


Fig. 5. Pie charts representing the relative frequency of each colour among the pooled errors performed by the lizards. Colour stimuli: O, orange; W, white; Y, yellow; A, achromatic stimulus matching the luminance of either orange or yellow.

more discriminable than yellow and orange combinations. Although behavioural results supporting this conclusion are lacking, chromatic distances obtained with visual modelling techniques may be good predictors of colour discriminability, even when distant colours are compared (Fleishman et al., 2016). Therefore, discriminability differences among pairs of ventral colours of *P. muralis* may have implications for signal detection and discrimination. This may be especially relevant for intrasexual and intersexual interactions that can be modulated by ventral colour, such as mate choice or male–male contests (Pérez i de Lanuza et al., 2013, 2016; Ábalos et al., 2016).

We found that sexes differ in colour morph discriminability, a finding that could have biological relevance (Zhou et al., 2015).

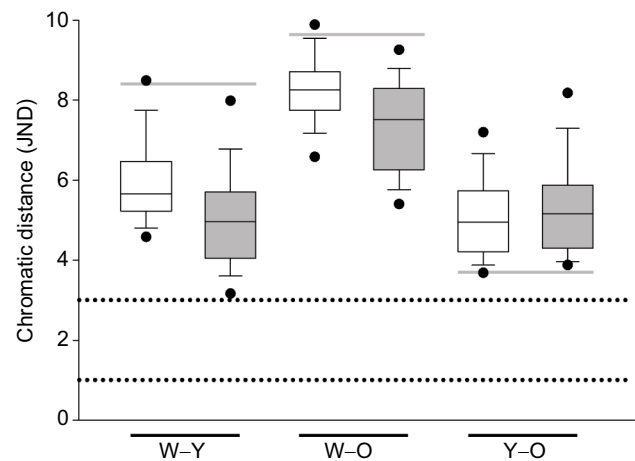


Fig. 7. Box-plots showing chromatic distances generated by pairs of colour morphs. Morphs: W, white; Y, yellow; O, orange. White box-plots correspond to males and grey box-plots correspond to females. In each case, horizontal lines, boxes, error bars and points indicate, respectively, the median, the 25–75% range, the 10th and 90th percentiles, and the 5th and 95th percentiles. Horizontal dotted lines indicate the discriminability thresholds of 1 just noticeable difference (JND; values above 1 JND indicate pairs of colours that are discriminable under good illumination conditions) and 3 JND (values above 3 JND indicate easily discriminable pairs of colours). Results considering other cone proportions and other Weber fraction values are detailed in Fig. S5. The impact of these variations is graphically reported in Fig. S6. Horizontal grey lines indicate chromatic distances of the experimental stimuli for each pair of colour morphs.

However, this result may be a consequence of sexual dichromatism (i.e. slight differences in spectra), resulting in small (but significant) differences in colour distances between males and females (see, for example, the chromaticity diagram in Fig. 6). We also found that males and females differ in the number of errors, but this difference may be caused by the small sample size used in the

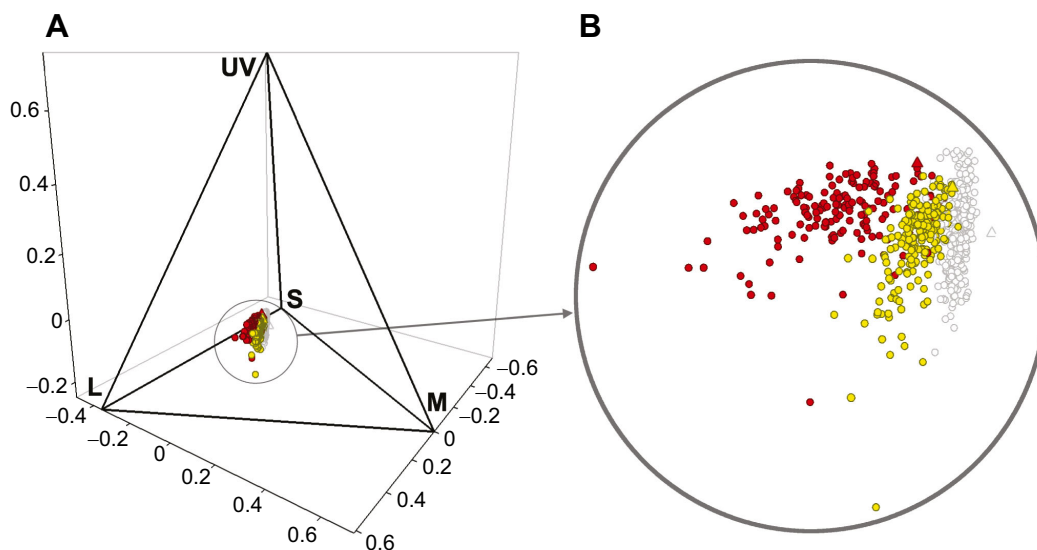


Fig. 6. Chromaticity diagram showing the location of chromatic points. (A) The entire receptor space; (B) detail of the volume occupied by the chromatic points. Circles correspond to chromatic points from the natural ventral colours (pooling males and females). Triangles correspond to the artificial stimuli. The colours of symbols indicate the morph. Sample sizes are given in Materials and methods. The overlap between the white and the yellow volumes amounts to 27.8% of the white volume and 4.9% of the yellow volume; the overlap between the white and the orange volumes represents 5.1% of the white volume and 0.7% of the orange volume; the overlap between the yellow and the orange volumes is 12.2% of the yellow volume and 9.1% of the orange volume. The white artificial stimulus is located outside (but close to) the cloud of white natural colours. The other two artificial stimuli fall within their respective cloud of natural colours, but are located at the periphery. However, note that the perceptual distance between the artificial stimuli is smaller than that of many chromatic points of different morphs. Wavelengths: S, short; M, middle; L, long; UV, ultraviolet.

experiment, which allows for extremely good performers to bias our results.

Although colour polymorphisms provide invaluable models to study the evolution and maintenance of polymorphisms generally (e.g. Roulin, 2004; Sinervo and Calsbeek, 2006; Chunco et al., 2007; Pryke and Griffith, 2009; McKinnon and Pierotti, 2010; McLean and Stuart-Fox, 2014; Wellenreuther et al., 2014; Svensson, 2017), insufficient attention has been paid to colour (morph) discrimination and its implications for understanding the significance of polymorphic coloration. It is often assumed that colour polymorphic animals perceive their own colour variation as different morphs, and that colour variants represent qualitatively different signals. However, this assumption has an unstable foundation if no evidence of colour discrimination is provided. We encourage other researchers to obtain evidence that their study animals are capable of chromatically discriminating their colour variation as independent colour morphs and show behavioural evidence of doing so.

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Competing interests

The authors declare no competing or financial interests.

Author contributions

Conceptualization: G.P.L.; Methodology: G.P.L., J.A., A.B.; Validation: G.P.L., E.F.; Formal analysis: G.P.L., J.A.; Investigation: G.P.L., J.A., A.B.; Writing - original draft: G.P.L., J.A.; Writing - review & editing: G.P.L., A.B., E.F.; Visualization: G.P.L., J.A., A.B.; Supervision: E.F.; Project administration: G.P.L., E.F.

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Supplementary information

Supplementary information available online at <http://jeb.biologists.org/lookup/doi/10.1242/jeb.169565.supplemental>

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