Cryptic ontogenetic changes in the ventral coloration of a colour polymorphic wall lizard (*Podarcis muralis*)

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Abstract (284 words)

Many animals undergo irreversible ontogenetic colour changes (OCCs), yet these changes are often overlooked despite their potential ethological relevance. The problem is compounded when OCCs involve wavelengths invisible to humans. Wall lizards can perceive ultraviolet (UV) light, and their conspicuous ventral and ventrolateral coloration —including UV-reflecting patches— likely serves social communication. Here, we describe OCCs in the ventral (throat and belly) and ventrolateral (outer ventral scales, OVS) coloration of juvenile common wall lizards (*Podarcis muralis*) as perceived by conspecifics.. We measured reflectance in newborn and yearling lizards raised under semi-natural conditions and used visual modelling to estimate chromatic distances within individuals and across life stages (i.e. newborns, yearlings, and adults). Newborns typically exhibit UV-enhanced white (UV^+white) on their ventral surfaces (throat, belly, and OVS), a colour that is likely discriminable to conspecifics from the most frequent adult colours in the throat (i.e. orange, yellow, and UV-reduced white; UV^-white) and OVS (i.e. UV-blue). The prevalence of UV^+white decreases with age, with the decline being less pronounced in female bellies. OCCs to UV-blue in the OVS are more apparent in males than in females and appear delayed relative to changes in the throat and belly. While throat colours in yearlings are indistinguishable to conspecifics from adult throat colours, yearling UV-blue patches remain chromatically distinct from those of adults. This delay may reflect variations in the mechanisms of colour production or distinct selective pressures acting on these patches. Overall, our results show that OCCs in *P. muralis* fulfil a key requirement for social signals by being perceptible to conspecifics. This supports the hypothesis that OCCs may play a role mediating interactions between juveniles and adults, as well as delaying the onset of colours involved in social communication.

Keywords: Ontogenetic colour changes; Colour polymorphism; Ultraviolet light perception; Sensory ecology; Visual modelling; Social communication; Wall lizards; *Podarcis muralis*

Introduction

Development exposes juvenile animals to varying selective forces arising from changes in size, vulnerability, diet, habitat, or social environment, which are sometimes associated with changes in body coloration. Ontogenetic colour change (OCCs) is defined as an irreversible colour change that is part of the normal development of individuals in a species (Buckman 1985; Booth 1990). External conditions may affect the timing of the change and the resulting colour expression (Frédérich et al. 2010; Stückler et al. 2022). OCCs can be so dramatic that the juvenile and corresponding adult forms were sometimes mistakenly labelled as different species (Smale and Kok 1983). Despite their potential ethological and selective relevance, research on OCCs has often lagged behind the study of adult coloration due to the logistical difficulties it poses, to the point that we sometimes ignore whether certain species undergo OCCs at all. The risk of inadvertently disregarding OCCs increases when colour changes take place out of the spectrum of light visible to humans (Rivas and Burghardt 2002; Caves et al. 2019). Despite its widespread occurrence and notable biological importance, the ultraviolet (UV) component in animal coloration has long gone unnoticed by scientists. However, its potential as a private communication channel hidden from animals lacking UV vision makes it particularly worthy of attention (Bradbury and Vehrencamp 2011; Cronin and Bok 2016).

Studies on lizard coloration have been crucial for advancing our understanding of a great range of evolutionary processes, from sexual selection and animal communication to the formation of new species (Olsson et al. 2013). Species showing heritable colour polymorphism (i.e. the coexistence of two or more alternative colour morphs of a species, with the rarer being too frequent to be solely the result of recurrent mutation (White and Kemp 2016) have been particularly popular in evolutionary biology and ethology (Majerus 2008; Svensson 2017; Endler et al. 2023). Ventral colour polymorphism has evolved in at least seven families of lizards, providing a unique opportunity to study the evolutionary processes responsible of maintaining intraspecific diversity (Stuart-Fox et al. 2020). Unfortunately, OCCs has rarely been examined in colour polymorphic lizards, and colour variation has often been described from the human perspective (which in some cases may have led to biologically irrelevant morph categorization; but see Rankin et al. 2016; Pérez i de Lanuza et al. 2018). Indeed, the historical neglect of UV colours in lizards has been corrected only in recent decades, revealing a great array of UV-coloured patches which may play a role as chromatic signals (e.g. involved in deimatic displays; Abramjan et al. 2015; Badiane et al. 2018); or male-male competition; Stapley and Whiting 2006; Whiting et al. 2006), but the relevance of UV in OCCs has not yet been examined (e.g. Yang et al. 2023).

Wall lizards (genus *Podarcis*, Lacertidae), comprising ca. 26 species with circum-Mediterranean distribution (Speybroeck et al. 2016; O'Shea 2021; Yang et al. 2021), have recently attracted attention as a suitable group in which to study colour (Pérez i de Lanuza et al. 2013, 2014; Andrade et al. 2019; Names et al. 2019; Miñano et al. 2021; Sacchi et al. 2021; de la Cruz et al. 2023; Abalos et al. 2024; Escoriza 2024). The dorsal coloration of *Podarcis* lizards is typically cryptic, consisting of dark melanin-based patches forming a reticulate pattern or bands over an olive background coloration (Salvador 2014; Ortega et al. 2019). In contrast, most species exhibit conspicuous ventral and ventrolateral coloration, often combining polymorphic throat and belly coloration, melanin-based patches, and conspicuous UV-reflecting patches in the shoulder region and/or the flanks (Arnold et al. 2007; Huyghe et al. 2007; Runemark et al. 2010; Marshall and Stevens 2014; Badiane and Font 2021; Brock et al. 2022b; de la Cruz et al. 2023; Solan et al. 2023). One such species (which is also the most widely distributed) is the European common wall lizard, *Podarcis muralis*. In common with many diurnal lizards, *P. muralis* has a sophisticated colour vision system with four different types of cones that are sensitive to light in the wavelengths between 320 and 700 nm (Pérez i de Lanuza and Font 2014a; Martin et al. 2015). Newborn *P. muralis* show a creamy white ventral coloration, but adults of both sexes may show up to 5 alternative ventral colour morphs to the human observer: three uniform (pure) morphs (orange, white, and yellow), and 2 mixed-morph mosaics combining orange and white or yellow and orange (Sacchi et al. 2007; Calsbeek et al. 2010; Pérez i de Lanuza et al. 2019). However, spectrophotometry and UV photography have revealed the existence of two types of whites differing in their UV reflectance (UV^{+}white and UV^{-}white) in the ventral coloration of both male and female *Podarcis* lizards, which may increase the number of discrete colours conforming lacertid colour polymorphism (Abalos et al. 2016; Pérez i de Lanuza & Font, 2024, *in press*). In addition, adults of both sexes show UV-blue patches in their outer ventral scales (OVS), but these are typically larger, more abundant, and more UV-biased and conspicuous in males (Pérez i de Lanuza and Font 2015).

Because of their ventral and ventrolateral location (allowing lizards to control their visibility through posturing) and conspicuousness, ventral polymorphic colours and UV-blue patches have been often thought to play a role in intraspecific communication (Pérez i de Lanuza et al. 2013, 2017; Abalos et al. 2016a, 2020; Names et al. 2019; Scali et al. 2019). The spectral properties of UV-blue patches in males are tuned to lacertid vision (Pérez i de Lanuza and Font 2014a; Martin et al. 2015), correlate with bite force and body condition (Pérez i de Lanuza et al. 2014), and behavioural evidence suggest that males making the OVS colour pattern visible during male-male confrontations have higher probability of prevailing over their rivals (Abalos et al. 2024). Research on *Podarcis* ventral colour polymorphism has largely focused on testing for the existence of alternative phenotypic optima, often in the form of alternative reproductive strategies involving differential sociosexual behaviour or breeding investment (Huyghe et al. 2007; Sacchi et al. 2009; Calsbeek et al. 2010; Galeotti et al. 2013; Mangiacotti et al. 2019; Brock et al. 2022a). Although the evidence in this regard is, at best, inconclusive (Sacchi et al. 2009; Stuart-Fox et al. 2020; Abalos et al. 2020, 2021), there are other lines of evidence suggesting a social role for alternative ventral colours. The average orange, yellow, and UV^{-}white colours are discriminable to conspecifics (Pérez i de Lanuza et al. 2018), a crucial prerequisite for alternative colours to function as social signals. In *P. muralis*, ventral colour may be playing a role in the formation of lasting male-female associations, with homomorphic pairs being more common than heteromorphic pairs in natural populations (Pérez i de Lanuza et al. 2013a, 2016b; but see Abalos et al. 2020; Aguilar et al. 2022a). The positive correlation observed between increased morph diversity and male-biased sex ratios across natural populations in the eastern Pyrenees further indicates that variation in ventral coloration among sympatric lizards may play a role in sexual selection under conditions of heightened male-male competition (Pérez i de Lanuza et al. 2017; Aguilar et al. 2024). Frequency-dependent effects of ventral colour on social interactions—such as a rare morph advantage or providing additional cues for social recognition—could potentially explain this finding but remain unexplored (Sheehan and Tibbetts 2009; Wellenreuther et al. 2014; Sheehan and Bergman 2016; Sheehan et al. 2017).

Despite the considerable attention given to the potential signalling role of these colour patches, research into their development (ontogeny) remains limited. For instance, newborn ventral coloration (which is perceived as identical to the adult white morph by human observers) has never been objectively characterized, and white morph adult lizards have been assumed to retain the juvenile coloration during growth (Pérez i de

Lanuza et al. 2013). Here, we set out to describe ontogenetic changes in the ventral coloration of juvenile *P. muralis* lizards both objectively (i.e. quantifying changes in reflectance) and as perceived by conspecifics (i.e. using visual models to simulate lacertid colour vision). To do so, we raised juveniles coming from two different breeding experiments under semi-natural conditions (Abalos et al. 2020, 2021), taking spectrophotometric measurements 3-4 weeks after hatching and 9-10 months later. We then used visual modelling to estimate chromatic distances between paired spectra from the same individual. Lastly, we assessed chromatic differences in ventral coloration between newborns, yearlings, and adult lizards by including ventral reflectance data from adult individuals sampled in the same localities where the parents of the juvenile lizards were captured.

Materials and methods

In 2018 and 2019 we conducted mesocosm experiments with *P. muralis* at the Station d'Écologie Théoretique et Expérimentale (Moulis, France). Lizards participating in these experiments (135 males and 225 females) were captured in 14 different localities across the Cerdanya plateau, in eastern Pyrenees (Abalos et al. 2020, 2021, 2024). Lizards mated under semi-natural conditions, after which females were housed individually until oviposition and their clutches were incubated (**Fig. S1**). In September, 3-4 weeks after hatching, we released 417 juveniles resulting from these experiments (2018: N = 45, 2019: N = 372) into 44 plastic tubs (170 cm diameter, 60 cm high; **Fig. S1**), that were kept outdoors, under natural temperature and illumination conditions, in groups of 10-12 individuals (Abalos et al. 2021). Prior to release into the tanks, we permanently marked each newborn on the ventral scales using a disposable medical cautery unit (Ekner et al. 2011). We took spectrophotometric measurements of the juveniles at two ontogenetic stages: as newborns (3-4 weeks after hatching) and as yearlings (10.5 months after hatching). Since newborn lizards show uniform coloration across their ventral and ventrolateral surface, we measured all newborn lizards in the throat (N = 417) and only a subset also in the belly (N = 43). Dorsal reflectance was measured in eight newborn lizards. Approximately ten months after hatching, we re-captured surviving yearlings in the tanks (June 2019: N= 16; July 2020: N = 50) and obtained spectrophotometric measurements of the throat, belly, and dorsum (N = 66), as well as the UV-blue patches, if present (N = 36). We also measured mass (± 0.01 g) and SVL (± 1 mm) in all newborn and yearling lizards using a ruler and a digital pocket scale.

Reflectance was measured using a USB 2000 portable diode-array spectrometer equipped with a QP200-2-UV/VIS-BX reading-illumination probe and a PX-2 Xenon strobe light for full spectrum illumination (Ocean Optics Inc., Dunedin, FL, USA; see details in Font et al. 2009). Small colour patches (such as UV-blue patches in juvenile lizards) may result in chimeric spectra when the cone of light projected by the spectrophotometer probe exceeds the diameter of the measured patch (Badiane et al. 2017). To avoid this problem, we attached an entomological pin with the nylon head downward to the side of the probe —ensuring a consistent 3 mm distance from the target surface— and limited measurements to colour patches with a diameter of at least 2 mm (Badiane et al. 2017). For analyses, we restricted the reflectance spectra to the 300-700 nm range to encompass the visual sensitivity of lacertids (Pérez i de Lanuza and Font 2014b; Martin et al. 2015). To control for noisy variation in luminance, spectra were normalized by subtracting the minimum value at all wavelengths. Spectral data were analysed in R v.4.0.3 (R Development Core Team 2017) using the package *pavo 2* (Maia et al. 2019).

We assigned specific colours (i.e. UV^+white, UV^-white, yellow, orange) to each juvenile colour patch based on the chromatic differences observed among adult throat and belly colours in the reflectance spectra used in Pérez i de Lanuza and Font (2015) (**Fig. 1**). These spectra correspond to adult males and females collected across various locations in the Cerdanya plateau, the same area where the parent lizards from the present experiment were captured. Notably, in these populations the orange and yellow colours seem to cover the entire ventral surface in males but are restricted to the throat in females (Pérez i de Lanuza et al. 2013a, 2017; Abalos et al. 2016, 2020). To determine objective thresholds for morph categorization, for each adult and juvenile spectrum we extracted five standard variables (**Table 1**): luminance, UV chroma (C_{UV}), and two variables describing hue (λ βmax, and λ Rmid) (Endler 1990; Kemp et al. 2015; Maia et al. 2019). We calculated luminance (Qt) as the sum of the reflectance across the visible range of lizards (i.e., $R_{300-700}$) and UV chroma (C_{UV}) as the relative reflectance in the UV waveband (i.e. summing the reflectance in the 300-400 range and dividing it by total reflectance; $R_{300-400}/R_{300-700}$). In adults, the wavelength corresponding to the maximum positive slope between 325 and 560 nm (λ $\beta max_{325-560}$) shows a gap between 440 and 500 nm that separates most lizards assigned to the orange and yellow colours from lizards assigned to the white morph (**Fig. 1**). Hence, juvenile spectra showing values of $\beta max_{325-560}$ equal or below 500 nm were classified as white, while lizards showing higher values where classified as either yellow or orange. We then distinguished between yellow and orange juveniles based on the wavelenght at which reflectance is halfway between its maximum and its minimum within the 400-650 nm waveband (λ $Rmid_{400-650}$) (**Fig. 1**). Specifically, juveniles were classified as yellow if showing values of λ $Rmid_{400-650}$ equal or lower than 550 nm, and orange if showing higher values. Following Pérez i de Lanuza & Font (2024, *in press*), we classified juvenile spectra as UV^+white if showing values of λ $Rmid_{300-450}$ equal or lower than 365 nm, and UV^-white if showing higher values (**Fig. 1**). To validate these thresholds for morph categorization, we reclassified a subset of 460 throat spectra from adult males, previously assigned to the white, orange, or yellow morphs by visual inspection. The high agreement between classifications confirms the reliability of the criteria (Cohen's *kappa* ± CI_{95} = 0.914 ± 0.031).

We built visual models using the Vorobyev and Osorio receptor noise model (Vorobyev and Osorio 1998) implemented in *pavo 2* to assess colour discrimination in terms of chromatic (dS) and achromatic (dL) distances, to test whether ontogenetic changes were large enough to be perceived by conspecifics (Maia et al. 2019). Specifically, we quantified within-individual chromatic and achromatic distances in throat and UV-blue coloration based on conspecific cone sensitivities and relative frequencies (Martin et al. 2015; Pérez i de Lanuza et al. 2018). We also estimated the colour distances between the different throat colours shown by yearling lizards. To quantify OCCs based on lacertid colour vision, we estimated the colour distances between the average ventral colour in newborn lizards (N = 417) and each of the colours found in full-blown adults (OVS and throat spectra from Pérez i de Lanuza and Font, 2015, the latter re-classified as either UV^+white, UV^-white, yellow, or orange according to the criteria specified above). We explored the similarity between yearling and adult throat colours when viewed by conspecifics by estimating colour distances among all possible combinations. Lastly, we examined OCCs in the OVS of yearling lizards by estimating within-sex colour distances between UV-reflecting patches in yearling lizards and full-blown UV patches from adult lizards.

We used the cone sensitivities (UVS:SWS:MSW:LSW, 367:456:497:562 nm) and cone ratios (1:1:1:4) published for *P. muralis* in Martin *et al.*, (2015). In the absence of behavioural estimates of the Weber fraction for colour discrimination in lizards, we set its value to 0.05 (Siddiqi et al. 2004; Pérez i de Lanuza and Font

2015; Pérez i de Lanuza et al. 2018), and a standard daylight "D65" irradiance spectrum, as implemented in *pavo*. Colour distances between pairs of colors were measured in units of just noticeable differences (JND), where one JND is assumed to be the threshold of discrimination between two colors under good illumination conditions (Vorobyev et al. 1998). However, as JND values between one and three could mean that two colors are barely discriminated, we also evaluated our results using a more conservative discrimination threshold of 3 JNDs (Siddiqi et al. 2004; Santiago et al. 2020). We then used distance-based MANOVAs or PERMANOVAs to test for discriminability between ventral colorations with respect to ontogeny (Anderson 2014). To do so, we first ran a MANOVA procedure on the chromatic and achromatic contrasts using the *adonis2* function from the *pairwiseAdonis* R package (Martinez Arbizu 2017). For comparisons between more than two groups, we ran a PERMANOVA using the *pairwise.adonis2* function in *pairwiseAdonis*, a modified version of the *adonis* function from the *vegan* R package (Oksanen et al. 2016). When comparing reflectance spectra from the same individual taken at different points in time, we accommodated the repeated measures nature of the data in the MANOVA by blocking contrasts at the within-individual level. Finally, as significance thresholds do not necessarily match the theoretical perceptual threshold of one JND above which colours can be said to be distinguishable, we used a bootstrap procedure to generate confidence intervals for the mean colour distance between the different colours. We used the *bootcoldist* function from the *pavo* package on the visual model described above with 999 replicates and a 0.95 level for confidence intervals.

Results

Juvenile lizards (yearlings) gained an average of 2.16 ± 0.19 g (mean ± CI$_{95}$) in body mass and grew by an average of 22.33 ± 1.21 mm of SVL in the period examined (ca. 10 months). Males grew slightly faster than females (m-f: 2.33 ± 2.34 mm, $t = -1.96$, $p = 0.054$) and increased their mass significantly more (m-f: 0.55 ± 0.36 g, $t = -3.07$, $p = 0.003$). We found strong evidence that *P. muralis* ventral coloration undergoes ontogenetic changes (**Table 1**, **Fig. 2**) that are large enough to be sensed by conspecifics (**Tables 2, 3** and **S2**). Most newborn lizards showed white throats (97%), with three quarters (74%) of them being classified as UV$^+$white according to their spectral properties. Yellow (39%), orange (17%) and UV$^-$white (30%) throats predominated in yearling lizards, with only a subset (8%) of re-sampled individuals showing UV$^+$white throats (**Fig. 3**). UV$^+$white coloration is particularly frequent in the bellies of adult and yearling females, even when their throats are UV$^-$white (**Fig. 4**). Sex differences in the prevalence and spectral properties of the UV-blue patches are already noticeable in yearlings (**Table 1**): UV-blue patches were present in 54% of the yearling lizards (29% of the females, 80% of the males). Dorsal coloration showed little differences between newborn, yearling and adult lizards (**Table S1**, **Fig. S2**). We did not quantify melanin-based patches, which were present in the ventral surface of many resampled yearlings but largely absent in the throat and belly of newborn lizards.

Within-individual contrasts (i.e. MANOVAs) found significant chromatic and achromatic differences between newborn and yearling throat colours for every yearling colour except UV$^+$white (**Table 2**).Chromatic distances between newborn-yearling paired spectra averaged 8.68 ± 1.55 JND, and were significantly greater than the theoretical threshold of 3 JND for orange, yellow, and UV$^-$white, but not for UV$^+$white (**Fig. 3**). Within-individual achromatic distances were shorter than the theoretical threshold of 3 JNDs for every yearling throat colour (**Table 2**).

Between-individual contrasts (PERMANOVA) found significant chromatic differences among all pairwise combinations of yearling throat colours (**Table 2**). In contrast, achromatic differences were non-significant for all contrasts except UV$^-$white–orange and yellow–orange (**Table 2**). Bootstrapped chromatic distances were larger than the threshold of 3 JNDs for all combinations, with Orange and UV$^+$white being the most different pair and Yellow–UV$^-$white the least different (**Fig. S3**).

Spectra from the UV-blue patches of yearlings showed a trough shape (with two peaks at the extremes of the spectral range), which differed from the single peak around longer wavelengths found in newborn lizards (**Fig. 5**). Paired spectra contrasting newborn ventral coloration and yearling UV-blue patches showed significant differences according to the MANOVAs (**Table 2**). Chromatic and achromatic distances were large enough to allow for discrimination, and more pronounced for males than females (**Table 2; Fig. 5**).

All contrasts between the average newborn colour ($N = 417$) and adult throat colours were statistically significant according to the PERMANOVA except the chromatic contrast against UV$^+$white adult throats (**Table 3**). Bootstrapped chromatic and achromatic distances followed this same pattern, with the contrasts against orange adult throats showing the largest distances, and the chromatic contrast against UV$^+$white adult throats being the only one below the theoretical threshold of 3 JNDs (**Fig. 6**). The distance-based PERMANOVA fitted on chromatic contrasts between yearlings and adult throat colours yielded significant results for all contrasts between lizards of different colours (**Tables 3** and **S2**). Chromatic contrasts between same-coloured lizards were non-significant except for yellow yearlings and adults. According to bootstrapped chromatic distances, all contrasts between same-coloured yearlings and adults result shorter distances than the theoretical threshold of 3 JNDs (**Fig 6** and **S5**).

Adult UV-blue patches were found to differ chromatically and achromatically from the average newborn coloration (**Table 3**), with contrasts in males resulting in larger bootstrapped distances than contrasts in females (**Fig. 6**). Within-sex contrasts between the UV-blue coloration found in yearling and adult lizards showed significant results only for chromatic differences (**Table 3**). Bootstrapped chromatic distances were similar for both sexes and approximately half of those estimated between newborns and adults. Achromatic distances were shorter than the theoretical threshold of 3 JNDs for both males and females (**Fig. 6**).

Discussion

We monitored colour expression in newborn (3–4 weeks old) and yearling (9–10 months old) *P. muralis* lizards raised under semi-natural conditions, providing the first account of OCCs in their ventral and ventrolateral coloration. Objective colour characterization revealed that newborn lizards exhibit enhanced UV reflectance compared to yearlings, which begin to show incipient morph expression (**Figs. 2**, **3**). Our results support the distinction of two types of white ventral coloration in *P. muralis*: UV$^+$white, typically found in newborns and some adult female bellies, and UV$^-$white, present in the throats of adults and the bellies of adult males (Abalos et al. 2016b; Pérez i de Lanuza and Font 2025, *in press*). Within-individual chromatic distances suggest that OCCs to orange, yellow, and UV$^-$white are perceptible to conspecifics. Among yearlings, throat colours are theoretically distinguishable, with orange and UV$^+$white being the most dissimilar and yellow and UV$^-$white the most similar. Contrasts with adults align with our repeated measures results, showing a similar rank order in divergence from average newborn coloration among throat colours (orange > yellow > UV^{-}white > UV^{+}white). Additionally, adult-yearling comparisons indicate that by 9–10 months after hatching, 92% of yearlings exhibit throat coloration that is indistinguishable to conspecifics from adult colours.

These findings have significant implications for understanding the ontogeny of ventral colour morphs in *P. muralis* and other lacertids. White morph lizards have often been assumed to retain their juvenile coloration into adulthood (unlike orange, yellow, or mosaic lizards; e.g., Pérez i de Lanuza et al. 2013a), but our results suggest that newborn lizards express a distinct UV^{+}white coloration that conspecifics likely perceive as chromatically different from adult throat colours. Similar UV^{+}white coloration is found in the bellies (but not throats) of many females in the eastern Pyrenees, suggesting that females in these populations may retain this juvenile trait into adulthood (**Figs. 2**, **4**, and Fig. 2 in Pérez i de Lanuza and Font 2015). We have previously highlighted the need to establish reliable criteria for adult colour morph classification (Pérez i de Lanuza et al. 2013a; Abalos et al. 2020). Based on our findings, we propose that decreased UV reflectance could be used to identify adult morph expression in white subadult lizards in future studies of *P. muralis* ventral colour variation.

Within-individual contrasts suggest that OCCs to UV-blue in the OVS are perceptible to conspecifics, and more apparent in males than in females (**Fig. 5**). However, nearly a year after hatching, yearling UV-blue patches remain chromatically distinguishable from adult colours, unlike the throat and belly coloration. This finding highlights an ontogenetic delay in the development of UV-blue patches, potentially reflecting differences in the underlying mechanisms of colour production (Pérez i de Lanuza et al. 2014; Andrade et al. 2019) and/or distinct selective pressures acting on these colour patches (Hebets and Papaj 2005; Cuthill et al. 2017; Tibbetts et al. 2017). Notably, UV-reflecting patches in the OVS undergo the most dramatic OCCs possible, shifting their reflectance from the extreme long-wavelength end to the minimum of the lacertid visual range in the UV wavelength band (Pérez i de Lanuza et al. 2014; Martin et al. 2015; Fleishman and Font 2019). This causes reflectance in the UV-blue patches of yearlings to adopt a characteristic trough shape (i.e. two peaks separated by a depression at intermediate wavelengths) which may explain the large chromatic distances found in this study. This result suggests that the ontogeny of UV-blue patches involves an increase in UV reflectance paired with a decrease in long-wavelength reflectance, instead of a progressive displacement towards shorter wavelengths of a single reflectance peak. The intermediate stages of this process would result in the trough-shaped spectra we observe in yearling lizards and adult females (**Fig. 6**).

Here, we did not test for possible adaptive explanations for the ventral and ventrolateral OCCs described in *P. muralis*, which could represent a nonfunctional by-product of chromatophore maturation (Bagnara et al. 2007; Umbers 2013). However, our findings demonstrate that OCCs fulfil a key requirement for social signals by being perceptible to conspecifics. Studies on OCCs in lizards have mostly focused on exploring the function of bright tail colorations as a decoy, acting in combination with striped dorsal patterns and autotomy to deflect predator attacks towards the expendable tail (Castilla et al. 1999; Hawlena et al. 2006; Hawlena 2009; Watson et al. 2012; Ortega et al. 2014; Fresnillo et al. 2015b, a, 2016; Murali et al. 2018). In contrast, a role in predator avoidance seems unlikely for ventral and ventrolateral OCCs. These colorations are rarely visible to avian predators, which typically attack from above (Marshall and Stevens 2014; Marshall et al. 2015, 2016), and are only occasionally visible to terrestrial predators as lizards are most commonly observed in postures where these scales remain largely hidden (Pérez i de Lanuza et al. 2016a). However, lizards shift their postures with increasing body temperature or during social interactions, making their ventral and ventrolateral scales visible to observers positioned parallel to and level with the lizard's flank (Noble and Bradley 1933; Kitzler 1941; Font and Carazo 2010; Pérez i de Lanuza et al. 2016a; Abalos et al. 2024). Considering the ontogenetic decline in UV$^+$white coloration and its distinct appearance to lizards compared to the colours predominantly found in adults, we suggest that OCCs affecting ventral and ventrolateral scales could influence social interactions by revealing juvenile status and sexual immaturity (Booth 1990). Juvenile-specific coloration may reduce aggression from adult conspecifics, as observed in several vertebrate species (Hill 1989; Bergman and Sheehan 2013; Ochi and Awata 2016; Hendershott et al. 2019), including lizards (Clark and Hall 1970; Hawlena et al. 2006; Fresnillo et al. 2015a). In wild populations of *P. muralis*, agonistic confrontations between adult males can escalate into physical fights, but juvenile or even subadult males (i.e. satellites) are often allowed to set their home-range within the boundaries of an adult male's territory (Waltz 1982; Barbault and Mou 1986; Edsman 1990, 2001; Brown et al. 1995; Font et al. 2012; Abalos et al. 2020). OCCs in ventral and ventrolateral coloration could mediate this tolerance by signalling the subordinate status and low reproductive threat posed by younger males, reducing the likelihood of aggression by resident males. Future studies should explore the role of ventral and ventrolateral OCCs in mediating male-male competition and territorial dynamics. The ontogenetic changes described here could also play a role in the context of mate choice. Evidence from lab experiments and field studies suggest that, as in many other lizards (Tokarz 1995; Cuadrado 2006; Uller and Olsson 2008; Vicente and Halloy 2016), pre-copulatory mate choice in wall lizards is largely under male control, with males selecting larger conspecific females based on either chemical or visual stimuli (Edsman 1990, 2001; Font and Desfilis 2002; Barbosa et al. 2006; Carazo et al. 2011; Font et al. 2012; Sacchi et al. 2015). Although rudimentary male traits in females are often assumed to represent a by-product of their function in males, OCCs in female ventral and ventrolateral scales may allow males to avoid courting immature females (mate recognition) (Edward and Chapman 2011; Swierk and Langkilde 2013). At the same time, immature females may benefit from being recognized as such if excessive male attention is costly to female fitness (Eberhard and Cordero 2003; Arnqvist and Rowe 2005; Le Galliard et al. 2008). An objection to this hypothesis, however, lies in explaining why body size alone might not be sufficient for receivers to identify young lizards. While body size is an obvious correlate of age in most reptiles, it may not provide enough information for conspecifics to distinguish between those that are sexually immature and those that are fully grown but still sexually inactive (Booth 1990; Roucurt Cezário et al. 2022).

Variation in the ventral and ventrolateral colour pattern of wall lizards could also be playing an overlooked role in sexual selection by providing visual cues for social recognition (Tibbetts 2004; Tibbetts et al. 2008; Sheehan and Bergman 2016). Many territorial lizards mitigate the costs of defence by showing attenuated aggression toward known neighbours while remaining aggressive toward unfamiliar intruders (Qualls and Jaeger 1991; Husak and Fox 2003; Osborne 2005; Baird 2013; Whiting and Miles 2019). In wall lizards, males discriminate familiar rivals based on scent marks, allocating aggression based on perceived threat (Carazo et al. 2008; Font et al. 2012). Given the sophistication of their visual system, it is plausible that wall lizards also use visual cues for social recognition (Font et al. 2012; Pérez i de Lanuza and Font 2014b; Fleishman and Font 2019). In other taxa, visual cues have been shown to play a crucial role alongside chemical signals in individual recognition (Tibbetts 2002; Sheehan and Tibbetts 2010), and in lizards like the tawny dragon (*Ctenophorus decresii*), throat coloration aids rival recognition (Osborne et al. 2012). While studies of social recognition in intersexual interactions in lizards are limited (e.g. Font and Desfilis 2002; Leu et al. 2015; Bordogna et al. 2016), evidence suggests that OCCs could influence mate choice. In *P. muralis*, ventral coloration is linked to male-female pair bond formation (Pérez i de Lanuza et al. 2013, 2016b; Aguilar et al. 2022a), potentially acting as mate-guarding or deterring harassment (in Den Bosch and Zandee 2001; Zaldívar-Rae and Drummond 2007; Olsson et al. 2019; Abalos et al. 2020). Subtle chromatic and achromatic variation within the orange, white, and yellow alternative colours, along with between-individual differences in patterning—such as melanin-based patches or mosaic coloration—may hold relevance for social recognition (Martin et al. 2015; Pérez i de Lanuza et al. 2018; Aguilar et al. 2022b). At the cohort level, ontogenetic transitions from uniform UV$^+$white coloration to distinct ventral and ventrolateral colour patterns enhance phenotypic divergence among maturing lizards, as expected if showing a distinctive appearance becomes increasingly advantageous with age (Sheehan and Tibbetts 2009; Sheehan and Bergman 2016; Gokcekus et al. 2021). Future studies could examine whether *P. muralis* OCCs may influence social interactions by delaying the onset of sexually-selected colour signals, as well as providing visual cues for individual recognition.

In conclusion, here we show that *P. muralis* ventral coloration undergoes OCCs perceptible to conspecifics, though not always to humans, providing valuable insights into the ontogeny of lacertid coloration. Future research should focus on detailed descriptions of OCCs, their cellular mechanisms, and their integration with melanin-based patches (Sheehan et al. 2017; Pérez-Rodríguez et al. 2017; Zhang et al. 2023). Altogether, our results underscore the importance of considering receiver perspectives in ethological studies of animal coloration (Endler et al. 2023).

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Author contributions

Conceptualization and experimental design: J.A., G.P.L., F.A. and E.F.; Investigation: J.A., A.B.; Statistical analysis: J.A.; Visualization: J.A.; Writing-original draft: J.A.; Writing-review & editing: all authors.

Conflict of interests

The authors declare no conflict of interest.

Data availability

The dataset used and analysed in this study will be made available upon acceptance.

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Tables

Table 1. Spectral variables (mean ± CI_{95}) describing reflectance curves in the ventral coloration of newborn, yearling, and adult lizards. Spectra have been normalized by subtracting the minimum value at all wavelengths. Qt = luminance ($R_{300\text{-}700}$), C_{UV} = UV chroma ($R_{300\text{-}400}/R_{300\text{-}700}$), $\lambda\ \beta max_{325\text{-}560}$ = wavelength at which reflectance shows the maximum positive slope in the 325-560 nm waveband, $\lambda\ Rmid_{300\text{-}450}$ and $\lambda\ Rmid_{400\text{-}650}$ = wavelength at which reflectance is halfway between its minimum and its maximum for the wavebands 300-450 nm and 400-650 nm respectively. Spectra from adult lizards correspond to Pérez i de Lanuza and Font (2015).

Colour patch	**Age**	***N***	**Qt**	**C_{UV}**	**$\lambda\ \beta\ max_{325\text{-}560}$ (nm)**	**$\lambda\ Rmid_{300\text{-}450}$ (nm)**	**$\lambda\ Rmid_{400\text{-}650}$ (nm)**
Conflated throats	Newborns (all)	417	8303.9 ± 133.0	.12 ± .00	345.1 ± 4.3	345.16 ± 2.0	513.4 ± 2.4
UV^{+}white throat	Newborns (resampled)	46	8384.1 ± 357.6	.13 ± .01	329.8 ± 0.1	334.5 ± 2.7	520.0 ± 5.5
	Yearlings	5	8303.9 ± 133.0	.12 ± .03	328.8 ± 1.6	329.4 ± 5.4	536.2 ± 27.5
	Adults	26	7306.0 ± 598.5	.13 ± .01	330.2 ± 0.2	336.8 ± 5.1	563.3 ± 10.2
UV^{-}white throat	Newborns (resampled)	11	8091.9 ± 909.3	.08 ± .01	388.2 ± 13.0	386.1 ± 4.1	483.1 ± 11.9
	Yearlings	20	6142.5 ± 547.3	.05 ± .01	402.0 ± 3.4	399.6 ± 5.3	511.6 ± 14.8
	Adults	159	5544.1 ± 173.5	.04 ± .00	410.9 ± 2.4	407.5 ± 1.9	505.9 ± 5.3
Yellow throat	Newborns (resampled)	5	8241.2 ± 2896.2	.09 ± .01	554.2 ± 7.3	355.8 ± 27.3	534.4 ± 11.2
	Yearlings	26	5754.7 ± 571.4	.05 ± .01	512.2 ± 4.3	376.7 ± 11.5	527.4 ± 4.2
	Adults	150	4764.8 ± 155.9	.04 ± .00	513.3 ± 1.5	384.4 ± 4.7	527.8 ± 1.4
Orange throat	Yearlings	11	4848.9 ± 1060.3	.05 ± .02	537.3 ± 15.1	361.4 ± 26.8	560.7 ± 4.7
	Adults	125	3443.3 ± 206.5	.03 ± .00	554.7 ± 1.4	363.9 ± 6.1	566.0 ± 1.1
OVS-UV females	Yearlings	10	4534.9 ± 997.2	.18 ± .05	329.5 ± .5	327.1 ± 11.0	544.5 ± 30.4
	Adults	37	6294.7 ± 420.6	.28 ± .02	330.2 ± 0.2	342.0 ± 12.8	498.2 ± 24.9
OVS-UV males	Yearlings	26	4710.1 ± 311.13	.24 ± .02	336.5 ± 14.1	336.7 ± 15.7	511.3 ± 23.9
	Adults	510	6620.9 ± 119.5	.36 ± .00	330.2 ± .1	367.7 ± 4.7	438.9 ± 1.7

Table 2. Pairwise comparisons between the ventral coloration of lizards measured as newborns and re-sampled as yearlings, per colour patch. Within-individual contrasts were calculated using a distance-based MANOVA on the chromatic and achromatic distances obtained by modelling the vision of conspecifics for the ventral coloration of each individual at birth and when re-captured one year after. Between-individual contrasts were calculated using a distance-based PERMANOVA on the chromatic and achromatic distances between the throat spectra of yearlings assigned into each of the four different morphs. Significant contrasts are indicated in bold ($p < 0.05$). *F* and R^2 represent pseudo *F*-statistics and effect size estimate, respectively. Adj. *P* represents adjusted *P* values (Bonferroni correction).

		Within-individual contrasts					
Colour patch		**Chromatic contrast**			**Achromatic contrast**		
Yearling colour	***N***	***F***	R^2	***P***	***F***	R^2	***P***
UV^+white throats	5	3.00	0.27	0.125	0.49	0.06	0.813
UV^-white throats	20	34.07	0.47	**< 0.001**	27.30	0.42	**< 0.001**
Yellow throats	26	42.54	0.46	**< 0.001**	20.92	0.29	**< 0.001**
Orange throats	11	12.31	0.38	**0.002**	14.82	0.43	**< 0.001**
OVS females	10	9.31	0.34	**0.010**	37.23	0.67	**0.002**
OVS males	26	71.96	0.59	**< 0.001**	185.89	0.79	**< 0.001**

		Between-individual contrasts					
Colour patch		**Chromatic contrast**			**Achromatic contrast**		
		F	R^2	**adj. *P***	***F***	R^2	**adj. *P***
UV^+white	Orange	3.36	0.19	**0.039**	2.88	0.17	0.091
UV^-white	Orange	9.59	0.25	**0.003**	5.27	0.15	**0.010**
UV^+white	Yellow	12.41	0.30	**0.001**	1.29	0.04	0.276
UV^+white	UV^-white	10.86	0.32	**0.001**	1.64	0.07	0.179
Yellow	Orange	9.44	0.21	**0.003**	4.31	0.11	**0.016**
UV^-white	Yellow	4.17	0.09	**0.020**	0.32	0.01	0.734

Table 3. Pairwise comparison contrasting the ventral coloration of adults with newborns, and adults with yearlings, per colour patch. In the former, every adult colour was contrasted against the average newborn ventral colour. In the latter, contrasts were estimated only between same-coloured yearling and adult lizards. Contrasts were calculated using a distance-based PERMANOVA on the chromatic and achromatic distances obtained by modelling the vision of conspecifics for the ventral coloration of newborn, yearling, and adult *P. muralis* lizards. Significant contrasts ($p < 0.05$) are indicated in bold. F and R^2 represent pseudo F-statistics and effect size estimate, respectively. Adj. P represents adjusted P values (Bonferroni correction).

	Newborn average - Adult colours					
Colour patch	**Chromatic contrast**			**Achromatic contrast**		
	F	R^2	adj. P	F	R^2	adj. P
UV$^+$white throat	-2.5	-0.01	1.00	416.78	0.49	**0.001**
UV$^-$white throat	705.5	0.55	**0.001**	2314.7	0.80	**0.001**
Orange throat	1406.8	0.72	**0.001**	1947.9	0.78	**0.001**
Yellow throat	1194.8	0.68	**0.001**	2270.9	0.80	**0.001**
OVS males	7252.7	0.89	**0.001**	5038.6	0.84	**0.001**
OVS females	556.2	0.56	**0.001**	623.85	0.58	**0.001**
	Yearlings - Adults (equivalent colours)					
Colour patch	**Chromatic contrast**			**Achromatic contrast**		
	F	R^2	adj. P	F	R^2	adj. P
UV$^+$white throat	1.29	0.04	0.255	0.77	0.03	0.393
UV$^-$white throat	2.91	0.02	0.069	3.66	0.02	**0.033**
Yellow throat	9.42	0.05	**0.002**	9.73	0.05	**0.001**
Orange throat	1.72	0.01	0.178	7.41	0.05	**0.003**
OVS females	33.52	0.43	**0.001**	1.73	0.04	0.189
OVS males	194.25	0.27	**0.001**	0.34	0.00	0.673

Figures

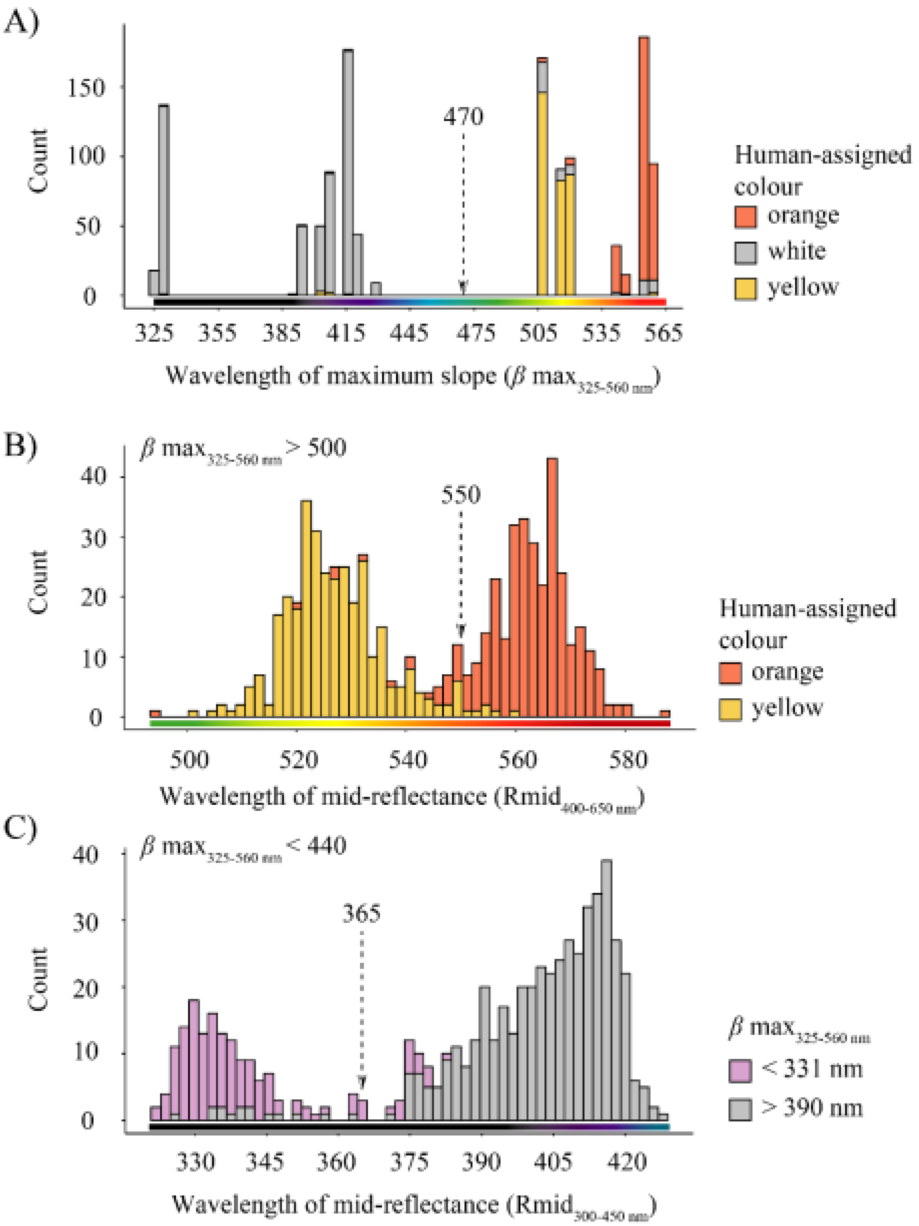

Figure 1. Categorization of *P. muralis* ventral colours according to their spectral properties in a sample of 1293 throat and belly spectra collected in adult males and females and assigned to a colour morph by human visual inspection. A) Stacked bar plot showing the discontinuous distribution of $\lambda\ \beta max_{325\text{-}560}$ (i.e. wavelength of maximum slope between 325 and 560 nm). A gap between 440 and 500 nm separates most lizards assigned to the orange and yellow colours from lizards assigned to the white morph. B) Stacked bar plot showing the bimodal distribution of $\lambda\ Rmid_{400\text{-}650}$ (i.e. wavelength at which reflectance is halfway between its minimum and its maximum in the 400-650 nm waveband). We set a threshold at 550 nm to separate orange and yellow lizards, which largely agrees with morph categorization by visual inspection. C) Stacked bar plot showing the bimodal distribution of $\lambda\ Rmid_{300\text{-}450}$. Filled bars show the high agreement between a threshold to distinguish between UV^{+}white and UV^{-}white based on $\lambda\ \beta\ max_{325\text{-}560}$ and one based on $\lambda\ Rmid_{300\text{-}450}$. For consistency with Pérez i de Lanuza and Font (2024, *in press*), we set a threshold at $\lambda\ Rmid_{300\text{-}450}$ = 365 nm to separate UV^{+}white from UV^{-}white lizards.

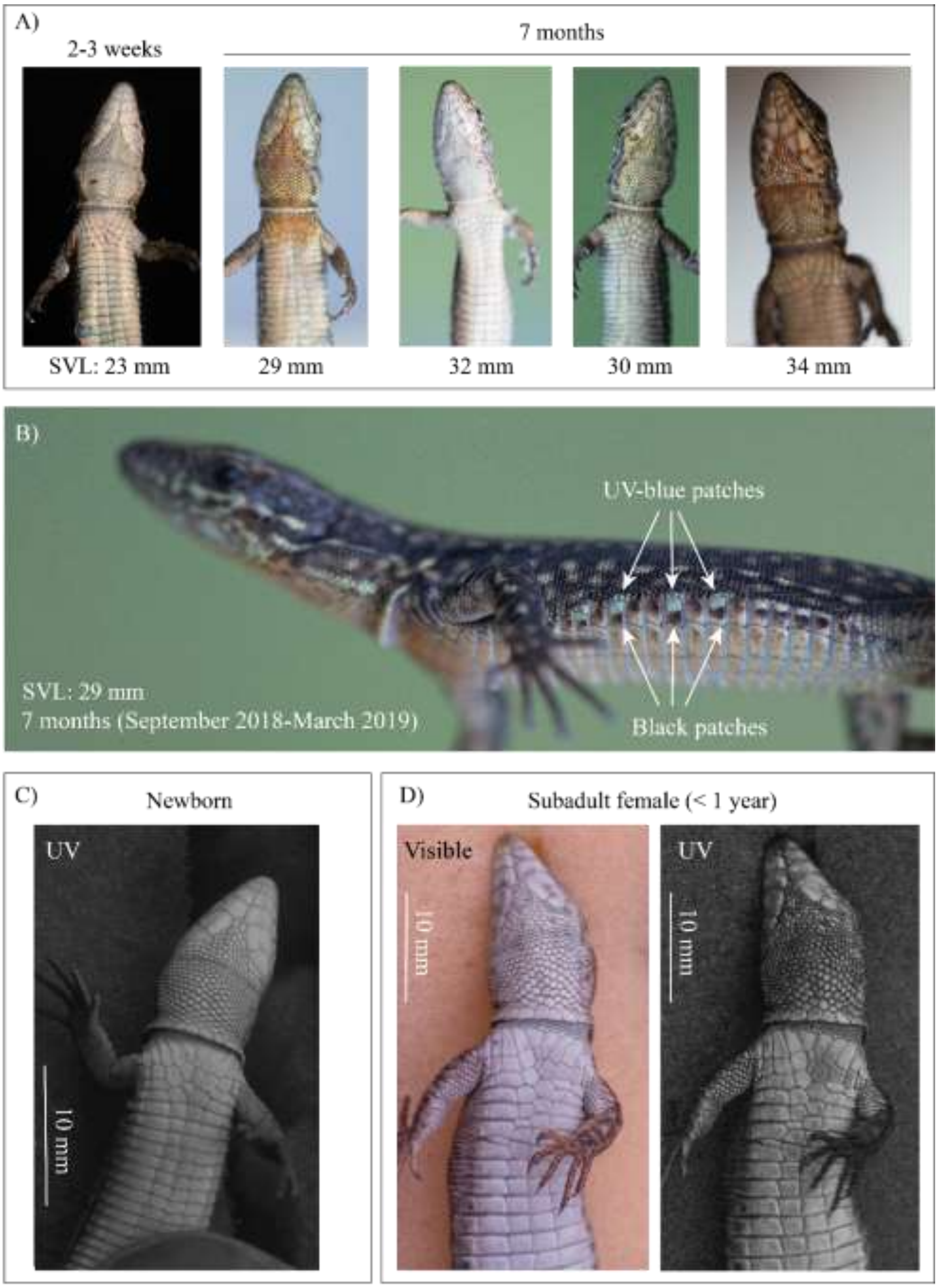

Figure 2. Ontogeny of ventral coloration in *P. muralis*. A) Representative photographs of ventral coloration in a newborn lizard 2-3 weeks after hatching (left), and in four yearlings re-captured in March 2019 (7 months after hatching). SVL stands for snout to vent length in mm. B) Young male of *P. muralis* showing incipient UV-blue and melanin-based black patches in the outer ventral scales (OVS). C) UV photograph of a newborn *P. muralis* lizard showing UV$^+$white colour in its ventral surface. D) Paired UV and visible photographs of the same subadult female (<1 year) showing UV$^-$white in the throat and UV$^+$white in the belly. The difference is only apparent in the UV image. Photographs in C and D were obtained with a full-spectrum camera and two filters, each transmitting light either in the visible (400-700 nm) or the near-UV (320-380 nm) range. Brighter areas in the UV image have higher UV reflectance (i.e. newborn ventral surface and female belly).

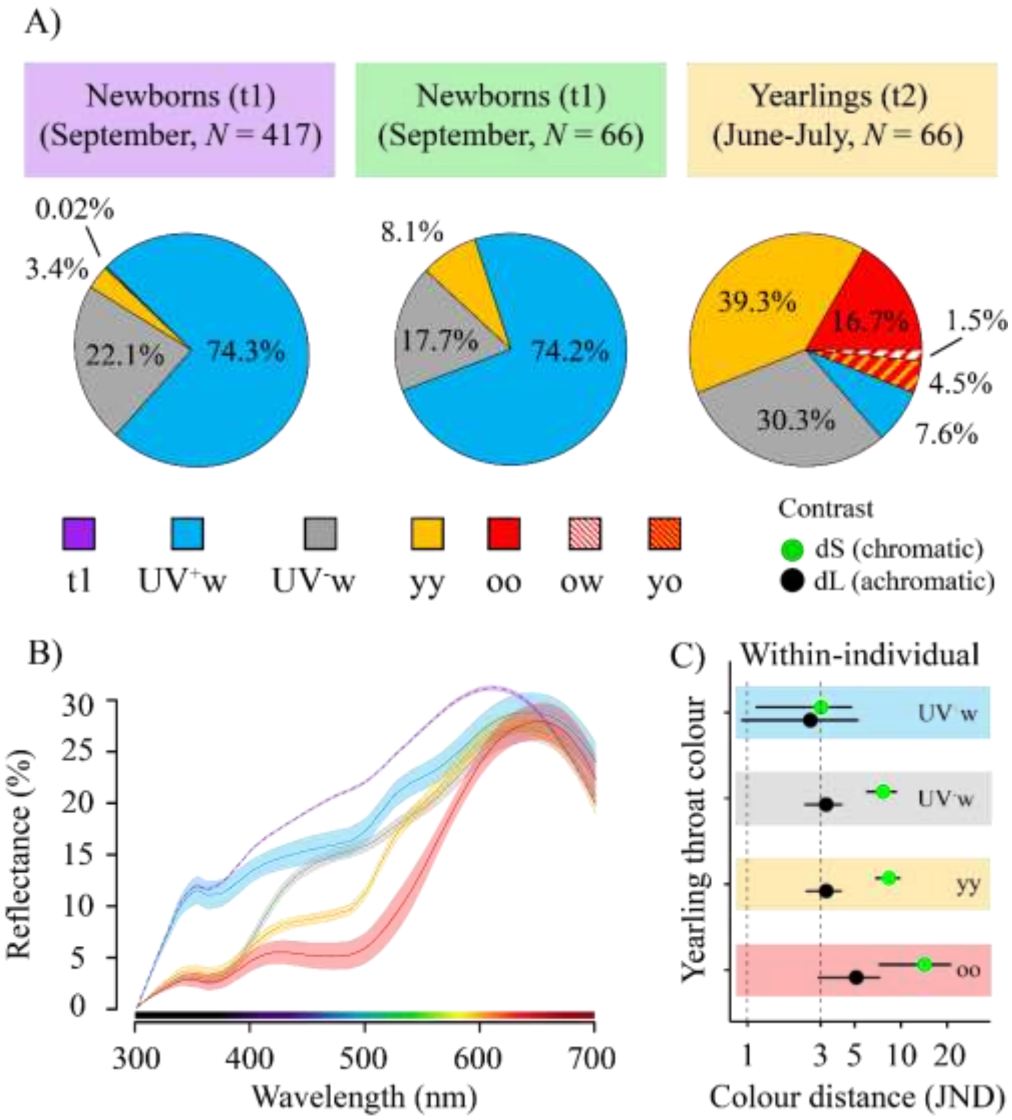

Figure 3. Ontogenetic changes in *P. muralis* throat coloration. A) Pie charts represent the proportions of juveniles showing different throat colours (UV$^+$w = UV$^+$white, UV$^-$w= UV$^-$white, oo = orange, yy = yellow, ow = orange-white, yo = yellow-orange) in September (t1; 3-4 weeks after hatching), and June-July (t2; one year after hatching). The three pie charts correspond to the full dataset of 417 newborns measured at t1 (purple), the subset of 66 surviving juveniles measured as newborns at t1 (green), and these same juveniles measured as yearlings in t2 (yellow). B) Reflectance spectra from the 62 surviving yearlings showing pure colour morphs (solid lines and shaded area represent means ± SEM). The dashed purple line represents the average throat spectra of 417 newborn lizards (similar to that of the 62 surviving yearlings when first measured, see central pie chart). Spectra have been normalized by subtracting the minimum reflectance of each spectrum at all wavelengths. C) Mean and CI$_{95}$ of the chromatic and achromatic distances (dS and dL respectively) between paired measurements of throat reflectance (i.e. within-individual newborn-yearling contrasts), separated by yearling throat colour. JND stands for "Just Noticeable Differences". Two dashed lines at 1 and 3 JNDs represent two theoretical discriminability thresholds. If the confidence interval of a point includes a discriminability threshold, the two colours are not distinguishable at this threshold according to receiver cone sensitivities and relative abundance.

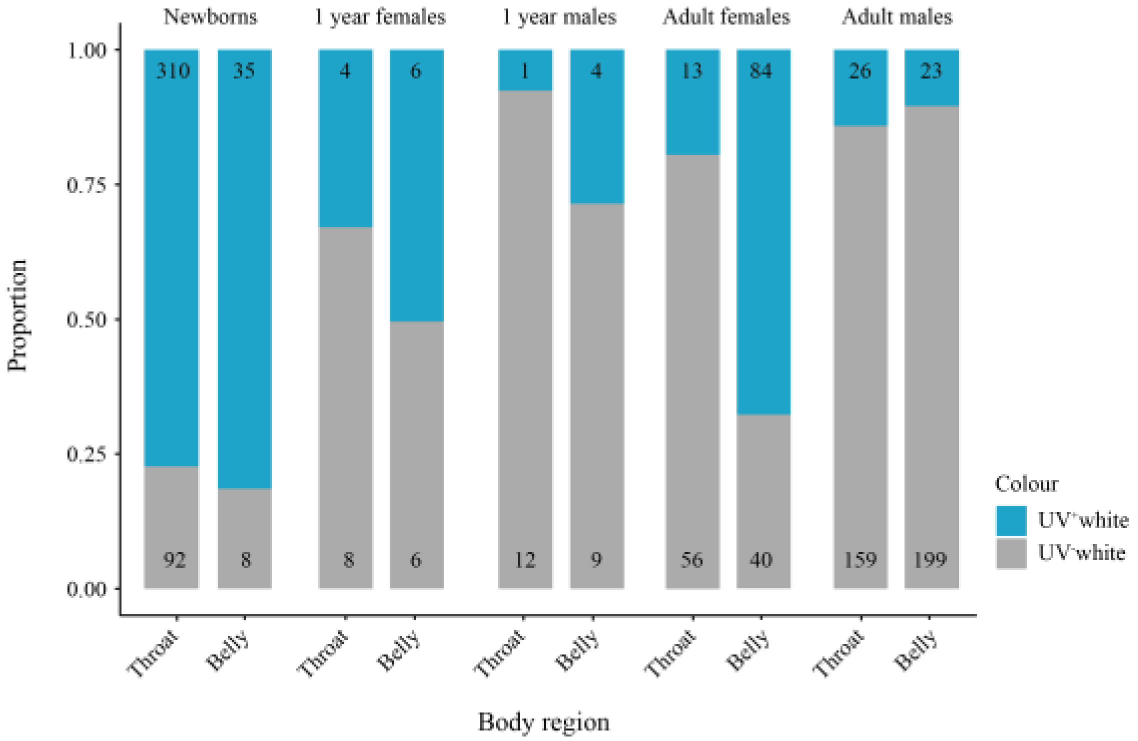

Figure 4. Stacked bar plot showing the proportion of UV$^+$white and UV$^-$white colorations in the throats and bellies of lizards classified according to the spectral properties of their reflectance curves (i.e. $\lambda\ \beta max_{325\text{-}560} \leq 500$): UV$^+$white if showing a $\lambda\ Rmid_{300\text{-}450} \leq 365$ nm, UV$^-$white if $\lambda\ Rmid_{300\text{-}450} > 365$ nm. Numbers inside filled bars indicate sample size. UV$^+$white coloration is particularly frequent among newborn lizards, and in the belly of yearling and adult females.

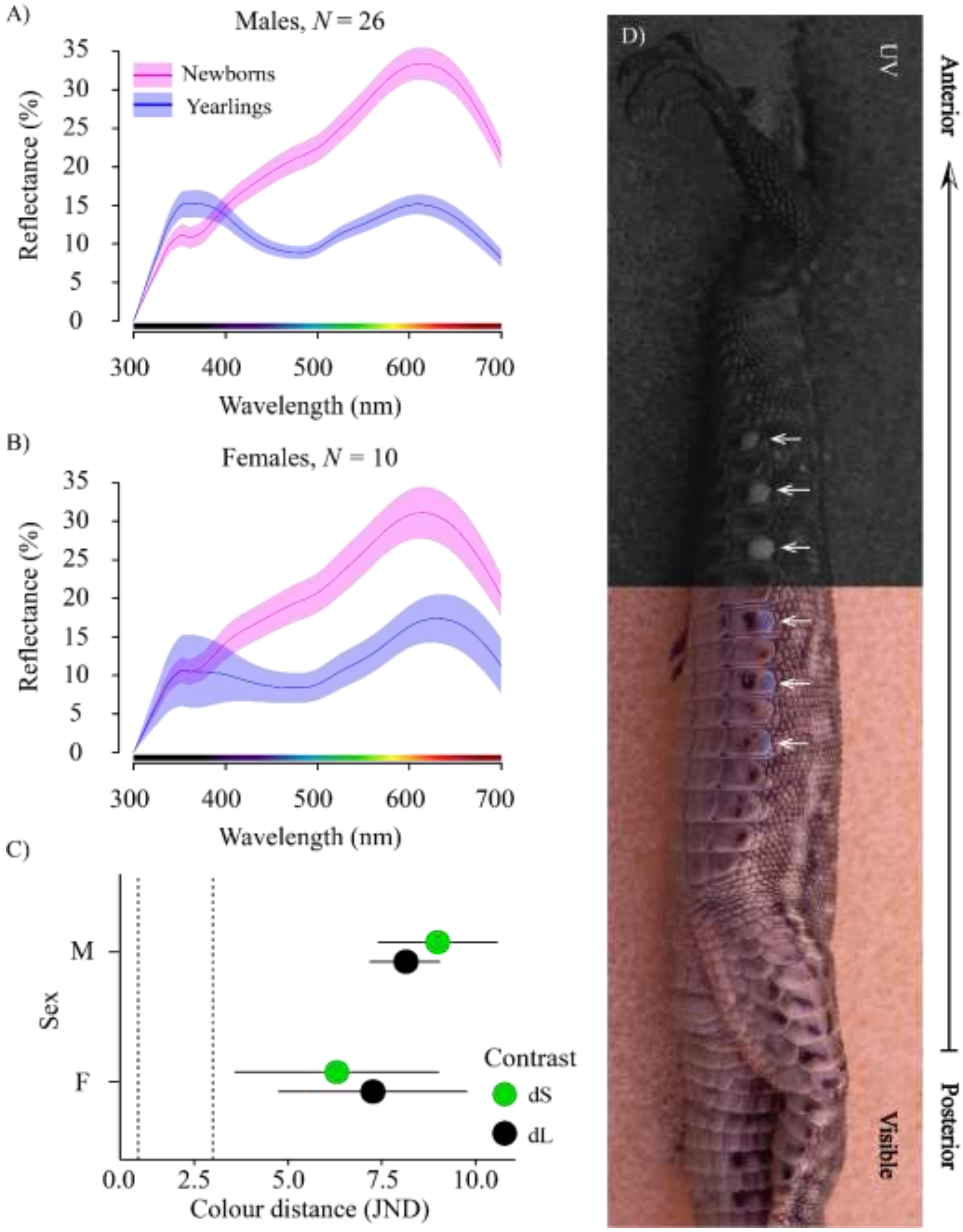

Figure 5. Ontogenetic change in *P. muralis* outer ventral scales (OVS) coloration. A) Reflectance spectra from the 36 lizards showing UV-blue patches as yearlings in their OVS (solid lines and shaded area represent means ± SEM). B) Mean and CI_{95} of the chromatic (dS) and achromatic (dL) distances between paired measurements of OVS reflectance (newborns-yearlings) in males and females. Two dashed lines at 1 and 3 JNDs represent two theoretical discriminability thresholds. If the confidence interval of a point includes a discriminability threshold, the two colours are not distinguishable at this threshold according to receiver cone sensitivities and relative abundance. D) Composite UV + visible image of a subadult (<1 year) *P. muralis* male showing incipient UV-blue coloration in the OVS.

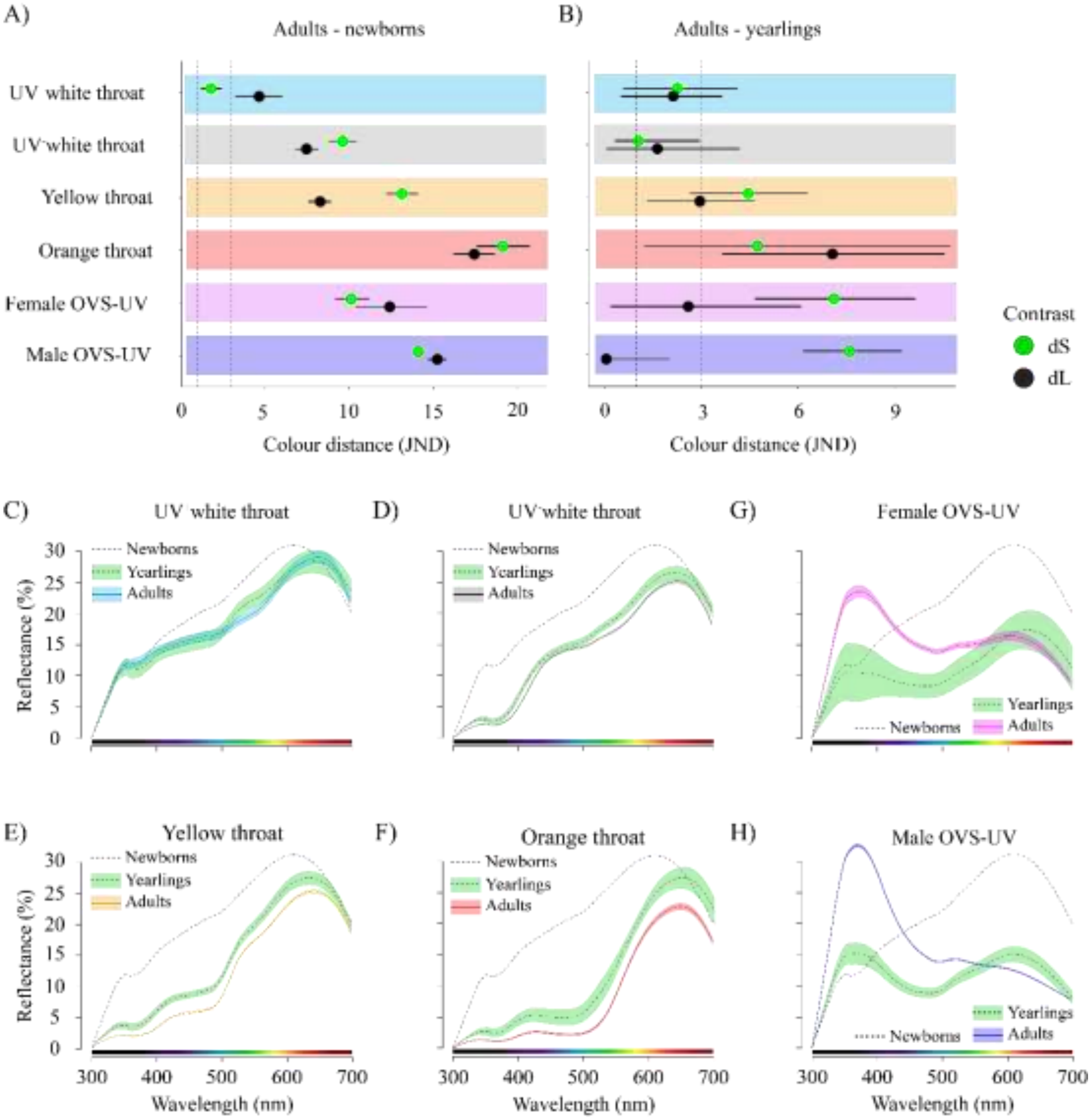

Figure 6. Comparison between the ventral coloration of newborn and yearling lizards with adult *P. muralis* from eastern Pyrenees. A) Mean and CI$_{95}$ of the chromatic (dS) and achromatic (dL) distances between the average ventral coloration of newborn and adult lizards, by adult colour. B) Mean and CI$_{95}$ of the chromatic and achromatic distances between equivalent colour patches in yearling and adult lizards (see **Fig. S5** for all possible pairwise contrasts between throat colours). Two dashed lines at 1 and 3 JNDs represent two theoretical discriminability thresholds. If the confidence interval of a point includes a discriminability threshold, the two colours are not distinguishable at this threshold according to receiver cone sensitivities and relative abundance. C-F) Throat reflectance spectra from yearlings and adults of each colour morph. G-H) Reflectance spectra of the UV-blue patches in the OVS of yearling and adult lizards, separated by sex. Solid lines and shaded area represent mean ± SEM. Dashed black line represents the average ventral reflectance of newborn lizards.

Appendix S1: Supplementary material of "Cryptic ontogenetic changes in the ventral coloration of a colour polymorphic wall lizard (*Podarcis muralis*)"

Tables

Table S1. Spectral variables (mean ± CI_{95}) describing reflectance curves in the dorsal coloration of 8 newborn, 66 yearlings, and 50 adult lizards of each sex. Spectra have been normalized by subtracting the minimum reflectance of each spectrum at all wavelengths. *N* = sample size, Qt = luminance ($R_{300\text{-}700}$), λ max = wavelength corresponding to peak reflectance in the 300-700 nm waveband, Chroma = Reflectance over the λ max ± 50 nm range, divided by total luminance (Qt).

Colour patch	**Age**	***N***	**Qt**	**λ max (nm)**	**Chroma**
Dorsum	Newborns	8	1315.7 ± 155.8	640.3 ± 9.5	0.53 ± 0.03
	Yearlings	66	1011.7 ± 74.6	642.0 ± 4.2	0.55 ± 0.01
	Adult males	50	1562.5 ± 183.0	631.5 ± 4.7	0.50 ± 0.01
	Adult females	50	1237.4 ± 132.1	642.8 ± 5.1	0.50 ± 0.01

Table S2. Pairwise comparisons contrasting the throat colours of adult and yearling *P. muralis* lizards. Contrasts were calculated using a distance-based PERMANOVA on the chromatic and achromatic distances obtained by modelling the vision of conspecifics for the ventral coloration of yearling and adult lizards. Significant contrasts (p < 0.05) are indicated in bold. F and R^2 represent pseudo F-statistics and effect size estimate, respectively. Adj. P represents adjusted P values (Bonferroni correction).

Yearling colour	Adult colour	**Chromatic contrast dS**			**Achromatic contrast dL**		
		F	R^2	adj. P	F	R^2	adj. P
UV^{+}white	UV^{+}white	1.29	0.04	0.255	0.77	0.03	0.393
	UV^{-}white	14.98	0.08	**0.001**	5.16	0.03	**0.010**
	Yellow	15.58	0.09	**0.001**	8.28	0.05	**0.002**
	Orange	8.28	0.06	**0.005**	9.71	0.07	**0.003**
UV^{-}white	UV^{+}white	77.92	0.64	**0.001**	0.54	0.01	0.548
	UV^{-}white	2.91	0.02	0.066	3.66	0.02	**0.033**
	Yellow	19.86	0.11	**0.001**	8.52	0.05	**0.001**
	Orange	32.76	0.19	**0.001**	32.65	0.19	**0.001**
Yellow	UV^{+}white	99.66	0.67	**0.001**	0.40	0.01	0.651
	UV^{-}white	14.50	0.07	**0.001**	4.17	0.02	**0.028**
	Yellow	9.42	0.05	**0.002**	9.73	0.05	**0.001**
	Orange	33.09	0.18	**0.001**	38.01	0.20	**0.001**
Orange	UV^{+}white	19.19	0.35	**0.001**	6.07	0.15	**0.006**
	UV^{-}white	30.60	0.15	**0.001**	3.94	0.02	**0.028**
	Yellow	9.64	0.06	**0.001**	3.61	0.02	**0.042**
	Orange	1.72	0.01	0.178	7.41	0.05	**0.003**

Figures

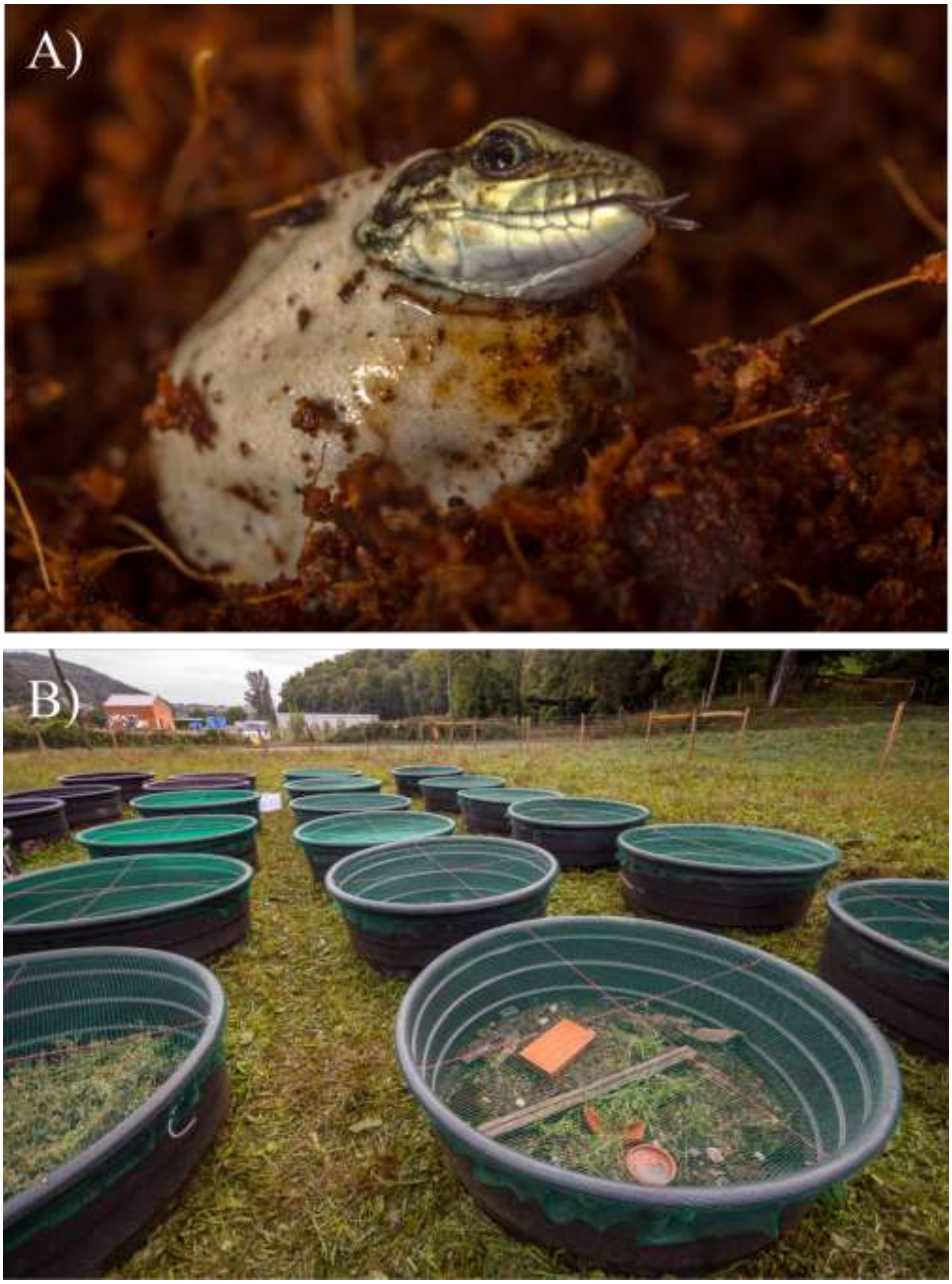

Figure S1. Breeding and housing of wall lizard juveniles. A) Newborn lizard hatching from the egg. Clutches were incubated in plastic cups filled with moist coco husk (1:2 coco:water by weigth) and covered with a perforated lid at a constant temperature of 28°C. B) Outdoor plastic tubs (170cm diameter, 60cm high) used to house juveniles under natural conditions at the Statión d'Ecologie Théorique et Expérimentale (SETE, Moulis, France). We covered each tank with a net, which excluded avian predators while allowing local invertebrates to get inside the tanks and serve as primary food source. To increase habitat complexity, we complemented the naturally occurring vegetation inside the tanks by providing a perforated brick to serve as shelter, two wood logs, and a water dish to collect rainwater. We maintained the tanks by regularly trimming weeds and supplementing the lizards' diet with *Tenebrio molitor* larvae and *Acheta domesticus* adults. Unfortunately, the COVID-19 lockdown caused a two-month interruption in tank maintenance, enabling some juveniles to escape through the overgrown vegetation. More details in Abalos *et al.*, (2021).

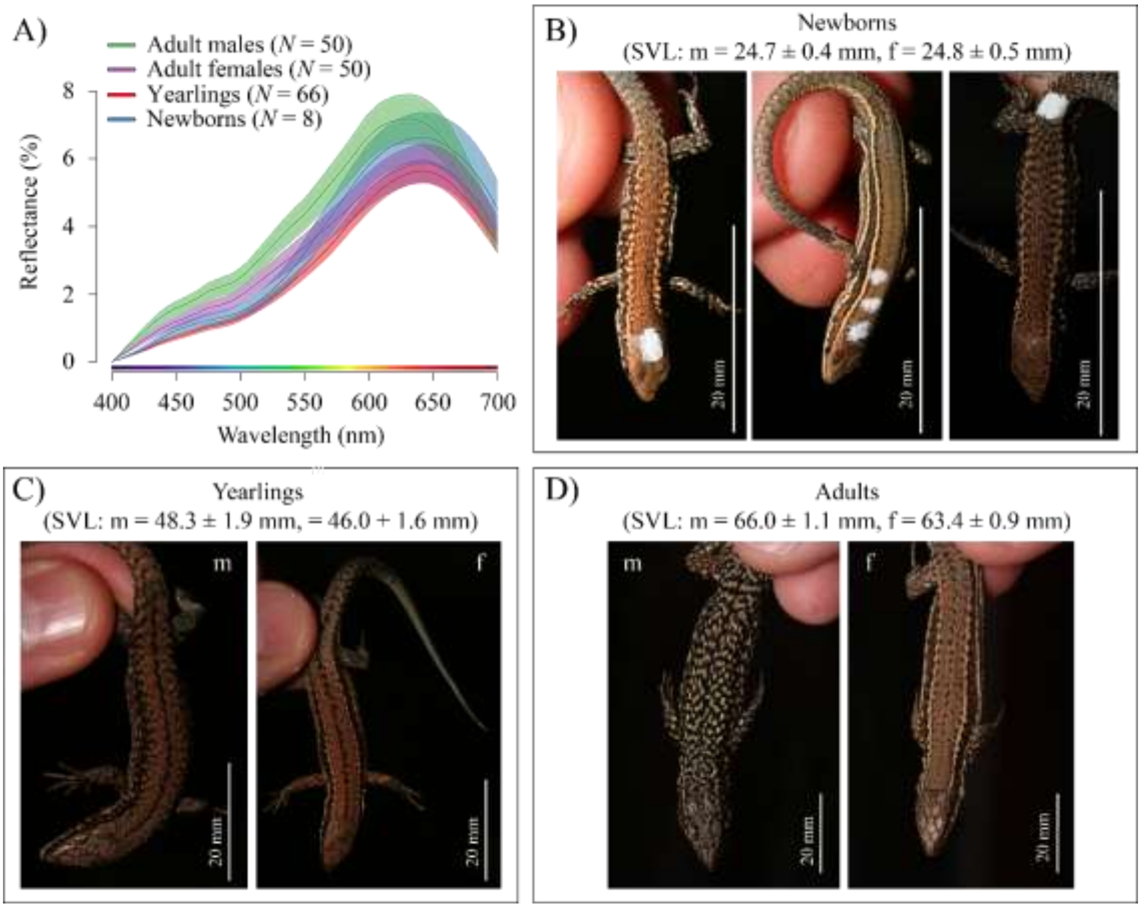

Figure S2. Ontogenetic variation in the dorsal coloration of *Podarcis muralis*. A) Reflectance spectra measured in eight newborn lizards, 66 yearlings, and 50 adults of each sex (solid lines and shaded area represent means ± CI_{95}). Spectra correspond to dorsal skin not covered by melanin patches and have been normalized by subtracting the minimum reflectance of each spectrum at all wavelengths. B) Photographs of three representative newborn lizards obtained 3-4 weeks after hatching. C) Photographs of two representative yearling lizards (one male and one female) obtained 10 months after hatching. D) Photographs of a male and female *P. muralis* captured in the same localities where the parent generation of the juveniles in B and C where sampled (i.e. along the Cerdanya plateau in Pyrénées-Orientales, France).

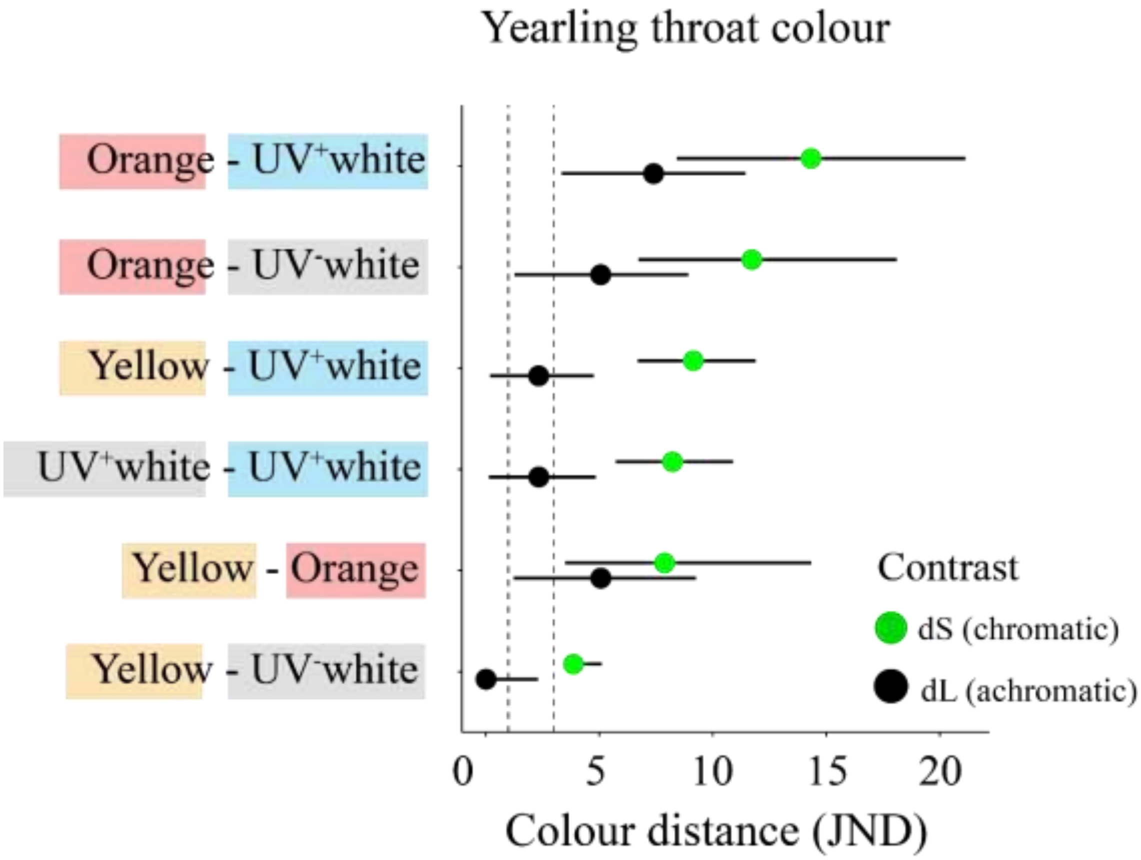

Figure S3. Mean and CI_{95} of the chromatic and achromatic distances between the four different colours found in the throat of yearling lizards. Two dashed lines at 1 and 3 JNDs represent two theoretical discriminability thresholds. If the confidence interval of a point includes a discriminability threshold, the two colours are not distinguishable at this threshold according to receiver cone sensitivities and relative abundance.

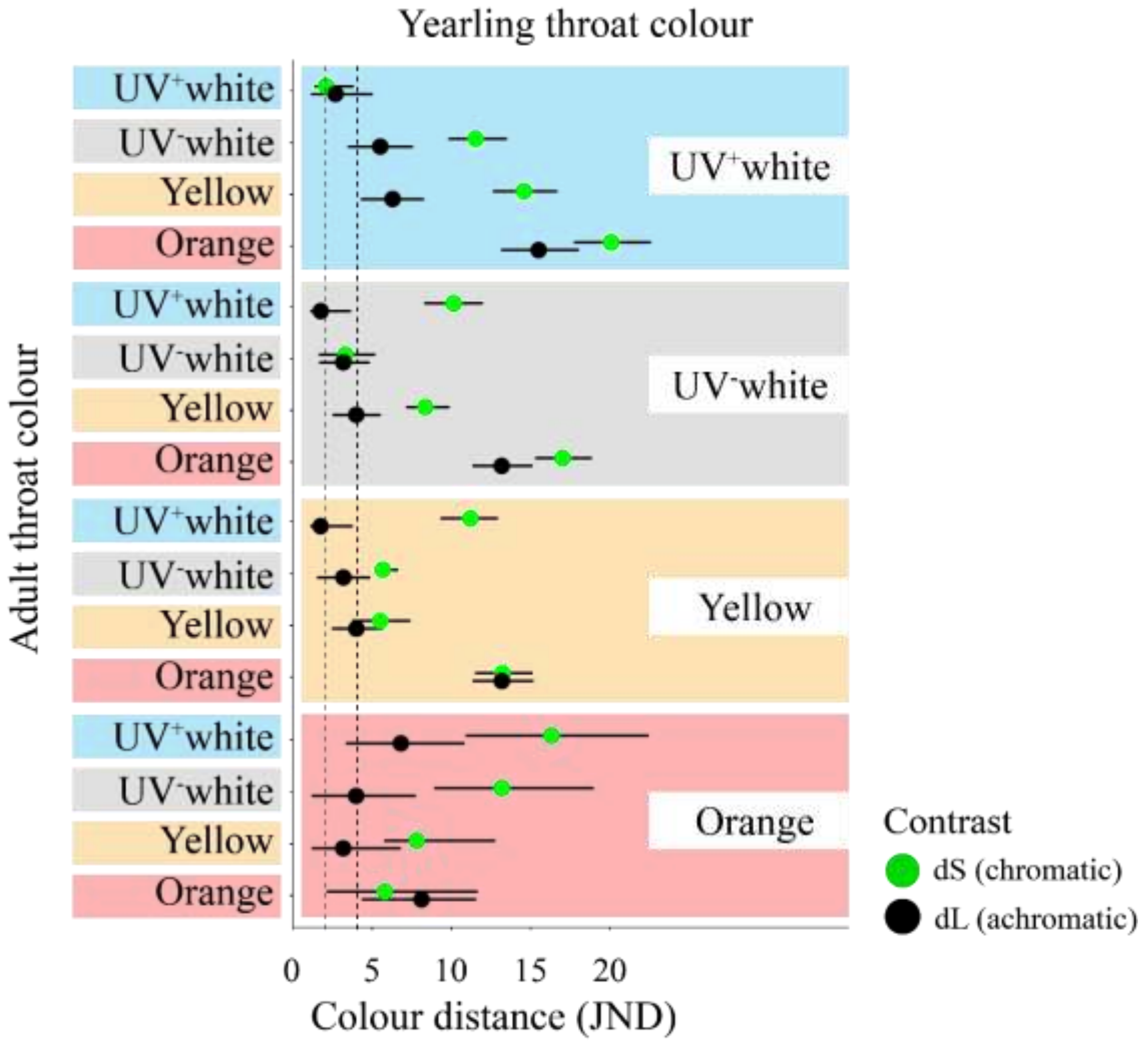

Figure S4. Mean and CI_{95} of the chromatic and achromatic distances between the colours found in the throat of yearling and adult lizards. Two dashed lines at 1 and 3 JNDs represent two theoretical discriminability thresholds. If the confidence interval of a point includes a discriminability threshold, the two colours are not distinguishable at this threshold according to receiver cone sensitivities and relative abundance.

References

Abalos, J., i de Lanuza, G.P., Bartolomé, A., Aubret, F., Uller, T. & Font, E. (2021). Viability, behavior, and colour expression in the offspring of matings between common wall lizard *Podarcis muralis* colour morphs. *Curr. Zool.* 1–15.

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