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Cryptic Ontogenetic Changes in the Ventral Coloration of a Color Polymorphic Wall Lizard (*Podarcis muralis*)

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ABSTRACT

Many animals undergo irreversible ontogenetic color 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 patched—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 hatchling and yearling lizards raised under semi-natural conditions and used visual modeling to estimate chromatic distances within individuals and across life stages (i.e., hatchlings, yearlings, and adults). Hatchlings typically exhibit UV-enhanced white (UV^+white) on their ventral surfaces (throat, belly, and OVS), a color that is likely discriminable to conspecifics from the most frequent adult colors 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 colors in yearlings are indistinguishable to conspecifics from adult throat colors, yearling UV-blue patches remain chromatically distinct from those of adults. This delay may reflect variations in the mechanisms of color production or distinct selective pressures acting on these patches. Overall, our results show that OCCs in *P. muralis* fulfill 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 colors involved in social communication.

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Summary

- Wall lizards' ventral coloration shows ontogenetic changes invisible without UV vision, demanding revision for overlooked changes in other taxa.
- Newborns show a UV-enhanced white color distinct to conspecifics, which changes differently across sexes and body regions.
- These changes may mediate juvenile-adult interactions, delaying the onset of adult colors involved in social communication.

1 | 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 color change (OCCs) is defined as an irreversible color 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 color expression (Frédérich et al. 2010; Stückler et al. 2022). OCCs can be so dramatic that the juvenile and corresponding adult forms were sometimes mistakenly labeled as different species (Smale and Kok 1983). Research on the adaptive value of OCCs in nature has found evidence of its function in three broad contexts: receiver deception, visual communication, and interaction with the abiotic environment (i.e. depending on the physical properties of color and pigments; (Booth 1990). Receiver deception contexts primarily involve predator-prey dynamics, where OCC aids in avoiding predator attacks through mechanisms such as mimicry, crypsis, deimatic displays, or deflection marks (Hawlena et al. 2006; Wilson et al. 2006; Grant 2007; Detto et al. 2008; Hawlena 2009; Natusch and Lyons 2012; Nyboer et al. 2014; Fresnillo et al. 2015a; Nokelainen et al. 2019; Medina et al. 2020). Communication contexts include aposematism, decreasing conspecific aggression or infanticide, promoting alloparental care, or signaling reproductive maturity (Caro et al. 2012; Hendershott et al. 2019). In relation with the abiotic environment, OCC may play a role in thermoregulation, water balance, protection against light or abrasion (Booth 1990; Hoppe 1979; San-Jose and Roulin 2018). In some cases, however, OCC may represent an unselected (or even slightly deleterious) by-product of pigment synthesis and degradation and be maintained due to pleiotropic associations with other strongly selected traits (Hedrick 1982; Kim and Stephan 2000). 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 color 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 color polymorphism (i.e. the coexistence of two or more alternative color 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; Kemp et al. 2023; Gefaell 2024; Gefaell, Vigo, González-Vázquez et al. 2023; Gefaell, Vigo, Galindo et al. 2023). Ventral color 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. 2021). Unfortunately, OCCs have rarely been examined in color polymorphic lizards, and color 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 colors in lizards has been corrected only in recent decades, revealing a great array of UV-colored 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 color (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; Feiner et al. 2024; Abalos et al. 2025). 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; Abalos, Pérez i de Lanuza, Carazo et al. 2016; Badiane and Font 2021; Brock, Madden et al. 2022; de 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 color 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 2014; Martin et al. 2015). Their retinas also contain large numbers of long-wavelength sensitive double cones that are thought to be involved in luminance perception (i.e. achromatic color discrimination) (Loew et al. 2002; Pérez i de Lanuza and Font 2014). Hatchling *P. muralis* show a creamy white ventral coloration, but adults of both sexes may show up to five alternative ventral color morphs to the human observer: three uniform (pure) morphs (orange, white, and yellow), and two 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 colors conforming lacertid color polymorphism (Abalos, Pérez i de Lanuza, Reguera et al. 2016). 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 colors and UV-blue patches have been often thought to play a role in intraspecific communication (Pérez i de Lanuza et al. 2013, 2017; Abalos, Pérez i de Lanuza, Carazo et al. 2016; Abalos et al. 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 2014; Martin et al. 2015), correlate with bite force and body condition (Pérez i de Lanuza et al. 2014), and behavioral evidence suggest that males making the OVS color pattern visible during male-male confrontations have higher probability of prevailing over their rivals (Abalos et al. 2024). Research on *Podarcis* ventral color polymorphism has largely focused on testing for the existence of alternative phenotypic optima, often in the form of alternative reproductive strategies involving differential sociosexual behavior or breeding investment (Huyghe et al. 2007; Sacchi et al. 2009; Calsbeek et al. 2010; Galeotti et al. 2013; Mangiacotti, Pezzi et al. 2019; Brock, Chelini et al. 2022). Although the evidence in this regard is, at best, inconclusive (Sacchi et al. 2009; Abalos et al. 2020, 2022; Stuart-Fox et al. 2021), there are other lines of evidence suggesting a social role for alternative ventral colors. The average orange, yellow, and UV$^-$white colors are discriminable to conspecifics (Pérez i de Lanuza et al. 2018), a crucial prerequisite for alternative colors to function as social signals. In *P. muralis*, ventral color 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. 2013; Pérez i de Lanuza, Font 2016; Aguilar, Andrade, Afonso et al. 2022). 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 color 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 signaling role of these color patches, research into their development (ontogeny) remains limited. For instance, hatchling 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 color vision). To do so, we raised juveniles coming from two different breeding experiments under seminatural conditions (Abalos et al. 2020, 2022), taking spectrophotometric measurements 3–4 weeks after hatching and 9–10 months later. We then used visual modeling to estimate chromatic distances between paired spectra from the same individual. Lastly, we assessed chromatic differences in ventral coloration between hatchlings, 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.

2 | Materials and Methods

2.1 | Lizard Rearing and Spectrophotometry

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, 2022, 2024). Lizards mated under seminatural 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: $N = 43$, 2019: $N = 374$) into 44 plastic tubs (170 cm diameter, 60 cm high; Figure S1), that were kept outdoors, under natural temperature and illumination conditions, in groups of 10–12 individuals (Abalos et al. 2022). Before release into the tanks, we permanently marked each hatchling on the ventral scales using a disposable medical cautery unit (Ekner et al. 2011). Interannual re-sighting was 16%, comparable to rates of hatchling survival estimated in a free-roaming population from south-western France (Barbault and Mou 1988). However, both estimates may conflate mortality with dispersal, as free-roaming lizards were not contained, and some of our juveniles may have escaped the outdoor tanks through overgrown vegetation during the COVID-19 lockdown. Additional details on egg incubation and juvenile husbandry are provided in Figure S1.

We took spectrophotometric measurements of the juveniles at two ontogenetic stages: as hatchlings (3–4 weeks after hatching) and as yearlings (10.5 months after hatching). Since hatchling lizards show uniform coloration across their ventral and ventrolateral surface (OVS), we measured all hatchling lizards in the throat ($N = 417$) and only a subset also in the belly ($N = 43$). Dorsal reflectance was measured in eight hatchling 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 hatchling 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 color 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 color 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 2014; 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 analyzed in R v.4.0.3 (R Core Team 2023) using the R package *pavo 2* (Maia et al. 2019).

2.2 | Spectral Data Analyses and Color Assignement

We assigned specific colors (i.e., UV^+white, UV^-white, yellow, orange) to each juvenile ventral color patch based on the chromatic differences observed among adult throat and belly colors in the reflectance spectra used in (Pérez i de Lanuza and Font 2015). 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 colors seem to cover the entire ventral surface in males but are restricted to the throat in females (Pérez i de Lanuza et al. 2013; 2017; Abalos et al. 2020, 2022). 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 colors from lizards assigned to the white morph (Figure 1a). 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

TABLE 1 | Spectral variables (mean ± CI_{95}) describing reflectance curves in the ventral coloration of hatchling, yearling, and adult lizards.

Color patch	Age	*N*	Qt	C_{UV}	λ β max$_{325–560}$ (nm)	λ Rmid$_{300–450}$ (nm)	λ Rmid$_{400–650}$ (nm)
Conflated throats	Hatchlings (all)	417	8303.9 ± 133.0	0.12 ± 0.00	345.1 ± 4.3	345.16 ± 2.0	513.4 ± 2.4
UV^+white throat	Hatchlings (resampled)	46	8384.1 ± 357.6	0.13 ± 0.01	329.8 ± 0.1	334.5 ± 2.7	520.0 ± 5.5
	Yearlings	5	8303.9 ± 133.0	0.12 ± 0.03	328.8 ± 1.6	329.4 ± 5.4	536.2 ± 27.5
	Adults	26	7306.0 ± 598.5	0.13 ± 0.01	330.2 ± 0.2	336.8 ± 5.1	563.3 ± 10.2
UV^-white throat	Hatchlings (resampled)	11	8091.9 ± 909.3	0.08 ± 0.01	388.2 ± 13.0	386.1 ± 4.1	483.1 ± 11.9
	Yearlings	20	6142.5 ± 547.3	0.05 ± 0.01	402.0 ± 3.4	399.6 ± 5.3	511.6 ± 14.8
	Adults	159	5544.1 ± 173.5	0.04 ± 0.00	410.9 ± 2.4	407.5 ± 1.9	505.9 ± 5.3
Yellow throat	Hatchlings (resampled)	5	8241.2 ± 2896.2	0.09 ± 0.01	554.2 ± 7.3	355.8 ± 27.3	534.4 ± 11.2
	Yearlings	26	5754.7 ± 571.4	0.05 ± 0.01	512.2 ± 4.3	376.7 ± 11.5	527.4 ± 4.2
	Adults	150	4764.8 ± 155.9	0.04 ± 0.00	513.3 ± 1.5	384.4 ± 4.7	527.8 ± 1.4
Orange throat	Yearlings	11	4848.9 ± 1060.3	0.05 ± 0.02	537.3 ± 15.1	361.4 ± 26.8	560.7 ± 4.7
	Adults	125	3443.3 ± 206.5	0.03 ± 0.00	554.7 ± 1.4	363.9 ± 6.1	566.0 ± 1.1
OVS-UV females	Yearlings	10	4534.9 ± 997.2	0.18 ± 0.05	329.5 ± 0.5	327.1 ± 11.0	544.5 ± 30.4
	Adults	37	6294.7 ± 420.6	0.28 ± 0.02	330.2 ± 0.2	342.0 ± 12.8	498.2 ± 24.9
OVS-UV males	Yearlings	26	4710.1 ± 311.13	0.24 ± 0.02	336.5 ± 14.1	336.7 ± 15.7	511.3 ± 23.9
	Adults	510	6620.9 ± 119.5	0.36 ± 0.00	330.2 ± 0.1	367.7 ± 4.7	438.9 ± 1.7

Note: Spectra have been normalized by subtracting the minimum value at all wavelengths. Qt = luminance ($R_{300–700}$), C_{UV} = UV chroma ($R_{300–400}/R_{300–700}$), λ $\beta max_{325–560}$ = wavelength at which reflectance shows the maximum positive slope in the 325–560 nm waveband, λ $Rmid_{300–450}$ and λ $Rmid_{400–650}$ = 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 (Perez i de Lanuza and Font 2015).

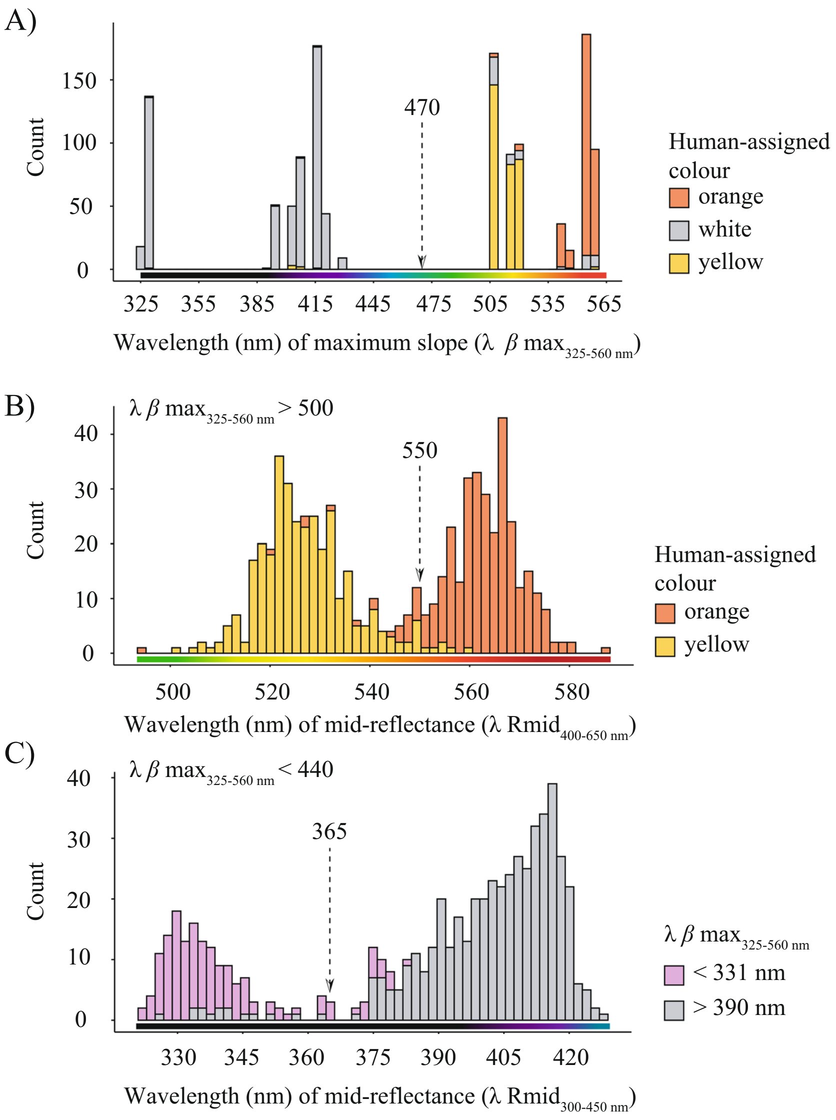

FIGURE 1 | Categorization of *Podarcis muralis* ventral colors according to their spectral properties in a sample of 1293 throat and belly spectra collected in adult males and females and assigned to a color morph by human visual inspection. (A) Stacked bar plot showing the discontinuous distribution of $\lambda\ \beta\mathrm{max}_{325–560}$ (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 colors from lizards assigned to the white morph. (B) Stacked bar plot showing the bimodal distribution of $\lambda\ \mathrm{Rmid}_{400–650}$ (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 $\lambda\ \mathrm{Rmid}_{300–450}$. Filled bars show the high agreement between a threshold to distinguish between UV^{+}white and UV^{-}white based on $\lambda\ \beta\ \mathrm{max}_{325–560}$ and one based on $\lambda\ \mathrm{Rmid}_{300–450}$. For consistency with (Pérez i de Lanuza and Font 2025), we set a threshold at $\lambda\ \mathrm{Rmid}_{300–450} = 365$ nm to separate UV^{+}white from UV^{-}white lizards.

between its maximum and its minimum within the 400–650 nm waveband ($\lambda\ \mathrm{Rmid}_{400–650}$) (Figure 1b). Specifically, juveniles were classified as yellow if showing values of $\lambda\ \mathrm{Rmid}_{400–650}$ equal or lower than 550 nm, and orange if showing higher values. We classified juvenile spectra as UV^{+}white if showing values of $\lambda\ \mathrm{Rmid}_{300–450}$ equal or lower than 365 nm, and UV^{-}white if showing higher values (Figure 1c). These thresholds correspond to troughs in the bimodal distribution of $\lambda\ \mathrm{Rmid}_{400–650}$ and $\lambda\ \mathrm{Rmid}_{400–650}$ in orange/yellow and white lizards, respectively (see Pérez i de Lanuza and Font 2025 for details on spectral differences between UV^{+}white and UV^{-}white). 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 $\varkappa \pm \mathrm{CI}_{95} = 0.914 \pm 0.031$).

2.3 | Visual Models and Color Contrast

We built visual models using the Vorobyev and Osorio receptor noise model (Vorobyev and Osorio 1998) implemented in *pavo* to assess color 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 color distances between the different throat colors shown by yearling lizards. To quantify OCCs based on lacertid color vision, we estimated the color distances between the average ventral color in hatchling lizards ($N = 417$) and each of the colors 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 colors when viewed by conspecifics by estimating color distances among all possible combinations. Lastly, we examined OCCs in the OVS of yearling lizards by estimating within-sex color distances between UV-reflecting patches in yearling lizards and full-blown UV patches from adult lizards.

In short, the receptor noise-limited model proposes that an animal's ability to discriminate color and luminance contrast depends on the intrinsic noise of individual photoreceptor cells (their firing rate without stimulation) in combination with the relative abundance of the different photoreceptor types (Vorobyev and Osorio 1998; Renoult et al. 2017). Together, these factors determine a channel-specific level of noise—commonly referred to as the Weber fraction—which is inversely related to discrimination ability (Norwich 1987; Jones et al. 2001). Briefly, we fitted visual models in *pavo* by estimating photoreceptor quantum catches with the *vismodel* function, and calculated chromatic and achromatic distances for a conservative Weber fraction using the function *coldist*. These distances were then evaluated for statistical significance using distance-based MANOVAs or PERMANOVAs (see below) and for theoretical discriminability using the *bootcoldist* function against conventionally-defined threshold values. We used the cone sensitivities (UVS:SWS:MSW:LSW, 367:456:497:562 nm) and cone ratios (1:1:1:4) for *P. muralis* available in the literature, which take into account the effect of oil droplet absorbance (Martin et al. 2015; Abalos et al. 2025). Based on evidence that luminance is processed via long-wavelength sensitive single or double cones (Fleishman and Persons 2001; Osorio and Vorobyev 2005; Fleishman and Font 2019), we fitted visual models assuming that achromatic discrimination depends on the stimulation of these cones (Pérez i de Lanuza et al. 2018; Badiane and Font 2021; de La Cruz et al. 2023).

In the absence of behavioral estimates of the Weber fraction for color discrimination in lizards, we set a conservative value of 0.05 (Siddiqi et al. 2004; Pérez i de Lanuza and Font 2015; Pérez i de Lanuza et al. 2018; Abalos et al. 2025), and a standard daylight "D65" irradiance spectrum, as implemented in *pavo*. Color 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). We followed a dual approach to evaluate statistical and perceptual differences in ventral coloration across ontogenetic stages, as recommended by Maia and White (2018). First, we evaluated statistical discriminability using distance-based MANOVAs or PERMANOVAs (Anderson 2014). We ran MANOVAs on the chromatic and achromatic distances between two groups of spectra 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) allowing for multilevel pairwise comparisons. For repeated-measures data (i.e., spectra from the same individuals at different time points), we accounted for within-individual dependence by including a blocking factor in the MANOVA using the parameter *strata*. In analyses based on group-level comparisons between individuals, we tested the assumption of homogeneity of multivariate dispersion using the *betadisper* function, a multivariate analogue of Levene's test (Anderson 2006). Second, because statistical significance does not always align with perceptual thresholds, we applied a bootstrap procedure using the *bootcoldist* function in the *pavo* package, generating confidence intervals for mean color distances under the visual models described above (999 replicates, 95% confidence). Finally, as JND values between one and three could mean that two colors are barely discriminated, we evaluated our results using a more conservative discrimination threshold of 3 JNDs (Siddiqi et al. 2004; Santiago et al. 2020; Abalos et al. 2025).

3 | Results

3.1 | Juvenile Growth and Color Expression

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, $t = -3.07$, $p = 0.003$). This sex difference limits our ability to test sex-by-morph interactions, as sample sizes become too small when split by both factors, but see descriptive statistics on juvenile growth in Table S1. Heavier juveniles had higher odds of being re-sighted after 1 year (logistic regression: std. $\beta \pm \mathrm{CI}_{95} = 0.29 \pm 0.27$, $\chi^2 = 4.33$, $p = 0.037$), whereas throat color did not influence re-sighting probability ($\chi^2 = 0.57$, $p = 0.903$). Elsewhere we have examined the effect of parental morph combination on juvenile viability and behavior (Abalos et al. 2022).

We found strong evidence that *P. muralis* ventral coloration undergoes ontogenetic changes (Table 1, Figure 2) that are large enough to be sensed by conspecifics (Tables 2 and 3). Whereas most hatchling lizards showed white throats (97%), with the majority (74%) classified as UV$^+$white according to their spectral properties, this category became markedly rare in yearlings—only 8% of re-sampled individuals retained UV$^+$-white throats. Instead, yellow (39%), UV$^-$white (30%), and orange (17%) morphs predominated in yearlings (Figure 3). Hatchlings exhibiting the UV$^+$white coloration tended to be slightly younger than orange and yellow individuals at the time of spectrophotometric measurement (Kruskal–Wallis $\chi^2 = 4.96$, $p = 0.084$). A logistic regression further indicated that the odds of being classified as UV$^+$white decreased by approximately 3.2% (i.e., multiply by 0.97) with each additional day of age ($\chi^2 = 2.00$, $p = 0.157$; Figure 4). UV$^+$white coloration is particularly frequent in the bellies of adult and yearling females, even when their throats are UV$^-$white (Figure 5). 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

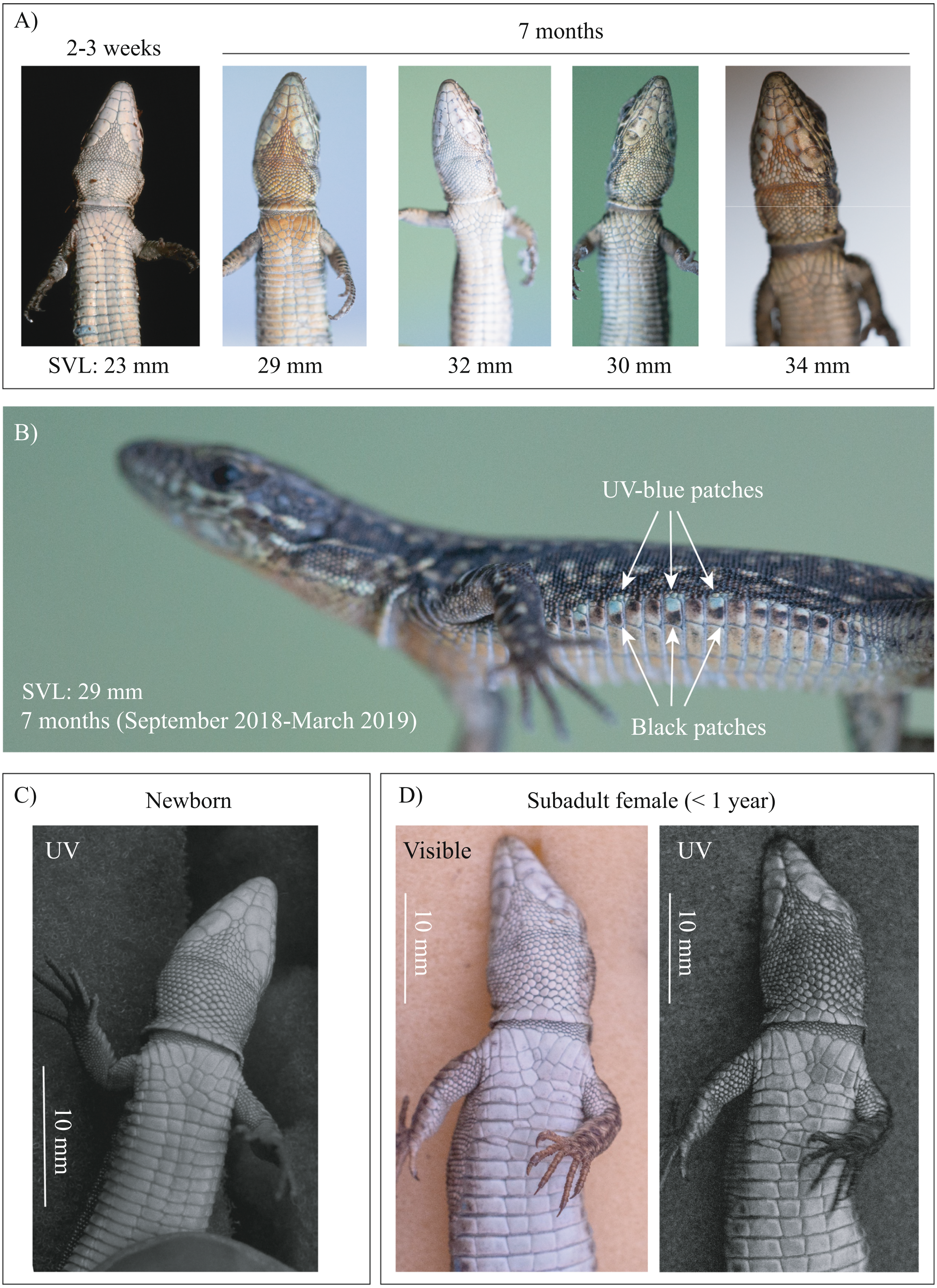

FIGURE 2 | Ontogeny of ventral coloration in *Podarcis muralis*. (A) Representative photographs of ventral coloration in a hatchling lizard 2–3 weeks after hatching (left), and in four yearlings re-captured in March 2019 (7 months after hatching). SVL stands for snout to vent length in mm. (B) Young male of *P. muralis* showing incipient UV-blue and melanin-based black patches in the outer ventral scales (OVS). (C) UV photograph of a hatchling *P. muralis* lizard showing UV^{+}white color 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., hatchling ventral surface and female belly).

TABLE 2 | Pairwise comparisons between the ventral coloration of lizards measured as hatchlings and re-sampled as yearlings, per color patch.

		Within-individual contrasts					
		Chromatic contrast			Achromatic contrast		
Color patch **Yearling color**	***N***	***F***	***R^2***	***p* value**	***F***	***R^2***	***p* value**
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					
		Chromatic contrast			Achromatic contrast		
Color patch		***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

Note: Within-individual contrasts were calculated using a distance-based MANOVA on the chromatic and achromatic distances obtained by modeling the vision of conspecifics for the ventral coloration of each individual at birth and when re-captured 1 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).

TABLE 3 | Pairwise comparisons assessing differences in ventral coloration between adults and hatchlings, and between adults and yearlings, for each color patch.

	Hatchling average-adult color patches					
	Chromatic contrast			Achromatic contrast		
Adult color patch	***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 color patches)					
	Chromatic contrast			Achromatic contrast		
Color patch	***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

Note: In the adult–hatchling comparison, each adult color was contrasted against the average ventral color of hatchlings (i.e., measured in the throat). In the adult–yearling comparison, the table presents only contrasts between color patches that were both spectrally equivalent and anatomically matched (i.e., located in the same body region), for clarity. Results for all adult–yearling throat color combinations are provided in Table S2 and Figure S4. Contrasts were calculated using a distance-based PERMANOVA on the chromatic and achromatic distances obtained by modeling the vision of conspecifics for the ventral coloration of hatchling, 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).

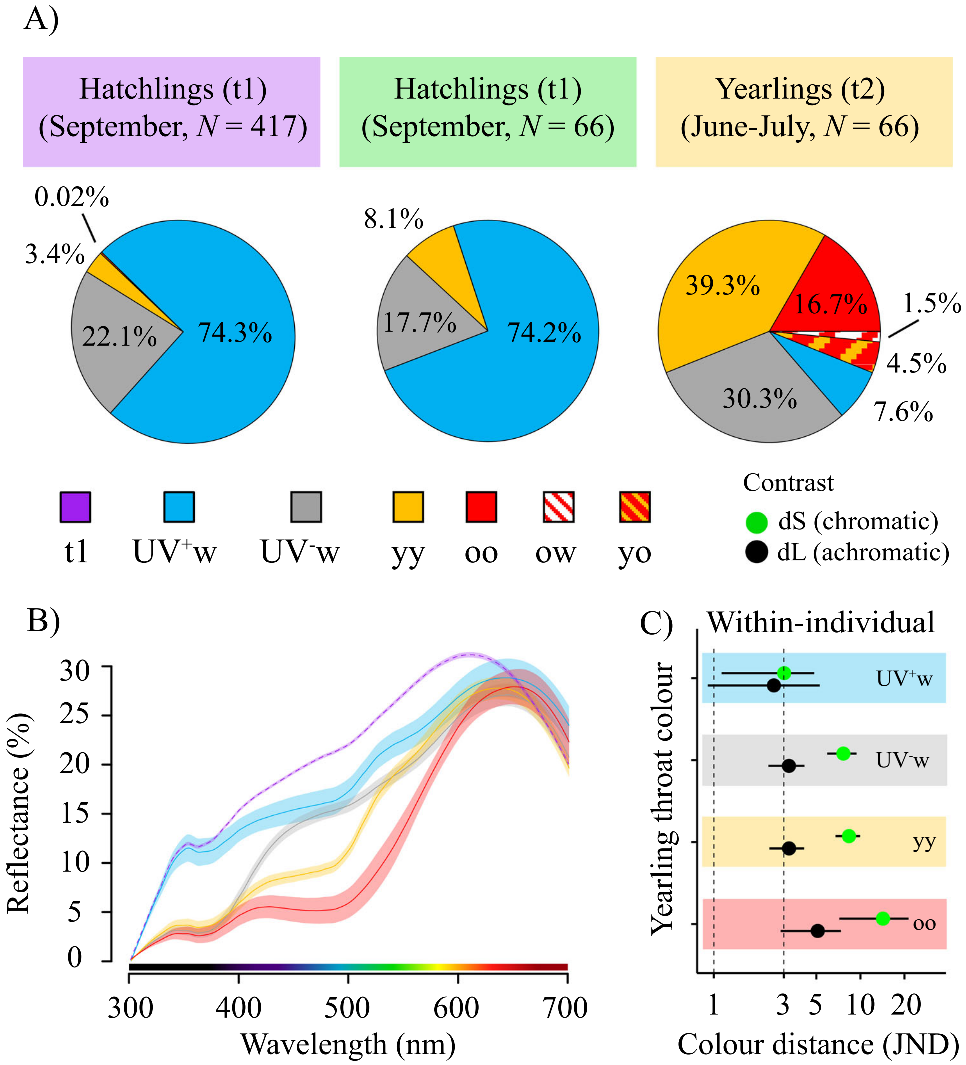

FIGURE 3 | Ontogenetic changes in *Podarcis muralis* throat coloration. (A) Pie charts represent the proportions of juveniles showing different throat colors (UV$^+$w = UV$^+$white, UV$^-$w = UV$^-$white, oo = orange, yy = yellow, ow = orange–white, yo = yellow–orange) in September (t1; 3–4 weeks after hatching), and June–July (t2; 1 year after hatching). The three pie charts correspond to the full data set of 417 hatchlings measured at t1 (purple), the subset of 66 surviving juveniles measured as hatchlings at t1 (green), and these same juveniles measured as yearlings in t2 (yellow). (B) Reflectance spectra from the 62 surviving yearlings showing pure color morphs (solid lines and shaded area represent means ± SEM). The dashed purple line represents the average throat spectra of 417 hatchling 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 hatchling-yearling contrasts), separated by yearling throat color. 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 colors are not distinguishable at this threshold according to receiver cone sensitivities and relative abundance.

between hatchling, yearling and adult lizards (Table S2, Figure 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 hatchling lizards.

3.2 | Visual Models and Discriminability of OCCs to Conspecifics

Within-individual contrasts (i.e., MANOVAs) found significant chromatic and achromatic differences between hatchling and yearling throat colors for every yearling color except UV$^+$white (Table 2). Chromatic distances between hatchling-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 (Figure 3). Within-individual achromatic distances were shorter than the theoretical threshold of 3 JNDs for every yearling throat color (Figure 3).

Between-individual contrasts (PERMANOVA) found significant chromatic differences among all pairwise combinations of yearling throat colors (Table 2). In contrast, achromatic differences were nonsignificant 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

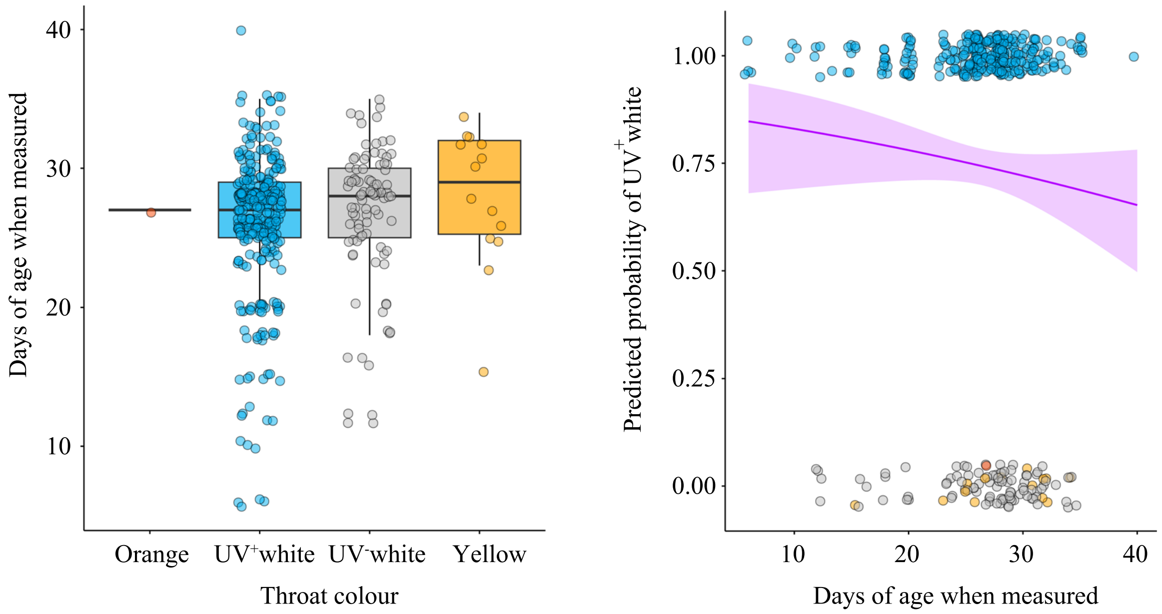

FIGURE 4 | Relationship between throat color and age (days since hatching to spectrophotometric measurement) in *Podarcis muralis* hatchlings ($N = 417$). A) Jittered boxplots showing variation in age across throat color categories. Horizontal lines represent medians; boxes span the interquartile range (IQR), and whiskers extend to the most extreme values within 1.5 × IQR. B) Negative association between age and the probability of exhibiting a UV$^+$white throat. The purple line and shaded area represent the predicted trend and CI$_{95}$ from a logistic regression model. Filled circles in both panels represent individual hatchlings, with point color indicating throat color.

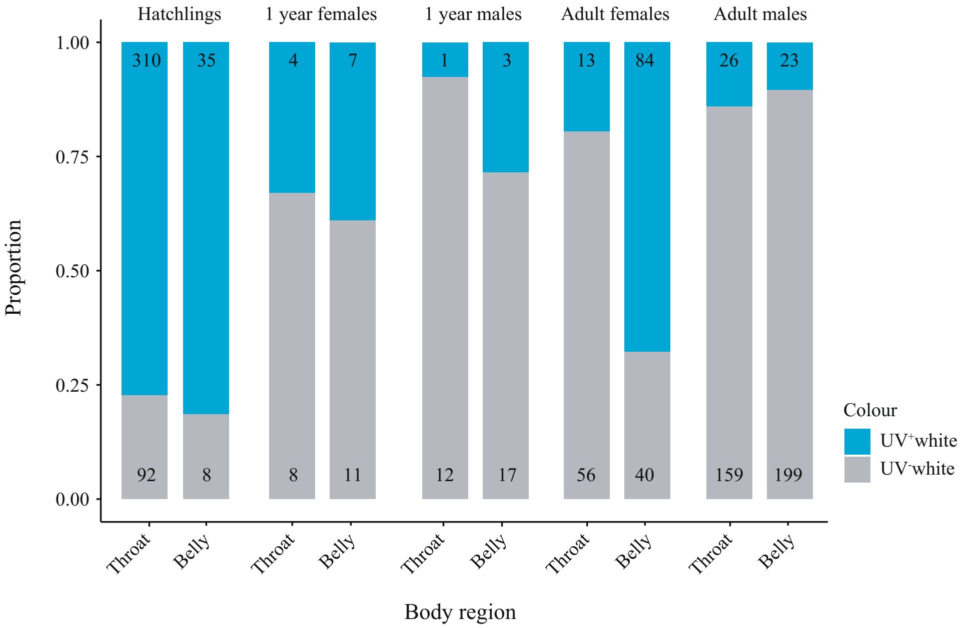

FIGURE 5 | Stacked bar plot showing the proportion of UV$^+$white and UV$^-$white colorations in the throats and bellies of lizards classified according to the spectral properties of their reflectance curves (i.e., $\lambda\ \beta\text{max}_{325–560} \leq 500$): UV$^+$white if showing a $\lambda\ \text{Rmid}_{300–450} \leq 365$ nm, UV$^-$white if $\lambda\ \text{Rmid}_{300–450} > 365$ nm. Numbers inside filled bars indicate sample size. UV$^+$white coloration is particularly frequent among hatchling lizards, and in the belly of yearling and adult females.

combinations, with Orange and UV$^+$white being the most different pair and Yellow–UV$^-$white the least different (Figure S3).

Spectra from the UV-blue patches of yearlings showed a trough shape (with two peaks at either end of the spectral range), which differed from the single peak around longer wavelengths found in hatchling lizards (Figure 6). Paired spectra contrasting hatchling 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; Figure 6).

All contrasts between the average hatchling ventral color ($N = 417$) and adult throat colors were statistically significant according to the PERMANOVA except the chromatic contrast

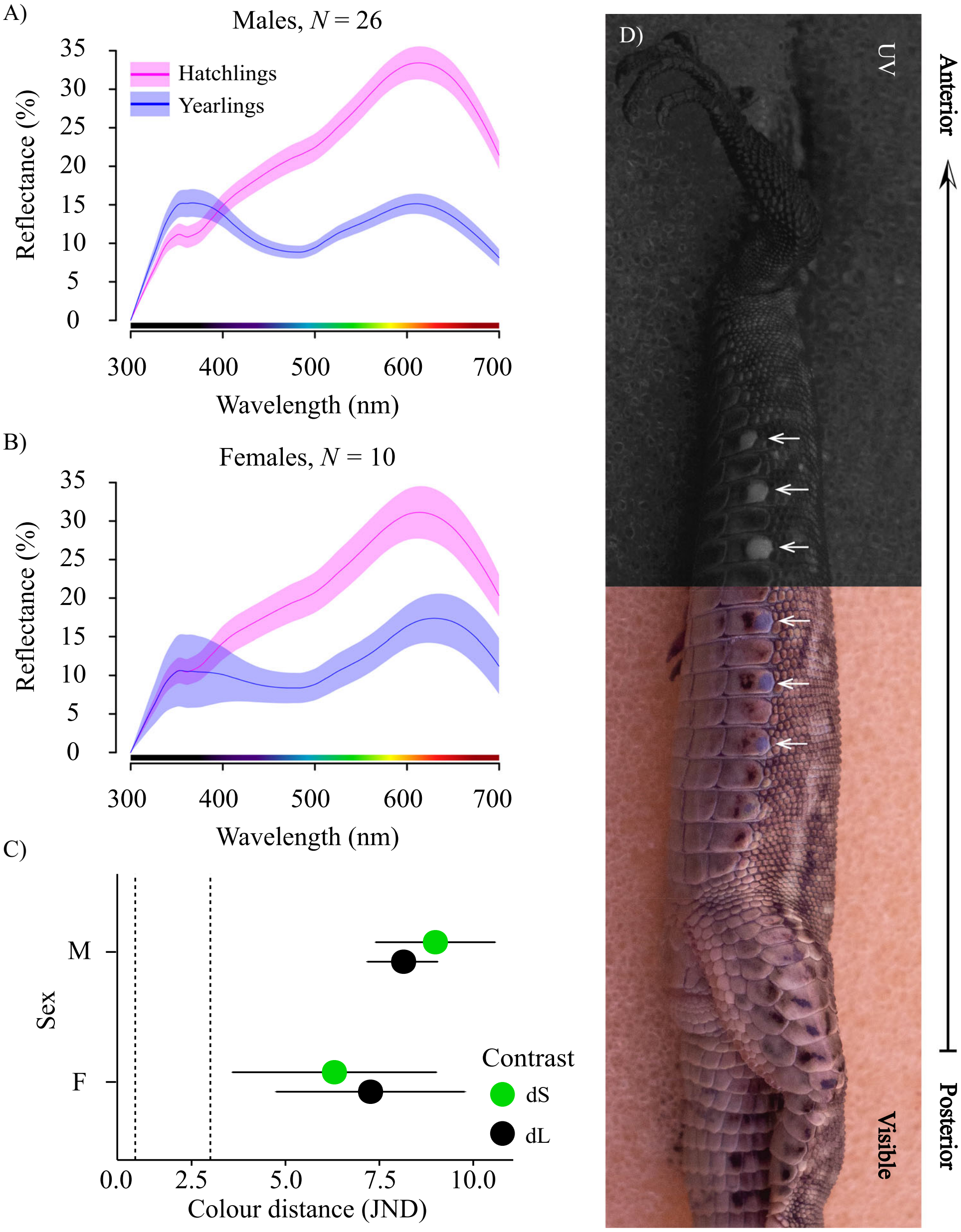

FIGURE 6 | Ontogenetic change in *Podarcis muralis* outer ventral scales (OVS) coloration. (A and B) Reflectance spectra from the 36 lizards (a = males, b = females) showing UV-blue patches as yearlings in their OVS (solid lines and shaded area represent means ± SEM). (C) Mean and CI_{95} of the chromatic (dS) and achromatic (dL) distances between paired hatchling-yearling measurements of reflectance in males and females. Hatchling throat spectra are comparable to yearling OVS spectra, as hatchlings exhibit uniform ventral coloration. 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 colors 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.

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 (Figure 7). The distance-based PERMANOVA fitted on chromatic contrasts between yearlings and adult throat colors yielded significant results for all contrasts between lizards of different colors (Table S3). Chromatic contrasts between same-colored lizards were nonsignificant except for yellow yearlings and adults (Table 3). According to bootstrapped chromatic distances, all contrasts between same-colored yearlings and adults resulted in shorter distances than the theoretical threshold of 3 JNDs (Figure 7 and S4).

Adult UV-blue patches were found to differ chromatically and achromatically from the average hatchling coloration (Table 3), with contrasts in males resulting in larger bootstrapped distances than contrasts in females (Figure 7). 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 hatchlings and adults. Achromatic distances were shorter than

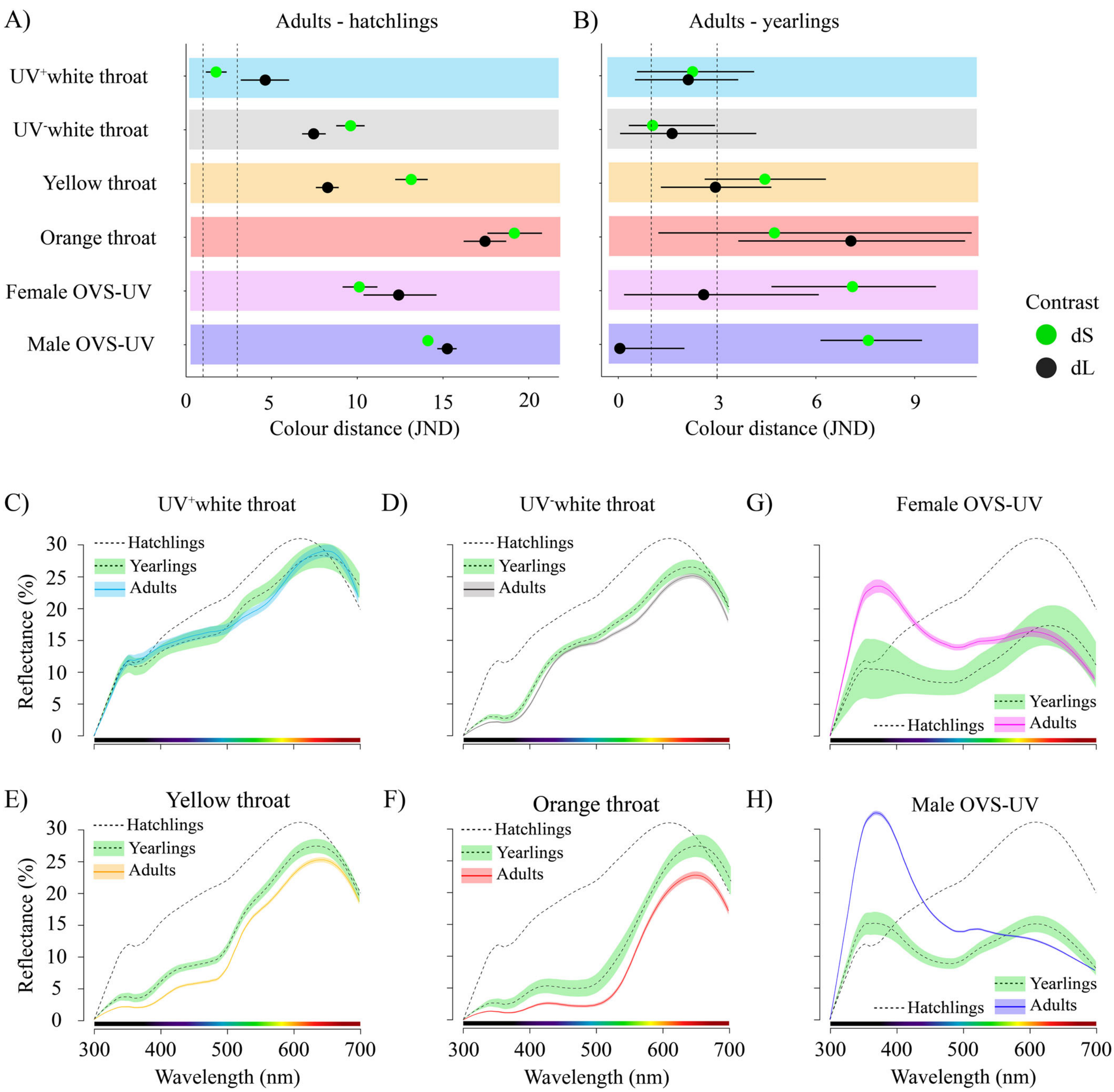

FIGURE 7 | Comparison between the ventral coloration of hatchling and yearling lizards with adult *Podarcis muralis* from eastern Pyrenees. (A) Mean and CI_{95} of the chromatic (dS) and achromatic (dL) distances between the average ventral coloration of hatchling and adult lizards, by adult color. (B) Mean and CI_{95} of the chromatic and achromatic distances between equivalent color patches in yearling and adult lizards (see Figure S4 for contrasts among all yearling-adult throat color combinations). 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 colors 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 color 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 hatchling lizards.

the theoretical threshold of 3 JNDs for both males and females (Figure 7).

4 | Discussion

We monitored color expression in hatchling (3–4 weeks old) and yearling (9–10 months old) *P. muralis* lizards raised under seminatural conditions, providing the first account of OCCs in their ventral and ventrolateral coloration. Objective color characterization revealed that hatchling lizards exhibit enhanced UV reflectance compared to yearlings, which begin to show incipient morph expression (Figures 2 and 3). Our results support the distinction of two types of white ventral coloration in *P. muralis*: UV^+white, typically found in hatchlings and some adult female bellies, and UV^-white, present in the throats of adults and the bellies of adult males (Abalos, Pérez i de Lanuza, Reguera et al. 2016). Within-individual chromatic distances suggest that OCCs to orange, yellow, and UV$^-$white are perceptible to conspecifics, at least based on visual models and their corresponding assumptions. Among yearlings, throat colors 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 hatchling coloration among throat colors (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 colors. A caveat worth acknowledging is that, although visual models estimate the sensory input reaching the visual system, the perceptual interpretation of that input is species-specific and shaped by neural processing (Kelber et al. 2003; Baden and Osorio 2019). As such, model predictions should be validated through behavioral experiments. Nonetheless, in *P. muralis*, previous studies have shown a close match between model predictions and experimentally confirmed perceptual differences (Pérez i de Lanuza et al. 2018), lending confidence to our interpretation.

These findings have significant implications for understanding the ontogeny of ventral color 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. [2013]), but our results suggest that hatchling lizards express a distinct UV$^+$white coloration that, based on our understanding of their visual system, conspecifics likely perceive as chromatically different from adult throat colors. Although 74% of hatchlings showed UV$^+$white coloration, some changed color even weeks after hatching, suggesting notable individual variation in OCC timing that merits further study. 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 (Figures 2, 5, and Figure 2 in Pérez i de Lanuza and Font 2015). We have previously highlighted the need to establish reliable criteria for adult color morph classification (Pérez i de Lanuza et al. 2013; 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 color 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 (Figure 6). However, nearly a year after hatching, yearling UV-blue patches remain chromatically distinguishable from adult colors, 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 color production and/or distinct selective pressures acting on these color 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 long-wavelength end of the spectrum to the minimum of the lacertid visual range in the UV wavelength band (Pérez i de Lanuza and Font 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 (Figure 7).

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 fulfill a key requirement for social signals by being perceptible to conspecifics. Studies on OCCs in lizards have 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; Watson et al. 2012; Ortega et al. 2014; Fresnillo et al. 2015a; b; Murali et al. 2018; Watson and Cox 2025). 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 hidden (Pérez i de Lanuza, Carretero et al. 2016). 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, Carretero et al. 2016; Abalos et al. 2024). Considering the ontogenetic decline in UV$^+$white coloration and its distinct appearance to lizards compared to the colors 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; Ochi and Awata 2009; Bergman and Sheehan 2013; Hendershott et al. 2019), including lizards (Clark and Hall 1970; Hawlena et al. 2006; Fresnillo et al. 2015b). 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 1988; 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 signaling 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 suggests that, as in many other lizards (Tokarz 1995; Cuadrado 2006; Uller and Olsson 2008; Vicente and Halloy 2016), precopulatory mate choice in lacertids, including wall lizards, is often largely under male control (Edsman 2001; Font and Desfilis 2002; Barbosa et al. 2006; Carazo et al. 2011; Font et al. 2012; Sacchi et al. 2015). A preference for larger, older, or clearly fertile females based on visual cues has been reported in male lizards (Cuadrado 1999, 2006; Whiting and Bateman 1999; Weiss 2006), including lacertids (Olsson 1993; Belliure et al. 2018). 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 *sensu* Paterson 1985) (Edward and Chapman 2011; Swierk and Langkilde 2013). Immature females may also 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). Although conspecifics might infer age and sexual maturity from body size, the widespread occurrence of ontogenetic color changes linked to maturity in other taxa suggests size alone may be insufficient (Booth 1990; Roucurt Cezário et al. 2022). Whether color signals offer more reliable cues than body size for assessing age and sexual maturity in wall lizards remains to be tested.

Variation in the ventral and ventrolateral color 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 neighbors 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 et al. 2014; Fleishman and Font 2019). In other taxa, visual and chemical cues have been shown to play a crucial role 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 (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 has been linked to lasting male-female pair bonds (Pérez i de Lanuza et al. 2013), which may play an important role in facilitating mate-guarding and reducing male harassment (in Den Bosch and Zandee 2001; Zaldívar-Rae and Drummond 2007; Olsson et al. 2019; Abalos et al. 2020). Although color-assortative pairings are more frequent in free-roaming populations (Pérez i de Lanuza et al. 2013; Pérez i de Lanuza, Font et al. 2016), these associations have neither led to genomic differentiation (Aguilar, Andrade, Afonso et al. 2022), nor been replicated in experiments with unfamiliar individuals (Abalos et al. 2020, 2022). These findings suggest that the prevalence of assortative pairing may not reflect selection for maintaining co-adapted trait combinations (Lancaster et al. 2014; Svensson et al. 2021; Aguilar et al. 2024), challenging the view that throat colors correspond to discrete, strategy-linked morphs (Mangiacotti, Fumagalli et al. 2019; Amer et al. 2024). Instead, they call for frameworks that better capture the full complexity of color polymorphism. Subtle chromatic and achromatic variation within the orange, white, and yellow alternative colors, along with between-individual differences in patterning may hold relevance for social recognition (Martin et al. 2015; Pérez i de Lanuza et al. 2018; Aguilar, Andrade and Pérez i de Lanuza 2022). At the cohort level, ontogenetic transitions from uniform UV^+-white coloration to distinct ventral and ventrolateral color 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 adult color signals, as well as providing visual cues for individual recognition.

In conclusion, here we show that *P. muralis* ventral coloration undergoes OCCs likely 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, including their cellular mechanisms, and how they involve or modify melanin-based patches (Pérez-Rodríguez et al. 2017; Sheehan et al. 2017; Zhang et al. 2023). Altogether, our results underscore the importance of considering receiver perspectives in ethological studies of animal coloration (Kemp et al. 2023).

Author Contributions

Javier Abalos: conceptualization and experimental design, investigation, statistical analysis, visualization, writing – original draft, writing – review and editing. **Guillem Pérez i de Lanuza:** conceptualization and experimental design, writing – review and editing. **Fabien Aubret:** conceptualization and experimental design, writing – review and editing. **Enrique Font:** conceptualization and experimental design, writing – review and editing. **Alicia Bartolomé:** investigation, writing – review and editing.

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Guidelines for the Use of Animals in Research and all applicable local, national, and European legislation.

Conflicts of Interest

The authors declare no conflicts of interest.

Data Availability Statement

The data set and R script used to generate results presented in this study are available at https://doi.org/10.5281/zenodo.15856719.

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Supporting Information

Additional supporting information can be found online in the Supporting Information section.
Figure S1: Breeding and housing of wall lizard juveniles. A) Hatchling lizard hatching from the egg. **Figure S2:** Ontogenetic variation in the dorsal coloration of *Podarcis muralis*. **Figure S3:** Mean and CI_{95} of the chromatic and achromatic distances between the four different colours found in the throat of yearling lizards. **Figure S4:** Mean and CI_{95} of the chromatic and achromatic distances between the colours found in the throat of yearling and adult lizards. **Table S1:** Mean change in body size (snout-to-vent length, SVL, in mm) and weight (in grams) for *P. muralis* juveniles housed in outdoor tanks and re-sampled approximately 10 months after hatching. **Table S2:** Spectral variables (mean ± CI_{95}) describing reflectance curves in the dorsal coloration of 8 hatchling, 66 yearlings, and 50 adult lizards of each sex. **Table S3:** Pairwise comparisons contrasting the throat colours of adult and yearling *P. muralis* lizards.