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

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Abstract (303 words)

During growth, many animals undergo irreversible colour changes. Despite their ecological and ethological relevance, ontogenetic colour changes (OCCs) are often overlooked. 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. To human vision, adults of the European common wall lizard (*Podarcis muralis*) may show throats and bellies with uniform orange, white, and/or yellow coloration, or two mosaic colorations. In addition, adult males (and some females) present a row of ventrolateral UV-blue patches in their outer ventral scales (OVS). Here we set out to describe OCCs in the ventral (throat and belly) and ventrolateral (OVS) coloration of juvenile *Podarcis muralis* lizards 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 perceived by conspecifics as distinct from the most frequent adult colours (i.e. orange, yellow, and UV-reduced white; UV^{-} white). This distinction, invisible to humans, highlights two types of white coloration differing in UV reflectance. The prevalence of UV^{+} white decreases with age, with the decline being less pronounced in female bellies. OCCs related to the UV-blue patches seem to be delayed with respect to changes in the throat and belly. Throat colours in yearling lizards are indistinguishable to conspecifics from the equivalent colours in adult throats. In contrast, chromatic distances between the UV-blue patches of adults and yearlings are large enough for discrimination by conspecifics. We discuss a possible function of *P. muralis* OCCs in delaying the onset of adult colours involved in social signalling.

Introduction

Growth 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 (Booth 1990). Ontogenetic colour change (OCC) is defined as a non-reversible 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). Due to the logistic difficulties posed by their study, research on OCCs has often lagged behind the study of adult coloration, up 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 (von Uexküll 1934; 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).

The most typical manifestation of OCC in nature occurs when juveniles initiate life with a drab or cryptic coloration, paying the costs of producing, maintaining and displaying bright colour signals only after they become sexually active (Schaller 1963; Martín and Forsman 1999; Hawkins et al. 2012; Ruell et al. 2013; Blas et al. 2013; Roucurt Cezário et al. 2022). However, juveniles of many species temporarily exhibit conspicuous colorations (such as in the François Langur *Trachypithecus francoisi* and other primates; Hendershott et al. 2019) that must offset the increased risk of predator detection by providing a survival advantage. Research on the adaptive value of OCCs in nature has found evidence of its function in two broad contexts: visual communication (either interspecific or intraspecific) and interaction with the abiotic environment (i.e. depending on the physical properties of colour and pigments; Booth 1990). Interspecific ecological and communication processes where OCC has been found to play a role concern mainly avoiding predator attacks (i.e. mimicry, crypsis, aposematism, deimatic displays or deflection marks; Wilson et al. 2006; Hawlena 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). Intraspecific communication contexts include decreasing conspecific aggression or infanticide, promoting alloparental care, or signalling 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, or just as an unselected by-product of nutrient synthesis and degradation (Booth 1990; Hoppe 2018; San-Jose and Roulin 2018). It is also possible that some OCCs are selectively neutral (or even slightly deleterious), and only maintained because of their association with other strongly selected characters (Hedrick 1982; Kim and Stephan 2000).

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

(Svensson 2017). Before the development of modern molecular methods, discrete colour morphs served as phenotypic markers allowing evolutionary biologists to study fundamental evolutionary processes such as selection, genetic drift, or gene-flow in natural populations (Kettlewell 1955; Cordero et al. 1998; Majerus 2008; Endler et al. 2023). Ventral colour polymorphism has evolved in at least seven different families of lizards, providing a unique opportunity to study the evolutionary processes responsible of maintaining intraspecific diversity (Stuart-Fox et al. 2020). Unfortunately, OCC 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 (in some cases) 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. 2013a, 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, 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; Brock et al. 2020; Badiane and Font 2021). 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. 2015a). 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). An intermediate white-yellow morph, previously considered, has been dismissed as these smaller lizards lack mosaic coloration and share the hue of pure yellow morphs but with lower intensity, likely representing subadult yellow morphs (Calsbeek et al. 2010; Sacchi et al. 2013). Recently, 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 to a total of seven (Pérez i de Lanuza & Font, 2024, *in press*). In some populations the orange and yellow colours 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). Adult morphs are heritable (Andrade et al. 2019) and behavioural evidence confirms that these colours are chromatically discriminable by conspecifics (Pérez i de Lanuza et al. 2018; Abalos et al. 2021; Pérez i de Lanuza & Font, 2024, *in press*). Regardless of their colour, adult lizards often feature melanin-based patches covering part of their ventral and ventrolateral scales (Gosá 1987; While et al. 2015; Abalos et al. 2016, 2024). Both sexes can develop 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, colour polymorphism and UV-blue patches have been often thought to play a role in communication (Pérez i de Lanuza et al. 2013a, 2017; Abalos et al. 2016, 2020). The spectral properties of UV-blue patches in males are tuned to lacertid vision (Pérez i de Lanuza and Font 2014a; Martin et al. 2015a) and behavioural evidence suggest that males making the OVS colour pattern visible during male-male confrontations —by adopting a characteristic raised-body posture and compressing their bodies laterally— have higher odds 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 underlying the different colours, often in the form of alternative reproductive strategies involving differential sociosexual behaviour or breeding investment (Sacchi et al. 2009; Calsbeek et al. 2010; Galeotti et al. 2013; Mangiacotti et al. 2019; Brock et al. 2022). 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 role of intraspecific ventral coloration in social interactions. 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 (Wellenreuther et al. 2014; Sheehan and Bergman 2016).

Despite the considerable attention given to the potential signaling role of these color 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 sometimes 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 at two different points in time (approximately 3-4 weeks and 9-10 months after hatching). 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 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.

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 were allowed to mate in semi-natural conditions (2018: nine males and nine females per enclosure; 2019: one male and three females per enclosure) after which pregnant females were brought to the laboratory and housed individually to lay their eggs. In September, 3-4 weeks after hatching, we released 417 juveniles resulting from these experiments (2018: *N* = 45, 2019: *N* = 372) into 44 outdoor 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. Parentage of the lizards was determined based on six known microsatellite loci and used to group unrelated juveniles together in the tubs so as to balance any potential effects arising from differences between the tubs (Heathcote et al. 2014; Abalos et al. 2021). 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. Prior to release into the tanks, we permanently marked each juvenile on the ventral scales using a disposable medical cautery unit (Ekner et al. 2011) and obtained one spectrophotometric measurement of reflectance in the ventral surface. Since newborn lizards show uniform coloration across their ventral surface (see results), we measured all newborn lizards in the throat (*N* = 417) and only a subset also in the belly (*N* = 43). We measured dorsal reflectance in eight newborn lizards. Approximately ten months after hatching, we re-captured every surviving lizard 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 to the side of the probe (nylon head down), which allowed us to maintain a constant distance of 3 mm between the tip of the probe and the target surface preventing the production of chimeric spectra in colour patches as small as 2 mm in diameter (Badiane et al. 2017). Measurements of the UV-blue patches were obtained from the largest patch of each individual also to prevent the obtention of erroneous spectra. 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. 2015a). 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 colours in the reflectance spectra used in Pérez i de Lanuza and Font (2015) (**Fig. 1**). These spectra correspond to adult individuals collected across various locations in the Cerdanya plateau, the same area where the parent lizards from the present experiment were captured. 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., $R_{300\text{-}700}$) 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; $R_{300\text{-}400}/R_{300\text{-}700}$). In adults, the wavelength corresponding to the maximum positive slope between 325 and 560 nm (λ $\beta max_{325\text{-}560}$) 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 $\beta max_{325\text{-}560}$ equal or below 500 nm were classified as white, while lizards showing higher values where classified as either orange or yellow. We then distinguished between orange and yellow juveniles based on the wavelenght at which reflectance is halfway between its maximum and its minimum within the 400-650 nm waveband (λ $Rmid_{400\text{-}650}$) (**Fig. 1**). Specifically, juveniles were classified as yellow if showing values of λ $Rmid_{400\text{-}650}$ 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 $Rmid_{300\text{-}450}$ equal or lower than 365 nm, and UV^- white if showing higher values (**Fig. 1**). To ensure the validity of these thresholds for morph categorization we re-classified 460 throat spectra from adult males, previously assigned into the white, orange or yellow morphs by visual inspection (Cohen's *kappa* ± CI_{95} = 0.914 ± 0.0313).

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, in order to test whether ontogenetic changes were large enough to be perceived by conspecifics. Specifically, we quantified within-individual chromatic and achromatic distances in throat and UV-blue coloration based on conspecific cone sensitivities and relative frequencies. To quantify colour similarity, we also estimated the colour distances between the different throat colours shown by yearling lizards. To quantify the impact of OCCs on lacertid sensory stimulation, 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, and 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 the progress of 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*. Contrasts 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). Whenever we wanted to contrast 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 ± 2.33 mm, t = -1.96, p = 0.054) and increased their mass significantly more (m-f: 0.55 ± 0.35 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 (**Fig. S3**).

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**). Accordingly, 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 (UV^+ white = 3.0 ± 1.9, UV^- white = 7.6 ± 1.7, yellow = 8.3 ± 1.6, orange = 14.3 ± 7.1; **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, except between Orange and UV$^+$ white (**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. S4**).

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 ventral coloration in newborns and UV-blue patches in yearlings showed significant differences according to the MANOVAs (**Table 2**). Chromatic and achromatic distances were more pronounced in males than in females (dS: males = 9.0 ± 1.6, females = 6.3 ± 2.7; dL: males = 8.1 ± 0.9, females = 7.3 ± 2.5) and large enough to allow for discrimination. (**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 distinctly coloured lizards (**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 ventral 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 controlled semi-natural conditions, providing the first account of ontogenetic colour changes in the ventral coloration of this species. Objective characterization of throat coloration revealed that the white coloration expressed by 74% of newborn lizards presents enhanced UV reflectance relative to yearling lizards showing incipient morph expression (**Fig. 3**). Our results support the distinction of two types of whites in the ventral coloration of *P. muralis*; UV$^+$ white and UV$^-$ white, the first typically found in newborn lizards and some adult female bellies, and the latter in the throat of adults (Pérez i de Lanuza et al. 2024 *in press*). Within-individual chromatic distances suggest that OCCs to orange, yellow and UV$^-$ white colours are likely perceptible to conspecifics. Although all combinations of yearling throat colours are theoretically discriminable, orange and

UV^+ white represent the two most dissimilar while yellow-UV^- white are the two most similar. Contrasts with adults align with our repeated measures results in finding a similar hierarchy in divergence from average newborn coloration among throat colours (orange > yellow > UV^- white > UV^+ white). In addition, results from adult-yearling contrasts suggest that 9-10 months after hatching, throat coloration in 92% of the yearlings is already indistinguishable to conspecifics from the colours found in adults.

These observations carry important implications for our understanding of the ontogeny of ventral colour polymorphism in *P. muralis* and other lacertid lizards, as white morph lizards have often been assumed to retain the juvenile ventral coloration during growth (in contrast with orange, yellow, and mixed-morph lizards; e.g. Pérez i de Lanuza et al. 2013). Our results instead suggest that newborn lizards tend to express a form of white coloration (UV^+ white) in their ventral surface that is likely perceived by conspecifics as chromatically distinct from the most frequent throat colours in adult lizards. Similar UV^+ white coloration is found in the belly (but not the throat) of many females from eastern Pyrenees suggesting that, in these populations, females may retain the newborn coloration in their bellies through adulthood (**Figs. 2**, 4, and Fig. 2 in Pérez i de Lanuza and Font 2015). Elsewhere we have argued the need to determine a reliable cut-off point for adult morph expression (which may vary across populations; Pérez i de Lanuza et al. 2013a; Abalos et al. 2020). Based on our results, we suggest that decreased UV reflectance should be used to identify adult morph expression among white subadult lizards in future studies focusing on *P. muralis* ventral colour variation.

Our results suggest that the ontogeny of UV-blue patches in the OVS is delayed with respect to colour changes in the throat and in the belly. Within-individual contrasts suggest that OCCs to UV-blue colour are perceptible to conspecifics, and more apparent in males than in females. However, almost a year after hatching, yearling UV-blue patches can still be chromatically discriminated by conspecifics from the colours exhibited by adults. Notably, UV-reflecting patches in the OVS undergo the most dramatic OCC possible, shifting their reflectance from peaking around the maximum range of lacertid sensitivity in the long wavelength band to peaking around the range's minimum in the UV wavelength band (Pérez i de Lanuza et al. 2014; Martin et al. 2015a; 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 valley 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. Future studies should confirm the observed delay in the ontogeny of UV-blue patches with respect to throat coloration, as well as explore its biological causes and consequences.

Here, we did not test for possible adaptive explanations for the ventral and ventrolateral OCC described in *P. muralis*, which could represent a nonfunctional by-product of chromatophore maturation (Bagnara et al. 2007; Umbers 2013). Studies on OCC 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. 2015a, b, 2016; Murali et al. 2018). However, a function in predator avoidance seems implausible given that OCCs in ventral and ventrolateral coloration are unlikely to be noticed by avian predators, which typically approach 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 oriented toward the substrate (Pérez i de Lanuza et al. 2016a). With rising body temperature and during social interactions, lizards shift their postures to reorient their ventral and ventrolateral scales, making them visible to observers positioned parallel 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 that the UV+ white coloration is mostly restricted to juveniles and distinct from the colours predominantly found in adults, we deem reasonable to suggest that OCCs affecting ventral and ventrolateral coloration could influence social interactions by revealing the juvenile status of lizards that have not yet developed adult full-blown coloration (Booth 1990; Fresnillo et al. 2015b; Yang et al. 2023; Zhang et al. 2023).

A wealth of studies have shown that lizards often inhabit dense populations where navigating a complex social environment is essential for their fitness (Edsman 1990; Stamps and Krishnan 1994, 1995, 1998; Tokarz 1995; Font et al. 2012; Whiting and While 2017). One way in which lizards assess potential rivals and mates is through evolved traits —shared by all senders— that enable comparison of relatively stable aspects of the senders' intrinsic quality (i.e. signalling) (Stapley and Whiting 2006; Weiss 2006; Pérez i de Lanuza et al. 2014; Baeckens et al. 2018; Ligon and McGraw 2018). In addition, lizards are able to discriminate among conspecifics and associate relevant information obtained in previous interactions with each specific social partner (i.e. social recognition) (Olsson 1994; Léna et al. 1998; Olsson and Shine 1998; Whiting 1999; Van Dyk and Evans 2007; Carazo et al. 2008; Whiting and While 2017). Aggression between males often plays a crucial role shaping social traits in lizards, particularly in territorial species (Calsbeek and Sinervo 2002; Baird 2013; Whiting and Miles 2019). Visual signals (including colour patches) have often found to play a role mediating aggression in intrasexual confrontations (Stapley and Whiting 2006; Stuart-Fox et al. 2006; Baird 2013; Olsson et al. 2013). In lacertid lizards, sexual dichromatism is positively associated with body size dimorphism, suggesting that conspicuous male coloration evolved to improve opponent assessment during intrasexual contests (Pérez i de Lanuza et al. 2013b; Fleishman and Font 2019). There are compelling reasons to believe that lacertid ventral and ventrolateral coloration may play a role in male-male competition. For instance, the spectral properties of lacertid UV-blue patches are tuned to conspecific vision (Marshall and Stevens 2014), males can control their visibility through posture (Pérez i de Lanuza et al. 2016a), and higher UV chroma and UV-biased hues correlate with bite force and body condition (Pérez i de Lanuza et al. 2014; Badiane and Font 2021). Although several studies have failed to find a quantitative relationship between contest outcome and UV-blue patches in lacertids (Martin et al. 2015b; Abalos et al. 2016, 2024; Names et al. 2019; Kawamoto et al. 2021), there is experimental evidence suggesting that signal suppression reduces received aggression (López et al. 2004; Kawamoto et al. 2021). 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 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). Our finding of an ontogenetic decline in the proportion of lizards showing UV$^+$ white coloration in their ventral and ventrolateral scales suggests that this colour may act as a social signal conveying information about the sender's young age and sexual immaturity (Booth 1990; Ligon and Hill 2013; Herberstein 2020). Infant-specific coloration has been found to reduce aggression from adult conspecifics in some 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. 2015b). 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 (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 nuanced 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). An additional point to consider is that *P. muralis* juveniles from Eastern Pyrenees display much duller tail coloration compared to the bright blue-green tails that are temporarily exhibited by juveniles in many congeneric species (*pers. obs.*). Although this trait is thought to function mainly in the context of predator avoidance (Castilla et al. 1999; Bateman and Fleming 2009; Ortega et al. 2014), in its absence adults have one less obvious cue to assess the age of juveniles (Grether et al. 2004).

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 territorial defence by showing attenuated aggression towards known neighbours, while still aggressively confronting unfamiliar intruders (Qualls and Jaeger 1991; Husak and Fox 2003; Osborne 2005; Baird 2013; Whiting and Miles 2019). In wall lizards, males have been shown to discriminate between familiar rivals with similar characteristics solely based on their scent marks, which allows them to allocate their aggressive behaviour according to the level of threat posed by each individual rival (López and Martín 2002; Carazo et al. 2008; Font et al. 2012). Given the sophistication of their visual system, akin to that found in other diurnal lizards, it seems plausible that wall lizards may also use visual cues for social recognition (Font et al. 2012; Pérez i de Lanuza and Font 2014b; Fleishman and Font 2019). Throat colour pattern has been found to mediate rival recognition (familiar/unfamiliar) in the tawny dragon *Ctenophorus decresii* (Osborne et al. 2012), and studies in other taxa which heavily rely on chemoreception demonstrate that visual cues can be just as crucial as chemical cues for true individual recognition (Tibbetts 2002; Sheehan and Tibbetts 2010; Gokcekus et al. 2021). Few studies have examined the effect of social recognition in intersexual interactions in lizards (e.g. Font and Desfilis 2002; Leu et al. 2015; Bordogna et al. 2016), yet behavioural evidence suggest that OCCs in adult coloration could also have an impact in this context. In *P. muralis,* ventral colour seems to be involved in the formation of lasting male-female pair bonds in natural populations (Pérez i de Lanuza et al. 2013a, 2016b; Aguilar et al. 2022a), an understudied behaviour often interpreted as mate-guarding and/or a deterrent of male harassment (in Den Bosch and Zandee 2001; Zaldívar-Rae and Drummond 2007; Olsson et al. 2019; Abalos et al. 2020). Colour variation among the average orange, white, and yellow ventral colours is likely discrete to conspecifics, however, there remains substantial chromatic and achromatic variation which could play a functionally relevant role in social recognition (Martin et al. 2015a; 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 — thus facilitating social recognition—becomes increasingly advantageous with age (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 that are perceptible by conspecifics. Our observation that hatchlings show a characteristic UV$^+$ white coloration (that differs from every adult throat colour) corrects a common misconception about the ontogeny of *P. muralis* colour morphs that is likely extensible to other *Podarcis* species. A host of questions remain unanswered. Detailed descriptions of OCCs affecting patch size, patterning, or integration with melanin-based patches should be tackled in future studies, as well as the cellular basis underlying the ontogenetic shift from UV$^+$ white to UV$^-$ white coloration in adults (Sheehan et al. 2017; Pérez-Rodríguez et al. 2017; Zhang et al. 2023). Altogether, our results highlight the importance of considering receiver perspective when studying animal coloration in an ecological context (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.

References

Abalos J, i de Lanuza GP, Bartolomé A, et al (2021) Viability, behavior, and colour expression in the offspring of matings between common wall lizard *Podarcis muralis* colour morphs. Curr Zool 1–15. https://doi.org/10.1093/cz/zoab039

Abalos J, Pérez i de Lanuza G, Bartolomé A, et al (2024) Behavioral threat and appeasement signals take precedence over static colors in lizard contests. Behav Ecol 35:. https://doi.org/10.1093/beheco/arae045

Abalos J, Pérez i de Lanuza G, Bartolomé A, et al (2020) No evidence for differential sociosexual behavior and space use in the color morphs of the European common wall lizard (Podarcis muralis). Ecol Evol 00:1–20. https://doi.org/10.1002/ece3.6659

Abalos J, Pérez i de Lanuza G, Carazo P, Font E (2016) The role of male coloration in the outcome of staged contests in the European common wall lizard (Podarcis muralis). Behaviour 153:607–631. https://doi.org/10.1163/1568539X-00003366

Abramjan A, Bauerová A, Somerová B, Frynta D (2015) Why is the tongue of blue-tongued skinks blue? Reflectance of lingual surface and its consequences for visual perception by conspecifics and predators. Sci Nat 102:. https://doi.org/10.1007/s00114-015-1293-4

Aguilar P, Andrade P, Afonso S, et al (2022a) No genomic repercussions of assortative pairing in a colour polymorphic lizard. J Evol Biol 35:648–656. https://doi.org/10.1111/jeb.13990

Aguilar P, Andrade P, Pérez I De Lanuza G (2022b) Epistatic interactions between pterin and carotenoid genes modulate intra-morph color variation in a lizard. Integr Zool 17:44–53. https://doi.org/10.1111/1749-4877.12570

Aguilar P, Pérez i de Lanuza G, Carneiro M, et al (2024) The role of historical biogeography in shaping colour morph diversity in the common wall lizard. Mol Ecol 33:e17338. https://doi.org/10.1111/MEC.17338

Anderson MJ (2014) Permutational Multivariate Analysis of Variance (PERMANOVA). Wiley StatsRef Stat Ref Online 1–15. https://doi.org/10.1002/9781118445112.stat07841

Andrade P, Pinho C, de Lanuza GP i., et al (2019) Regulatory changes in pterin and carotenoid genes underlie balanced color polymorphisms in the wall lizard. Proc Natl Acad Sci U S A 116:5633–5642. https://doi.org/10.1073/pnas.1820320116

Andrade P, Pinho C, de Lanuza GP i., et al (2018) Regulatory Changes in Pterin and Carotenoid Genes Underlie Balanced Color Polymorphisms in the Wall Lizard. bioRxiv. https://doi.org/10.1101/481895

Arnold EN, Arribas O, Carranza S (2007) Systematics of the Palaearctic and Oriental lizard tribe Lacertini

Arnqvist G, Rowe L (2005) Sexual conflict. Princeton university press

Badiane A, Carazo P, Price-Rees SJ, et al (2018) Why blue tongue? A potential UV-based deimatic display in a lizard. Behav Ecol Sociobiol 72:1–11. https://doi.org/10.1007/s00265-018-2512-8

Badiane A, Font E (2021) Information content of ultraviolet - reflecting colour patches and visual perception of body coloration in the Tyrrhenian wall lizard Podarcis tiliguerta. Behav Ecol Sociobiol 1–15. https://doi.org/10.1007/s00265-021-03023-2

Badiane A, Pérez i de Lanuza G, García-Custodio M del C, et al (2017) Colour patch size and measurement error using reflectance spectrophotometry. Methods Ecol Evol 8:1585–1593. https://doi.org/10.1111/2041-210X.12801

Baeckens S, Martín J, García-Roa R, Van Damme R (2018) Sexual selection and the chemical signal design of lacertid lizards. Zool J Linn Soc 183:445–457. https://doi.org/10.1093/zoolinnean/zlx075

Bagnara JT, Fernandez PJ, Fujii R (2007) On the blue coloration of vertebrates. Pigment Cell Res 20:14–26. https://doi.org/10.1111/j.1600-0749.2006.00360.x

Baird TA (2013) Lizards and other reptiles as model systems for the study of contest behaviour. In: Hardy ICW, Briffa M (eds) Animal Contests. Cambridge University Press, Cambridge, pp 258–286

Barbault R, Mou YP (1986) A Population Analysis of the Common Wall Lizard Podarcis muralis in Southwestern France. Stud Herpetol Rocek Z (ed) 513–518

Barbosa D, Font E, Desfilis E, Carretero MA (2006) Chemically mediated species recognition in closely related Podarcis wall lizards. J Chem Ecol 32:1587–1598. https://doi.org/10.1007/s10886-006-9072-5

Bateman PW, Fleming PA (2009) To cut a long tail short: A review of lizard caudal autotomy studies carried out over the last 20 years. J Zool 277:1–14. https://doi.org/10.1111/j.1469-7998.2008.00484.x

Bergman TJ, Sheehan MJ (2013) Social knowledge and signals in primates. Am J Primatol 75:683–694. https://doi.org/10.1002/ajp.22103

Blas J, Cabezas S, Figuerola J, et al (2013) Carotenoids and Skin Coloration in a Social Raptor. J Raptor Res 47:174–184. https://doi.org/10.3356/JRR-12-46.1

Booth CL (1990) Evolutionary significance of ontogenetic colour change in animals. Biol J Linn Soc 40:125–163. https://doi.org/10.1111/j.1095-8312.1990.tb01973.x

Bordogna G, Cunningham G, Fitzpatrick LJ, et al (2016) An experimental test of relatedness-based mate discrimination in a social lizard. Behav Ecol Sociobiol 70:2139–2147

Bradbury JW, Vehrencamp SL (2011) Principles of Animal Communication, 2nd edn. Sinauer Associates, Sunderland (MA)

Brock KM, Chelini MC, Ayton C, et al (2022) Colour morph predicts social behaviour and contest outcomes in a polymorphic lizard (Podarcis erhardii). Anim Behav 191:91–103. https://doi.org/10.1016/j.anbehav.2022.06.017

Brock KM, McTavish EJ, Edwards DL (2020) Color polymorphism is a driver of diversification in the lizard family Lacertidae. bioRxiv 2020.08.27.270207. https://doi.org/10.1101/2020.08.27.270207

Brown RM, Gist DH, Taylor DH (1995) Home range ecology of an introduced population of the European wall lizard Podarcis muralis (Lacertilia; Lacertidae) in Cincinnati, Ohio. Am Midl Nat 344–359

Buckman D (1985) Color change in insects. In: Bagnara J, Klaus SN, Paul E, Schartl M (eds) Pigment Cell. University of Tokyo Press, Tokyo, pp 209–217

Calsbeek B, Hasselquist D, Clobert J (2010) Multivariate phenotypes and the potential for alternative phenotypic optima in wall lizard (*Podarcis muralis*) ventral colour morphs. J Evol Biol 23:1138–1147. https://doi.org/10.1111/j.1420-9101.2010.01978.x

Calsbeek R, Sinervo B (2002) An experimental test of the ideal despotic distribution. J Anim Ecol 71:513–523. https://doi.org/10.1046/j.1365-2656.2002.00619.x

Carazo P, Font E, Desfilis E (2008) Beyond “nasty neighbours” and “dear enemies”? Individual recognition by scent marks in a lizard (*Podarcis hispanica*). Anim Behav 76:1953–1963. https://doi.org/10.1016/j.anbehav.2008.08.018

Carazo P, Font E, Desfilis E (2011) The role of scent marks in female choice of territories and refuges in a lizard (Podarcis hispanica). J Comp Psychol 125:362–365. https://doi.org/10.1037/a0023404

Caro T, Stankowich T, Mesnick SL, et al (2012) Pelage coloration in pinnipeds: functional considerations. Behav Ecol 23:765–774. https://doi.org/10.1093/BEHECO/ARS025

Castilla AM., Gosá A, Galán P, Pérez-Mellado V (1999) Green Tails in Lizards of the Genus Podarcis : Do They Influence the Intensity of Predation ? Herpe 55:530–537. https://doi.org/https://www.jstor.org/stable/3893319

Caves EM, Nowicki S, Johnsen S (2019) Von uexküll revisited: Addressing human biases in the study of animal perception. Integr Comp Biol 59:1451–1462. https://doi.org/10.1093/icb/icz073

Clark DR, Hall RJ (1970) Function of the blue tail coloration of the five-lined skink *Eumeces fasciatus*. Herpetologica 26:271–274

Cordero A, Carbone SS, Utzeri C (1998) Mating opportunities and mating costs are reduced in androchrome female damselflies, *Ischnura elegans* (Odonata). Anim Behav 55:185–197. https://doi.org/10.1006/anbe.1997.0603

Cronin TW, Bok MJ (2016) Photoreception and vision in the ultraviolet. J Exp Biol 219:2790–2801. https://doi.org/10.1242/jeb.128769

Cuadrado M (2006) Mate guarding and social mating system in male common chameleons (*Chamaeleo chamaeleon*). J Zool 255:425–435. https://doi.org/10.1017/S0952836901001510

de la Cruz F, Pérez i de Lanuza G, Font E (2023) Signalling on islands : the case of Lilford ' s wall lizard (Podarcis lilfordi gigliolii) from Dragonera. Biol J Linn Soc 138:1–20. https://doi.org/https://doi.org/10.1093/biolinnean/blac152

Detto T, Hemmi JM, Backwell PRY (2008) Colouration and Colour Changes of the Fiddler Crab, Uca capricornis: A Descriptive Study. PLoS One 3:e1629. https://doi.org/10.1371/JOURNAL.PONE.0001629

Eberhard WG, Cordero C (2003) Sexual conflict and female choice. Trends Ecol Evol 18:438–439. https://doi.org/10.1016/S0169-5347(03)00180-0

Edsman L (2001) Female mate choice of male characteristics and resources in the wall lizard. In: Vicente L, Crespo EG (eds) Mediterranean basin lizards: a biological approach. Instituto de Conservaçao da Natureza, Lisboa, pp 133–134

Edsman L (1990) Territoriality and competition in wall lizards. Dept. of Zool., Univ. of Stockholm

Edward DA, Chapman T (2011) The evolution and significance of male mate choice. Trends Ecol Evol 26:647–654

Ekner A, Sajkowska Z, Dudek K, Tryjanowski P (2011) Medical cautery units as a permanent and non-invasive method of marking lizards. Acta Herpetol 6:229–236. https://doi.org/10.13128/Acta_Herpetol-9346

Endler JA (1990) On the measurement and classification of colour in studies of animal colour patterns. Biol J Linn Soc 41:315–352. https://doi.org/10.1111/j.1095-8312.1990.tb00839.x

Endler JA, Kemp DJ, Reznick DN, et al (2023) How to generate and test hypotheses about colour : insights from half a century of guppy research

Escoriza D (2024) Environmental colour pattern variation in Mediterranean Podarcis. 1–8

Fleishman LJ, Font E (2019) Sensory Processing in Relation to Signaling Behavior

Font E, Barbosa D, Sampedro C, Carazo P (2012) Social behavior, chemical communication, and adult neurogenesis: Studies of scent mark function in Podarcis wall lizards. Gen Comp Endocrinol 177:9–17. https://doi.org/10.1016/j.ygcen.2012.02.015

Font E, Carazo P (2010) Animals in translation: Why there is meaning (but probably no message) in animal communication. Anim Behav 80:e1–e6. https://doi.org/10.1016/j.anbehav.2010.05.015

Font E, Desfilis E (2002) Chemosensory recognition of familiar and unfamiliar conspecifics by juveniles of the Iberian wall lizard *Podarcis hispanica*. Ethology 108:319–330. https://doi.org/10.1046/j.1439-0310.2002.00782.x

Font E, Pérez i de Lanuza G, Sampedro C (2009) Ultraviolet reflectance and cryptic sexual dichromatism in the ocellated lizard, Lacerta (Timon) lepida (Squamata: Lacertidae). Biol J Linn Soc 97:766–780. https://doi.org/10.1111/j.1095-8312.2009.01251.x

Frédérich B, Mills SC, Denoël M, et al (2010) Colour differentiation in a coral reef fish throughout ontogeny: habitat background and flexibility. Aquat Biol 9:271–277

Fresnillo B, Belliure J, Cuervo JJ (2015a) Red tails are effective decoys for avian predators. Evol Ecol 29:123–135. https://doi.org/10.1007/S10682-014-9739-2/TABLES/2

Fresnillo B, Belliure J, Cuervo JJ (2015b) Red coloration in juvenile spiny-footed lizards, Acanthodactylus erythrurus, reduces adult aggression. Anim Behav 102:59–67. https://doi.org/10.1016/j.anbehav.2015.01.004

Fresnillo B, Belliure J, Cuervo JJ (2016) Ontogenetic shifts in risk behaviours are related to body size and coloration in spiny-footed lizards. Anim Behav 119:165–172. https://doi.org/10.1016/J.ANBEHAV.2016.07.009

Galeotti P, Sacchi R, Pellitteri-Rosa D, et al (2013) Colour polymorphism and alternative breeding strategies:effects of parent’s colour morph on fitness traits in the common wall lizard. Evol Biol 40:385–394. https://doi.org/10.1007/s11692-012-9222-3

Gokcekus S, Firth JA, Regan C, Sheldon BC (2021) Recognising the key role of individual recognition in social networks. Trends Ecol Evol 36:1024–1035. https://doi.org/10.1016/j.tree.2021.06.009

Gosá A (1987) Observaciones sobre el colorido y diseño en poblaciones ibéricas de lagartija roquera, *Podarcis muralis* (Laurenti, 1768). Rev Española Herpetol 2:7–27

Grant JB (2007) Ontogenetic colour change and the evolution of aposematism: A case study in panic moth caterpillars. J Anim Ecol 76:439–447. https://doi.org/10.1111/j.1365-2656.2007.01216.x

Grether GF, Kolluru GR, Nersissian K (2004) Individual colour patches as multicomponent signals. Biol. Rev. Camb. Philos. Soc. 79:583–610

Hawkins GL, Hill GE, Mercadante A (2012) Delayed plumage maturation and delayed reproductive investment in birds. Biol Rev 87:257–274. https://doi.org/10.1111/J.1469-185X.2011.00193.X

Hawlena D (2009) Colorful tails fade when lizards adopt less risky behaviors. Behav Ecol Sociobiol 64:205–213. https://doi.org/10.1007/s00265-009-0837-z

Hawlena D, Boochnik R, Abramsky Z, Bouskila A (2006) Blue tail and striped body: why do lizards change their infant costume when growing up? Behav Ecol 17:889–896. https://doi.org/10.1093/BEHECO/ARL023

Heathcote RJP, Dawson DA, Uller T (2014) Characterisation of nine European wall lizard (*Podarcis muralis*) microsatellite loci of utility across sub-species. Conserv. Genet. Resour. 7:85–87

Hedrick PW (1982) Hitchhiking: A New Factor in Evolution ? Bioscience 32:845–848

Hendershott R, Hu G, Groves C, Behie A (2019) Natal-to-juvenile pelage change in free-living François' (Trachypithecus francoisi) and Cat Ba langurs (T. poliocephalus). Vietnamese J Primatol 3:55–69

Herberstein ME (2020) Ontogenetic colour change signals sexual maturity in a non - territorial damselfly Md Kawsar Khan. 51–58. https://doi.org/10.1111/eth.12959

Hill GE (1989) Late spring arrival and dull nuptial plumage: aggression avoidance by yearling males? Anim Behav 37:665–673. https://doi.org/10.1016/0003-3472(89)90045-6

Hoppe DM (2018) The influence of color on behavioral thermoregulation and hydroregulation. Behav significance Color 35–74

Husak JF, Fox SF (2003) Adult male collared lizards, *Crotaphytus collaris*, increase aggression towards displaced neighbours. Anim Behav 65:391–396. https://doi.org/10.1006/anbe.2003.2058

Huyghe K, Vanhooydonck B, Herrel A, et al (2007) Morphology, performance, behavior and ecology of three color morphs in males of the lizard *Podarcis melisellensis*. Integr Comp Biol 47:211–220. https://doi.org/10.1093/icb/icm043

in Den Bosch HAJ, Zandee M (2001) Courtship behaviour in lacertid lizards: phylogenetic interpretations of the *Lacerta kulzeri* complex (Reptilia: Lacertidae). Netherlands J Zool 51:263–284

Kawamoto A, Le Galliard JF, Badiane A (2021) The role of social costs as a mechanism enforcing the honesty of ultraviolet-reflecting signals in a lizard. Biol J Linn Soc 133:1126–1138. https://doi.org/10.1093/biolinnean/blab008

Kemp DJ, Herberstein ME, Fleishman LJ, et al (2015) An integrative framework for the appraisal of coloration in nature. Am Nat 185:705–724. https://doi.org/10.1086/681021

Kettlewell HBD (1955) Selection experiments on industrial melanism in the Lepidoptera. Heredity (Edinb) 9:323–342. https://doi.org/10.1038/hdy.1955.36

Kim Y, Stephan W (2000) Joint Effects of Genetic Hitchhiking and Background Selection on Neutral Variation. Genetics 155:1415–1427. https://doi.org/10.1093/GENETICS/155.3.1415

Kitzler G (1941) Die Paarungsbiologie einiger Eidechsen. Z Tierpsychol 353–402

Le Galliard J-F, Cote J, Fitze PS (2008) Lifetime and intergenerational fitness consequences of harmful male interactions for female lizards. Ecology 89:56–64

Léna JP, de Fraipont M, Léna JP (1998) Kin recognition in the common lizard. Behav Ecol Sociobiol 42:341–347

Leu ST, Burzacott D, Whiting MJ, Bull CM (2015) Mate Familiarity Affects Pairing Behaviour in a Long-Term Monogamous Lizard: Evidence from Detailed Bio-Logging and a 31-Year Field Study. Ethology 121:760–768. https://doi.org/10.1111/eth.12390

Ligon RA, Hill GE (2013) Is the juvenal plumage of altricial songbirds an honest signal of age ? Evidence from a comparative study of thrushes (Passeriformes : Turdidae). 51:64–71. https://doi.org/10.1111/j.1439-0469.2012.00668.x

Ligon RA, McGraw KJ (2018) A chorus of color: Hierarchical and graded information content of rapid color change signals in chameleons. Behav Ecol 29:1075–1087. https://doi.org/10.1093/beheco/ary076

López P, Martín J (2002) Chemical rival recognition decreases aggression levels in male Iberian wall lizards, Podarcis hispanica. Behav Ecol Sociobiol 51:461–465. https://doi.org/10.1007/s00265-001-0447-x

López P, Martín J, Cuadrado M (2004) The role of lateral blue spots in intrasexual relationships between male Iberian rock-lizards, Lacerta monticola. Ethology 110:543–561. https://doi.org/10.1111/j.1439-0310.2004.00996.x

Maia R, Gruson H, Endler JA, White TE (2019) pavo 2: New tools for the spectral and spatial analysis of colour in r. Methods Ecol Evol 10:1097–1107. https://doi.org/10.1111/2041-210X.13174

Majerus MEN (2008) Industrial Melanism in the Peppered Moth, Biston betularia: An Excellent Teaching Example of Darwinian Evolution in Action. Evol Educ Outreach 2:63–74. https://doi.org/10.1007/s12052-008-0107-y

Mangiacotti M, Pezzi S, Fumagalli M, et al (2019) Seasonal Variations in Femoral Gland Secretions Reveals some Unexpected Correlations Between Protein and Lipid Components in a Lacertid Lizard. J Chem Ecol 45:673–683. https://doi.org/10.1007/s10886-019-01092-2

Marshall KLA, Philpot KE, Damas-Moreira I, Stevens M (2015) Intraspecific colour variation among lizards in distinct island environments enhances local camouflage. PLoS One 10:1–20. https://doi.org/10.1371/journal.pone.0135241

Marshall KLA, Philpot KE, Stevens M (2016) Microhabitat choice in island lizards enhances camouflage against avian predators. Sci Rep 6:1–10. https://doi.org/10.1038/srep19815

Marshall KLA, Stevens M (2014) Wall lizards display conspicuous signals to conspecifics and reduce detection by avian predators. Behav Ecol 25:1325–1337. https://doi.org/10.1093/beheco/aru126

Martín J, Forsman A (1999) Social costs and development of nuptial coloration in male Psammodromus algirus lizards: An experiment. Behav Ecol 10:396–400. https://doi.org/10.1093/beheco/10.4.396

Martin M, Le Galliard JF, Meylan S, Loew ER (2015a) The importance of ultraviolet and near-infrared sensitivity for visual discrimination in two species of lacertid lizards. J Exp Biol 218:458–465. https://doi.org/10.1242/jeb.115923

Martin M, Meylan S, Perret S, Le Galliard JF (2015b) UV coloration influences spatial dominance but not agonistic behaviors in male wall lizards. Behav Ecol Sociobiol 69:1483–1491. https://doi.org/10.1007/s00265-015-1960-7

Martinez Arbizu P (2017) pairwiseAdonis: Pairwise multilevel comparison using adonis. R Packag version 1:

Medina I, Vega-Trejo R, Wallenius T, et al (2020) From cryptic to colorful: Evolutionary decoupling of larval and adult color in butterflies. Evol Lett 4:34–43. https://doi.org/10.1002/EVL3.149

Miñano MR, While GM, Yang W, et al (2021) Climate shapes the geographic distribution and introgressive spread of color ornamentation in common wall lizards. Am Nat. https://doi.org/10.1086/715186

Murali G, Merilaita S, Kodandaramaiah U (2018) Grab my tail: evolution of dazzle stripes and colourful tails in lizards. J Evol Biol 31:1675–1688

Names G, Martin M, Badiane A, Le Galliard JF (2019) The relative importance of body size and UV coloration in influencing male-male competition in a lacertid lizard. Behav Ecol Sociobiol 73:. https://doi.org/10.1007/s00265-019-2710-z

Natusch DJD, Lyons JA (2012) Relationships between ontogenetic changes in prey selection, head shape, sexual maturity, and colour in an Australasian python (Morelia viridis). Biol J Linn Soc 107:269–276. https://doi.org/10.1111/J.1095-8312.2012.01941.X

Noble GK, Bradley HT (1933) The mating behavior of lizards; its bearing on the theory of sexual selection. Ann N Y Acad Sci 35:25–100. https://doi.org/10.1111/j.1749-6632.1933.tb55365.x

Nokelainen O, Maynes R, Mynott S, et al (2019) Improved camouflage through ontogenetic colour change confers reduced detection risk in shore crabs. Funct Ecol 33:654–669. https://doi.org/10.1111/1365-2435.13280/SUPPINFO

Nyboer EA, Gray SM, Chapman LJ (2014) A colourful youth: Ontogenetic colour change is habitat specific in the invasive Nile perch. Hydrobiologia 738:221–234. https://doi.org/10.1007/S10750-014-1961-Y/FIGURES/4

O'Shea M (2021) Lizards of the World: A Guide to Every Family. Princeton University Press

Ochi H, Awata S (2016) Resembling the Juvenile Colour of Host Cichlid Facilitates Access of the Guest Cichlid to Host Territory Author (s): Haruki Ochi and Satoshi Awata Published by : Brill Stable URL : http://www.jstor.org/stable/40296094 REFERENCES Linked references are av. 146:741–756

Oksanen AJ, Blanchet FG, Friendly M, et al (2016) Vegan: community ecology package. R Packag version 2.0:321–326

Olsson M (1994) Rival recognition affects male contest behavior in sand lizards (*Lacerta agilis*). Behav Ecol Sociobiol 35:249–252. https://doi.org/10.1007/BF00170705

Olsson M, Schwartz TS, Wapstra E, Shine R (2019) How accurately do behavioural observations predict reproductive success in free-ranging lizards? Biol Lett 15:. https://doi.org/10.1098/rsbl.2019.0030

Olsson M, Shine R (1998) Chemosensory mate recognition may facilitate prolonged mate guarding by male snow skinks, Niveoscincus microlepidotus. Behav Ecol Sociobiol 43:359–363

Olsson M, Stuart-Fox D, Ballen C (2013) Genetics and evolution of colour patterns in reptiles. Semin Cell Dev Biol 24:529–541. https://doi.org/10.1016/j.semcdb.2013.04.001

Ortega J, López P, Martín J (2014) Conspicuous blue tails, dorsal pattern morphs and escape behaviour in hatchling Iberian wall lizards (Podarcis hispanicus). Biol J Linn Soc 113:1094–1106

Ortega J, Martín J, Crochet PA, et al (2019) Seasonal and interpopulational phenotypic variation in morphology and sexual signals of Podarcis liolepis lizards. PLoS One 14:1–25. https://doi.org/10.1371/journal.pone.0211686

Osborne L (2005) Rival recognition in the territorial tawny dragon (Ctenophorus decresii). Acta Ethol 8:45–50. https://doi.org/10.1007/s10211-005-0108-6

Osborne L, Umbers KDL, Backwell PRY, Keogh JS (2012) Male tawny dragons use throat patterns to recognize rivals. Naturwissenschaften 99:869–872. https://doi.org/10.1007/s00114-012-0968-3

Pérez-Rodríguez L, Jovani R, Stevens M (2017) Shape matters: Animal colour patterns as signals of individual quality. Proc. R. Soc. B Biol. Sci. 284

Pérez i de Lanuza G, Abalos J, Bartolomé A, Font E (2018) Through the eye of a lizard: hue discrimination in a lizard with ventral polymorphic coloration. J Exp Biol 221:jeb.169565. https://doi.org/10.1242/jeb.169565

Pérez i de Lanuza G, Bellati A, Pellitteri-Rosa D, et al (2019) Colour variation between different lineages of a colour polymorphic lizard. J Zool 308:175–187. https://doi.org/10.1111/jzo.12658

Pérez i de Lanuza G, Carazo P, Font E (2014) Colours of quality: Structural (but not pigment) coloration informs about male quality in a polychromatic lizard. Anim Behav 90:73–81. https://doi.org/10.1016/j.anbehav.2014.01.017

Pérez i de Lanuza G, Carretero MA, Font E (2017) Intensity of male-male competition predicts morph diversity in a color polymorphic lizard. Evolution (N Y) 71:1832–1840. https://doi.org/10.1111/evo.13256

Pérez i de Lanuza G, Carretero MÁ, Font E (2016a) Thermal dependence of signalling: do polymorphic wall lizards compensate for morph-specific differences in conspicuousness? Behav Ecol Sociobiol 70:1151–1159. https://doi.org/10.1007/s00265-016-2123-1

Pérez i de Lanuza G, Font E (2014a) Ultraviolet vision in lacertid lizards: evidence from retinal structure, eye transmittance, SWS1 visual pigment genes and behaviour. J Exp Biol 217:2899–909. https://doi.org/10.1242/jeb.104281

Pérez i de Lanuza G, Font E (2015) Differences in conspicuousness between alternative color morphs in a polychromatic lizard. Behav Ecol 26:1432–1446. https://doi.org/10.1093/beheco/arv075

Pérez i de Lanuza G, Font E (2014b) Ultraviolet vision in lacertid lizards: evidence from retinal structure, eye transmittance, SWS1 visual pigment genes and behaviour. J Exp Biol 217:2899–909. https://doi.org/10.1242/jeb.104281

Pérez i de Lanuza G, Font E, Carazo P (2013a) Color-assortative mating in a color-polymorphic lacertid lizard. Behav Ecol 24:273–279. https://doi.org/10.1093/beheco/ars164

Pérez i de Lanuza G, Font E, Carretero MÁ (2016b) Colour assortative pairing in a colour polymorphic lizard is independent of population morph diversity. Sci Nat 103:82. https://doi.org/10.1007/s00114-016-1407-7

Pérez i de Lanuza G, Font E, Monterde JL (2013b) Using visual modelling to study the evolution of lizard coloration: Sexual selection drives the evolution of sexual dichromatism in lacertids. J Evol Biol 26:1826–1835. https://doi.org/10.1111/jeb.12185

Qualls CP, Jaeger RG (1991) Dear enemy recognition in *Anolis carolinenis*. J Herpetol 25:361. https://doi.org/10.2307/1564599

R Development Core Team (2017) R: A Language and Environment for Statistical Computing

Rankin KJ, McLean CA, Kemp DJ, Stuart-Fox D (2016) The genetic basis of discrete and quantitative colour variation in the polymorphic lizard, *Ctenophorus decresii*. BMC Evol Biol 16:179. https://doi.org/10.1186/s12862-016-0757-2

Rivas JA, Burghardt GM (2002) Crotalomoprhism: A metaphor to understand anthropomorfism by omission. In: Bekoff M, Colin A, Burghardt GM (eds) The cognitive animal: empirical and theoretical perspectives on animal cognition. MIT Press, Cambridge, pp 9–17

Roucurt Cezário R, Moreira Therézio E, Marletta A, et al (2022) Ontogenetic colour change of a sexual ornament in males of a damselfly: female mimicry, crypsis or both? Sci Nat 109:2. https://doi.org/10.1007/s00114-021-01775-5

Ruell EW, Handelsman CA, Hawkins CL, et al (2013) Fear, food and sexual ornamentation: plasticity of colour development in Trinidadian guppies. Proc R Soc B Biol Sci 280:. https://doi.org/10.1098/RSPB.2012.2019

Runemark A, Hansson B, Pafilis P, et al (2010) Island biology and morphological divergence of the Skyros wall lizard *Podarcis gaigeae*: a combined role for local selection and genetic drift on color morph frequency divergence? BMC Evol Biol 10:269. https://doi.org/10.1186/1471-2148-10-269

Sacchi R, Coladonato AJ, Battaiola M, et al (2021) Subjective resource value affects aggressive behavior independently of resource-holding-potential and color morphs in male common wall lizard. J Ethol 39:179–189. https://doi.org/10.1007/s10164-021-00690-6

Sacchi R, Ghitti M, Scali S, et al (2015) Common wall lizard females (*Podarcis muralis*) do not actively choose males based on their colour morph. Ethology 121:1145–1153. https://doi.org/10.1111/eth.12431

Sacchi R, Pellitteri-Rosa D, Bellati A, et al (2013) Colour variation in the polymorphic common wall lizard (*Podarcis muralis*): An analysis using the RGB colour system. Zool Anzeiger - A J Comp Zool 252:431–439. https://doi.org/10.1016/J.JCZ.2013.03.001

Sacchi R, Pupin F, Gentilli A, et al (2009) Male-male combats in a polymorphic lizard: Residency and size, but not color, affect fighting rules and contest outcome. Aggress Behav 35:274–283. https://doi.org/10.1002/ab.20305

Sacchi R, Scali S, Pupin F, et al (2007) Microgeographic variation of colour morph frequency and biometry of common wall lizards. 273:389–396. https://doi.org/10.1111/j.1469-7998.2007.00342.x

Salvador A (2014) Reptiles, 2ª edición revisada y aumentada. Fauna Ibérica 10:

San-Jose LM, Roulin A (2018) Toward understanding the repeated occurrence of associations between melanin-based coloration and multiple phenotypes. Am Nat 192:111–130. https://doi.org/10.1086/698010

Santiago C, Green NF, Hamilton N, et al (2020) Does conspicuousness scale linearly with colour distance? A test using reef fish: Detectability of suprathreshold colours. Proc R Soc B Biol Sci 287:. https://doi.org/10.1098/rspb.2020.1456

Schaller GE (1963) The mountain gorilla: Ecology and behavior.

Sheehan MJ, Bergman TJ (2016) Is there an evolutionary trade-off between quality signaling and social recognition? Behav Ecol 27:2–13. https://doi.org/10.1093/beheco/arv109

Sheehan MJ, Choo J, Tibbetts EA (2017) Heritable variation in colour patterns mediating individual recognition. R Soc Open Sci 4:. https://doi.org/10.1098/rsos.161008

Sheehan MJ, Tibbetts EA (2010) Selection for individual recognition and the evolution of polymorphic identity signals in polistes paper wasps. J Evol Biol 23:570–577. https://doi.org/10.1111/j.1420-9101.2009.01923.x

Siddiqi A, Cronin TW, Loew ER, et al (2004) Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. J Exp Biol 207:2471–2485. https://doi.org/10.1242/jeb.01047

Smale MJ, Kok HM (1983) The occurrence and feeding of Pomatomus saltarix (el) and Lichia amia (leervis) juveniles in two Cape south coast estuaries. South African J Zool 18:337–342. https://doi.org/10.1080/02541858.1983.11447836

Speybroeck J, Beukema W, Bok B, et al (2016) Field guide to the amphibians and reptiles of Britain and Europe. Bloomsbury Publishing Plc, London

Stamps JA, Krishnan V V. (1995) Territory acquisition in lizards: III. Competing for space. Anim Behav 49:679–693. https://doi.org/10.1016/0003-3472(95)80201-0

Stamps JA, Krishnan V V (1998) Territory acquisition in lizards. IV. Obtaining high status and exclusive home ranges. Anim Behav 55:461–72. https://doi.org/10.1006/anbe.1997.0612

Stamps JA, Krishnan V V (1994) Territory acquisition in lizards: II. Establishing social and spatial relationships. Anim Behav 47:1387–1400. https://doi.org/10.1006/anbe.1994.1186

Stapley J, Whiting MJ (2006) Ultraviolet signals fighting ability in a lizard. Biol Lett 2:169–172. https://doi.org/10.1098/rsbl.2005.0419

Stuart-Fox D, Aulsebrook A, Rankin KJ, et al (2020) Convergence and divergence in lizard colour polymorphisms. Biol Rev 000–000:1–21. https://doi.org/10.1111/brv.12656

Stuart-Fox DM, Firth D, Moussalli A, Whiting MJ (2006) Multiple signals in chameleon contests: designing and analysing animal contests as a tournament. Anim Behav 71:1263–1271. https://doi.org/10.1016/j.anbehav.2005.07.028

Stückler S, Cloer S, Hödl W, Preininger D (2022) Carotenoid intake during early life mediates ontogenetic colour shifts and dynamic colour change during adulthood. Anim Behav 187:121–135

Svensson EI (2017) Back to basics: using colour polymorphisms to study evolutionary processes. Mol Ecol 26:2204–2211. https://doi.org/10.1111/mec.14025

Swierk L, Langkilde T (2013) Bearded ladies: Females suffer fitness consequences when bearing male traits. Biol Lett 9:. https://doi.org/10.1098/rsbl.2013.0644

Tibbetts EA (2004) Complex social behaviour can select for variability in visual features: A case study in Polistes wasps. Proc R Soc B Biol Sci 271:1955–1960. https://doi.org/10.1098/rspb.2004.2784

Tibbetts EA (2002) Visual signals of individual identity in the wasp *Polistes fuscatus*. Proc R Soc B Biol Sci 269:1423–1428. https://doi.org/10.1098/rspb.2002.2031

Tibbetts EA, Sheehan MJ, Dale J (2008) A testable definition of individual recognition. Trends Ecol Evol 23:356. https://doi.org/10.1016/j.tree.2008.03.007

Tokarz RR (1995) Mate choice in lizards: a review. Herpetol Monogr 9:17–40. https://doi.org/10.2307/1466994

Uller T, Olsson M (2008) Multiple paternity in reptiles: Patterns and processes. Mol Ecol 17:2566–2580. https://doi.org/10.1111/j.1365-294X.2008.03772.x

Umbers KDL (2013) On the perception, production and function of blue colouration in animals. J Zool 289:229–242. https://doi.org/10.1111/jzo.12001

Van Dyk DA, Evans CS (2007) Familiar–unfamiliar discrimination based on visual cues in the Jacky dragon, Amphibolurus muricatus. Anim Behav 74:33–44

Vicente NS, Halloy M (2016) Chemical recognition of conspecifics in a neotropical lizard, Liolaemus pacha (Iguania: Liolaemidae): relation to visual displays, season and sex. J Ethol 34:329–335

von Uexküll J (1934) A foray into the world of animals and humans with a theory of meaning. University of Minnessota Press, Minneapolis

Vorobyev M, Osorio D (1998) Receptor noise as a determinant of colour thresholds. Proc R Soc London Ser B Biol Sci 265:351–358. https://doi.org/10.1098/rspb.1998.0302

Vorobyev M, Osorio D, Bennett ATD, et al (1998) Tetrachromacy, oil droplets and bird plumage colours. J Comp Physiol - A Sensory, Neural, Behav Physiol 183:621–633. https://doi.org/10.1007/s003590050286

Waltz EC (1982) Alternative mating tactics and the law of diminishing returns: The satellite threshold model. Behav Ecol Sociobiol 10:75–83. https://doi.org/10.1007/BF00300166

Watson CM, Roelke CE, Pasichnyk PN, Cox CL (2012) The fitness consequences of the autotomous blue tail in lizards : an empirical test of predator response using clay models. 115:339–344

Weiss SL (2006) Female-specific color is a signal of quality in the striped plateau lizard (Sceloporus virgatus). Behav Ecol 17:726–732. https://doi.org/10.1093/beheco/arl001

Wellenreuther M, Svensson EI, Hansson B (2014) Sexual selection and genetic colour polymorphisms in animals. Mol Ecol 23:5398–5414. https://doi.org/10.1111/mec.12935

While GM, Michaelides S, Heathcote RJP, et al (2015) Sexual selection drives asymmetric introgression in wall lizards. Ecol Lett 18:1366–1375. https://doi.org/10.1111/ele.12531

White TE, Kemp DJ (2016) Colour polymorphism. Curr Biol 26:R517–R518. https://doi.org/10.1016/j.cub.2016.03.017

Whiting MJ (1999) When to be neighbourly: differential agonistic responses in the lizard *Platysaurus broadleyi*. Behav Ecol Sociobiol 46:210–214. https://doi.org/10.1007/s002650050611

Whiting MJ, Miles DB (2019) Behavioral ecology of aggressive behavior in lizards. In: Bels VL, Russel AP (eds) Behavior of Lizards. CRC Press, Boca Ratón, FL, pp 289-319.

Whiting MJ, Stuart-Fox DM, O'Connor D, et al (2006) Ultraviolet signals ultra-aggression in a lizard. Anim Behav 72:353–363. https://doi.org/10.1016/j.anbehav.2005.10.018

Whiting MJ, While GM (2017) Sociality in lizards. Comp Soc Evol 390–426. https://doi.org/10.1017/9781107338319.014

Wilson D, Heinsohn R, Endler JA (2006) The adaptive significance of ontogenetic colour change in a tropical python. Biol Lett 3:40–43. https://doi.org/10.1098/RSBL.2006.0574

Yang C, Chen S, Wang J (2023) Ontogenetic color change in the tail of blue‐tailed skinks (Plestodion elegans). Ecol Evol 13:e10152

Yang W, Feiner N, Pinho C, et al (2021) Extensive introgression and mosaic genomes of Mediterranean endemic lizards. Nat Commun 2021 121 12:1–8. https://doi.org/10.1038/s41467-021-22949-9

Zaldívar-Rae J, Drummond H (2007) Female accompaniment by male whiptail lizards: Is it mate guarding? Behaviour 144:1383–1402. https://doi.org/10.1163/156853907782418187

Zhang G, Yallapragada VJ, Halperin T, et al (2023) Lizards exploit the changing optics of developing chromatophore cells to switch defensive colors during ontogeny. Proc Natl Acad Sci 120:e2215193120

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, λ Rmid = wavelength at which reflectance is halfway between its minimum and its maximum for a given waveband (e.g. 300-450 nm and 400-650 nm).

Colour patch	**Age**	***N***	**Qt (300-700 nm)**	**C_{UV} (%)**	**λ β max (325-560 nm)**	**λ Rmid (300-450 nm)**	**λ Rmid (400-650 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 newborns, 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**		
Colour 1	**Colour 2**	F	R^2	**adj.** P	F	R^2	**adj.** P
UV$^+$ white	Orange	2.67	0.16	0.073	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	0.066	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

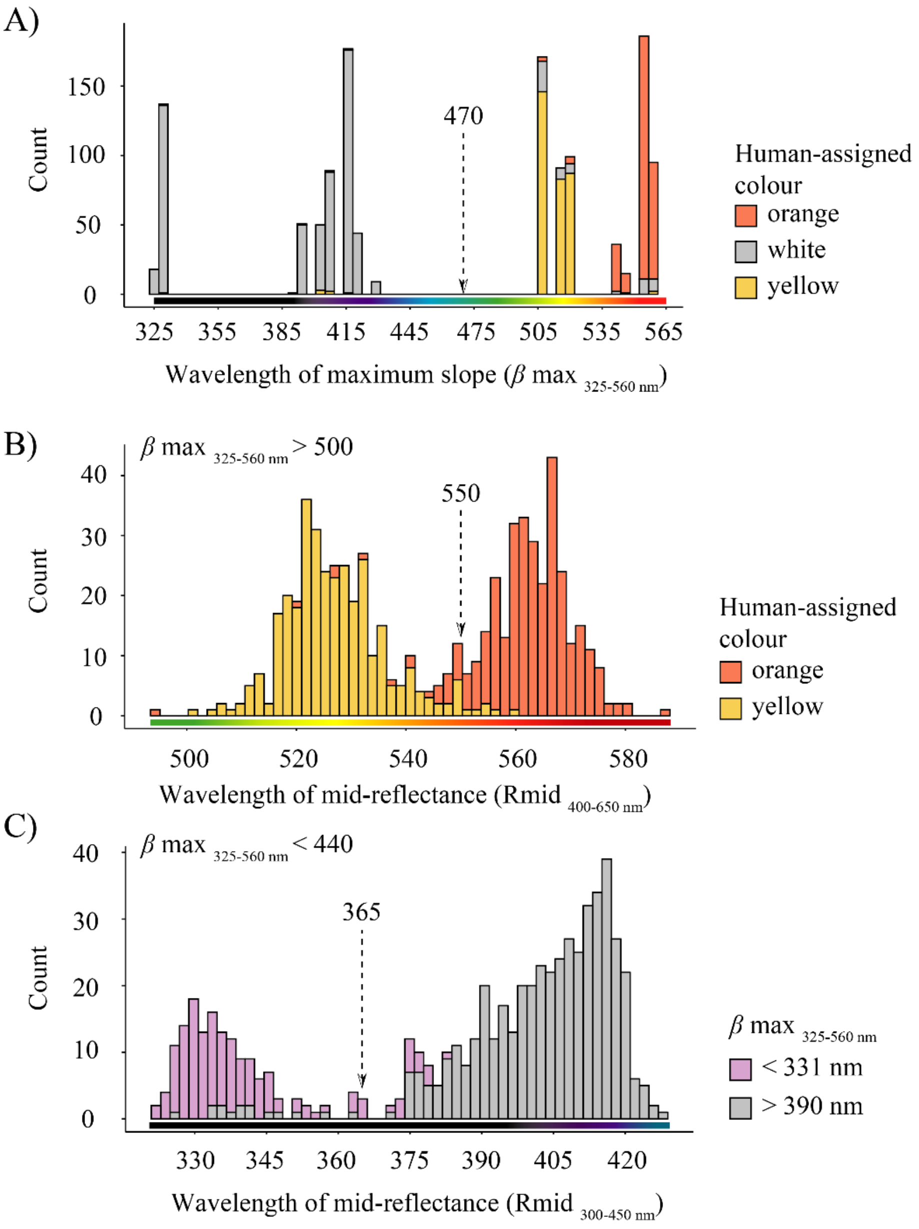

Figure 1. Categorization of *P. muralis* ventral colours according to their spectral properties in a sample of 1293 throat and belly spectra collected in adult males and females and assigned to a colour morph by human visual inspection. A) Stacked bar plot showing the discontinuous distribution of λ $\beta max_{325\text{-}560}$ (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 λ $Rmid_{400\text{-}650}$ (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 λ $Rmid_{300\text{-}450}$. Filled bars show the high agreement between a threshold to distinguish between UV^+ white and UV^- white based on β $max_{325\text{-}560}$ and one based on $Rmid_{300\text{-}450}$. For consistency with Pérez i de Lanuza et al. (2024, *in press*), we set a threshold at $Rmid_{300\text{-}450}$ = 365 nm to separate UV^+ white from UV^- white lizards.

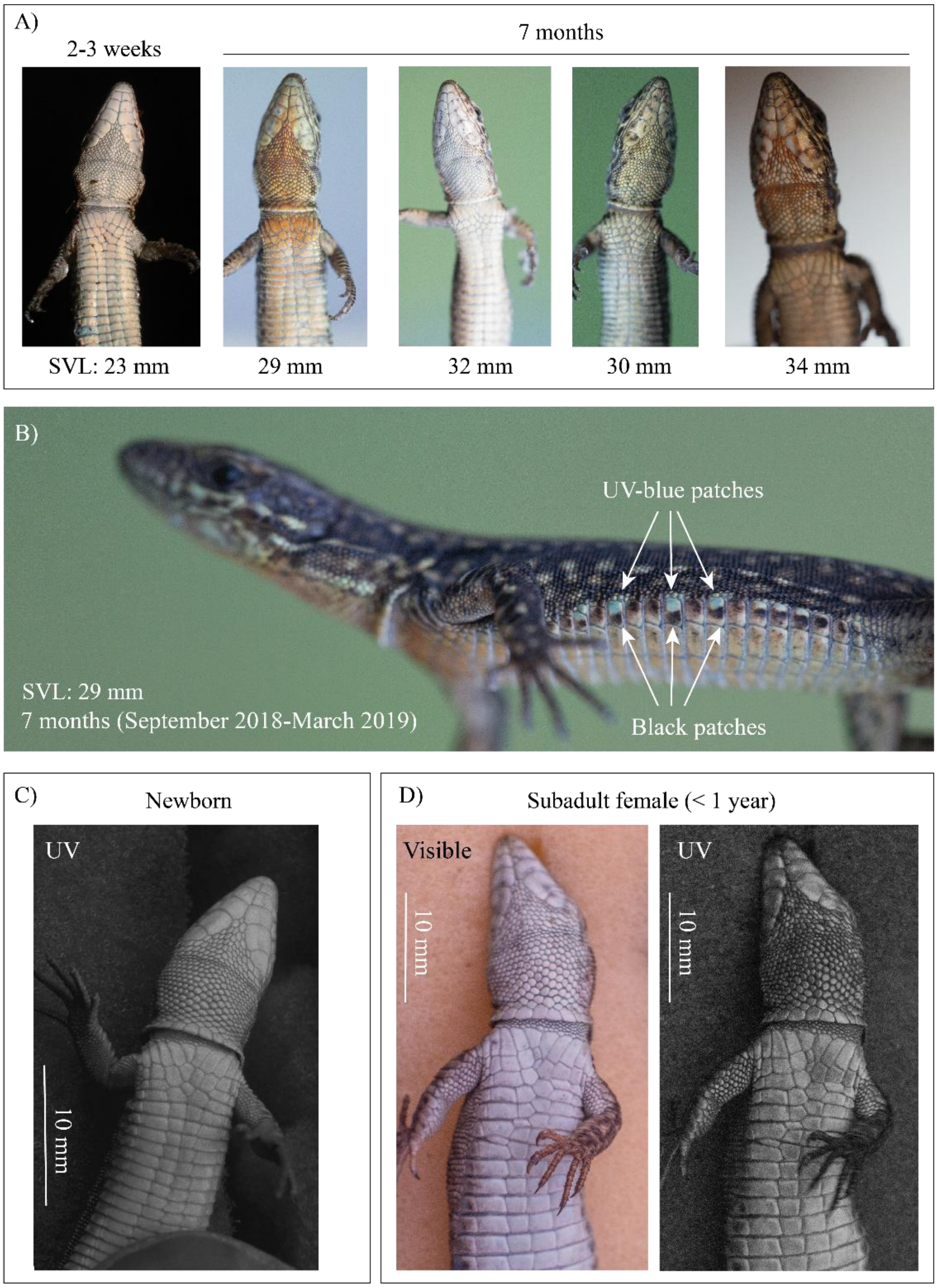

Figure 2. Ontogeny of ventral coloration in *P. muralis*. A) Representative photographs of ventral coloration in a newborn lizard 2-3 weeks after hatching (left), and in four yearlings re-captured in March 2019 (7 months after hatching). SVL stands for snout to vent length in mm. B) Young male of *P. 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. Surfaces with higher UV reflectance (i.e. newborn ventral surface and female belly) appear brighter in the UV photograph.

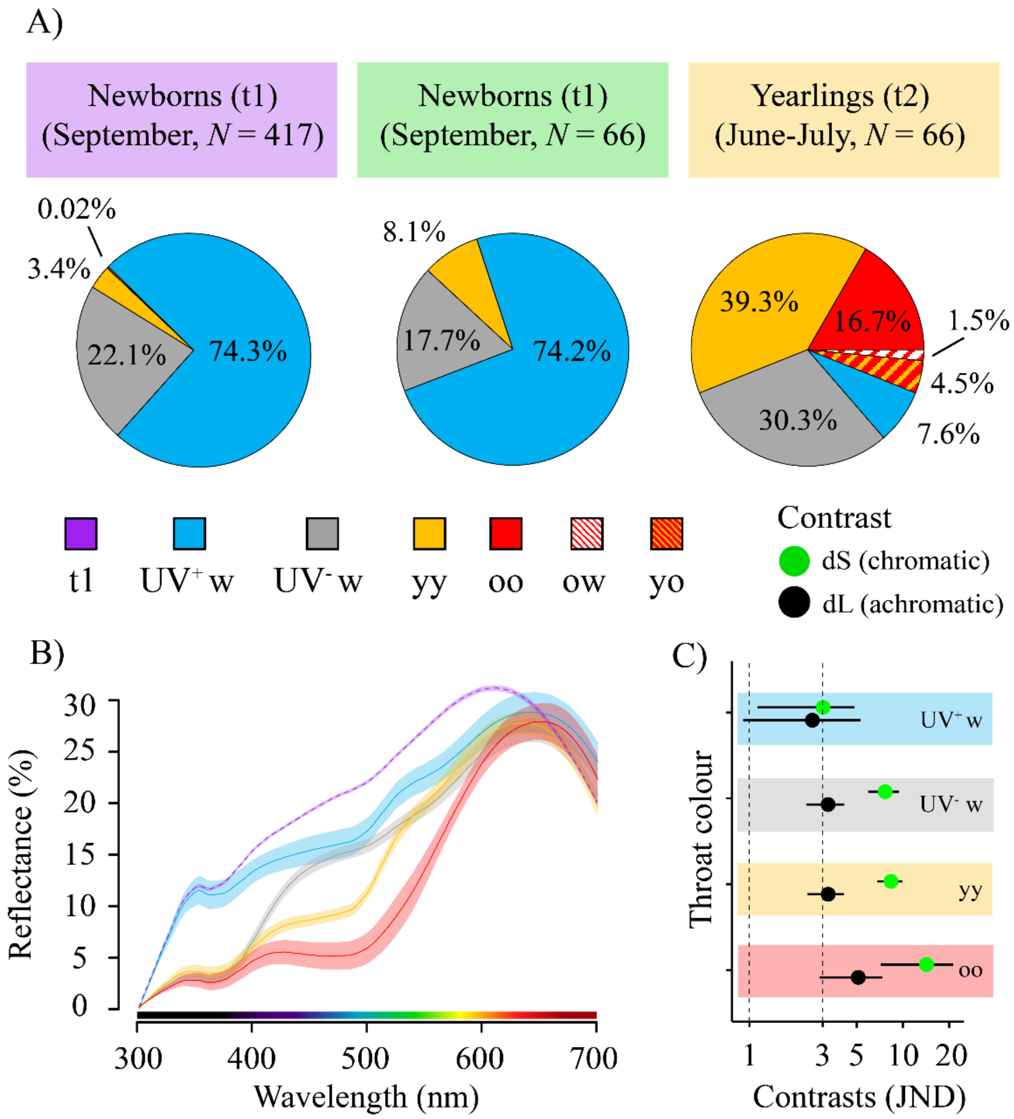

Figure 3. Ontogenetic changes in *P. muralis* throat coloration. A) Pie charts represent the proportions of juveniles showing different throat colours (UV$^+$ w = UV$^+$ white, UV$^-$ w = UV$^-$ white, oo = orange, yy = yellow, ow = orange-white, yo = yellow-orange) in September (t1; 3-4 weeks after 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.

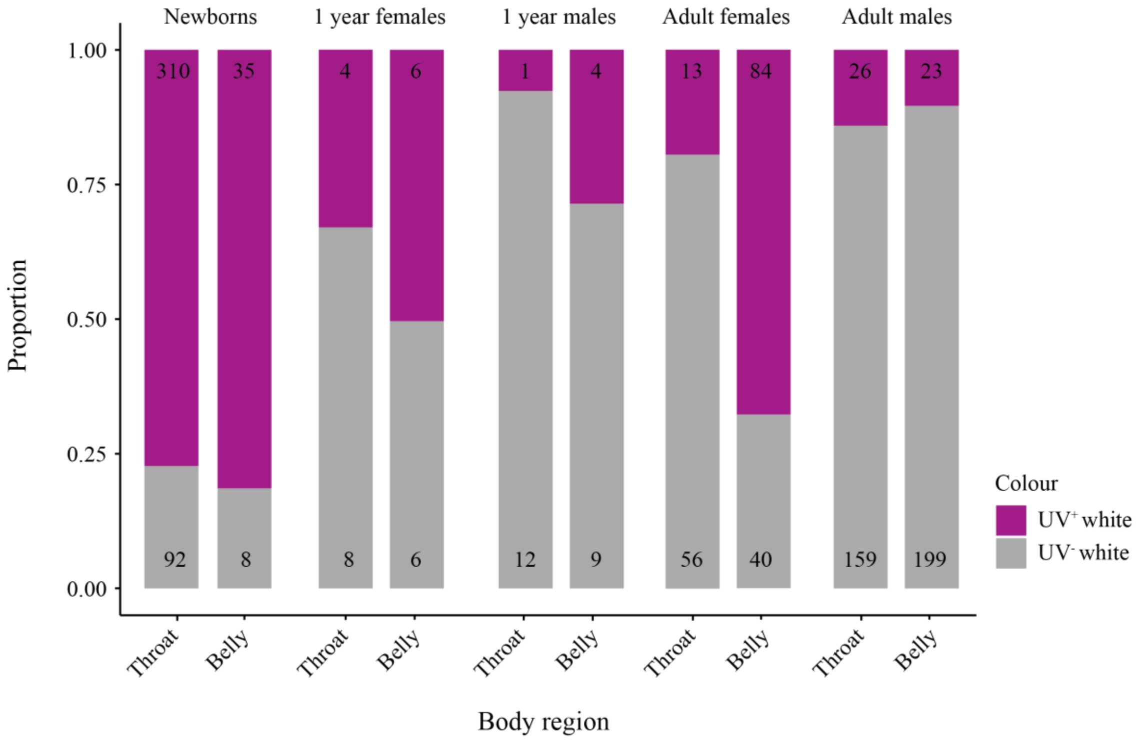

Figure 4. Stacked bar plot showing the proportion of UV$^+$ white and UV$^-$ white colorations in the throats and bellies of lizards classified according to the spectral properties of their reflectance curves (i.e. λ $\beta\text{max}_{325\text{-}560} \leq 500$): UV$^+$ white if showing a λ $\text{Rmid}_{300\text{-}450} \leq 365$ nm, UV$^-$ white if λ $\text{Rmid}_{300\text{-}450} > 365$ 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.

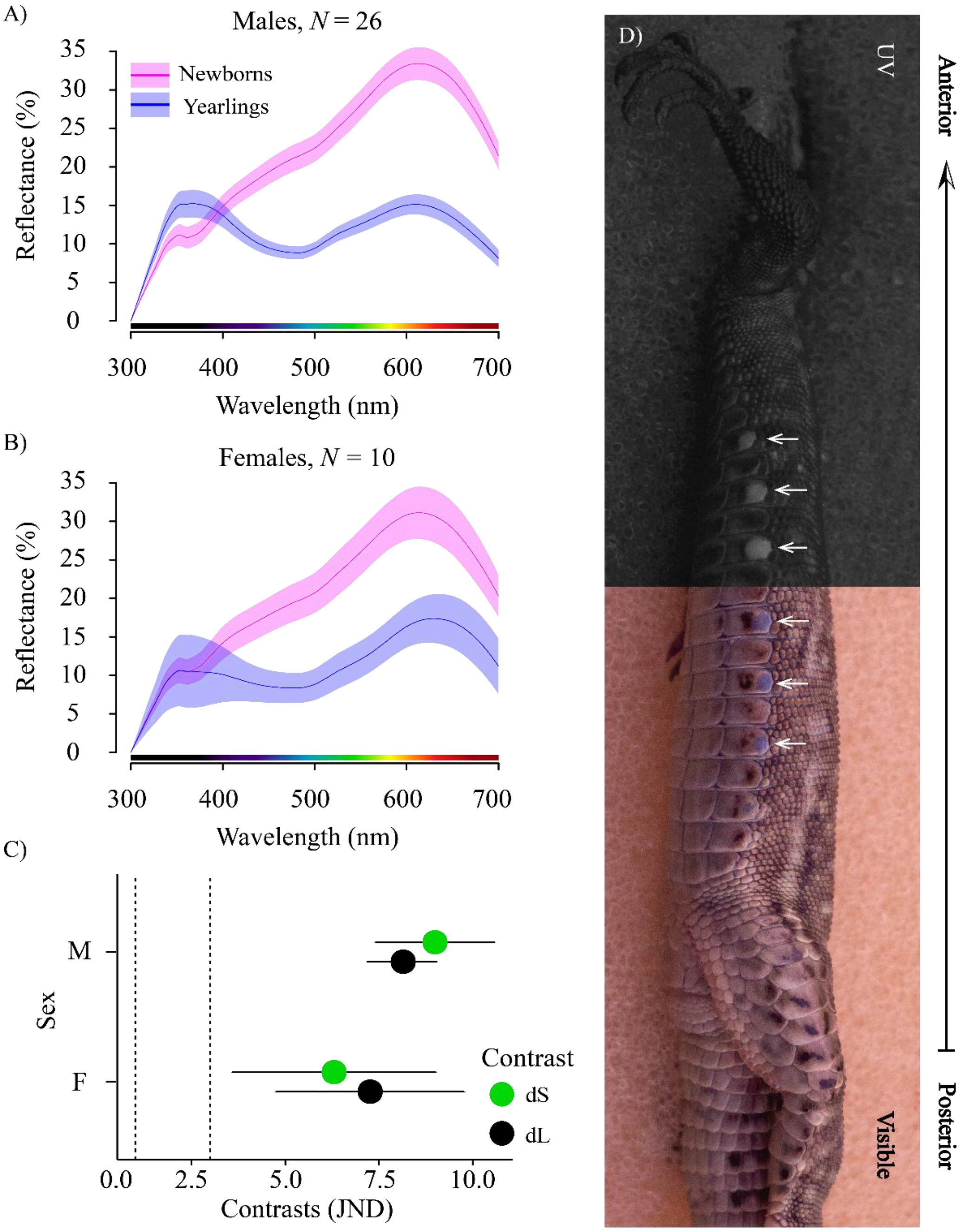

Figure 5. Ontogenetic change in *P. muralis* outer ventral scales (OVS) coloration. A) Reflectance spectra from the 36 lizards showing UV-blue patches as yearlings in their OVS (solid lines and shaded area represent means ± SEM). B) Mean and CI$_{95}$ of the chromatic (dS) and achromatic (dL) distances 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. C) Composite UV + visible image of a subadult (<1 year) *P. muralis* male showing incipient UV-blue coloration in the OVS.

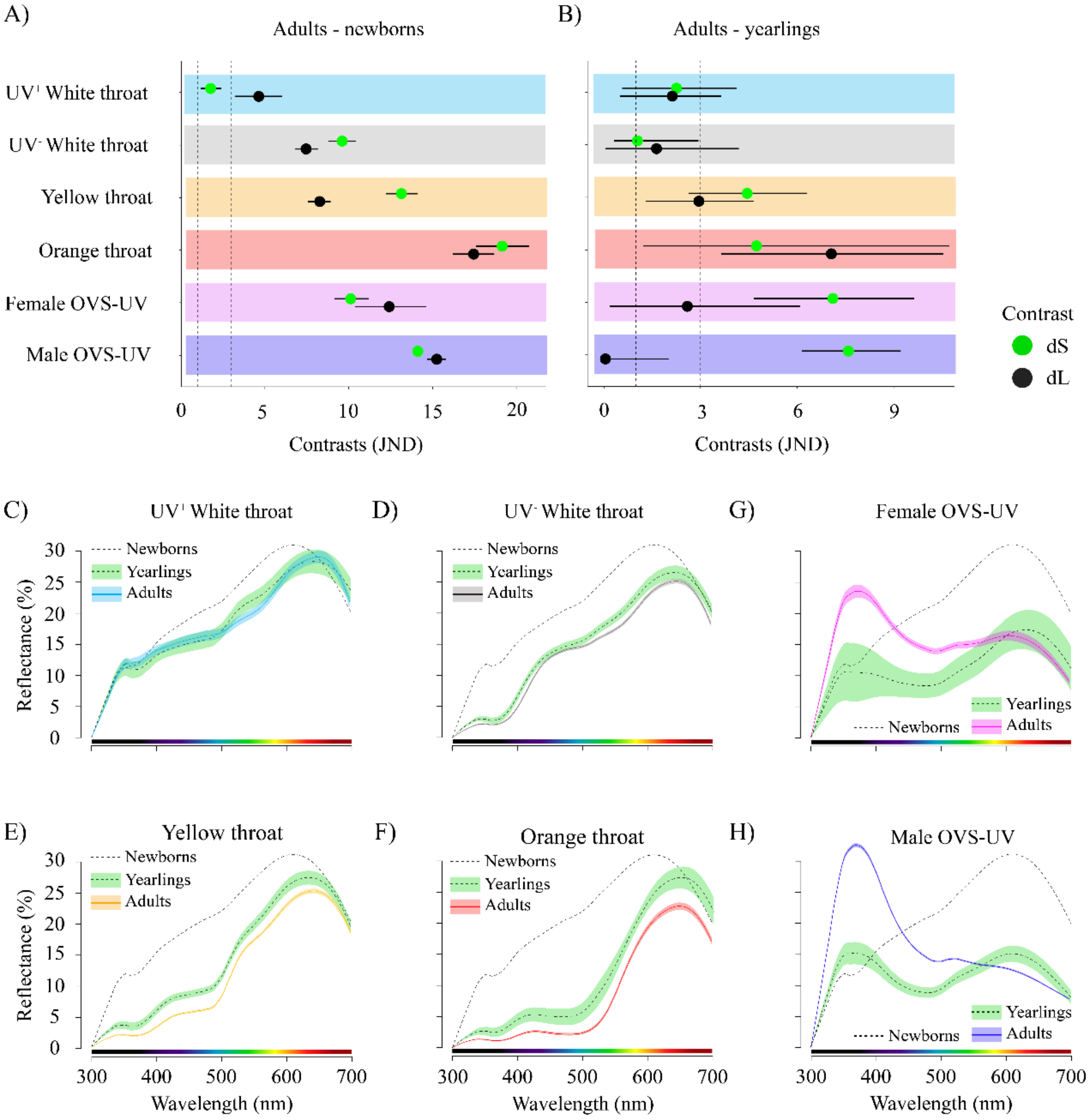

Figure 6. Comparison between the ventral coloration of newborn and yearling lizards with adult *P. muralis* from eastern Pyrenees. A) Mean and CI$_{95}$ of the chromatic (dS) and achromatic (dL) distances between the average ventral coloration of newborn and adult lizards, by adult colour. B) Mean and 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 (300-700 nm)**	**λ max (300-700 nm)**	**Chroma (300-700 nm)**
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 28ºC. 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). More details in Abalos *et al.*, (2021).

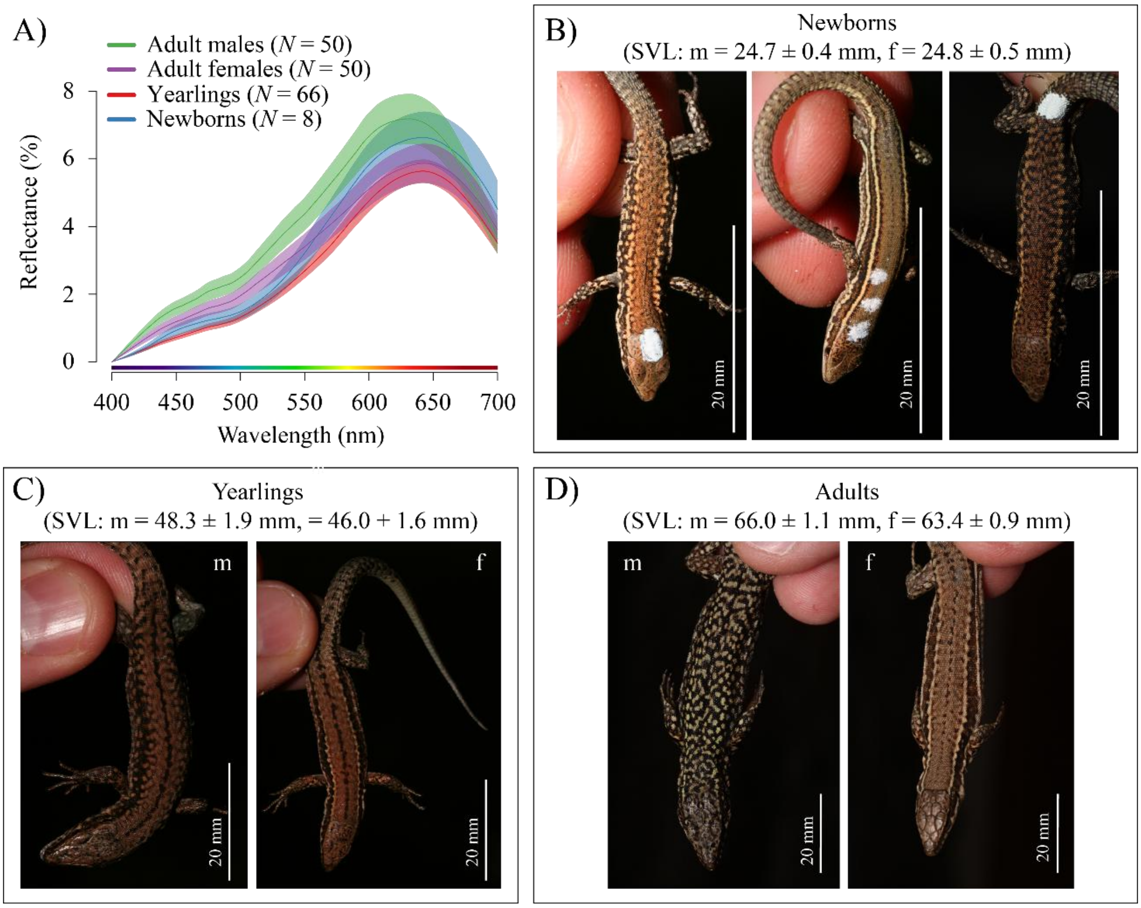

Figure S2. Ontogenetic variation in the dorsal coloration of *Podarcis muralis*. A) Reflectance spectra measured in eight newborn lizards, 66 yearlings, and 50 adults of each sex (solid lines and shaded area represent means ± CI_{95}). Spectra correspond to dorsal skin not covered by melanin patches 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. Ontogenetic variation in the melanin-based coloration covering the throat, belly, and outer ventral scales of an individual *Podarcis muralis* lizard. The photographs correspond to the same individual and were obtained 3-4 weeks after hatching and 7 months later when the lizard was recaptured in its outdoor enclosure. This individual showed melanin-based patches only in its outer ventral scales as a newborn, later extending into the adjacent row of ventral scales.

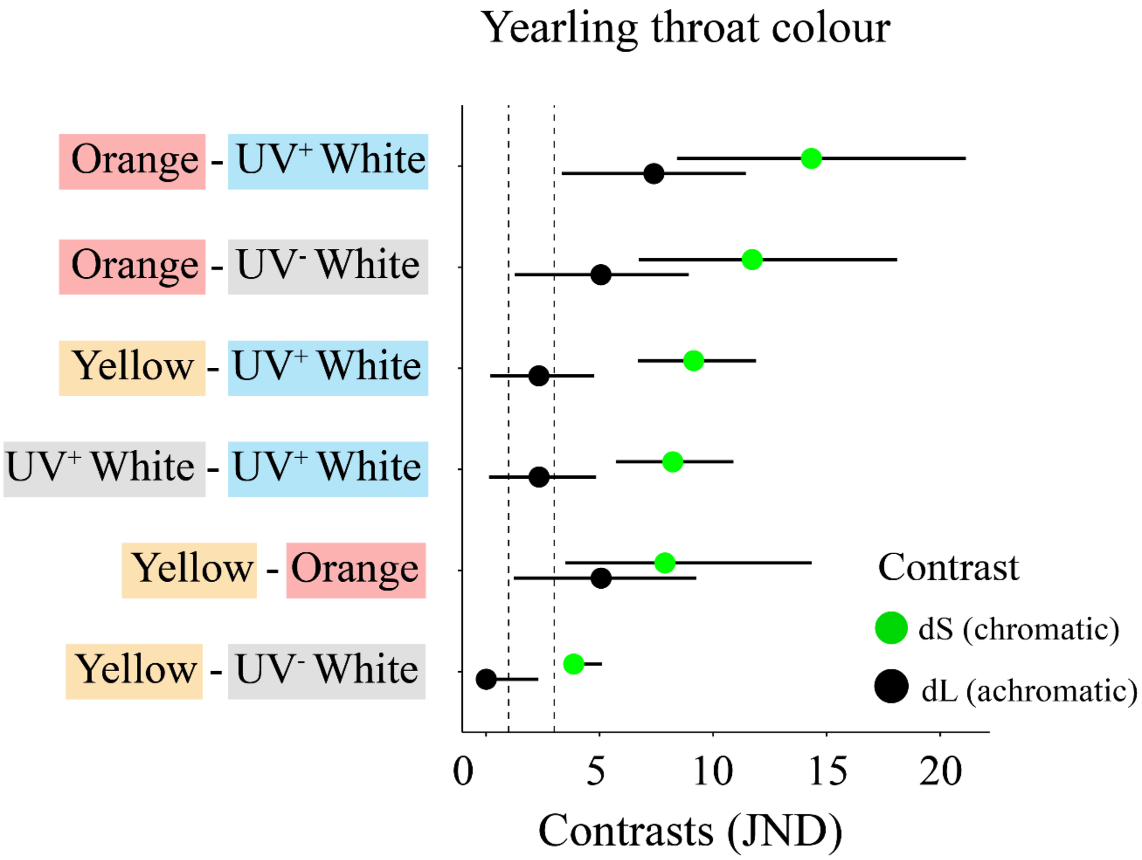

Figure S4. Mean and CI$_{95}$ of the chromatic and achromatic distances between the four different colours found in the throat of yearling lizards. Two dashed lines at 1 and 3 JNDs represent two theoretical discriminability thresholds. If the confidence interval of a point includes a discriminability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

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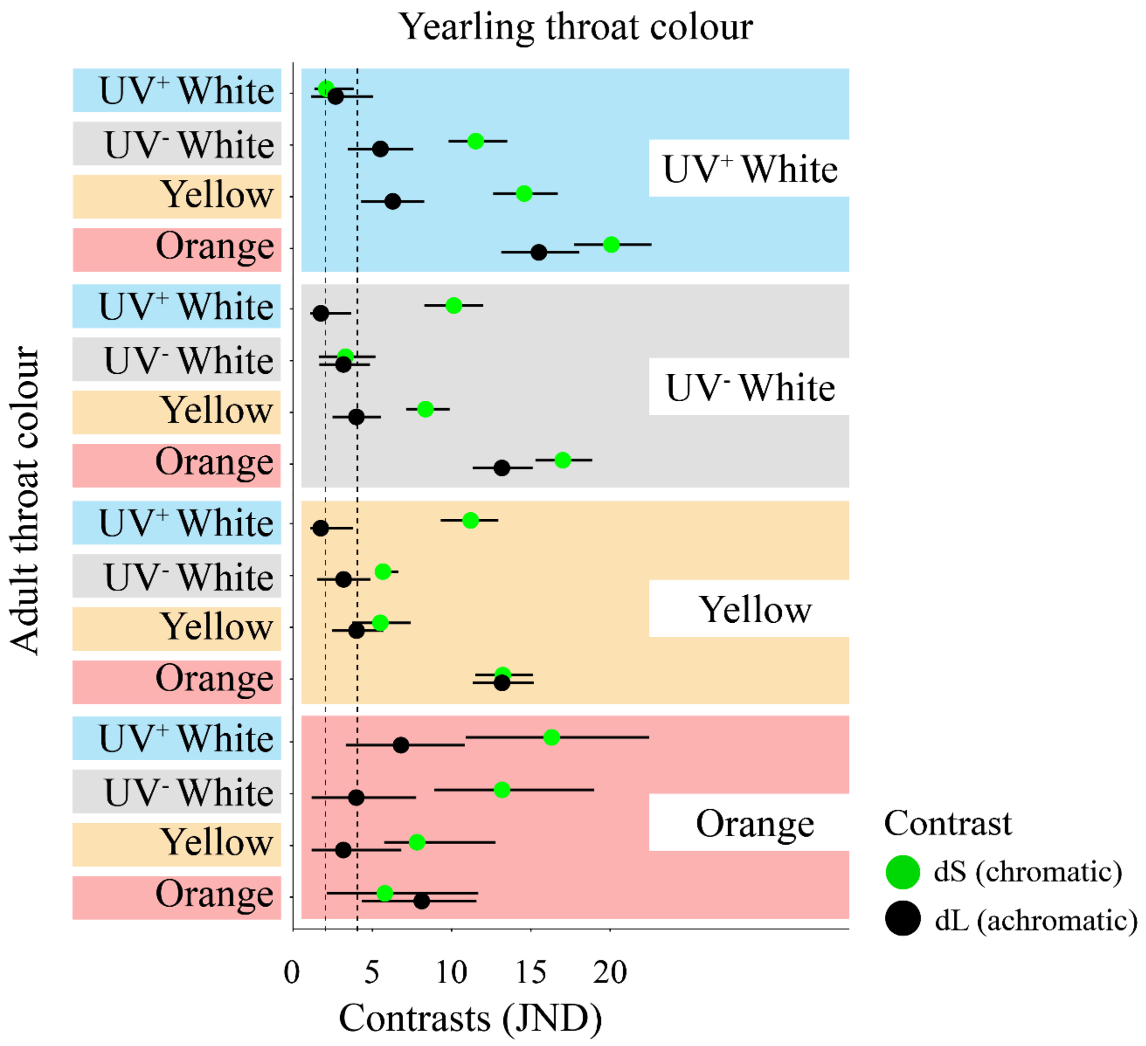

1083

1084 **Figure S5.** Mean and CI_{95} of the chromatic and achromatic distances between the colours found in the throat
1085 of yearling and adult lizards. Two dashed lines at 1 and 3 JNDs represent two theoretical discriminability
1086 thresholds. If the confidence interval of a point includes a discriminability threshold, the two colours are not
1087 distinguishable at this threshold according to receiver cone sensitivities and relative abundance.

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