Journal of Thermal Biology 132 (2025) 104262

Contents lists available at ScienceDirect

Journal of Thermal Biology

journal homepage: www.elsevier.com/locate/jtherbio

Thermal stability of pigment- and structurally based body coloration in a polymorphic lizard

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ARTICLE INFO

Keywords:
Communication
Predation
Temperature
Thermal biology
Thermal imaging
Visual modeling

ABSTRACT

Animal coloration plays a fundamental role in communication, camouflage, aposematism, mimicry and thermoregulation, and has strong implications for adaptation and diversification. Phenotypic plasticity of color traits can thus affect social, reproductive, antipredator, or thermoregulatory behavior and determining the causes and consequences of color change helps us understand evolution. In contrast to seasonal or ontogenetic color changes, physiological color change in response to fine-scale changes in environmental conditions has received less attention. Temperature-driven, rapid changes in coloration can have profound implications for ecophysiology, particularly in ectotherms. Here, using a widespread color polymorphic lacertid, *Podarcis muralis*, we study the impact of temperature on the chromatic properties and perception of pigment- and structurally based coloration of different body regions. We subjected male and female adult lizards from different color morphs to two different temperature regimes: cold (25 °C) and hot (≥34 °C) temperature, and quantified color change in the dorsum, belly, throat and ultraviolet (UV)-blue ventrolateral patches using a spectrophotometer. We then applied visual modeling to assess color variation from the perspective of a conspecific and two visual predators. We show that despite minor differences in spectral reflectance metrics, temperature had no significant effect on how color patches are perceived by receivers. Moreover, temperature did not affect existing sex and morph differences in color properties, suggesting that the minor changes we observed have little functional/adaptive consequences in this context. Contrary to results reported in other lizard taxa (iguanians and geckos), our findings suggest that temperature-induced rapid visual color change is unlikely in this lacertid species.

1. Introduction

Animal colors play important roles in communication, camouflage, aposematism, thermoregulation, and protection from the environment, and have strong implications for adaptation and diversification (Caro, 2005; Cuthill et al., 2017; Stevens, 2013). Phenotypic plasticity of color traits can thus affect social, reproductive, antipredator, or thermoregulatory behavior and determining the causes of color change helps us understand evolution (Cuthill et al., 2017). In contrast to seasonal or ontogenetic color changes (i.e. morphological changes), physiological color change occurs rapidly, in seconds to minutes, and responds to fine-scale changes in conditions such as acute stress, background color, social interactions, or temperature (Caro et al., 2016; Cooper and Greenberg, 1992; Duarte et al., 2017; Figon and Casas, 2018). For example, in laboratory experiments, within 15–30 min of exposure, the coloration of fiddler crabs (*Uca panacea*) became lighter on a white background and when exposed to high temperature, and it became darker on a black background and at low temperature (Kronstadt et al., 2013). Similarly, in under 4 min, dorsal and lateral surfaces of water anoles (*Anolis aquaticus*) brightened substantially in response to a mild stressor (Boyer and Swierk, 2017) while green anoles (*A. carolinensis*) change body color between brown and green within seconds multiple times during social interactions (Greenberg and Crews, 1990; Horr et al., 2023).

Ambient temperature is a factor of special relevance for ectotherm ecophysiology (Angilletta et al., 2002). Since dark (i.e. low-reflectance) colors heat up faster than light (i.e. high-reflectance) colors, plastic color change can serve to increase or decrease heat absorption from the environment, facilitating thermoregulation in thermally heterogeneous habitats. Indeed, the thermal melanism hypothesis predicts that increased body temperatures will produce lighter colorations and lower temperatures will produce darker colorations in ectothermic individuals

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https://doi.org/10.1016/j.jtherbio.2025.104262
Received 5 June 2025; Received in revised form 22 August 2025; Accepted 22 August 2025

(Clusella Trullas et al., 2007). Despite thermal melanism yielding mixed empirical support, this prediction is intuitive and generally accepted, having implications in the fields of animal coloration and visual communication research.

From a research perspective, rapid color changes could affect the reliability of color measurements, especially when standardization of measuring conditions is not possible (e.g. *in situ* field measurements). In many signaling contexts, color variation correlates with some feature of the individual, providing different sorts of information (Cuthill et al., 2017; Stuart-Fox and Moussalli, 2009), and thus conflating color change with color variation can lead to flawed conclusions. Unaccounted color plasticity may impact color quantification by adding uncontrolled variability to, for instance, repeated measurements of the same individuals made at different times (or environments) or to comparisons across individuals, populations and species, complicating their biological interpretation (Romero-Diaz et al., 2022). Nevertheless, color constancy of visual systems (i.e. the ability to perceive colors as relatively constant despite changes in illumination), and categorical discrimination of continuous color variation (Caves et al., 2018; Fleishman et al., 2016; Pérez i de Lanuza et al., 2018; Szabo et al., 2021), for example, can minimize the perceptual effects of dynamic color changes. It is thus important to determine the impact of rapid responses to short-term environmental change from the perspective of relevant observers, if and when they occur.

Among ectotherms, lizards are an ideal model to study plastic color changes. Most lizards are diurnal and terrestrial and exhibit exceptional diversity in body colorations, which serve a wide variety of functions (Olsson et al., 2013). Physiological color changes have been described mainly in agamids (Madsen and Loman, 1987), anoles (Boyer and Swierk, 2017; Taylor and Hadley, 1970; Wuthrich et al., 2022), chameleons (Stuart-Fox and Moussalli, 2008), iguanas (Norris, 1967) and phrynosomatids (Langkilde and Boronow, 2012; Zucker, 1989), which are all in the suborder Iguania, and in geckos (Vroonen et al., 2012), and thus the extent to which these responses can be generalized is unclear. Most colors are produced by a combination of specialized chromatophore cells that contain pigments which selectively absorb natural light, or nanoscale structures which selectively reflect or scatter light (Bagnara and Hadley, 1973; Ligon and McCartney, 2016; Olsson et al., 2013). As in other vertebrate ectotherms, physiological color change in lizards involves the mobilization (dispersion and aggregation) of pigments and/or the reorganization of nanostructures in dermal chromatophore units (Cooper and Greenberg, 1992; Hadley and Goldman, 1969; Teyssier et al., 2015).

The mechanistic basis of color production in different body regions can differ, as often does the combination of selective pressures these patches are under (Cooper and Greenberg, 1992; Stuart-Fox and Moussalli, 2008; Stuart-Fox et al., 2004). In general, dorsal coloration is affected by the degree of reliance on crypsis for predator avoidance and thermoregulatory needs (Gunderson et al., 2022; Romero-Diaz et al., 2019; Rosenblum, 2006). Heliothermy is one of the main thermoregulatory strategies in diurnal lizards, and dorsal surfaces receive the highest exposure to solar radiation. In contrast, colors that are located ventrally or ventrolaterally are likely hidden from view most of the time and may be revealed only behaviorally, when adopting specific body postures (e.g. during basking or displays of social communication; Driessens et al., 2014; Hews and Martins, 2013; Pérez i de Lanuza et al., 2016; Pérez i de Lanuza and Font, 2015). This difference in selective regime can make the stability or plasticity of color vary substantially among different body regions. For example, dorsal but not ventral skin reflectance in bearded dragons (*Pogona vitticeps*) changed significantly in response to temperature (Smith et al., 2016b). In the eastern fence lizard, *Sceloporus undulatus*, belly and throat patches shifted from green to blue hue in response to increasing temperatures but dorsal hue was unaffected (Assis et al., 2022; Langkilde and Boronow, 2012).

Here, we study whether the different colors shown by the European wall lizard (*Podarcis muralis*, family Lacertidae) exhibit rapid changes induced by temperature variation. This species is color polymorphic, with up to five color morphs, and is often the focus of visual signaling, behavior and ecology research (Abalos et al., 2025; Kawamoto et al., 2025; Olsson et al., 2013; Pérez i de Lanuza et al., 2018; Pérez i de Lanuza et al., 2019; Pérez i de Lanuza and Font, 2015; Pérez i de Lanuza and Font, 2016). As in other lizards (e.g. Haisten et al., 2015; Kuriyama et al., 2017; Morrison et al., 1995; Taylor and Hadley, 1970), *P. muralis* skin coloration results from the combined action of three dermal chromatophore layers, from top to bottom: xanthophores, iridophores, and melanophores (Andrade et al., 2019). In both sexes, ventral scales exhibit one of three distinct colors (white, yellow, orange) or a mosaic pattern combining two colors (orange-white and orange-yellow), with differences in pterin and carotenoid content underlying morph differences (Andrade et al., 2019). Dorsal surfaces are iridescent green-brown (Pérez i de Lanuza and Font, 2016). Additionally, conspicuous ventrolateral ultraviolet (UV)-blue patches that overlap some of the outer ventral scales (OVS) are present in the flanks of males and some females (Pérez i de Lanuza and Font, 2015). Dorsal coloration seems to function primarily as camouflage and enables thermoregulation (Marshall et al., 2015; Pérez i de Lanuza and Font, 2015; Pérez i de Lanuza and Font, 2016; Tosini et al., 1992). UV-blue patches are good predictors of size-independent bite force and body condition (Pérez i de Lanuza et al., 2014) and thus hypothesized to function as a social signal in opponent assessment of male fighting ability, yet their precise role in agonistic encounters is still unclear (Abalos et al., 2016, 2024b; Names et al., 2019). Ventral coloration (belly and throat) does not seem to influence behavioral thermoregulation (Pérez i de Lanuza et al., 2016) nor is associated to alternative reproductive/behavioral strategies (Abalos et al., 2020) and its function, if any, remains elusive.

We experimentally tested the short-term effects of temperature on color patches from different body regions by measuring spectral reflectance of dorsal, ventral and ventrolateral color patches in adult lizards from both sexes and different color morphs. We then assessed whether any potential color changes may be perceived by conspecifics, a common avian predator (a raptor), or a saurophagous snake. Evidence of physiological color change in lacertids is scant. From the adaptive perspective of the thermal melanism hypothesis, we may expect temperature-induced rapid changes in color patches directly involved in thermoregulation and not in patches under selection for crypsis or social signaling, especially if these color changes increase or decrease the conspicuousness of the color patch. The absence of color changes, or the occurrence of color changes that are ultimately not discriminable by relevant receivers would instead suggest that *P. muralis'* coloration is not affected by short-term changes in body temperature and that temperature is unlikely to impact color patch function.

2. Methods

In July 2024, we collected 16 adult (SVL >55 mm) female and 40 adult male *P. muralis* from a population in Llívia, in the Pyrenean plateau of la Cerdanya (Spain). Only lizards of pure ventral color were used in the experiment to avoid spectra that artifactually combine properties from multiple color patches (Badiane et al., 2017): 23 white, 25 yellow and 8 orange lizards. Lizards were placed individually in numbered cloth bags for the duration of the experiment and released at their exact point of capture within 3 days. Bags were moistened with water and kept in a dark fresh (23 °C) room.

2.1. *Temperature treatment*

We tested the short-term impact of temperature on color by measuring and comparing the coloration of each lizard after being exposed to two temperature treatments: "cold" and "hot", in that order, since warming may produce faster color changes than cooling (Stephenson et al., 2017). We split lizards into two batches of 27 and 29 lizards to treat and measure over 3 days. On the first day, we measured the first batch of cold-treated lizards. On the second day, we measured the first batch of hot-treated lizards and the second batch of cold-treated lizards. On the third day, we measured the second batch of hot-treated lizards. In the "cold" temperature treatment, lizards were acclimated in a portable incubator (R-COM Juragon RX Suro), in dark conditions, until their body temperatures reached 25 ± 1 °C. Temperature within the incubator was monitored in real time using a wireless temperature and humidity sensor (RuuviTag bluetooth sensor, Ruuvi Inc.). In the "hot" temperature treatment, lizards were placed in an empty terrarium (60 × 42.5 × 29 cm) under direct sunlight until they reached a temperature of 34 °C or above (average ± SD: 34.9 ± 0.7 °C), guaranteeing a minimum 8-degree difference between the two treatments. Hours of measurement and weather conditions (temperature, relative humidity, windspeed and solar irradiation) were similar on both days of outdoor treatment (Table S1). In previous studies with lizards, a 4 or 5-degree difference was enough to induce temperature-dependent color changes (Langkilde and Boronow, 2012; Stephenson et al., 2017). The mean body temperature of free-ranging *P. muralis* in the field is 33.8 °C (Braña, 1991). In a laboratory photothermal gradient, their median preferred body temperature is 34.1 °C with a breath of 4.6 °C (Bauwens et al., 1995). The hot treatment target temperatures thus represent the temperature that lizards would select and maintain if they had unrestricted access to a full range of biologically relevant thermal conditions. Moreover, cold and hot target temperatures are within the natural range of body temperatures observed in the wild (Braña, 1991).

Lizards' body temperatures were verified right before color measurement (see below) with a handheld infrared (IR) thermometer (PeakMeter PM659B) set at an emissivity of 0.97 (Luna et al., 2013) (Table S2). Temperature measurements were taken at room temperature over a standardized background, while holding the lizard by the upper half of its body with one hand, with the thermometer's laser pointed right above its cloaca at a distance of 10 cm (<1 cm Ø spot). IR measurements of body surface temperature strongly correlate with cloacal temperature obtained through contact thermometry, and thus they accurately reflect internal body temperatures in small-sized lacertids (Barroso et al., 2016; Luna et al., 2013).

2.2. *Color measurement*

We obtained reflectance spectra relative to a white standard (Spectralon WS1) using a USB2000 spectrometer with a PX-2 pulsed xenon lamp and an R200-7-UV-VIS reflection probe (Ocean Optics Inc., Dunedin, FL, USA). The spectrometer averaged 20 spectral acquisitions, and we restricted analyses to the range 300–700 nm. We took measurements from four body regions: the throat, the belly, the dorsum and UV-blue patches in the outer ventral scales ("UV-blue OVS" henceforth) (Fig. 1). We measured i) the center point of the throat; ii) a homogeneously colored, and preferably central, scale within the first third of the belly (the most colorful part); iii) the midpoint between the front legs in the dorsum, avoiding dark lines or melanized spots; iv) and the 2nd UV-blue OVS of the right side of the lizard. If there were no clear or large enough UV-blue OVS on the right side, we would choose one on the left side. When *P. muralis* females present UV-blue patches, they are often too small to measure correctly (Badiane et al., 2017). This was also the case in our sample, and thus we only measured them in males. During measurements, we held the reflectance probe at a constant 90° angle and a distance of 3 mm to the lizard's surface with the aid of an entomological pin attached to the probe's tip, nylon pinhead down. This resulted in a circular reading spot of under 2 mm in diameter (Badiane et al., 2017). We conducted two consecutive rounds of measurements for each lizard, obtaining a repeated measure of the exact same points to account for unexplained variance stemming from measurement geometry (Johnsen, 2016), and used the average of the two measures in subsequent analyses. We measured the lizard's temperature before each round of measurements to make sure it conformed to the target temperature. In cases when it did not, we placed the lizard back into the incubator (cold treatment) or the sunlit terrarium (hot treatment) and waited for it to achieve the target temperature again.

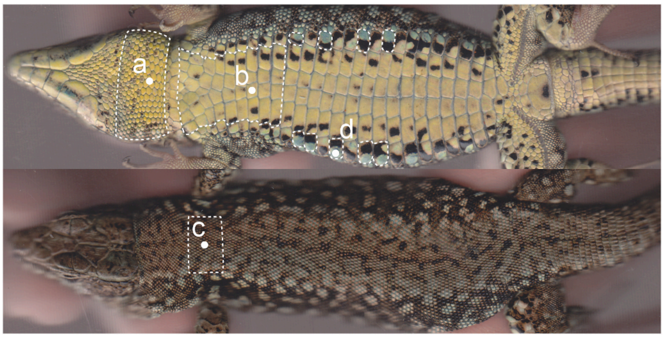

Fig. 1. Location of the four points for which we quantified color on a representative adult male *Podarcis muralis*: a) throat, b) belly, c) dorsum, and d) UV-blue patches in the outer ventral scales (OVS). See text for details.

We used the R package "pavo" (v. 2.9.0; Maia et al., 2019) to import and process spectral reflectance data. First, we zeroed negative values and smoothed spectra with a span of 0.1 using the *prospec* function of pavo. Second, we extracted colorimetric variables for hue, chroma and brightness that describe the shape of the spectral curves of the colors of these lizards (Badiane et al., 2017; Montgomerie, 2006). We measured hue as the wavelength of maximum reflectance (λ_{peak}) in unimodal spectra with a narrow peak (i.e. the dorsum and UV-blue OVS), and as the wavelength at the midpoint between the minimum and maximum reflectance (λ_{Rmid}) in spectra with a wide plateau (i.e. the throat and belly, which do not differ in peak location but in the wavelength range in which reflectance decreases) (Pérez i de Lanuza et al., 2019). We calculated UV chroma (C_{UV}) and green chroma (C_G) as the relative contribution of the 300–400 nm and 510–605 nm range to the sum of the relative reflectance over the entire spectral range (300–700 nm), respectively, and brightness (B) as the mean reflectance over the entire spectral range.

We also applied visual modeling to determine whether there were chromatic or achromatic differences between cold and hot color measurements taking into account the visual perception system of conspecifics and visual predators, namely, a bird and a snake (e.g. Abalos et al., 2025; Pérez i de Lanuza et al., 2019). We conducted visual modeling according to the receptor noise-limited model developed by Vorobyev and Osorio (1998) to convert reflectance spectra into perceived colors represented in tetrachromatic color space. For conspecifics, we used the photoreceptor sensitivities (UVS:SWS:MSW:LSW, 367:456:497:562 nm) and cone ratios (1:1:1:4) estimated for *P. muralis* (Martin et al., 2015), and a Weber fraction of 0.05 as suggested for amphibians (Siddiqi et al., 2004). For avian predators, we chose the violet sensitive (VS)-averaged visual system available in pavo, which is representative of raptors (Accipitridae and Falconidae), as they are the most common avian predators of *P. muralis* (Martín and López, 1990). We used cone ratios of 1:2:2:4, and a Weber fraction of 0.1 (Vorobyev et al., 1998). For snakes, we used the photoreceptor sensitivities of a visually hunting whip snake, *Masticophis flagellum* (UVS:SWS:LWS, 362:458:561 nm), the cone ratios of *Thamnophis sirtalis* (1:2:17), and a Weber fraction of 0.1 (Macedonia et al., 2009; Sillman et al., 1997) to represent the visual system of saurophagous colubrids known to predate on *P. muralis* in the area of study (e.g. *Hierophis viridiflavus*) (Pérez i de Lanuza and Font, 2015). In all cases, we assumed a "D65" standard daylight illuminant. We calculated bootstrapped chromatic and achromatic color distances in just-noticeable differences (JNDs) between cold and hot spectra for each body region, lizard color morph and sex, with 95 % confidence intervals (C.I.). Values ≥ 1 JND indicate that two colors are perceived as distinct; however, in practice, JNDs between 1 and 3 may be difficult to discriminate under non-optimal light conditions, and a more conservative threshold (≥3 JNDs) is frequently adopted (Marshall and Stevens, 2014; Pérez i de Lanuza et al., 2018; Siddiqi et al., 2004).

2.3. Statistical analyses

In R (v. 4.3.3; R Core Team, 2024), we ran linear mixed effects models (LMM) with the function *lmer* (package lme4, v. 1.1–27.1; Bates et al., 2015) using each of the four color metrics (hue, brightness and two measures of chroma) as dependent variables, "temperature" (cold/hot), "sex" (M/F) and "morph" (Y/W/O) as fixed factors, and lizard ID as a random effect to account for repeated measures of the same lizards. We conducted Tukey tests for post-hoc comparisons of significant morph differences with the function *glht* (package multcomp, v. 1.4–25; Hothorn et al., 2008) and confirmed that assumptions of linear regression, normality and homoscedasticity of residuals were met with normal Q-Q plots and Levene's tests. We used a ranked weighted LMM to correct for violation of normality and homogeneity of variance for morph in the models for throat and ventral λ_{Rmid}, and a weighted LMM to correct for heteroscedasticity in UV-blue OVS λ_{peak} using the nlme package (v. 3.1–164; Pinheiro et al., 2023) and the *weights* argument.

3. Results

3.1. Temperature, sex and morph differences in spectral shape descriptors

We found no temperature effects on dorsal coloration for any metric (Table 1). The two sexes and three morphs significantly differed in dorsal hue (λ_{peak}; sex: $X_1^2 = 10.05$, $P = 0.001$; morph: $X_2^2 = 11.82$, $P = 0.003$), and green chroma (C_G; sex: $X_1^2 = 10.01$, $P = 0.001$; morph: $X_2^2 = 8.25$, $P = 0.016$) (Fig. S1). W lizards had dorsal λ_{peak} at shorter wavelengths than Y and O lizards (Table 2), and so did males when compared to females (estimate ± S.E.: −14.2 ± 4.4 nm). W lizards showed higher C_G than O and Y lizards (Table 2), and males had higher C_G than females (Fig. S1).

We found temperature-dependent changes in throat coloration restricted to brightness (B; $X_1^2 = 5.08$, $P = 0.024$; Table 1, Fig. 2), which increased in hot lizards compared to cold (1.97 ± 0.36 %). In addition, we found sexual dichromatism in C_G ($X_1^2 = 7.20$, $P = 0.007$) and B ($X_1^2 = 8.07$, $P = 0.004$), with females being overall more reflective than males (C_G: 0.01 ± 0.004 %; B: 1.9 ± 0.7 %) (Fig. S1). Morphs differed in three color metrics, namely, λ_{Rmid} ($X_1^2 = 99.11$, $P < 0.001$), C_G ($X_1^2 = 28.94$, $P < 0.001$) and B ($X_1^2 = 36.0$, $P = 0.003$) (Table 1, Fig. S1). Y and O lizards had longer throat λ_{Rmid} than W lizards and O lizards had longer λ_{Rmid} than Y (Table 2). All morphs differed in throat C_G with Y lizards being the most reflective in this region of the spectrum, followed by W, which was more reflective than O (Table 2). W and Y lizards also had significantly brighter throats than O lizards (Table 2).

Table 1

Summary of the statistical significance found in LMMs for the variance associated to lizard ID and the effects of temperature, morph and sex on color metrics for each of the measured body regions. Asterisks indicate the level of significance: ***$P < 0.001$, **$P < 0.01$, *$P < 0.05$, ns = not significant. See text for details.

Patch location	Treatment	Color metric			
		$\lambda_{peak}/\lambda_{Rmid}$	C_{UV}	C_G	B
Dorsum	lizard ID	***	***	***	***
	temperature	ns	ns	ns	ns
	sex	***	ns	***	ns
	morph	**	ns	**	ns
Throat	lizard ID	***	***	***	***
	temperature	ns	ns	ns	*
	sex	ns	ns	**	**
	morph	***	ns	***	**
Belly	lizard ID	***	***	***	**
	temperature	ns	*	*	***
	sex	ns	***	***	ns
	morph	***	ns	***	***
UV-blue OVS	lizard ID	***	***	***	*
	temperature	***	***	***	ns
	morph	ns	ns	ns	ns

Temperature affected both measures of chroma (C_{UV}: $X_1^2 = 4.85$, $P = 0.028$; C_G: $X_1^2 = 6.47$, $P = 0.011$) and B ($X_1^2 = 10.86$, $P < 0.001$) of ventral coloration (Table 1, Fig. 2). Hot lizards showed reduced C_{UV} (0.006 ± 0.002), and increased C_G (0.004 ± 0.001) and B (1.36 ± 0.40 %). We also found sexual dichromatism in both metrics of chroma (C_{UV}: $X_1^2 = 12.57$, $P < 0.001$; C_G: $X_1^2 = 23.39$, $P < 0.001$), and morph differences in all metrics except C_{UV} (λ_{Rmid}: $X_1^2 = 70.64$, $P < 0.001$; C_G: $X_1^2 = 31.11$, $P < 0.001$; B: $X_1^2 = 49.90$, $P < 0.001$; Table 1, Fig. S1). Females were more reflective in the UV region (0.028 ± 0.007), while less reflective in the green (−0.025 ± 0.005), compared to males (Fig. S1). The O morph had longer λ_{Rmid} compared to W and Y lizards, and Y had longer λ_{Rmid} than W (Table 2). C_G was highest in Y lizards, followed by W and O (Table 2). Consequently, both Y and W morphs were overall brighter than O (Table 2).

In males, temperature affected λ_{peak} ($X_1^2 = 32.98$, $P < 0.001$), C_{UV} ($X_1^2 = 17.53$, $P < 0.001$) and C_G ($X_1^2 = 12.57$, $P < 0.001$) of UV-blue OVS but we found no morph differences (Table 1; Fig. 2). Hot lizards had λ_{peak} at longer wavelengths than cold lizards (9.3 ± 1.3 nm), were less reflective in the UV (−0.02 ± 0.004) and more reflective in the green (0.009 ± 0.002) region of the spectrum.

3.2. Perceived color differences

Visual models suggested that none of the rapid color changes reflected by metrics describing the spectral shape can be perceived by a conspecific observer or diurnal visual predators, such as a raptor or a whip snake (Fig. 3 and S3). In all body regions, JNDs for comparisons between cold and hot treatment colors in tetrahedral colorspace were either below 1 or exhibited bootstrap 95 % confidence intervals (C.I.) overlapping 1, with only one exception. Throat achromatic contrast between cold and hot measurements in W males was 3.18 JNDs (95 % C.I.: 1. 4, 5.0) to a conspecific lizard visual system.

4. Discussion

Temperature-driven, rapid changes in coloration have been described in some lizard taxa. Such color plasticity may affect social, antipredator, or thermoregulatory behavior (Dickerson et al., 2020; Geen and Johnston, 2014; Horr et al., 2023; Smith et al., 2016b), yet the causes and consequences of physiological color changes are seldom investigated (Figon and Casas, 2018). Here, using a color polymorphic lacertid lizard, we show that despite minor differences in metrics describing color spectral shape, temperature had no significant short-term impact on how color patches from different body regions are perceived by conspecifics or predators. Moreover, temperature did not affect existing sex and morph differences in color properties, suggesting that these dynamic changes have little to no functional consequences for wall lizards, at least within the context of our study.

Minor temperature-induced color changes mostly involved brightness and chroma while patch hue across different body regions was largely unaffected (Table 1). Only in UV-blue OVS we found a slight shift toward bluer wavelengths in the hot treatment (Fig. 2). Interestingly, UV-blue OVS and belly patches, which show variation in their ultrastructure (Andrade et al., 2019; E. Font unpub. data) and thus may differ in their color-producing mechanisms, showed similar changes in chroma in response to hot temperature. Both decreased and increased relative reflectance in the UV and green regions of the spectrum, respectively (Fig. 2). This suggests that the proximate mechanism of color change in response to temperature may be shared across types of colorations. Surprisingly, brightness of throat and belly patches, but not of dorsal or UV-blue OVS increased in hot compared to cold lizards. Environmentally-induced changes in brightness (or luminance) are more frequently reported in dorsal and/or lateral skin of lizards (e.g.

Table 2

Results from post-hoc Tukey's multiple comparison test for color metrics of the dorsum, throat and belly of lizards to identify differences among morphs. Shown are mean differences (MD), standard errors (S.E.) and test statistics for all pairwise comparisons. ns: not significant.

	$\lambda_{peak}/\lambda_{Rmid}$			C_G			B		
	MD (S.E.) (nm)	*Z*	*P*	MD (S.E.)	*Z*	*P*	MD (S.E.) (%)	*Z*	*P*
Dorsum									
W – O	−19.5 (6.1)	−3.20	0.004	0.024 (0.01)	2.28	0.057	ns	ns	ns
Y – W	10.5 (4.2)	2.53	0.030	−0.017 (0.01)	−2.46	0.036	ns	ns	ns
Y – O	ns	ns	ns	ns	ns	ns	ns	ns	ns
Throat									
W – O	−79.2 (4.9)	−16.24	<0.001	0.022 (0.006)	3.46	<0.001	6.46 (0.97)	6.66	<0.001
Y – W	46.5 (3.6)	12.83	<0.001	0.014 (0.004)	3.34	0.002	ns	ns	ns
Y – O	−32.7 (4.9)	−6.70	<0.001	0.035 (0.006)	5.71	<0.001	5.98 (0.95)	6.26	<0.001
Belly									
W – O	−76.2 (6.6)	−11.45	<0.001	0.023 (0.007)	3.46	0.001	7.94 (0.93)	8.53	<0.001
Y – W	38.7 (5.0)	7.71	<0.001	0.016 (0.005)	3.55	0.001	ns	ns	ns
Y – O	−37.4 (6.6)	−2.62	0.023	0.040 (0.007)	5.97	<0.001	7.03 (0.92)	7.63	<0.001

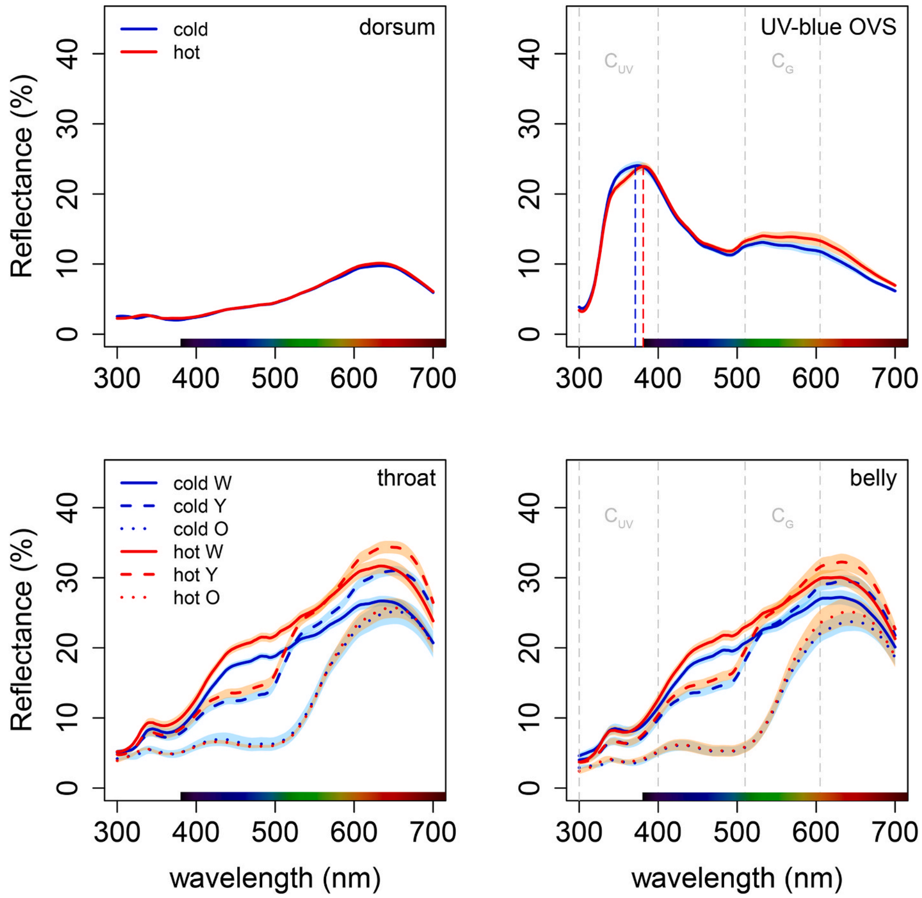

Fig. 2. Mean ± S.E. spectral reflectance of four body regions in cold (T = 25 ± 1 °C; blue) and hot (T ≥ 34 °C; red) lizards from orange (O), yellow (Y) and white (W) morphs. For clarity, different morphs and/or sexes are pooled in dorsum and UV-blue OVS, where all spectral curves are very similar. In the throat and belly, morphs are plotted separately. Where relevant, regions of C_{uv} and C_G, and the λ_{peak} for cold and hot lizards are indicated with dashed vertical lines. Sample sizes: 56 (dorsum and belly), 55 (throat), and 38 (UV-blue OVS) lizards.

Cooper and Greenberg, 1992; Sherbrooke, 1997; Smith et al., 2016b; Vroonen et al., 2012). From an adaptive lens, more exposed patches may benefit more from color changing capacity to better meet the conflicting demands of camouflage, communication and thermoregulation functions (Marshall and Stevens, 2014; Stuart-Fox and Moussalli, 2009). In contrast, here we found that the most exposed patches (dorsal skin and lateral UV-blue OVS) changed the least in brightness (Table 1).

Spectrophotometric readings offer an objective way to quantify color but need to be interpreted from a biologically relevant perspective that considers the ability of potential receivers to detect color differences. For example, the temperature-induced differences we found on color metrics for throat, belly and UV-blue patches were of smaller magnitude than intra-morph ventral color variation in this species (Aguilar et al., 2021). While some of this intra-morph color variation (e.g. red vs. orange) is partially discriminable by conspecifics, we found no evidence that temperature-induced color change can be perceived by other wall lizards nor by their main predators. The largest change we found was the throat patch in W males, which was distinguishable in achromatic terms between cold and hot lizards by conspecifics (Fig. 3), on account of changes to brightness. Temperature-induced changes in brightness

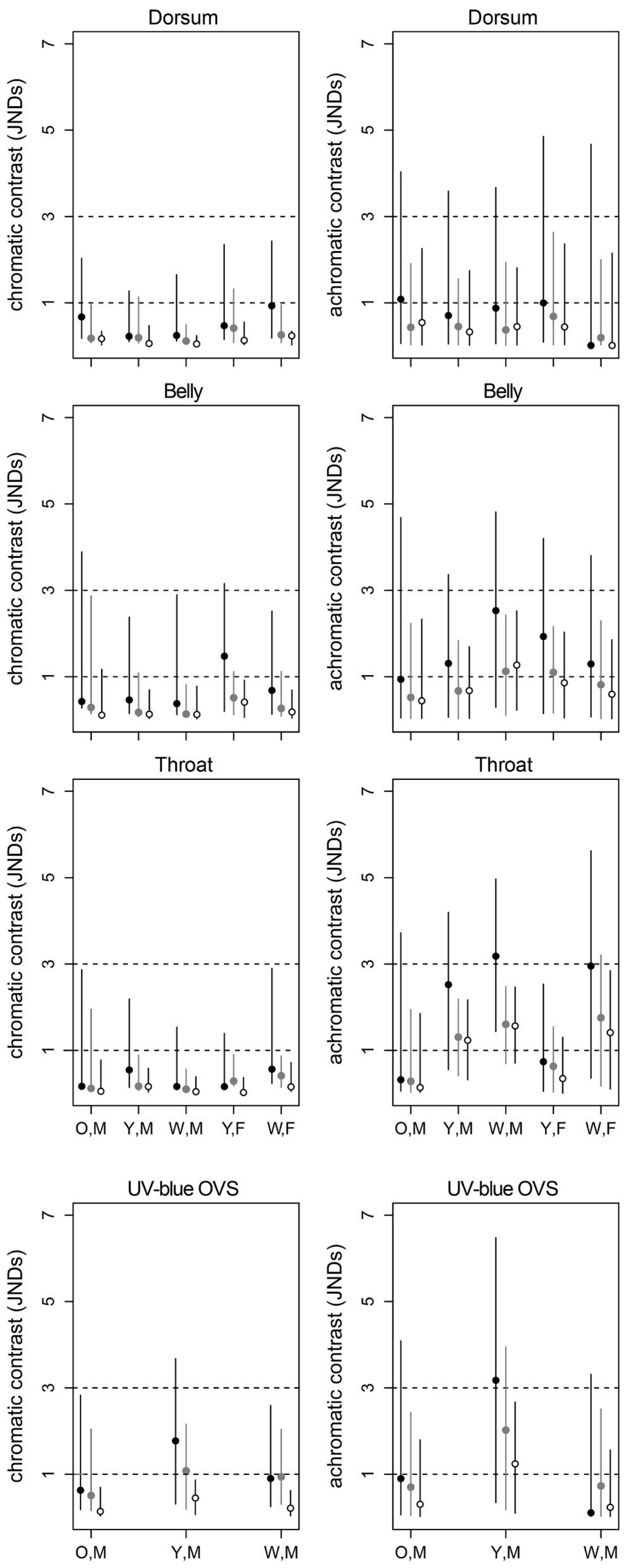

Fig. 3. Chromatic and achromatic color distances in units of just noticeable differences (JNDs) between cold and hot color measurements as perceived by conspecifics (black circles), an avian predator (gray circles), and a saurophagous snake (empty circles). The horizontal dashed lines indicate 1 and 3 JNDs thresholds. Points indicate means and 95 % bootstrap C.I. distances by morph (O = orange, Y = yellow, W = white) and sex (M = male, F = female). For overall JNDs between cold and hot coloration in each body region (pooling morph and sexes together) see Supplementary Fig. S2.

represented a <2 % reflectance difference between cold and hot lizards, less than the 7 % change in dorsal mean reflectance reported in bearded dragons (Smith et al., 2016a, 2016b), and well under the 15–37 % dorsal reflectance change exhibited by horned lizards (Sherbrooke, 1997) in response to a change in temperature. Throat coloration has been associated with mate choice and intrasexual competition in some lizards, acting as a sexual ornament (Olsson et al., 2013). However, despite several studies having been conducted, there is no evidence for a signaling role of throat coloration in *P. muralis*. Throat color is largely unrelated to body size, body condition and fighting ability (Pérez i de Lanuza et al., 2014), immunocompetence (Calsbeek et al., 2010), aggressiveness, space use and reproductive success (Abalos et al., 2020). White throats, in particular, are the least conspicuous of them all in their environments (Pérez i de Lanuza and Font, 2015), making the hypothesis of a W-limited signal even more unlikely.

In the UV-blue patches, which may function as a social signal of male fighting ability, λ_{peak} between hot and cold lizards differed by < 10 nm on average (Fig. 2). This difference is within the natural range of variation in peak spectral sensitivities described for *P. muralis'* photoreceptors (Martin et al., 2015) and much less than the change in hue (>30 nm) that results from iridescence on dorsal coloration (Pérez i de Lanuza and Font, 2016). In stark contrast, the blue patches of eastern fence lizards experience a near-100 nm shift in λ_{peak} soon after a change in temperature of similar magnitude to the one used in this study (Assis et al., 2020). Accordingly, the relatively minor color changes that we found here were inconspicuous. Perhaps these small changes were simply the result of passive alteration of some temperature-sensitive elements of the skin's ultrastructure, such as guanine crystals within iridophores, or of temperature-induced changes in the skin's osmolarity (Morrison et al., 1996), which have shown to impact spectral reflectance in other lizards (e.g. lacertids: Kuriyama et al., 2017; San-Jose et al., 2013; chameleons: Teyssier et al., 2015). The results from the visual modeling also indicated that there is substantial intrapopulation variability in the degree of plastic color change caused by temperature, which overall makes them unlikely to be perceived and used reliably in a signaling context.

Perhaps unexpectedly, we found no rapid changes in dorsal coloration with temperature, notably in terms of brightness, which influences the rate of heating and cooling in ectotherms. The dorsum is the body part most directly involved in *P. muralis* heliothermic thermoregulation (Braña, 1991). There is striking intra-specific variation in dorsal coloration in this species, ranging from brown to bright green, within and across populations, which has been hypothesized to respond to climatic or microclimatic differences (e.g. Ruiz Miñano et al., 2024). In *Anolis* lizards, body color dynamically changes from green to brown in high and low temperature, respectively (Hadley and Goldman, 1969) and similar physiological darkening has been reported in other lizards and snakes in reduced temperatures (Cooper and Greenberg, 1992). In *P. muralis*, dorsal reflectance differences on account of color seem to contribute very little to individual heating rates (Tosini et al., 1992) and it is likely that the potential contribution of color to thermoregulation is negligible in comparison to other factors, such as body size (Herczeg et al., 2007), site selection, orientation or postural changes (Pérez i de Lanuza et al., 2016). However, temperature-induced changes in the near-infrared part of the spectrum (NIR, 700–2600 nm), which was not measured here, cannot be discarded. NIR reflectance is usually independent from visible color (Stuart-Fox et al., 2017), it affects heating rates and thus could influence thermoregulation (Smith et al., 2016b; Stuart-Fox et al., 2017). Alternatively, dorsal coloration may be primarily involved in other functions such as camouflage, or UV protection, for which rapid color changes may be less critical. For example, while bearded dragons dynamically change color to improve both thermoregulation and camouflage, they predominantly adjust for camouflage, suggesting a more critical role of crypsis-related than temperature-dependent changes (Smith et al., 2016a). Other environmental factors such as changes in illumination, background coloration, environmental stressors, and hormonal activity (e.g. catecholamines, corticosterone) can induce physiological color changes in lizards (Cooper and Greenberg, 1992) and could be the focus of future studies.

The lack of evidence regarding rapid color change does not preclude the existence of color changes over longer timescales. For example, small temperature-induced changes could accumulate over time, or there may be seasonal or ontogenetic color changes. Long-term individual data indicates that *P. muralis* ventral coloration undergoes ontogenetic changes that can be perceived by conspecifics (Abalos et al., 2024a). Seasonal changes in dorsal coloration tracking shifts in background habitat have been reported in other *Podarcis* species (e.g. *P. raffonei*, Gambioli et al., 2024; *P. sicula*, Pellitteri-Rosa et al., 2020) and hypothesized to be an anti-predatory adaptation. However, the cause, the magnitude and biological relevance of these changes is yet to be determined. More generally, the environmental causes and mechanisms of plastic color change, particularly in lacertids, need further testing.

Where present, sexual dichromatism and color morph differences were maintained under cold and hot temperatures, demonstrating that interindividual differences in *P. muralis* body color can be assessed reliably at room temperature (the most common setting in which color measurements are taken) and compared safely across thermal contexts. The perceptual stability of wall lizard body coloration at different temperatures within its natural range and to different observers indicates that short-term, temperature-induced changes likely have little or no functional impact on thermoregulation, crypsis, or social communication. Instead, intraspecific variability of body coloration may more readily respond or be caused by alternative individual condition, environmental and historical factors, as is the case in other communication traits (e.g. Romero-Diaz et al., 2024), or mediated by mechanisms that take longer to cause an effect.

CRediT authorship contribution statement

Cristina Romero-Diaz: Writing – review & editing, Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Data curation, Conceptualization. **Enrique Font:** Writing – review & editing, Resources, Funding acquisition. **Guillem Pérez i de Lanuza:** Writing – review & editing, Resources, Investigation, Funding acquisition, Conceptualization.

Funding sources

This work was financially supported by the Spanish Ministry of Science and Innovation (MICINN) [project ref.: PID2019-104721 GB-I00].

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Acknowledgements

C.R-D. was supported by a César Nombela fellowship (ref: 2024-T1/ECO-31254) from the Comunidad de Madrid, and a fellowship (ref: CIAPOS/2021/111) from the Consellería de Innovación, Universidades, Ciencia y Sociedad Digital of the Generalitat Valenciana, co-financed by the European Social Fund (ESF).

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.jtherbio.2025.104262.

Data availability

Data are available from figshare (https://doi.org/10.6084/m9.figshare.29533793)

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