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ORIGINAL RESEARCH

Intraspecific variation and detectability of iridescence in the dorsal coloration of a wall lizard

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Abstract

Iridescence refers to the optical property of surfaces for which the reflected wavelengths depend on viewing geometry. Although iridescence underlies some of the most striking animal colours, the sensory stimulation elicited by iridescent spectral shifts in relevant observers has seldom been explored. Wall lizards (genus *Podarcis*), with remarkable intraspecific colour variation and possible iridescence, offer a unique opportunity to investigate how these traits interact to shape overall colour appearance. Here, we set out to study iridescence in *Podarcis liolepis* in two localities in which lizards differ in dorsal coloration: the València Botanical Garden (EB) and La Murta Natural Park (LM). To determine the presence of angle-dependent reflectance, we measured dorsal coloration at three different configurations (0°, 60° and 90° angles between incident light and observer location) in 87 lizards of either sex and used visual modelling to determine their detectability when viewed by conspecifics, raptors and humans. Our results show that *P. liolepis* dorsal coloration varies chromatically with sex and locality and also shows iridescence (i.e. reflectance peaks at shorter wavelengths with increasing viewing angle). Lizards from EB are brown dorsally, whereas most lizards from LM, especially males, show a green dorsal background coloration, reflectance peaking at shorter wavelengths in lizards from LM compared to lizards from EB. Angle-dependent shifts in peak location are smaller in LM males than in other groups, yet iridescence appears more pronounced (i.e. larger chromatic distances between viewing angles) in LM than in EB due to greater overlap between the involved waveband and receiver cone sensitivities. Additionally, *P. liolepis* dorsal iridescence may be more noticeable to humans and raptors than to lizards. Our findings suggest that intraspecific colour variation influences iridescence detectability across observers, underscoring the need for objective colour quantification and visual modelling to assess the ecological consequences of animal coloration.

Introduction

Iridescence refers to the optical property of a surface for which the spectral composition of reflected light changes with the angle between the observer and illumination source (i.e. hereafter, viewing geometry or angle) (Ospina-Rozo et al., 2022; Stuart-Fox et al., 2021). While iridescence describes angle-dependent shifts in the chromatic component of spectral shape (e.g. pointedness and wavelength of peak reflectance), the term specularity is used to refer to any angle-dependent achromatic changes (Stuart-Fox et al., 2021). Iridescence underlies some of the most striking animal colours and is a particularly challenging case for researchers, as its cellular basis, development and adaptive significance are still poorly understood. Iridescence is produced by the physical interaction between light and nanometre-scale variation in the arrangement and refractive indices of biological structures in the integument (Doucet & Meadows, 2009; Land, 1972; Onslow, 1923). While the mechanisms underlying iridescence have received considerable attention and significant progress understanding the mechanisms that distinguish iridescent from non-iridescent structural colours has been made (Debruyn et al., 2025; Meadows et al., 2009; Nicolaï et al., 2024; Seago et al., 2009), the perceptual aspects of iridescence remain comparatively understudied. The perception of objective shifts in spectral shape as subjective chromatic changes depends on the interplay between the range of reflected wavelengths and features of the receiver's visual system (Kelber & Osorio, 2010; Renoult et al., 2017). Therefore, research on iridescence must clearly differentiate between the physical, sensory and psychophysical aspects of the phenomenon (Cuthill et al., 2017; Ospina-Rozo et al., 2022). Although some studies have incorporated perceptual aspects by combining spectrophotometry and visual modelling, they often consider a single observer's vision (Fabricant et al., 2014; Pegram et al., 2015; Ng et al., 2022) or focus on iridescence's consequences for background-matching rather than perceived colour changes (Pérez i de Lanuza & Font, 2014a). Consequently, potential differences in iridescence detectability across multiple ecologically relevant observers remain unquantified. Addressing these differences is essential for capturing the full ecological and evolutionary significance of iridescent signals (Doucet & Meadows, 2009; Stuart-Fox et al., 2021).

Iridescence is relatively common in invertebrates (e.g. crustaceans (Parker, 2000); molluscs (Mäthger et al., 2009); insects (Miaoulis & Heilman, 1998; Seago et al., 2009)). Within vertebrates, iridescence has been most extensively documented in birds and fish, while fewer reports exist for reptiles and mammals (Denton, 1970; Lythgoe & Shand, 1989; Osorio & Ham, 2002; Prum, 2006). While iridescent colorations have been described in some species of lizards and snakes (Morrison, 1995; Rohrlich & Porter, 1972); reviewed in (Doucet & Meadows, 2009), their occurrence within the family Lacertidae (a widely distributed clade comprising about 360 species) is limited to two species: the Iberian emerald lizard, *Lacerta schreibeiri* (Pérez i de Lanuza & Font, 2014a), and the common wall lizard, *Podarcis muralis* (Pérez i de Lanuza & Font, 2016). Given the vast diversity of body colorations in lacertid lizards (Pérez i de Lanuza et al., 2013), iridescence within this group may be underreported. Non-directional reflectance properties (e.g. hue, saturation) may modulate the perception of iridescence, as seen in certain Rutelinae beetles, where broad-band golden reflectance can mask iridescence (Mitov, 2017; Ospina-Rozo et al., 2022). Wall lizards (genus *Podarcis*) exhibit substantial intraspecific colour variation (Aguilar et al., 2024; Brock et al., 2022; Miñano et al., 2021; Storniolo et al., 2021), which could influence the appearance of angle-dependent colour changes (i.e. the detectability of iridescence) by altering the range of reflected wavelengths. This interplay between colour variation and iridescence may lead human observers to perceive iridescence as being restricted to certain localities when, in fact, unrecognized iridescence could be a factor in the observed colour differences. Measuring iridescence is therefore essential—not only to determine whether reported colour differences persist independently of iridescence but also to assess geographic variation in iridescence and its interaction with intraspecific colour variation in shaping visual perception.

Podarcis liolepis (Boulenger, 1905; formerly *P. hispanica*) is a small lacertid lizard found in relatively dry Mediterranean areas with rocky substrates throughout the eastern Iberian Peninsula and the Mediterranean coast of France (Renoult et al., 2009). Dorsal coloration of *P. liolepis* is variable across its distribution range (Renoult et al., 2010), although this geographical chromatic variability remains understudied. Across most of its range, dorsal coloration features a brownish background with black spots or stripes, though this patterning is more subtle or even absent in some areas, such as the city of Valencia (i.e. *concolor* phenotype; Salvador, 2014). In contrast, in some areas, especially in the southern part of the species' distribution range, lizards often exhibit a green background dorsal coloration, especially males (Fig. 1). Although the taxonomic status of the species originating from the former *P. hispanica* complex is still under scrutiny, it is unlikely that this chromatic variation may result from hybridization between different species (Kaliontzopoulou et al., 2011; Renoult et al., 2009, 2010; Salvador & Carretero, 2014). In fact, despite the notable colour differentiation, lizards from localities towards the southern end of the species distribution range (including the city of Valencia) have been repeatedly found to cluster together in genetic analyses based on mitochondrial DNA (Bassitta et al., 2020; Caeiro-Dias et al., 2018; Renoult et al., 2009). Iridescence has been anecdotally reported in this

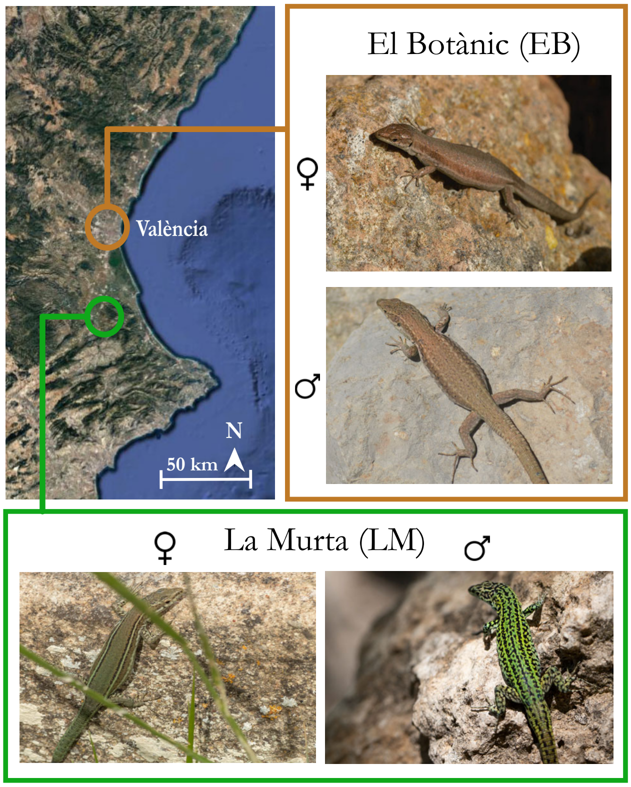

Figure 1 Satellite image of the Mediterranean coast of Valencia marking the position of the two sampling localities: EB (Botanical garden within the city of Valencia) and LM (La Murta, Alzira, 35 km south of Valencia). On the right and below, photographs of one representative male and female from each locality.

species, particularly on the ventral surface (Pérez i de Lanuza & Font, 2016). However, while dorsal iridescence is apparent in wild lizards (Fig. 2), it has never been objectively quantified, especially when considering its perceptual effects across different observers.

Our aims here are (1) to describe the spectral differences in the dorsal coloration of male and female *P. liolepis* lizards, (2) to confirm the existence of angle-dependent reflectance properties (i.e. iridescence) and (3) to explore the consequences of intraspecific colour variation on the detectability of iridescence by modelling the sensory response of a range of selected observers (i.e. lizards, raptors, humans). Our focus for this last objective is to explore whether intraspecific colour variation may consistently affect the detectability of iridescence across viewers. Therefore, we modelled the sensory response of lizards and raptors (two ecologically relevant observers possessing four different types of cones in their retina, yet differing in their peak wavelength sensitivities), as well as humans (i.e. possessing three types of cones and responsible for descriptions of intraspecific colour variation in field guides and scientific reports).

(a) El Bòtanic (male)

(b) La Murta (female)

Figure 2 Representative examples of iridescence in the dorsal coloration of *Podarcis liolepis* from the two examined localities. (a) Photographs of the same male from EB with different viewing geometries. On the left, the sun is located in front of the camera and thus the angle between incident light and observer viewpoint is wider than 90°. On the right, the sun is located behind the camera and therefore, the viewing angle is wider than 90°. (b) Photographs of the same female from LM with different viewing geometries. In the picture above, the angle between incident light and observer viewpoint is narrower than 90°. In the picture below, the viewing angle is wider than 90°. Change in the same individual female can be viewed in Video S1, available as Supplementary material.

Materials and methods

Subjects

In May 2021, we captured by noosing 38 adult *P. liolepis* (21 females and 17 males) in the Botanical Garden of the University of Valencia (EB, 39°28′ N, 0°23′ W; Valencia), and 49 adults (17 females and 32 males) in la Murta i la Casella Natural Park (LM, 39°07′ N, 0°21′ W; Alzira). We visited both localities, separated by approximately 35 km, in two consecutive days. Whereas all the lizards from EB are brown dorsally, most lizards from LM, especially males, show a green dorsal background coloration (Fig. 1). *P. iolepis* do not show drastic changes in dorsal coloration when handled, exposed to bright light, or retained in captivity for several weeks (pers. obs., Fig. S1). Thus, we placed lizards in moistened individual cloth bags (which minimizes stress and ensures ventilation) and transferred them to the Ethology lab at the University of Valencia (<1 h by car) for measurements. All lizards were released at their geotagged capture location in <36 h.

Spectrophotometry

To study dorsal coloration and its angle-dependent spectral properties, we measured dorsal reflectance in each lizard at three different viewing geometries, determined by the angle between the incident light and the measuring probe (0°, 60° and 90°). Spectrophotometric measurements were obtained by the same researcher (GPL) in a single session using a USB-2000 portable diode-array spectrometer and a PX-2 xenon strobe light source (Ocean Optics, Dunedin, FL) in a darkened room. We set the integration time to 70 ms, the number of readings per average to 20, and boxcar width to 10 (Badiane et al., 2017; Font et al., 2009). Spectra were recorded in 0.37-nm steps and expressed as per cent reflectance relative to a Spectralon diffuse (Lambertian) white standard (99% reflectance, Labsphere, North Sutton, NH, USA). A dark current reading was subtracted before data collection, and calibration was reassessed between individuals and viewing geometries. We restricted the reflectance spectra to the 300–700 nm range to cover the entire visual spectrum of lacertid lizards (Pérez i de Lanuza & Font, 2014b; Martin et al., 2015).

For the 0° set-up, we used a single probe combining six emissive fibres and a recording fibre held perpendicularly to the lizard's skin surface, that is, coincident normal measuring geometry (Andersson & Prager, 2006). 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. By preventing chimeric spectra in small (<1 mm in diameter) patches, this set-up ensures accurate sampling of dorsal skin, where patches typically exceed 2 mm (Badiane et al., 2017). For the 60° and 90° set-ups, we used two aligned emissive and recording probes mounted on a purpose-built goniometer which allows the probes to be rotated into a precise angular position (Meadows et al., 2011). Both probes were positioned symmetrically to the sample normal, ensuring that light is both emitted and collected symmetrically relative to the surface, hence minimizing directional bias in measurement. For 60° and 90°, we took two subsets of measurements to control for the lizard orientation in relation to the emissive and recording probes. Following Pérez i de Lanuza and Font (2016), we assessed repeatability along the longitudinal axis, as lateral scales are symmetric, but anterior and posterior ones may not be. Thus, we first placed lizards with their head closer to the emissive probe (i.e., head-to-tail) and then with their tail closer to the emissive probe (i.e., tail-to-head). Unlike the 0° set-up, we could not keep the distance from both probes to the subjects constant using an entomological pin. Hence, we measured lizards at the distance from both probes which maximized the signal-to-noise ratio in the real-time spectrophotometry software window. This distance was comparable between sampled lizards and reflectance standards, ruling out potential artefacts caused by the difficulty of keeping the sample perfectly flat. Reflectance data were recorded only after consecutive readings exhibited minimal variation over time (see Results for estimates of repeatability at the within-individual level). The order in which we took the 60° and 90° measurements was reversed among individuals, and all spectra with the 0° set-up were taken after the 60° and 90° measurements (see Fig. 3 for a photograph and a schematic diagram of this set-up).

Measurements taken at wider angles between the emissive and receptive probes will cover a larger elliptical area and are therefore more prone to result in chimeric spectra by contamination with non-target parts of the colour pattern (Akkaynak, 2014). To account for this, we focused on patches of background dorsal coloration exceeding the size of the diameter of the cone of light projected onto the lizard's surface. It is also worth noting that the only possible contamination in the lizard's dorsal surface is with melanic patches, which will result in an overall decrease in luminance with limited impact on chromatic features (Badiane et al., 2017). Despite calibrating between viewing geometries, we still observe a negative relationship between intensity and viewing angle, along with considerable noise in the UV range (300–400 nm) (Fig. S2). While genuine specularity cannot be ruled out, an artefactual origin remains possible, likely due to the tilt in the incident beam reducing the amount of reflected light reaching the receptive probe. Disentangling these effects would require analytical approaches that are not feasible for live lizards (Gruson et al., 2018). To address this, we restricted all analyses involving the 60° and 90° spectra to their chromatic aspects and standardized all values below 400 nm to the recorded value at 400 nm for each spectrum. This homogenization should not alter the results because the dorsal coloration has no UV reflection in this species (Fig. 1 in Pérez i de Lanuza & Font, 2016).

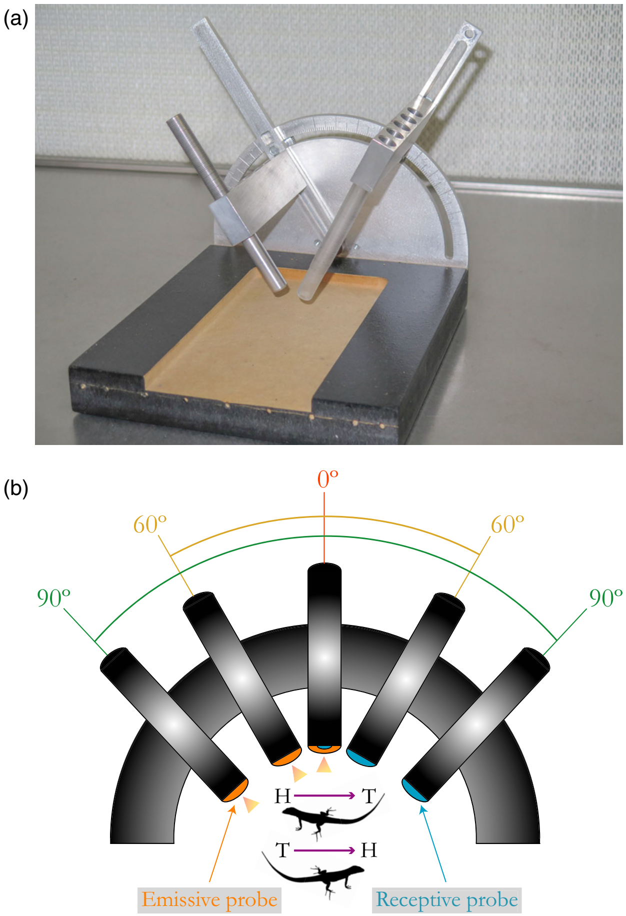

Figure 3 Experimental set-up for measuring angle-dependent dorsal reflectance in wall lizards. (a) Photograph of the apparatus used, consisting of two hollow tubes attached to a goniometer, which allow two independent optic fibres (i.e. an emissive and a receptive probes) to be rotated into a precise angular position over a platform, where the subject is positioned. (b) Schematic diagram illustrating the setup for measurements at angles of 0°, 60° and 90° between the emission and receptive probes. Measurements at 0° were not obtained using the goniometer but are represented here to show coincident illumination and recording points (normal measuring geometry). For the 60° and 90° set-ups, we used the goniometer, measuring each lizard at two orientations parallel to the plane defined by the two probes, first with their head closer to the emissive probe (head-to-tail), and then with their tail closer to the emissive probe (tail-to-head).

Statistics

Spectral data were analysed in R v.4.0.3 (R Core Team, 2022) using the package *pavo 2* (Maia et al., 2019). Spectra were smoothed (span = 0.2) and normalized by subtracting the minimum reflectance value across all wavelengths from each individual spectrum. This normalization enhances comparability by aligning all spectra to a common baseline, minimizing variability from slight probe distance differences (Badiane & Font, 2021; White et al., 2015). In natural spectra, brightness differences typically affect the entire spectrum, so this normalization does not mask biologically relevant achromatic variation (Fig. S2). For each spectrum, we calculated four standard variables: total reflectance (i.e. luminance; just for the 0° set-up), peak location and two measures of chroma (Endler, 1990; Kemp et al., 2015). We calculated total reflectance (Qt) as the sum of the reflectance across the visible range of lizards (i.e. $R_{300-700}$) and peak location as the wavelength of maximum reflectance (λ_{max}). To study the purity of green and brown dorsal colorations, we calculated green chroma (GC) as the relative reflectance in the middle-wavelength range (i.e. summing the reflectance in the 490–570 nm range and dividing it by total reflectance; $R_{490\text{-}570}/R_{300\text{-}700}$) and brown chroma (BC) as the relative reflectance in the long-wavelength range (i.e. $R_{571\text{-}700}/R_{300\text{-}700}$) (Pérez i de Lanuza et al., 2014; Endler, 1990).

We assessed differences in reflectance between the two spectra obtained per individual (head-to-tail and tail-to-head) at 60° and 90° by computing the wavelength-specific difference in per cent reflectance. We then averaged these differences for each locality and viewing angle. To estimate the 95% confidence interval (CI_{95}) for the overall difference, as well as for each locality and angle separately, we applied a bootstrapping approach with 1000 resampling iterations. Following Centore (2016), we also estimated the standard deviation and coefficient of variation at a nm scale for each individual and viewing angle, using the two paired spectra per individual at 60° and the two paired spectra at 90°. These values were then averaged for each locality and viewing angle as a proxy for repeatability. To estimate the mean difference in λ_{max} between measurements taken from the same individual at 60° and 90°, we fitted generalized linear models (GLMs) with lizard orientation as a fixed effect and lizard ID as a random intercept to account for repeated measurements. Pairwise contrasts were performed using estimated marginal means (EMMs) to obtain mean differences and CI_{95}. To assess the repeatability of λ_{max} measurements, we used the *rptR* package in R (Stoffel et al., 2017), which provides a framework for estimating intra-class correlation coefficients (ICC) based on mixed effect models. Uncertainty in repeatability estimates was quantified using parametric bootstrapping with 1000 resampling iterations. We conducted this analysis for the full dataset, which included both lizard orientation and viewing angle as fixed effects, and separately for each combination of locality and viewing angle to explore potential variation in repeatability across conditions. Overall, the variation between paired head-to-tail and tail-to-head spectra was minimal (see Results and Fig. S3) and consistent with published repeatability estimates for spectrophotometric data (i.e. CV < 30%) (Dhawale et al., 2013; Nunes et al., 2017). We therefore used the reflectance spectra averaged across orientations within individuals and viewing angles in all subsequent analyses.

To assess objective iridescence (i.e. angle-dependent shifts in peak location) across both localities and sexes, we fitted a linear mixed model on λ_{max} with a triple interaction between locality, sex and viewing angle as fixed factors. To further explore differences in the magnitude of objective iridescence between localities and sexes, we fitted a linear model on the difference between λ_{max} at 0° and λ_{max} at 90° (i.e. 0°–90° $\Delta\lambda_{max}$), including the interaction between locality and sex as fixed factors. To account for the repeated measurements nature of our data, we included lizard identity as a random factor in every mixed model.

All models were fitted using functions available in the *glmmTMB* package of R (Brooks et al., 2017). We graphically explored that residuals conformed to homoscedasticity and normality assumptions using the function *simulateResiduals* from the package DHARMa (Hartig, 2017). Model selection was conducted using the corrected Akaike's information criterion (AICc), implemented via the *dredge* function in the R package *MuMin* (Barton, 2022). Models with AICc differences (ΔAICc) < 2 are considered essentially as good as the best model, and models with ΔAICc < 6 should not be discounted (Burnham & Anderson, 2004; Richards, 2005; Symonds & Moussalli, 2011). To enhance the likelihood of retaining the best model, we expanded the selection threshold to ΔAICc < 4 (Wang et al., 2021). We examined interactions in the top-ranked models using estimated marginal means (EMMs), computed with the *emmeans* function in the homonym R package (Midway et al., 2020). Pairwise contrasts were performed with Tukey-adjusted *P* values to account for multiple comparisons (Lenth, 2023).

Visual models

We built visual models using the Vorobyev and Osorio receptor noise model (Vorobyev & Osorio, 1998) implemented in *pavo2* to assess colour discrimination in terms of chromatic and achromatic distances. We built visual models to test whether conspecifics, avian predators, and humans are able to sense the differences between the dorsal colorations of lizards when observed with different viewing geometries. Since detailed information on the visual system of *P. liolepis* is not available, we used cone sensitivities (UVS:SWS:MSW:LSW, 367:456:497:562 nm) and cone ratios (1:1:1:4) of its close relative *P. muralis* (Martin et al., 2015). In the absence of behavioural estimates of the correct Weber fraction for colour discrimination in lizards, we set the Weber fraction to 0.1 (as it has been estimated for bird long-wavelength sensitive class cones; Vorobyev & Osorio, 1998), and a standard daylight "D65" irradiance spectrum, as implemented in *pavo*. For the bird predator model, we used the violet sensitive (VS)-averaged cone sensitivity included in *pavo*, as it approximates the visual system of the Falconiformes (Ödeen & Håstad, 2003; Stoddard & Prum, 2008), which are the most typical avian predators of *P. liolepis* (Martin & López, 1990; Salvador, 2014). We used a cone ratio of 1:2:2:4 (UVS:SWS:MSW:LSW) and a Weber fraction of 0.1 (Vorobyev et al., 1998). Cone sensitivities used to model bird and lizard vision take into account the effect of oil droplet absorbance (Martin et al., 2015; Stoddard & Prum, 2008). For the human models, we used the LMS cone sensitivities (Stockman & Sharpe, 2000), cone ratios 0.057:0.314:0.629 (SWS:LWS1:LWS2; Hofer et al., 2005) and two different Weber fractions: 0.02 (as has been estimated for the human LWS cone class; Wyszecki & Stiles, 2000) but also 0.1 for the sake of comparison with birds and lizards.

Contrasts between pairs of colours were measured in units of just noticeable differences (JND), where one JND is the threshold of discrimination between two colours under good illumination conditions (Vorobyev & Osorio, 1998). However, as JND values between one and three could mean that two colours are barely discriminated, we also evaluated our results using a more conservative discrimination threshold of 3 JND (Santiago et al., 2020; Siddiqi et al., 2004). We used a distance-based PERMANOVA (Anderson, 2014) to test for statistical differences between dorsal colorations with respect to sex, locality and viewing angle. To do so, we ran a PERMANOVA procedure on the chromatic and achromatic contrasts using the *pairwise.adonis* function from the *pairwiseAdonis* R package (Martinez Arbizu, 2017), a modified version of the *adonis* function from the *vegan* R package (Oksanen et al., 2016) allowing for multilevel pairwise comparisons taking into account repeated measures. For analyses on reflectance spectra measured at 60° and 90°, we only ran the PERMANOVA procedure on chromatic contrasts since the procedure to measure reflectance with increasing angle geometry generates spurious luminance changes. When comparing reflectance spectra from the same individual taken at different angles, we accommodated the repeated measure nature of the data in the PERMANOVA by blocking contrasts at the within-individual level. Finally, as significance does not reliably indicate whether colour differences exceed the three JND discriminability threshold, we used bootstrapping to generate confidence intervals for mean colour distance while accounting for variability and normal uncertainty in the data. We used the *bootcoldist* function from the *pavo* package on the visual model described above with 1000 replicates and a 0.95 level for confidence intervals (Maia et al., 2019).

Results

Repeatability of reflectance with lizard orientation

The global mean standard deviation of per cent reflectance between corresponding head-to-tail and tail-to-head spectra was 0.66 (CI_{95} = [0.65, 0.67]). The global mean coefficient of variation between corresponding head-to-tail and tail-to-head spectra was 17.40% (CI_{95} = [17.24%, 17.56%]). The global difference in per cent reflectance between corresponding head-to-tail and tail-to-head spectra was 0.05%, with a CI_{95} including zero [−0.04%, 0.14%]. The global mean difference in λ_{max} between spectra of the same individual with different orientations was −1.03 nm with a CI_{95} including zero [−2.87, 0.81]. Lastly, the global within-individual repeatability of λ_{max} was 0.91 (CI_{95} = [0.87, 0.93]). Global averages are calculated from a total of 348 repeated spectra (87 at each orientation and angle). For results detailed by combination of locality and angle see Table S1. Close alignment between head-to-tail and tail-to-head spectra can be examined graphically in Fig. S3. See Table 1 for summary spectral variables, calculated within each combination of sex, locality, and viewing angle.

Variation in λ_{max} with sex, locality and angle

A total of 128 models fitted on λ_{max} were evaluated, with the top-ranked model including all three main effects (sex, locality and viewing angle) and their three-way interaction. This model had the lowest AICc value (AICc = 2080.8) and a model weight of 0.996, indicating overwhelming support compared to alternative models (i.e. next best model ΔAICc = 11.26, weight = 0.004; Table S2). The three-way interaction indicates that the effect of viewing angle on dorsal coloration varies by locality and sex (Fig. 4). At each viewing angle, coloration peaks at shorter wavelengths in LM than in EB and in LM males compared to LM females, though no sex difference is observed in EB. Additionally, while dorsal coloration shifts towards shorter wavelengths with increasing viewing angle in all groups, this shift is less pronounced in LM males than in their female counterparts and lizards from EB. Together, these patterns fully describe the three-way interaction between angle, sex, and locality. See Table S3 and Fig. S4 for pairwise Tukey contrasts among combinations of locality, sex and angle, based on estimated marginal means.

Table 1 Mean ± SEM total reflectance (Qt), green chroma (GC), brown chroma (BC) and peak location (λ_{max}) of *Podarcis liolepis* by locality (LM = la Murta, EB = el Botànic), sex (m = males, f = females) and viewing angle

Locality	Sex	N	Angle	Qt	GC	BC	λ_{max} (nm)
LM	m	32	0°	1262 ± 61	0.33 ± 0.02	0.60 ± 0.02	592.7 ± 4.4
			60°	—	0.45 ± 0.01	0.47 ± 0.01	558.2 ± 2.8
			90°	—	0.50 ± 0.01	0.39 ± 0.01	535.9 ± 1.5
	f	17	0°	1007 ± 46	0.23 ± 0.01	0.70 ± 0.01	625.6 ± 3.3
			60°	—	0.34 ± 0.02	0.60 ± 0.02	586.0 ± 3.4
			90°	—	0.46 ± 0.02	0.43 ± 0.02	550.4 ± 3.1
EB	m	17	0°	1653 ± 97	0.19 ± 0.00	0.75 ± 0.01	662.2 ± 3.5
			60°	—	0.25 ± 0.01	0.67 ± 0.01	617.1 ± 3.8
			90°	—	0.35 ± 0.01	0.55 ± 0.01	579.8 ± 3.6
	f	21	0°	1516 ± 58	0.18 ± 0.00	0.76 ± 0.01	662.6 ± 3.2
			60°	—	0.25 ± 0.01	0.68 ± 0.01	621.7 ± 3.6
			90°	—	0.56 ± 0.01	0.26 ± 0.01	583.9 ± 3.9

Total reflectance with the 60° and 90° set-ups are not reported because of the possibly artefactual negative relationship between intensity and viewing angle.

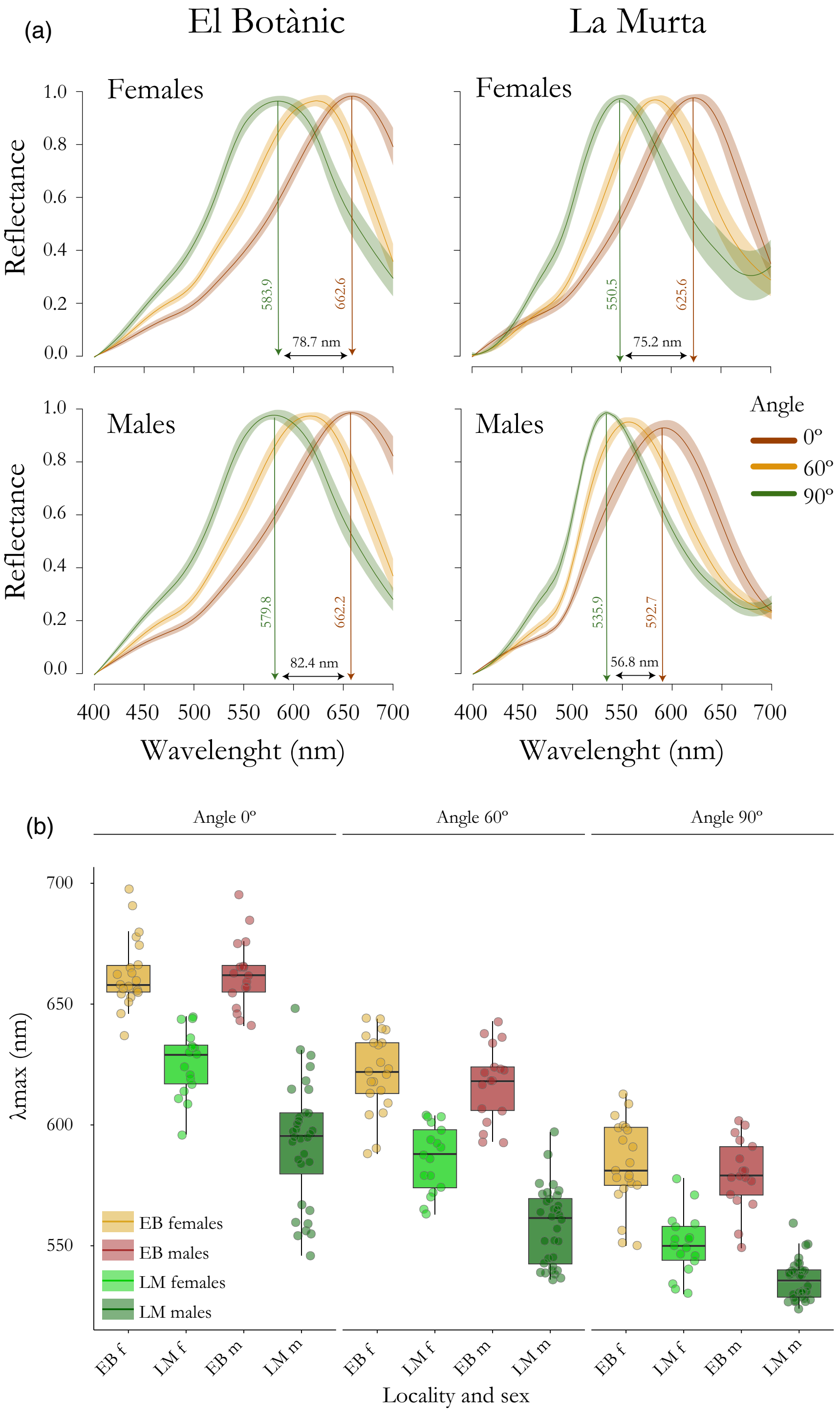

Figure 4 Chromatic variation in the dorsal coloration of *Podarcis liolepis* according to viewing angle, sex and locality. (a) Mean normalized reflectance spectra (line) and 95% CI (shaded area) of *P. liolepis* dorsal coloration measured at a viewing angle of 0°, 60° and 90°. For analysis, spectra were normalized by subtracting the minimum reflectance value at each wavelength. However, for improved visualization, spectra were further bounded between 0 and 1 by subsequently dividing by the new maximum reflectance at each wavelength (see Fig. S2 for non-normalized spectra). Peak location (λ_{max}) for 0° and 90° is indicated (single arrows) as well as 0°–90° spectral shift (0°–]90° $\Delta\lambda_{max}$; double arrows). (b) Jittered boxplots showing variation in λ_{max} with locality, sex, and viewing angle. The horizontal line represents the median, boxes indicate the interquartile range (IQR, 50% of the data), and vertical bars extend to the last observation within 1.5 IQR. Filled circles represent individual observations, with colour fill indicating combinations of locality and sex.

Table 2 Tukey-adjusted pairwise contrasts for differences in 0°–90° $\Delta\lambda_{max}$ (i.e. maximum angle-dependent variation in λ_{max}; nm) for *Podarcis liolepis* lizards (N = 87) across both localities and sexes

Contrast	Difference	Standard error	d.f.	*t* ratio	*P*-value	Significance
EB f—LM f	3.57	5.09	82	0.70	0.896	NS
EB f—EB m	−3.72	5.09	82	−0.73	0.885	NS
EB f—LM m	22.00	4.38	82	5.02	<0.001	*
LM f—EB m	−7.29	5.35	82	−1.36	0.526	NS
LM f—LM m	18.42	4.68	82	3.93	0.001	*
EB m—LM m	25.72	4.68	82	5.49	<0.001	*

d.f., degrees of freedom; difference, model-estimated difference in mean 0°–90° $\Delta\lambda_{max}$; EB, el Botànic; f, female; LM, la Murta; m, male.
*$P \leq 0.05$; NS, $P > 0.05$.

The top-ranked model among those fitted on 0°–90° $\Delta\lambda_{max}$ was found to be the saturated model, including the two-way interaction between locality and angle, and their corresponding main effects (AICc = 735.7, weight = 0.971). The next model, without the interaction, showed an ΔAICc above the established threshold (ΔAICc = 7.43, weight = 0.024; Table S4). This interaction arises because LM males exhibit a less pronounced peak shift compared to both LM females and EB lizards, despite no significant differences among these three groups (Table 2, Fig. S5).

Detectability of spectral differences

For every potential receiver examined, chromatic distances between spectra measured at different viewing angles (measured in JNDs) were larger in LM than in EB. According to our visual models, angle-dependent chromatic changes are more noticeable to conspecifics in LM than in EB (Fig. 5). In lizards from LM, angle-dependent changes are significant for every pair of angles compared (Table 3) and likely chromatically discriminable to conspecifics between 0° and 90° (JND ± CI_{95} > 3; Fig. 5). By contrast, angle-dependent changes in lizards from EB are less noticeable to conspecifics and perhaps not sensed as chromatically distinct (JND ± CI_{95} < 3; Table 3; Fig. 5).

To putative avian predators and humans, angle-dependent changes are significant for every pair of angles compared (Table 3), but iridescent shifts are probably only sensed as categorically distinct colours in LM (JND ± CI_{95} > 3; Fig. 5). Chromatic distances between paired spectra measured at different viewing angles are larger in raptors and humans with respect to lizards (e.g. mean 0°-90° JNDs in females from la Murta: lizards = 4.09, humans = 6.13, birds = 7.91).

Discussion

Our results show that the dorsal coloration of *Podarcis liolepis* varies with locality and sex, but also with viewing geometry. Dorsal reflectance peaks at shorter wavelengths in lizards from LM than in lizards from EB. Lizards from LM are sexually dichromatic, with males peaking at shorter wavelengths than females (irrespective of viewing angle) and therefore appearing greener to the human eye, while there are no sex differences in dorsal background reflectance in EB, where both males and females look brownish (Fig. 1, Fig. S4). We also found that the dorsal coloration of *P. liolepis* is iridescent, peaking at shorter wavelengths with increasing angle between incident light and observer viewpoint (Video S1, Table 1, Figs. 4 and 5). However, angle-dependent peak variation is not uniform across localities and sexes, with LM males exhibiting a less pronounced peak shift compared to both LM females and EB lizards, despite no significant pairwise differences among these three other groups (Fig. 4 and Fig. S5). The iridescent properties of *P. liolepis*' dorsal coloration are similar to those reported in the closely related *P. muralis* (Pérez i de Lanuza & Font, 2016).

Intra-specific variation in dorsal coloration along a green-brown axis is widespread in *Podarcis* lizards, sparking interest in its underlying mechanisms and functions (e.g. Feiner et al., 2024). This pattern has been documented across multiple species, including *P. muralis*, *P. vaucheri*, *P. pityusensis*, *P. lilfordi*, *P. melisellensis*, *P. gaigae*, *P. filfolensis*, *P. cretensis*, *P. peloponnesiacus*, *P. raffonei*, *P. tauricus*, *P. virescens* and *P. wagleriana* (Bauwens & Castilla, 1998; Cirer, 2020; Faria, 2020; Gorman et al., 1975; Podnar et al., 2004; Salvador, 2014; While et al., 2015). Sexual dichromatism along this axis is common in *Podarcis*, with males typically exhibiting green-biased dorsal coloration and females more often appearing brown (e.g., *P. bocagei*, *P. siculus*, *P. melisellensis, P. pityusensis*; Galán, 2008; Salvador, 2014; Storniolo et al., 2021). Dorsal coloration in wall lizards is typically cryptic and thus local adaptation to maximize background matching is often thought to explain geographical colour variation in *Podarcis* lizards (Pérez i de Lanuza & Font, 2015; Marshall, Philpot, Damas-Moreira, et al., 2015; Ortega et al., 2019). Differences between sexes could be explained by the greater intensity of sexual selection experienced by males, as there is evidence that male–male competition has played a key role in the evolution of male-biased conspicuousness in lacertid lizards (Abalos et al., 2020; Pérez i de Lanuza et al., 2013; While et al., 2015). In addition, although LM constitutes a more natural and vegetated setting than EB, lizards from both localities are preferentially found in similar patches of habitat (limestone outcrops in open areas), suggesting the possibility of consistent differences in detectability between localities (and sexes in LM). Future studies should investigate whether intraspecific variation in *Podarcis* dorsal colour reflects differences in the trade-off between predator avoidance and intraspecific

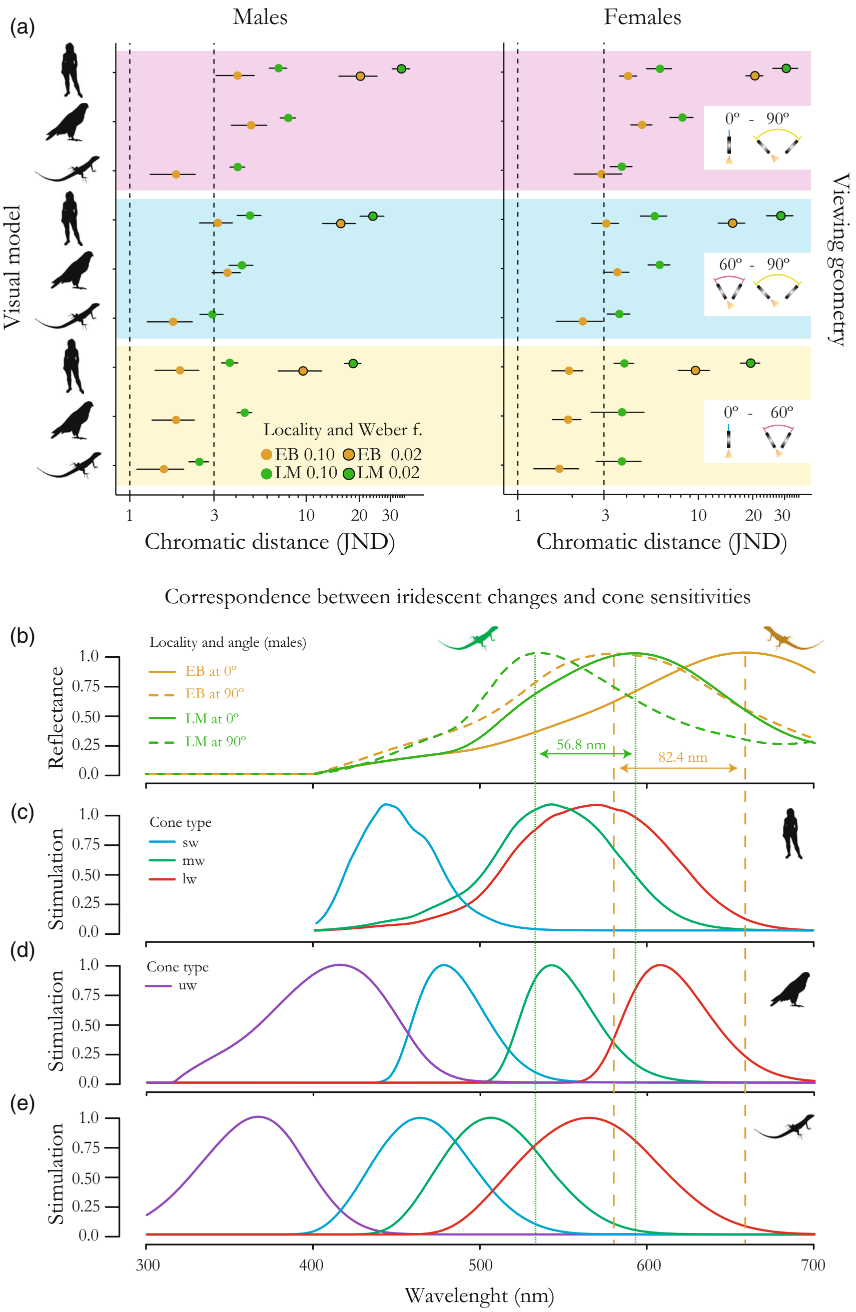

Figure 5 Visual models on *Podarcis liolepis* dorsal iridescence. (a) Mean and 95% confidence intervals of the within-individual chromatic distances between the dorsal coloration of *P. liolepis* lizards by sex and locality when viewed with three different viewing geometries (i.e. 0°, 60°, 90°), and according to the visual system of humans, VS raptors, and wall lizards (Weber fraction = 0.10). For humans, we also show distances estimated with a Weber fraction of 0.02 (Wyszecki & Stiles, 2000). JND stands for 'Just Noticeable Differences'. Two vertical dashed lines at 1 and 3 JNDs represent two theoretical discriminability thresholds. If the CI_{95} of a point includes a discriminability threshold, the two colours are not distinguishable at this threshold according to receiver cone sensitivities and relative abundance. (b) Correspondence between the iridescent spectral shifts in males from both localities and the cone sensitivities used for modelling (c) human, (d) raptor and (e) *Podarcis* vision. Vertical lines bound the waveband affected by peak shifts in LM (dotted green) and EB (dashed brown). Despite larger spectral shifts in EB than LM, reduced overlap with cone sensitivities leads to lower sensory stimulation (i.e. shorter chromatic distances). Note, however, that sensory stimulation and perceptual distance are not always linearly related. For visualization, sensitivity curves have been normalized to the maximum reflectance for each cone type in each species.

Table 3 Pairwise comparison among different viewing angles of *Podarcis liolepis* dorsal coloration (i.e. 0°, 60°, 90°), by sex (m = males, f = females) and locality (La Murta, El Botànic)

				Chromatic contrast ΔS			
Receptor	Locality	Sex	Pairwise	*F*	R^2	*P*	adj. *P*
Lizard	La Murta	m	0°–60°	11.03	0.15	0.001	**0.001**
			60°–90°	11.77	0.16	0.001	**0.001**
			0°–90°	38.717	0.38	0.001	**0.001**
		f	0°–60°	6.08	0.16	0.028	**0.020**
			60°–90°	5.73	0.15	0.001	**0.001**
			0°–90°	17.85	0.36	0.001	**0.001**
	El Botànic	m	0°–60°	2.67	0.08	0.041	**0.035**
			60°–90°	5.14	0.14	0.008	**0.004**
			0°–90°	5.04	0.14	0.001	**0.001**
		f	0°–60°	1.87	0.04	0.122	0.101
			60°–90°	2.33	0.06	0.072	0.067
			0°–90°	6.64	0.14	0.002	**0.002**
Raptor	La Murta	m	0°–60°	29.45	0.32	0.001	**0.001**
			60°–90°	26.0	0.30	0.001	**0.001**
			0°–90°	99.46	0.62	0.001	**0.001**
		f	0°–60°	13.69	0.30	0.001	**0.001**
			60°–90°	30.52	0.49	0.001	**0.001**
			0°–90°	63.34	0.66	0.001	**0.001**
	El Botànic	m	0°–60°	8.39	0.21	0.001	**0.001**
			60°–90°	35.54	0.53	0.001	**0.001**
			0°–90°	51.24	0.62	0.001	**0.001**
		f	0°–60°	9.51	0.19	0.001	**0.001**
			60°–90°	35.0	0.47	0.001	**0.001**
			0°–90°	50.25	0.56	0.001	**0.001**
Human	La Murta	m	0°–60°	13.09	0.17	0.001	**0.001**
			60°–90°	25.31	0.29	0.001	**0.001**
			0°–90°	64.80	0.51	0.001	**0.001**
		f	0°–60°	7.21	0.18	0.001	**0.001**
			60°–90°	24.06	0.43	0.001	**0.001**
			0°–90°	29.65	0.48	0.001	**0.001**
	El Botànic	m	0°–60°	3.13	0.09	0.003	**0.005**
			60°–90°	20.08	0.39	0.001	**0.001**
			0°–90°	27.40	0.46	0.001	**0.001**
		f	0°–60°	3.65	0.08	0.001	**0.002**
			60°–90°	16.98	0.30	0.001	**0.001**
			0°–90°	24.97	0.38	0.001	**0.001**

Contrasts were calculated using a distance-based PERMANOVA on the chromatic distances obtained when modelling the vision of lizards, raptors and humans (Weber fraction = 0.1). Significant contrasts ($P < 0.05$) are indicated in bold. *F* and R^2 represent pseudo-*F*-statistics and effect size estimates, respectively. Adj. *P* represents adjusted *P* values (Bonferroni correction).

signalling. This would require assessing subjective contrast against a range of locally available backgrounds, paired with information on the lizard's microhabitat choice, sexual dimorphism and the local abundance of potential predators (Marshall, Philpot, Damas-Moreira, et al., 2015; Marshall, Philpot, & Stevens, 2015; Marshall et al., 2016).

Relying solely on human vision to characterize animal coloration can lead to misleading conclusions, particularly when iridescence and other chromatic phenomena are involved (Brebner et al., 2024; Caves et al., 2019). For many *Podarcis* species, colour variation has often been described based on human perception—sometimes even from preserved museum specimens—without considering the visual systems of lizards or other ecologically relevant observers (Escoriza, 2024). Our findings emphasize the need to re-evaluate these descriptions considering the visual system of lizards and other (potentially) relevant observers, as well as viewing geometry, since iridescence can play a crucial role in the detection of colour for all receivers, including humans. In turn, colour descriptions coming from field guides, standard photography-based sampling, or citizen science projects may need to be updated with new information on the potential angle-dependent properties of animal coloration. In particular, methods based on photography should ensure images are captured under non-directional lighting conditions, such as in the shade, to minimize misleading effects of directional illumination on colour appearance

(Hemingson et al., 2024; Stevens et al., 2007; Troscianko & Stevens, 2015). Additionally, our results suggest that non-directional coloration can influence iridescence perception and do so differently across receivers. Although iridescence is present in *P. liolepis* from both studied localities, for all receivers examined, similar angle-dependent spectral shifts should result in a larger perceived hue difference in LM lizards than in EB lizards, at least based on visual models and their corresponding assumptions. This results from the existence of a sensory dimension to iridescence by which spectral shift is a poor predictor of stimulation in the observer (Fig. 5). Sensory stimulation increases when the range of variation encompasses a larger fraction of the overlap in sensitivity between more than one type of cone in the retina of the receiver (Kelber et al., 2003; Kelber & Osorio, 2010). For instance, the spectral shift between the 0° and 90° set-ups is as large in females from EB as in females from LM (~75 nm). Nonetheless, this spectral shift results in a relatively smaller chromatic distance to conspecifics in EB because the range of variation falls within 663 and 584 nm, while in LM, it falls within the 626–550 nm range (thus matching a larger fraction of the overlap between the MW and the LW *Podarcis* cones; Pérez i de Lanuza & Font, 2014b; Martin et al., 2015). Likewise, the spectral shift between 0° and 90° set-ups is larger in males from EB than in males from LM (EB = 82 nm; LM = 57 nm), but the chromatic distances to conspecifics are considerably larger in LM than in EB (EB = 1.83 JND; LM = 4.09 JND). Increased overlap between angle-dependent spectral changes and cone sensitivities is likely responsible also for our results considering other potential receivers, which according to visual modelling may perceive iridescent changes in *P. liolepis* dorsal coloration even better than the lizards themselves (Fig. 5). This is particularly evident in our avian vision models, which estimate larger chromatic distances compared to lizards (and slightly larger than humans) despite using the same Weber fraction of 0.1. Although iridescence being more pronounced in LM than in EB matches our own visual perception, we should be cautious when interpreting results coming from visual models. The relationship between differential sensory stimulation and perceptual distance is often intricate and non-linear (Luo, 2023; Vienot, 2002; Witzel, 2019). In the coral reef fish *Rhinecanthus aculeatus*, the relationship between behaviourally determined detectability of colour stimuli and model-based chromatic contrast against background varied across the colour space and followed a sigmoidal function (Cheney et al., 2019; Santiago et al., 2020). Therefore, results from visual modelling should be interpreted as providing information on the sensory input available to the colour-processing neural channels in a given species, which in turn interpret sensory information in species-specific ways (Baden & Osorio, 2019; Pérez i de Lanuza et al., 2018; Kelber et al., 2003; Osorio & Vorobyev, 2008).

The functional significance of iridescence in *Podarcis* lizards remains unclear. Several hypotheses have been put forward regarding the functional consequences of animal iridescence in contexts such as communication, predator avoidance, orientation, thermoregulation, photoprotection, friction reduction, water repellence and strengthening (Doucet & Meadows, 2009; Pérez i de Lanuza & Font, 2014a). Traits involved in intraspecific communication are usually tailored to be more noticeable to conspecifics than to unintended observers (Cronin et al., 2000; Marshall & Stevens, 2014). The animals' ability to exploit light directionality is key for iridescence to play a role mediating detectability to intended and unintended receivers (Stuart-Fox et al., 2021). For instance, blue head iridescence in *L. schreiberi* males enhances conspicuousness at midday when observed from wider viewing angles (more commonly experienced by conspecifics) rather than the acute angles typical of avian predators. This suggests an adaptive function related to signal detection and predator avoidance under a simplified scenario pending validation from field studies (Pérez i de Lanuza & Font, 2014a). A similar explanation is unlikely to apply to the dorsal iridescence of *Podarcis* lizards. First, dorsal iridescence in wall lizards lacks key adaptations tailoring detectability to intended receivers such as the anatomical localization and increased conspicuousness to conspecifics reported in *L. schreiberi* iridescent coloration (Pérez i de Lanuza & Font, 2015; Ortega et al., 2019; Storniolo et al., 2021). Second, wall lizards show decreased activity at the central hours of the day, when the viewing angles of avian predators and conspecifics should differ the most (Abalos et al., 2024; Castilla & Bauwens, 1991; Foa et al., 1992; Pérez Mellado, 1983). Third, *Podarcis* lizards often perch on vertical surfaces (e.g. stone-walls), adopting varied orientations in relation to observers and sunlight so that both conspecifics and predators are unlikely to differ significantly in their average viewing angles when observing the lizards' dorsal surface (Barbault & Mou, 1988; Pérez i de Lanuza & Font, 2016; Edsman, 1990). However, iridescence may still play a role in predator avoidance if a more changeable appearance may startle potential predators, thwart their ability to judge distances or hinder the acquisition of a search image (Doucet & Meadows, 2009; Kjernsmo et al., 2020; Stevens & Ruxton, 2019; Troscianko et al., 2018). Our finding that iridescence-induced changes in colour sensation may be more apparent to other potential observers than to lizards themselves underscores the need to explore the impact of lacertid dorsal iridescence on predator avoidance. However, we should also consider the possibility that iridescence may not confer any selective advantage and constitute a non-adaptive by-product of genetic drift or a correlate of other traits under selection (Doucet & Meadows, 2009; Snyder et al., 2012). For instance, iridescent properties have also been described in the ventral surface of *P. liolepis* (Pérez i de Lanuza & Font, 2016), an observation that is difficult to interpret from a purely adaptationist point of view (e.g. the ventral surface of lacertid lizards is rarely exposed to predators or conspecifics).

Altogether these findings imply that iridescence may be underreported in reptiles, introducing an additional dimension of variation to the already remarkable colour diversity of *Podarcis* lizards (Abalos et al., 2021; de la Cruz et al., 2023; Pérez i de Lanuza et al., 2013; Escoriza, 2024). Understanding the mechanisms underlying iridescence in these lizards remains an open question, as well as the selective pressures shaping its variation across sexes and localities. Our results show that intraspecific differences in non-directional colour properties influence the detectability of iridescence, suggesting that similar yet overlooked angle-dependent effects may exist in other taxa. Overall, our research demonstrates that objective colour quantification at different viewing geometries and the use of visual modelling to evaluate detectability by relevant observers is crucial to understanding the evolutionary causes and consequences of iridescence in nature.

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Author contributions

Conceptualization: F.C., J.A., G.P.L., E.F. Investigation: F.C., J.A., G.P.L., E.F. Statistical analysis: F.C. J.A. Writing—original draft: F.C. and J.A. Writing—review and editing: F.C., J.A., G.P.L. and E.F.

Conflict of interest

The authors declare no conflicts of interest.

Data availability statement

The dataset used for this study can be obtained at https://zenodo.org/records/15150400.

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Supporting Information

Additional Supporting Information may be found in the online version of this article:

Video S1. Video recording of the female in Fig. 2b, illustrating the change in apparent coloration as the camera moves from a narrow to a wide viewing angle. Two representative frames from the video can be found in the Supporting Information.

Table S1. Variation in percent reflectance and $\lambda_{\max}$ (wavelength of peak reflectance) between paired spectra ($N = 2$) of the same lizard obtained with different lizard orientations (head-to-tail and tail-to-head), presented by locality and viewing angle (EB, el Botànic; LM, la Murta).

Table S2. Model selection based on corrected Akaike's information criterion (AICc) exploring angle-dependent variation in $\lambda_{\max}$ (i.e. wavelength of peak reflectance) across both localities and sexes.

Table S3. Tukey-adjusted pairwise contrasts for differences in $\lambda_{\max}$ (wavelength of peak reflectance; nm) across combinations of sex (f, female; m, male), locality (EB, el Botànic; LM, la Murta), and viewing geometry (0°, 60°, 90°) for *Podarcis liolepis* lizards ($N =$ 87).

Table S4. Model selection based on corrected Akaike's information criterion (AICc) exploring variation in 0°–90° $\Delta\lambda_{\max}$ (i.e. maximum angle-dependent variation in $\lambda_{\max}$; nm) across both localities and sexes.

Figure S1. Repeated reflectance spectra of 16 males from LM showing green dorsal coloration and 16 males from Godella (6.3 km distant from EB) showing brown dorsal coloration.

Figure S2. Raw, non-normalized reflectance spectra illustrating variation in the dorsal coloration of *Podarcis liolepis* as a function of viewing angle, sex, and locality.

Figure S3. Differences in reflectance between paired measurements of the same lizards taken with different lizard orientations (head-to-tail and tail-to-head), presented by locality and viewing angle (EB: $N = 38$ head-to-tail, $N = 38$ tail-to-head; LM: $N = 49$ head-to-tail, $N = 49$ tail-to-head).

Figure S4. Forest plot depicting the results of pairwise contrasts on estimated marginal means (EMMs) of $\lambda_{\max}$ for different combinations of sex, locality, and viewing angle.

Figure S5. Jittered boxplots showing variation in 0°–90° $\Delta\lambda_{\max}$ (i.e. maximum angle-dependent variation in $\lambda_{\max}$; nm) across both localities and sexes.