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Research Article

Environmental determinants of interpopulation variation in chemical and visual signals in an insular lizard

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Understanding how communication systems evolve across heterogeneous environments requires examining multiple signalling modalities. In 2017 and 2018, we examined geographic variation in chemical signals of the insular lizard *Gallotia galloti* across 16 sites on Tenerife (Canary Islands). We analysed interpopulation variation in the lipophilic fraction of male femoral gland secretions in relation to vegetation cover (NDVI), local sex ratio, ectoparasite load and macroclimatic factors. In 2023, we also analysed visual signals of two lizard phenotypes that occur in contrasting habitats of Tenerife. We modelled the chromatic and achromatic conspicuousness of colour patches under both a conspecific (lacertid) and an avian predator visual system to examine habitat-dependent divergence in signal detectability. Chemical signal diversity decreased with increasing shrub vegetation cover, while males from sites with male-biased sex ratios exhibited greater individual chemical richness, consistent with heightened intrasexual competition. Populations in xeric habitats and with higher mite loads showed relatively higher proportions of α-tocopherol, whereas greener habitats were associated with higher proportions of steroids. In contrast, visual analyses revealed that lizards from densely vegetated habitats exhibited greater chromatic conspicuousness and larger chromatic volumes, particularly under the conspecific visual model. Achromatic contrast showed weaker habitat-dependent differentiation, consistent with the hypothesis that luminance divergence is constrained by predator-mediated selection due to the high luminance sensitivity of avian visual systems. Thus, in open habitats, persistent and chemically diverse secretions may enhance communication efficiency under increased exposure, whereas in vegetated environments chromatic visual signals appear to be amplified, potentially driven by sexual selection while constrained by predation risk. These findings suggest

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that environmental heterogeneity can promote complementary divergence across signalling modalities, highlighting the importance of integrating sensory ecology and social context to understand the evolution of animal communication.

Keywords: animal communication, ecological gradients, *Gallotia galloti*, local adaptation, sexual versus natural selection

Introduction

Animal communication systems are shaped by natural and sexual selection to optimize detection by the intended receivers (e.g. conspecifics) while minimizing detection by unintended receivers (e.g. predators) (Searcy and Nowicki 2005, Bradbury and Vehrencamp 2011). Signal transmission and detection are constrained by habitat-specific characteristics – such as climate, light availability, vegetation structure and background noise – that can affect the performance of different sensory modalities (Gómez-Catasús et al. 2022, Whitcher et al. 2024). Furthermore, environmental change driven by human activities, such as habitat fragmentation, acoustic and visual pollution, or changes in population densities, can further alter the effectiveness of communication signals and impose additional selection pressures (Rosenthal and Stuart-Fox 2012, Kelley et al. 2018). In response, animals can adjust their signalling behaviour or alter signal composition to maintain reliability and efficiency (Candolin and Wong 2012, Sierro et al. 2017).

Chemical communication is widespread in animal taxa (Müller-Schwarze 2006, Wyatt 2014). In lizards, chemical signals are often produced by the femoral or other exocrine glands and consist of complex mixtures of lipophilic and proteinaceous compounds (Mangiacotti et al. 2019, Martín and López 2024). The relative abundances of these secretions can vary due to environmental influences, including diet, climate, parasite load and social context (Martín et al. 2008, García-Roa et al. 2017a, Baeckens et al. 2018, Donihue et al. 2020). Environmental factors can influence not only communication but also population demography (e.g. density and local sex ratio), thereby modulating the strength of sexual selection and intrasexual competition (Clutton-Brock 2017, Pérez i de Lanuza et al. 2018, Cronin et al. 2022). In populations with male-biased sex ratios, for example, selection may favour increased investment in chemically rich or complex olfactory signals in this sex (West-Eberhard 1983, Donihue et al. 2020, Choi et al. 2022). However, empirical evidence for how social or environmental variation shapes chemical signals across geographic gradients remains limited (Baeckens et al. 2018, 2025, 2026, Donihue et al. 2020).

Visual signals are also integral to intraspecific communication in many lizards and are often subject to social context evolving both by natural and sexual selection (Pérez i de Lanuza and Font 2014a, Klomp 2016, Kawamoto et al. 2021). Colour signals, especially those with high chromatic and/or achromatic contrast, can improve detectability against complex backgrounds, enhancing their efficacy in specific visual environments (Marshall and Stevens 2014). Lizards can tune the complexity, hue, or placement of these signals to optimize conspicuousness to conspecifics while simultaneously reducing detection by predators (Macedonia et al. 2009, Hews et al. 2013). Some colour traits, particularly carotenoid-based colour (yellow to orange) patches, are largely, but not only, constrained by dietary intake and endocrine factors (Cote et al. 2010, San-Jose et al. 2012). In contrast, the expression of structural (blue/UV-blue) coloration is strongly modulated by a combination of melanophore content and layers of iridophores in the skin of lizards (Quinn and Hews 2003). Lizard colour traits are often sexually dimorphic and males under strong sexual selection typically exhibit more elaborate coloration (Pérez i de Lanuza et al. 2013). Furthermore, habitat itself, through its influence on vegetation cover, light conditions, and predator density, can mediate the benefits of investment in visual signalling (Théry 2001, Badiane et al. 2022, Lu et al. 2024). However, chemical signals are more persistent than visual signals and can remain effective in the absence of the producer (Martín and López 2013). Whereas the role of chemical signalization in female lizards has been rarely explored, due to an absence or reduction of femoral pores in many species, females do often have colour patches with a potentially similar signalling function as in males (Kopena et al. 2020). In some species, female coloration also has a sexual function (Belliure et al. 2018), although sexual selection may not be a primary force driving the evolution of female coloration in lacertid lizards (Pérez i de Lanuza et al. 2013).

Animals often use more than one sensory channel to communicate: visual displays, chemical cues, acoustic signals or combinations thereof. Studying multimodal communication is key, as the overall communication context may not be fully understood when focusing on a single communication channel. Several studies illustrate this: for example, lizards of the genus *Sceloporus* (Squamata: Phrynosomatidae) use chemical signals more when visual displays are reduced or lost (Pruett et al. 2016). In another case, the lizard *Liolaemus pacha* (Squamata: Liolaemidae) responds with a different combination of behavioral responses (tongue flicks and head-bob displays) to visual, chemical and combined stimuli, indicating synergy or interaction between modalities (Vicente and Halloy 2017). In geckos of the genus *Cnemaspis* (Squamata: Gekkonidae), visual traits (like colour patches), and chemical secretions both vary among species in ways that correlate with environment and receiver responses (Kabir et al. 2020). However, this is one of the first studies that models the conspicuousness of visual signals to conspecifics and predators and examines environmental predictors of chemical signals across ecological gradients of climate and vegetation in an insular lizard.

The western Canaries lizard *Gallotia galloti* (Squamata: Lacertidae), is a colour dimorphic species that is widespread

on the island of Tenerife (Canary Islands, Spain). Its UV-based coloration varies across seasons and habitats (Thorpe and Brown 1989, Bohórquez-Alonso and Molina-Borja 2014) and a previous study suggested the role of ventrolateral patches in intrasexual selection with males with blue-skewed patches winning contexts more often (Bohórquez-Alonso and Molina-Borja 2018). The colour phenotypes of *G. galloti* promoted the description of two subspecies on this island. Lizards with yellow stripes in highly dense shrub and humid habitats in the north of Tenerife were classified as *Gallotia galloti eisentrauti* (Fig. 1a–b), whereas lizards with prominent blue patches in less vegetated habitats in the centre and south of this island (Fig. 1c–d) were classified as *Gallotia galloti galloti* (Bischoff 1982). Current evidence suggests that northern and southern phenotypes show genetic differentiation. However, these differences could well be explained by distance and/or environmental differences. Additionally, these phenotypes do not constitute two distinct genetic clusters but rather appear as a continuum. In other words, genome-wide variation is correlated to, but does not explain colour differences (Brown et al. 2016). This further suggests that colour expression in *G. galloti* is controlled by a few genes of major phenotypic effect (Andrade et al. 2019). However, previous RADseq analyses only represent ~1–2% of the genome and subtle genomic differences between colour morphs can be easily missed or, if not missed, they represent a small portion of the genome-wide differences. Male chemical signals in this system also vary between colour phenotypes with higher relative proportion of cholesterol in *G. galloti galloti* and higher relative proportion of vitamin E in *G. galloti eisentrauti* (García-Roa et al. 2017b). Although chemicals were analysed in a single geographic site per subspecies, these differences suggested context-dependent communication strategies in *G. galloti* (García-Roa et al. 2017b). According to the same study, chemical composition also varied between spring and winter, with a relatively higher proportion of carboxylic acids, terpenoids and waxy esters in spring, and a relatively higher proportion of aldehydes and steroids in winter.

Here, we investigated how visual and chemical signals vary between populations of the lizard *G. galloti* in Tenerife. Specifically, 1) we examined population differences in the lipophilic chemical profiles of male femoral gland secretions.

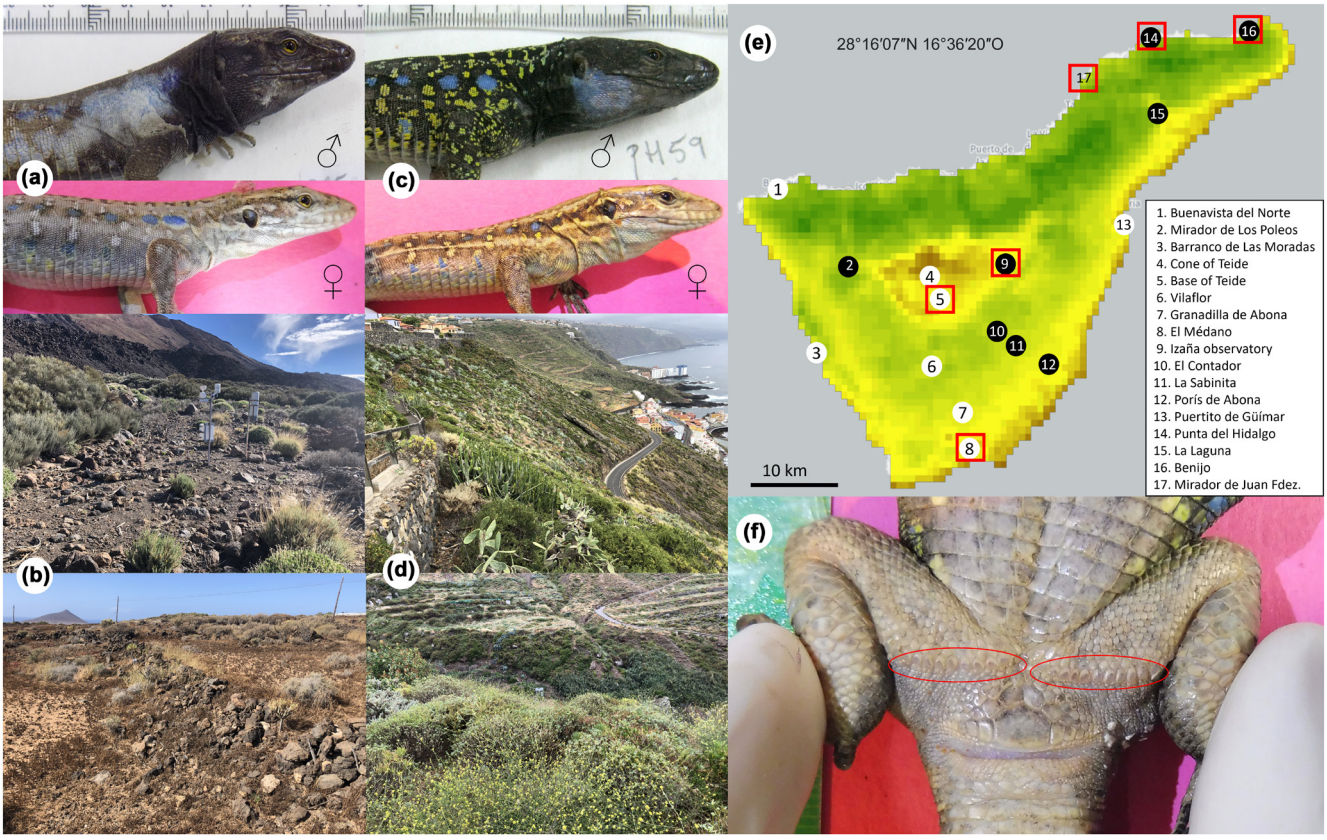

Figure 1. (a) Males and females of the phenotype 'galloti' and (b) xeric habitats of the center and south of Tenerife that it occupies. (c) Male and female of the phenotype 'eisentrauti' and (d) humid and more vegetated habitats that it occupies in the north. Note the relatively greener shrub vegetation and higher shrub cover of northern sites in 'd'. (e) Geographic location of sampling sites in Tenerife for femoral pore secretions of males of *G. galloti* represented in a vegetation (NDVI) model of Tenerife. The white and black circles represent sites sampled in summer 2017 (white) and 2018 (black). Red squares indicate the sites where spectral data was collected (14, 16, 17 – 'eisentrauti'; 5, 8, 9 – 'galloti'). (f) Precloacal femoral pores in a male of *G. galloti* are indicated with red ovals (note: only males have femoral secretions).

We expect that the diversity of lipid compounds in male femoral secretions will be lower in habitats with greener and denser shrub vegetation and that lizards will produce chemical signals with more compounds in contexts of higher intrasexual competition (lower local proportion of females) (Donihue et al. 2020). 2) We used visual models of a lacertid lizard and a raptor of genus *Falco*, one major natural predator of *G. galloti* (Carrillo et al. 2017), to investigate how colour patches of male and female lizards may be perceived by different receivers against field background colour items. We hypothesize that habitat-dependent divergence in visual signalling in *G. galloti* primarily occurs through chromatic channels, whereas achromatic contrast (luminance) is constrained by predation risk imposed by the high spatial acuity of raptor visual systems and favoured by a high density of cones and strong luminance sensitivity (Potier et al. 2018). This prediction is grounded on visual ecology, because luminance contrast contributes strongly to edge detection and spatial resolution in avian visual systems and increased achromatic contrast may elevate detectability to aerial predators, potentially constraining divergence in brightness-based signalling (Fialko 2023). Therefore, divergence in achromatic channels may be constrained by predation risk, resulting in weaker habitat-dependent differentiation compared to chromatic contrast. As a result, chromatic contrast should show stronger phenotypic and receiver-dependent differentiation than achromatic contrast. In turn, in more vegetated habitats, we expect that lizards will have more conspicuous coloration, i.e. higher chromatic contrast against background coloration (Théry 2001, Gomez and Théry 2004). Thus, we anticipate a stronger effect on lizards of phenotype 'eisentrauti', because they occur in more densely vegetated habitats, and for male lizards, due to strong sexual selection operating on this sex (Pérez i de Lanuza et al. 2013, Algar and López-Darias 2016). However, by including colour data also from females in the analyses, we can model how conspecifics and predators perceive sexually selected differences in colour. Altogether, results from this study will shed light on how multiple signals of this lizard species are shaped by ecological and social variation.

Material and methods

Geographic and anthropic context

Tenerife, the largest of the Canary Islands (28°16′N,16°36′O), lies in the subtropical region of the northern Atlantic, covering an area of 2034 km^2. The island supports a growing human population of > 900 000 residents and up to six million tourists annually (ISTAC 2018). With the Teide volcano in the centre of the island, Tenerife peaks at 3718 m a.s.l. The geography of the island promotes strong heterogeneity in climate regimes, habitats and human pressure.

Study species

The west Canaries lizard, *G. galloti*, is an omnivorous species whose diet shifts toward increased plant consumption with body size (Roca et al. 2005). It occurs across ecological and anthropogenic pressure gradients on the islands of Tenerife and La Palma (Canary Islands, Spain) with varying local abundances (Megía-Palma et al. 2024) and elevated densities of lizards in some coastal areas (Del Arco et al. 2006). This ecological flexibility makes it an ideal model for investigating how communication signals respond to social and environmental variability.

Lizard sampling for chemicals and local sex ratios (2017 and 2018)

In July 2017 and 2018, we sampled adult male and female lizards from 16 localities in Tenerife using baited pitfall traps (Fig. 1e). We sexed the lizards based on coloration, head size, and the presence of developed femoral pores in males. We calculated a local sex ratio index as the number of females divided by the number of males found in the traps per sampling site (Mills et al. 2007). Adults were defined as individuals measuring < 75 mm (female) or 100 mm (male) snout-to-vent length (SVL) (Salvador 2015). We counted ectoparasitic mites using a 10× magnifying glass and calculated the median abundance of mites on male lizards per locality (Megía-Palma et al. 2020). The lizards were not injured by the sampling protocol and were released in the same place where they had been captured within a few hours.

Human development, vegetation and bioclimatic indices

A human development index, normalized by area and biome, was obtained from a global dataset of 1 km covering human population pressure (population density), human land use and infrastructure (built-up areas, nighttime lights, land use/land cover), and human access (roads) (Sanderson et al. 2002, WCS and CIESIN 2005). Higher values of this index indicate more intense human pressure (Megía-Palma et al. 2020). A normalized difference vegetation index (NDVI) was extracted from satellite images taken during the first week of July 2017 and 2018 (eMODIS ver. 6.0 NASA) where the NDVI values are positively correlated with vegetation cover and primary production (Jenkerson et al. 2010). We also downloaded information on 19 bioclimatic modelled variables from the WorldClim-Global Climate Data 2.1 dataset, at 30 arc sec (~1 km^2) that is available for the period 1970–2000 (Fick and Hijmans 2017). These climatic data were validated in the field using automated dataloggers (Supporting information). We summarized the eight bioclimatic variables (bio) selected along with the geographic elevation of the sampling sites using a principal component analysis that produced a single factor with eigenvalue >1 and that explained 88.5% of the original variance (Supporting information). PC1 was negatively correlated with bio4 (Temperature seasonality), bio7 (Temperature annual range), bio14 (Precipitation of driest month), bio17 (Precipitation of driest quarter), and elevation and positively correlated with bio5 (Maximum temperature of warmest month), bio6 (Minimum temperature of coldest month), bio9 (Mean temperature of driest quarter) and bio10 (Mean temperature of warmest quarter).

Lipid fraction of male chemical signals

We collected waxy secretions of a total of 150 adult males (n = 4–13 per locality, $n_{2017} = 64$, $n_{2018} = 86$). A single researcher (RMP) used clean forceps to gently exert pressure on the skin area around the femoral pores (Fig. 1f) (García-Roa et al. 2017b). The waxy secretions were directly collected in glass chromatography vials equipped with 250 µl glass inserts and teflon-lined stoppers (Aijiren, Quzhou, China) that were preserved at -20ºC (García-Roa et al. 2017b). Blank control vials containing no secretion were used during further chemical analyses. Before analyses, male femoral gland secretions were dissolved in 200 µl of n-hexane (99%; obtained from JT Baker, Deventer, the Netherlands). We analysed the samples using a gas chromatograph (GC) (Agilent 7890A) coupled to a mass spectrometer (MS) (Agilent 5975C with Triple-Axis HED-EM detector). Further methodological details are provided in the Supporting information. Our analyses focused on the lipophilic fraction of femoral gland secretions and not on their proteins because, at least in some *Podarcis* wall lizards (Squamata, Lacertidae), the protein fraction is involved in individual identification (Mangiacotti et al. 2019) and because the composition and complexity of the two fractions can be strongly correlated (Mangiacotti et al. 2023). Impurities identified in the control vial samples were not considered.

Data analyses were performed using Software Xcalibur 2.2 (Thermo Fischer Scientific). For the initial identification of compounds embodied in femoral gland secretions, we used the NIST/EPA/NIH 2010 computerized mass spectral library, through chemical mass spectra comparison, and we also used published information on chemicals of the same lizard species (García-Roa et al. 2017b). When possible, identifications were confirmed by comparison of spectra and retention times with those of authentic standards (Sigma-Aldrich Chemical). To calculate the relative proportions of each compound in each sample, we used the percent of the total ion current (TIC = the total abundance of all ions detected within a defined mass range over the course of the analysis). The proportion was calculated by dividing the TIC area of each individual peak – compound – by the total TIC area of all mass spectral peaks belonging to the same scan and multiplying by 100 (García-Roa et al. 2017b).

Diversity indices and functional summary of the lipophilic fraction of male chemical signals

We calculated 1) the mean richness of compounds per individual male (MCCR), as the average of the sum of different chemical compounds per male in that locality; 2) the chemical compound richness per locality (LCCR), as the total sum of different chemical compounds in that locality; 3) the mean Shannon diversity of chemicals per individual (MSDC) in that locality; and 4) the mean Shannon diversity of chemicals per locality (LSDC), calculated from the individual means. Furthermore, we classified chemical compounds into seven major functional classes (aldehydes, alcohols, fatty acids, ketones, terpenoids, steroids and tocopherol) (Martín and López 2014). We calculated the mean value per locality of each of these seven functional classes, and a principal component analysis (PCA) was performed to summarize them using a varimax normalized rotation of factors (Budaev et al. 2010). We retained the first two components ($PC1_{chemicals}$ and $PC2_{chemicals}$) because they had eigenvalues > 1.

Statistics analysis of the lipophilic fraction of male chemical signals

Spatial autocorrelation (SAC)

We used Moran's matrix I, where the null hypothesis equals the spatial independence of the data (Legendre and Legendre 1998). The following variables were spatially independent: MCCR (SD = 0.056, p = 0.46), LCCR (SD = 0.064, p = 0.66), MSDC (SD = 0.060, p = 0.76) and LSDC (SD = 0.060, p = 0.31). However, the PC1 chemicals (SD = 0.055, p = 0.049) and the $PC2_{chemicals}$ were spatially autocorrelated (SD = 0.062, p = 0.009). To control SAC in the models analysing $PC1_{chemicals}$ and $PC2_{chemicals}$, we included as predictors an inverse distance-weighted function of neighbouring response (autocovariate) (Dormann et al. 2007).

Model building

Statistical analyses were performed in R ver. 4.0.4 (www.r-project.org). The sampling year (2017 or 2018) and the colour phenotype (i.e. 'galloti' or 'eisentrauti') were established as factor predictors in a general linear model. We included local sex ratios as continuous predictors (as a proxy of intrasexual competition), median abundance of mites per site in males (as proxies of parasitic pressure), a normalized difference vegetation index (NDVI) (and index that is used to quantify vegetation greenness and approach vegetation density, Weier and Herring 2020), the human activity index (a proxy of human footprint pressure), and the two bioclimatic/elevation principal factors. We checked the multicollinearity of the predictors in the models using a variance inflation factor (VIF) criterion (Schroeder et al. 1990). We also checked the parametric assumption of model residuals by simulating the residual distribution with the package 'DHARMa' (Hartig 2024). All models for the chemical composition indices of male lipids in femoral secretions showed a good fit to a Gaussian error distribution. A weighting term, namely, the corresponding sample size of lizards sampled for chemicals per locality, was included in the models.

Model selection and model averaging on male chemical signals

We analysed the geographic variation in the relative abundance of lipids in male femoral secretions performing model selection and model averaging on the Gaussian models with the functions *dredge()* and *model.avg()* of the package 'MuMIn' (Bartoń 2024). This statistical method is recommended for small sample sizes because it removes effects with low influence for the final model (Hegyi and Garamszegi 2011). For this, the models were considered sufficiently informative when their $\Delta AICc \leq 2$ (Burnham and Anderson 2004). We calculated the relative importance of each predictor as the

frequency in which it appeared in the equally likely models. Furthermore, a final model was calculated by averaging all equally likely models. We calculate the adjusted SE of the z-standardized ß coefficient ± adjusted SE of the predictors in this final model.

Colour measurements of male and female lizards (2023)

In April 2023, we collected spectral data from the colour patches of 100 adult lizards (52 males and 48 females). Specifically, 49 lizards (26 males and 23 females) were sampled in the north of Tenerife for phenotype 'eisentrauti', which were clearly differentiated because they have yellow stripes, and 51 lizards (26 males and 25 females) in the centre and southern localities for phenotype 'galloti', which only had UV-blue patches (Fig. 1c). Each of the colour phenotypes was sampled at three different localities (5–6 individuals by sex and locality, Fig. 1e). We collected the spectral reflectance from their first and second eyespots, first and second ventrolateral patches, cheek, yellow patch and dorsum (Supporting information). This represents most of the colour patches they have (Fig. 1a). The yellow patch as well as the blue cheek is only present in 'eisentrauti', so to obtain a proper comparison, we measured reflectance in individuals of phenotype 'galloti' in the same body regions. In addition, we sampled a single reflectance spectrum for each of a total of 27 background items (that is, stones, soil, flowers, leaves; Supporting information) on the same sites of Tenerife where colour of lizards was measured. We chose these items based on their apparent representativeness of the sampled habitats and to be used as a background colouration in the visual models (below). We measured their reflectance spectra in the field as well as the colour patches of lizards using a Jaz portable spectrophotometer connected to a pulsed xenon lamp (Ocean Optics). We used as reference spectrum one measurement performed on four layers of white-matte Teflon tape mounted on top of a commercial white standard that provided a flat and constant reference white surface. These layers of clean teflon were replaced by new ones every time they showed signs of dirt. The probe of the spectrophotometer was fitted inside a fully opaque plastic piece that enabled placing the spectrometer probe at constant distance of 3 mm from the measured surface, forming an angle of 90º, and avoiding environmental light to bias the spectral measurements (Megía-Palma et al. 2022). We used an integration time of 10 ms and a boxcar width of four units.

We built two visual models based on an ultraviolet sensitive (UVS) lacertid and a violet sensitive (VS) predatory bird and measured the conspicuousness of the coloration of *G. galloti* against natural backgrounds. To test whether colour patches of lizards are more visible to conspecifics than to predators, conspicuousness was measured as chromatic (i.e. chromaticity) and achromatic (i.e. luminance) distances, expressed as just noticeable differences (JND). JND values over three units were considered discriminable, whereas those between one and three units were considered discriminable under good light conditions (Siddiqi et al. 2004). For the predator model, we focus on the common kestrel *Falco tinnunculus*, as *G. galloti* individuals represent one of the main diet items of this species in Tenerife (Carrillo et al. 2017). To model its vision, we assumed the same parameters as Goedert et al. (2021) for a close relative, *Falco sparverius* (405, 449, 504 and 567 nm, corresponding to VWS, SWS, MWS and LWS cones in proportions of 1:2:3:3). For the lacertid model, we assumed cone absorbances and abundances from another species in the same family, *Podarcis muralis* (367, 456, 497 and 562 nm, corresponding to UVWS, SWS, MWS and LWS cones in proportions of 1:1:1:4; Martin et al. 2014). To fit these models, we used the *sensmodel* function of 'pavo' ver. 2.7.1 (Maia et al. 2019), which is based on the templates of Govardovskii et al. (2000) and Hart and Vorobyev (2005). For both models, we used the receptor noise limited model (Vorobyev and Osorio 1998). We used an irradiance spectrum corresponding to daylight conditions 'D65' implemented in pavo for both visual models. We used the same irradiance spectrum (instead of irradiance spectra from every site where spectral data was collected) to avoid introducing biases related to the date and climatological conditions associated with each of the sampling events. The Weber fraction value was set to 0.1 for the visual model of *Falco* (Olsson et al. 2018) and to 0.05 for the lacertid visual model (Martin et al. 2014). To estimate the conspicuousness between the colour patches of *G. galloti* and the items present in their habitats, we retained all comparisons between colour patches and background elements. Pairwise comparisons between lizard colour patch and field background colour item resulted in 16 200 chromatic/achromatic JND scores per visual model. Given that the conspicuousness between colour patches greatly depends on the background against which they are compared (Caves et al. 2024), we used an averaged dorsum spectrum from the darkest (nearly black) dorsal surface of the lizards as a reference background that was measured in every case avoiding, in 'eisentrauti', the dorsal yellow stripes. The estimates of JND were not averaged per phenotype, instead they were obtained separately for each sex (×2) and colour phenotype (×2) due to the differences they show in their dorsal spectra (Supporting information). To examine our hypothesis that chromatic contrast would show stronger phenotypic and receiver-dependent differentiation than achromatic contrast, we performed a pairwise within-colour patch analysis with both chromatic and achromatic contrasts simultaneously set as response variables and the three-way interaction between visual model, lizard phenotype and sex, and all surrogate two-way interactions and main effects, as predictors. We inspected the resulting model residuals to ensure that they conformed to assumptions of normality, homoscedasticity, autocorrelation and kurtosis. We performed a Bonferroni post hoc test to inspect for significant differences across levels of the three-way interaction.

Further, we explored whether colour patches showed greater variability under the conspecific visual model, which would suggest that colour may be optimized for intraspecific communication. To do so, we used the *voloverlap* function from 'pavo' ver. 2.7.1 (Maia et al. 2019) to calculate the

chromatic volume (i.e. the spectral variability of a colour as perceived by the receptor's tetrachromatic vision represented in a 3-dimensional visual space) of each colour patch of lizards from the six sampling sites separately. We did this using the visual models built using the *Falco* and *Podarcis* cone absorbances and proportions. Therefore, this analysis provided a single chromatic volume score per colour patch (resulting from all individuals analysed per locality), receptor visual model and locality. For this analysis, we used an idealized homogeneous background (i.e. constant illuminance value of 1 across all wavelengths), which also allowed us to obtain the chromatic volume of the dorsum. Then, we fitted a generalized linear mixed model (GLMM) with chromatic volumes as response, lizard colour phenotype, receptor visual model (i.e. conspecific or predator), and their two-way interaction as fixed factors. We also included the body region and locality as random terms in the analysis.

Results

Lipophilic fraction of male chemical signals

We identified a total of 63 lipophilic compounds in the secretions of the femoral gland of 150 adult males (mean ± SE = 9.4 ± 0.6 males/locality). The minimum number of compounds in a single individual was 25 and the maximum 55 (mean ± SE = 44.9 ± 0.4 compounds/individual), while at a locality level (considering all the individuals sampled in that locality), the number of compounds ranged between 55 and 63 (mean ± SE = 58.6 ± 0.7 compounds/population).

The main lipophilic compounds found in femoral secretions were steroids (44 different compounds and 82.08% of the TIC area), with cholesterol and campesterol as the main lipids, followed by α-tocopherol (15.68%). We also found other minor compounds, such as seven fatty acids and their esters (1.04), five alcohols (0.50), four aldehydes (0.45), one terpenoid (squalene) (0.22) and one ketone (0.03%) (Supporting information).

The average model for the mean chemical richness per individual (MCCR), resulting from the average of three equally likely models (Supporting information), indicated that MCCR was best predicted only by the lizard sex ratio (importance = 1.00, estimate = −19.71 ± 6.58, z = 2.99, p = 0.003). The average number of different lipids in the femoral secretions of male lizards was the highest in those localities with the lowest proportion of females (Fig. 2a).

The average model for the chemical compound richness per locality (LCCR) was derived from the average of two equally likely models (Supporting information). It indicated that LCCR was best predicted only by the median abundance of mites found on male lizards (importance = 0.92, estimate = −0.04 ± 0.02, z = 2.17, p = 0.030). The total number of compounds per locality was lower where males had more mites (Fig. 2b).

None of the predictors tested explained the variance in the Shannon diversity of compounds per male (MSDC) (Supporitng information). The average model for the diversity of chemicals per locality (LSDC) resulted from averaging two equally likely models (Supporting information) and indicated that the LSDC was best predicted only by the vegetation index (importance = 1.00, estimate = −0.91 ± 0.37, z = 2.49, p = 0.013). That is, Shannon's diversity of chemicals was lower in those localities with greener vegetation (Fig. 2c).

The PCA performed on the seven functional classes of chemical compounds produced two factors with eigenvalues > 1 that together accounted for 83.14% of the observed variance in mean chemical secretions in 16 localities. $PC1_{chemicals}$ had an eigenvalue of 3.94 and represented 56.28% of the variance. Aldehydes, alcohols, fatty acids, ketones and terpenoids had strong and positive correlations with $PC1_{chemicals}$ (Table 1). A single model explained the variance between populations in $PC1_{chemicals}$ (Supporting information) and indicated that the year of sampling was the most important predictor (importance = 1, estimate = 0.84 ± 0.23, z = 3.36, p < 0.001). Indeed, lizard femoral secretions contained more aldehydes, alcohols, fatty acids, ketones and terpenoids in 2017.

$PC2_{chemicals}$ had an eigenvalue of 1.88 and accounted for 26.86% of the variance in chemical compounds. Steroid compounds were negatively correlated with $PC2_{chemicals}$, while tocopherol was positively correlated with it (Table 1). A single model resulted from the selection of the model (Supporting information). The normalized vegetation index, the median abundance of mites in male lizards, and the colour phenotype best explained the interlocal variation of the $PC2_{chemicals}$ (Table 2). The mean ± SE percent of tocopherol was lower in phenotype 'eisentrauti' (11.86 ± 1.58%) than in phenotype 'galloti' (17.10 ± 1.57%). On the contrary, the mean ± SE for steroids was higher in phenotype 'eisentrauti' (86.99 ± 1.55%) than in phenotype 'galloti' (80.41 ± 1.70%) (Fig. 2d). Male chemical signals had relatively more tocopherol and less steroids in those localities where they had higher mite loads (Fig. 2e), while the opposite occurred in localities with higher normalized vegetation indices (Fig. 2f).

Colour conspicuousness

The conspicuousness estimates showed high variability, but most fell above the 3 JND units threshold (Supporting information), suggesting that colour patches of *G. galloti* can both achromatically and chromatically be discriminated from the background by the visual models of both receivers tested. Interestingly, we found a significant effect of the three-way interaction between colour phenotype, visual model, and sex that explained the pairwise within-colour patch differences in achromatic and chromatic distances (F = 12.1, p < 0.001) (Table 3). This indicated that colour patches of males of the 'eisentrauti' phenotype showed the highest chromatic contrast (JND) under the lacertid visual model (Fig. 3, Supporting information). Importantly, the differences in achromatic contrast were significantly lower than for the chromatic one (Fig. 3, Supporting information). This suggests, in line with our

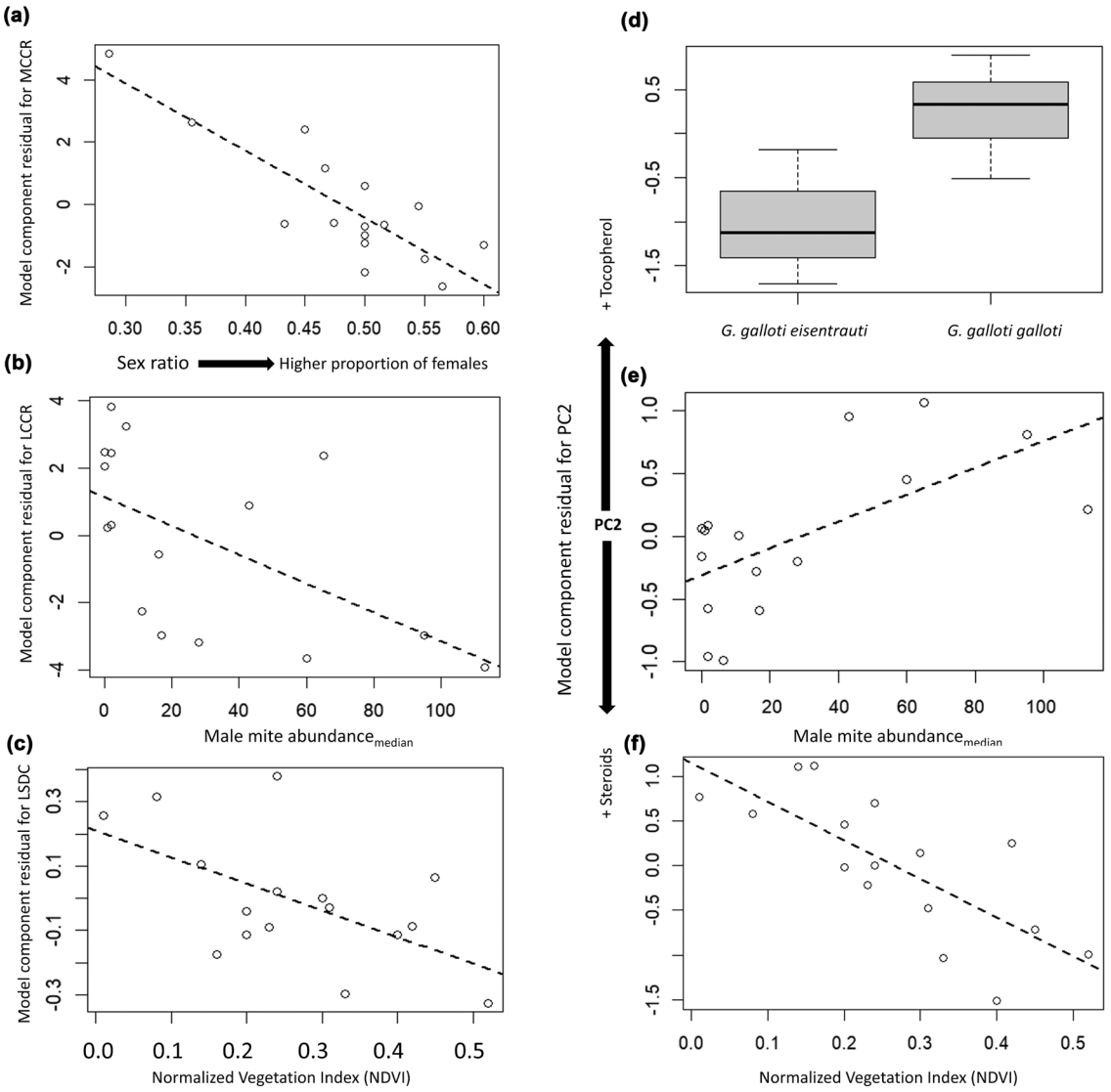

Figure 2. Relationship between (a) mean chemical compound richness (MCCR) and lizard sex ratio, (b) between chemical total richness (LCCR) and median mite abundance in males, (c) between Shannon chemical diversity (LSDC) and a vegetation index, (d) between $PC2_{chemicals}$ and an index of vegetation, (e) mite median abundance on male lizards and, (f) between colour phenotype and tocopherol and steroids contend. The relationships were represented after controlling all other effects.

Table 1. Results of a principal component analysis on the seven main classes of compounds found in the femoral gland secretions of male *G. galloti* in Tenerife based on varimax normalized rotation of factors. Chemicals shown in bold have significant correlations with the corresponding PC.

Variable	$PC1_{chemicals}$	$PC2_{chemicals}$
Aldehydes	**0.91**	0.18
Alcohols	**0.91**	0.20
Fatty acids	**0.78**	0.11
Steroids	−0.30	**−0.94**
Ketones	**0.93**	0.20
Terpenoids	**0.72**	−0.35
Tocopherol	−0.02	**0.99**
Explained variance (%)	56.28	26.86

initial prediction, that colour patches of *G. galloti* were primarily differentiated from the background through chromatic (dS) rather than achromatic (dL) contrast, and that the phenotype 'eisentrauti' was more discriminable to conspecific visual systems.

Also according to our initial predictions, we found an effect of both the colour phenotype ($\chi^2 = 22.59$, df = 1, $p < 0.001$) and the visual model on the lizards' chromatic volumes ($\chi^2 = 15.20$, df = 1, $p < 0.001$), but not their interaction ($\chi^2 = 0.49$, df = 1, $p = 0.482$), indicating that colour patches of lizards of the phenotype 'eisentrauti' were associated with larger chromatic volumes when modelled with the visual system of a lacertid (Fig. 4).

Table 2. Results of the averaged model that analyses the mean relative abundance of steroids and tocopherol ($PC2_{chemicals}$) between locations in the femoral gland secretions of male *G. galloti* in Tenerife. Adj SE = adjusted standard error.

	Importance	Estimate	Adj SE	z-value	Pr(>|z|)
(Intercept)		−0.16	1.38	0.12	0.906
Vegetation index (NDVI)	**1.00**	**−4.26**	**1.77**	**2.40**	**0.016**
Mite median intensity on the males	**1.00**	**0.02**	**0.01**	**2.28**	**0.023**
Colour phenotype (*G.g.eisentrauti*)	**1.00**	**−0.70**	**0.31**	**2.28**	**0.022**
PC1 climate	0.00	−0.37	0.32	1.15	0.250
Spatial autocovariate	0.00	0.03	0.02	1.67	0.095
Lizard sex ratio	0.00	4.30	3.98	1.08	0.280
PC2 climate + elevation	0.00	−0.30	0.34	0.87	0.382
Year (2017)	0.00	−0.24	0.25	0.96	0.339
Human development index	0.00	0.00	0.04	0.03	0.979

Discussion

In the summer of 2017 and 2018, lizards had less diverse chemical signals in environments with higher NDVI scores (i.e. greener and denser vegetation, Weier and Herring 2020). More specifically, chemical richness per male increased with male-biased sex ratios, while chemical diversity per locality decreased with increasing greener vegetation and mite load. Greener habitats and lizards of phenotype 'eisentrauti' showed higher steroid proportions, whereas drier habitats, higher mite loads, and lizards of phenotype 'galloti' showed higher proportions of α-tocopherol, with no environmental effects detected for aldehydes, alcohols, fatty acids, ketones and terpenoids. Moreover, male femoral secretions contained more lipids at sites with a lower proportion of females, implying greater investment in chemical signalling under increased male–male competition. Importantly, the latter relationship was detected at the individual level (mean chemical compound richness per male), suggesting an adaptive functional response, either behavioural or physiological, by males to their social context (Donihue et al. 2020). These results align well with sexual selection theory, which predicts an elevated investment in sexual signals when mating opportunities are scarce or contested (Chen et al. 2012).

In the spring of 2023, lizard colour patches were chromatically conspicuous to both lizard and bird visual models, particularly in males of phenotype 'eisentrauti'. The relatively higher chromatic conspicuousness of male 'eisentrauti' lizards, that combine yellow with UV-blue patches, was consistent with the relatively denser and greener shrub habitats that this bright phenotype occupies in Tenerife. According to results in other systems, this was due to ecological contexts of high intrasexual competition, high environmental light, and low predation pressure facilitated by a complex habitat structure, favouring evolution in colour elaboration/conspicuousness (e.g. in birds, Delhey et al. 2023). Although some caution must be taken because chemicals and visual signals were sampled in different years and months, our findings suggest that the vegetation acts as a key ecological driver of multimodal communication in this species.

The environmental variation found in the lipidic composition of femoral secretions contrasts with a previous study that analysed 64 species of lacertid lizards across three continents and found that in species from xeric habitats, femoral secretion composition generally had a large proportion of fatty acid esters, whereas in species from habitats with high precipitation, humidity and solar radiation lizards produced highly rich chemical secretions with a large proportion of aldehydes (Baeckens et al. 2018). However, the same authors recognize that the chemical signal design in lacertids seems highly evolutionary malleable and appears to have changed rapidly over a small evolutionary time (Baeckens et al. 2018). This suggests that specific ecological contexts promote local adaptation in chemical communication strategies. Certainly, chemical composition may also be subject to seasonal oscillation, as reported for a single sampling site, where males of phenotype 'galloti' had a relatively low proportion of tocopherol in spring (García-Roa et al. 2017b). A longitudinal study in an island introduction experiment showed that the chemical signal design of *Podarcis erhardii* lizards can shift rapidly

Table 3. Results of a linear model testing for pairwise within-patch differences in achromatic and chromatic difference (JNDs) as perceived by a lacertid lizard and a *Falco* raptor. df = degrees of freedom; SM = sum of squares; MS = mean square. Significant p-values are highlighted in bold.

	SS	df	MS	F	p-value
Sex	**2791.92**	**1.00**	**2791.92**	**46.88**	**< 0.001**
Receiver	**113 044.89**	**1.00**	**113 044.89**	**1898.34**	**< 0.001**
Colour phenotype	**15 671.98**	**1.00**	**15 671.98**	**263.18**	**< 0.001**
Sex × Receiver	95.62	1.00	95.62	1.61	0.205
Sex × Colour phenotype	**11 440.16**	**1.00**	**11 440.16**	**192.11**	**< 0.001**
Receiver × Colour phenotype	**2791.98**	**1.00**	**2791.98**	**46.89**	**< 0.001**
Sex × Receiver × Colour phenotype	**718.26**	**1.00**	**718.26**	**12.06**	**< 0.001**
Error	**1 928 920.81**	**32 392.00**	**59.55**		

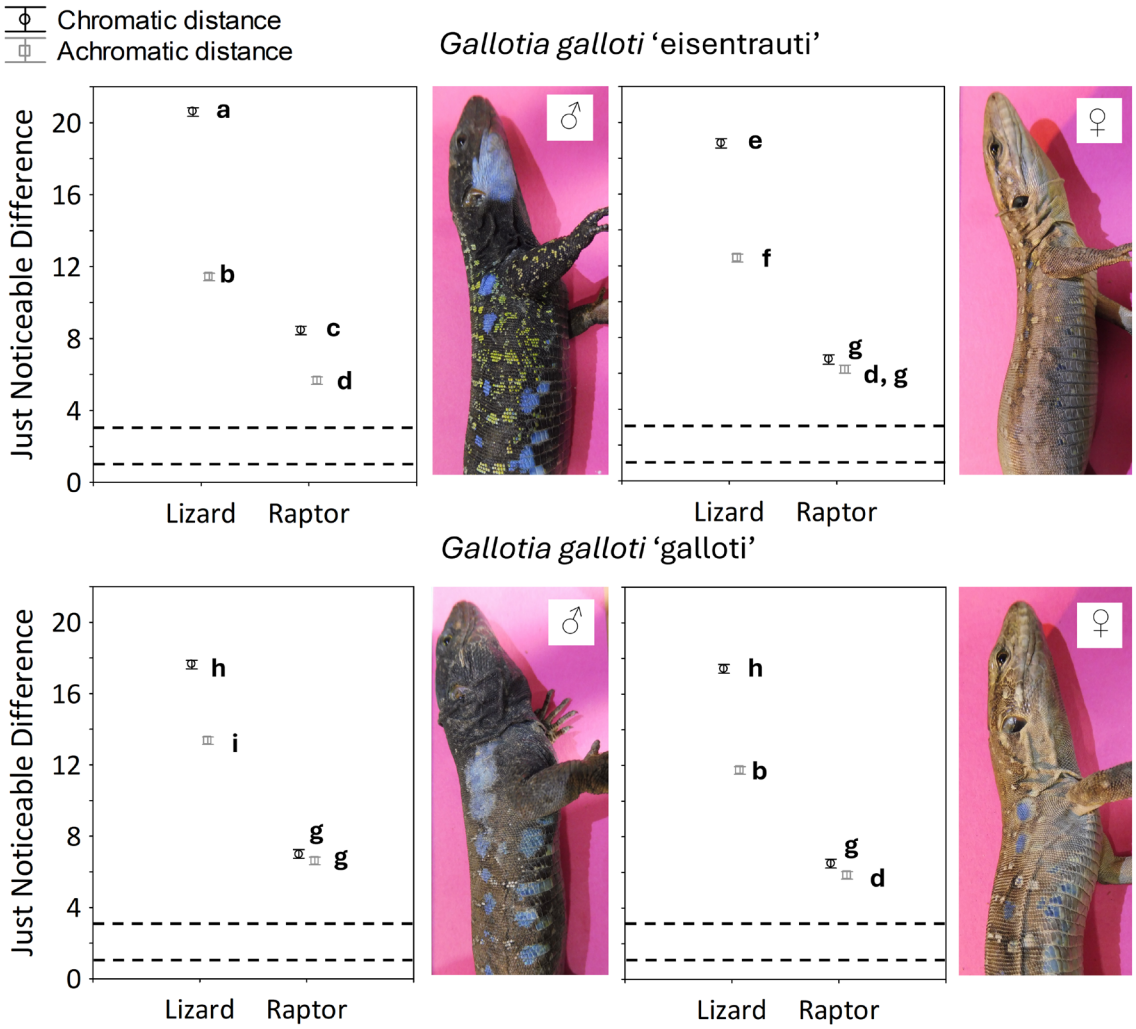

Figure 3. Mean ± 0.95 confidence intervals of pairwise achromatic versus chromatic difference within colour patches of *G. galloti* as perceived by a raptor of genus *Falco* and a lacertid lizard against background colour items and expressed as just noticeable difference (JND). Horizontal dashed lines correspond to the established JND thresholds of 1 and 3. The plots depict the significant effect in Table 3 of a three-way interaction between receiver visual model, sex of the lizard, and colour phenotype as a significant predictor. Different letters indicate significant differences after a Bonferroni post hoc analysis (Supporting information).

and predictably in novel ecological context (Donihue et al. 2020), and that the overall scent mark composition of individual lizards may change over time (Baeckens et al. 2025). Although lizards in greener habitats secreted less diverse lipids, they also contained a relatively higher proportion of steroids, especially cholesterol, in femoral secretions. Steroids are acquired through the diet and are key antioxidant components of chemical signals from lizards because they form a non-reactive apolar matrix that stabilizes the signal (Martín and López 2014, García-Roa et al. 2017b). While this suggests potential environmental adaptation of the chemical signals to local xeric/mesic conditions, it could still reflect the different biochemical composition of plants across xeric and mesic environments in Tenerife (Otto et al. 2001) because each plant species has a different biochemical profile (Gunaherath and Gunatilaka 2014). Indeed, the relative abundances of steroids and tocopherol are expected to change with the plant community (DellaPenna and Pogson 2006, Patel and Savjani 2015).

On the contrary, in localities with sparse and xeric vegetation, which are typically the warmest habitats of Tenerife, male chemical secretions had a lower total richness of lipids, with a high proportion of α-tocopherol (vitamin E). This pattern may reflect a functional response to the joint stressors of food scarcity related to aridity and higher environmental temperatures (Zhang et al. 2023). The higher proportion of tocopherol, an antioxidant acquired through the diet (Kopena et al. 2014), is consistent with the important fraction of fleshy fruits consumed by *G. galloti* in xeric environments. It has previously been reported that in xeric habitats of Tenerife, lizards take advantage of the widespread invasive plants of the genus *Opuntia* (Cactaceae) and feed on pear fruit both in summer and winter (Padrón et al. 2011). *Opuntia* spp. can be very abundant locally and tocopherol

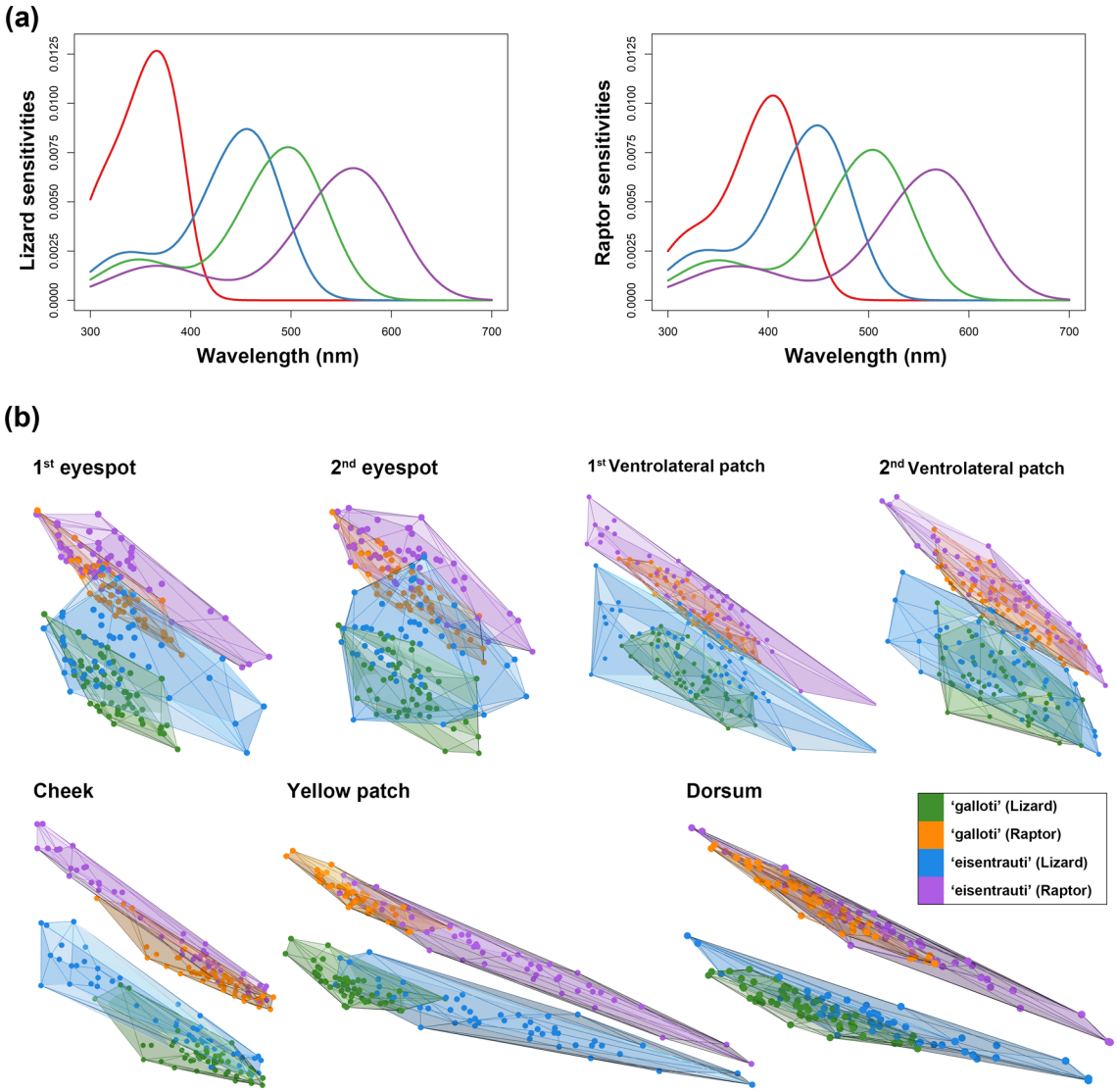

Figure 4. (a) Colour sensitivities of the visual models of the lacertid (ultraviolet sensitive) and a raptor of genus *Falco* (violet sensitive). (b) Spatial representation of the chromatic volumes of the 'eisentrauti' and 'galloti' colour phenotypes depicting the spectral variability of each colour patch as perceived by the receptor's tetrachromatic vision (raptor bird versus lacertid lizard) and represented in the visual spaces of the 3-dimensional model receptors.

can reach 50 mg per 100 g of fruit (Matthäus and Özcan 2011). A high proportion of tocopherol in femoral secretions could contribute to the oxidative stability of chemical signals (Martín and López 2014). Therefore, the difference in the proportion of tocopherol and steroids between xeric and mesic environments suggests context-dependent antioxidant strategies for signal stability in *G. gallotia*. Future studies should include gradients of trophic availability and selection.

Our results also showed that lizards from localities with high ectoparasitic loads had a lower total lipid richness, with a high proportion of α-tocopherol (vitamin E). The link between mite abundance and low lipid richness may be driven by the converging effects of environmental factors such as vegetation structure or microclimate, rather than direct parasite-mediated suppression of signal investment. A stronger test of such putative tradeoff would require within-population, individual-level analysis that simultaneously models parasite load, chemical investment and habitat features.

The relatively higher total richness and Shannon diversity of lipids in xeric habitats of Tenerife were consistent with our initial predictions because male lizards invested more in chemically complex secretions where these signals are likely to persist for longer. This may be adaptive in open landscapes where the predation pressure by kestrels can be high (Carrillo-Hidalgo et al. 2020). In contrast, the relatively lower total richness and Shannon diversity of lipids in greener habitats of Tenerife are consistent with the earlier indications that chemical communication becomes less efficient in humid environments, where volatile signals degrade more rapidly (Baeckens et al. 2018). In such

contexts, visual signals may be favoured because lizards of phenotype 'eisentrauti', which occur in the greener northern regions of Tenerife (Thorpe and Brown 1989), exhibited larger chromatic volumes and greater chromatic conspicuousness than lizards of phenotype 'galloti' that inhabits less vegetated areas. The colour patches of both sexes were generally more conspicuous in a lacertid visual model than in an avian predator model, due to the greater sensitivity to ultraviolet (UV) of the vision of the lizard (Pérez i de Lanuza et al. 2014b). However, males of phenotype 'eisentrauti' were significantly more chromatically conspicuous and had higher chromatic volumes. Our results do not conflict with previous hypotheses suggesting that dorsal stripes in lizards of phenotype 'eisentrauti', typically occurring in highly vegetated sites, may serve a dual function: increasing disruption of the body silhouette against the background vegetation for aerial predators (Thorpe and Brown 1989) and providing conspicuous lateral coloration for conspecific communication (Bohórquez-Alonso et al. 2018). Such signal partitioning, where different body regions are optimized for different receivers, has been described in other species of lizards and may be a widespread strategy under conflicting selection pressures (Stuart-Fox and Ord 2004). Thus, the interaction between sex, habitat structure, and predator pressure may shape the evolution of dimorphic coloration and chemical signals of *G. galloti*.

It should be noted that, despite the higher chromatic conspicuousness in both sexes, females were generally less chromatically conspicuous than males, particularly in an avian predator visual space. This, together with a generally lower achromatic conspicuousness under this raptor visual model, suggests that predation can exert an important selection on colour patch evolution in *G. galloti.* Furthermore, the similarly low achromatic versus chromatic contrasts against background in females suggests that crypsis upon a predator's eye is naturally selected. In support of our results, a previous study showed positive relationships of hue and chroma of colour patches of males, but not females, with body condition and parasite load, suggesting a relatively stronger influence of sexual selection on the evolution of male coloration (Megía-Palma et al. 2016).

Conclusion

Our findings add to a growing body of evidence that visual and chemical divergence between *G. galloti* phenotypes is driven by ecological adaptation (Thorpe and Brown 1989, Brown et al. 2016). The different signalling profiles of lizards of phenotypes 'eisentrauti' and 'galloti' appear to reflect local environmental pressures, particularly vegetation cover and social structure, and suggest that environmental and social factors interact to shape multimodal signalling in this insular lizard (Pérez i de Lanuza and Font 2016). *Gallotia galloti* exhibits habitat- and sex-specific adjustments in their signalling phenotypes, modulating investment across chemical and visual channels in response to ecological pressures. The results underscore the importance of considering multimodal communication in the context of local environmental conditions and suggest that such flexibility may be the key to maintaining reproductive success across heterogeneous landscapes. The spatial heterogeneity of Tenerife, driven by its complex orography, vegetation gradients, and localized anthropogenic pressures (Otto et al. 2001) has previously been linked to physiological and genomic adaptations in *G. galloti* (Serén et al. 2023, 2024, Gilbert et al. 2024). We extend this framework to sexual signalling, showing that both colour traits and male chemical profiles are geographically structured and likely adaptive to local social and environmental conditions.

Speculations

Our results suggest that multi-modal signalling in *Gallotia galloti* may reflect a dynamic allocation strategy across sensory channels shaped by environmental constraints. Rather than acting independently, chemical and visual signals could be rebalanced depending on habitat-specific transmission efficiency and social context. Xeric environments may favour persistent and information-rich chemical cues due to increased signal longevity, whereas structurally complex habitats may promote chromatic visual signals that exploit heterogeneous light conditions.

This pattern raises the possibility of trade-offs between modalities, mediated by physiological constraints (e.g. antioxidant availability), ecological factors (e.g. diet), and social dynamics (e.g. intrasexual competition). The increase in chemical richness under male-biased sex ratios suggests that social competition may override environmental constraints, leading to elevated signalling investment.

Environmental heterogeneity may also generate multiple adaptive optima, where different combinations of signal traits achieve similar functional outcomes. Finally, the decoupling of chromatic and achromatic divergence suggests asymmetric predator-mediated constraints, potentially allowing chromatic signalling to evolve under reduced predation risk.

Alternative viewpoints

Alternative explanations should be considered. First, geographic variation in chemical profiles may reflect differences in resource availability rather than adaptive signalling. Because many compounds are diet-derived, spatial variation in plant communities could passively generate chemical differences without direct selection on communication.

Second, the association between mite load and chemical composition may arise from shared environmental drivers (e.g. microclimate) rather than a tradeoff between parasitism and signal investment. Similarly, the relationship between sex ratio and chemical richness could reflect demographic or sampling effects.

Third, historical and demographic processes may contribute. Partial genetic structure across Tenerife could interact with environmental gradients, meaning that phenotypic differences between colour forms are not solely due to contemporary adaptation.

Finally, temporal mismatches between datasets (2017–2018 for chemical signals, 2023 for colour) limit inference about multimodal integration. Seasonal variation in both traits suggests that longitudinal, within-population studies are needed to confirm whether the inferred relationships persist over time.

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Rodrigo Megía-Palma: Conceptualization (lead); Data curation (lead); Formal analysis (lead); Investigation (equal); Methodology (equal); Writing – original draft (lead). **Prem Aguilar**: Conceptualization (supporting); Formal analysis (equal); Methodology (equal); Writing – original draft (supporting). **Anamarija Žagar**: Conceptualization (supporting); Investigation (supporting); Writing – original draft (supporting). **Marcio R. Pie**: Investigation (supporting); Resources (lead); Writing – original draft (supporting). **Urban Dajčman**: Formal analysis (supporting); Investigation (supporting); Writing – original draft (supporting). **Santiago Merino**: Conceptualization (supporting); Project administration (supporting); Resources (lead); Writing – original draft (supporting). **Miguel A. Carretero**: Conceptualization (supporting); Funding acquisition (lead); Project administration (equal); Writing – original draft (supporting). **José Martín**: Conceptualization (equal); Data curation (equal); Resources (equal); Writing – original draft (supporting).

Data availability statement

Data are available from the Dryad Digital Repository: https://doi.org/10.5061/dryad.vmcvdnd54 (Megía-Palma et al. 2026).

Supporting information

The Supporting information associated with this article is available with the online version.

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