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Signalling on islands: the case of Lilford's wall lizard (*Podarcis lilfordi gigliolii*) from Dragonera

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Studies of the effects of insularity on animal signals are scarce, particularly in lizards. Here, we use Lilford's wall lizard from Dragonera (*Podarcis lilfordi gigliolii*) to ask how island conditions have affected its repertoire of social signals, focusing on two visual signals shared by many *Podarcis* species: ultraviolet (UV)–blue-reflecting ventrolateral colour patches and visual displays. We examined whether the number or spectral characteristics of the UV–blue patches are associated with traits related to individual quality. We also used visual models to assess visual conspicuousness and to measure sexual dichromatism. We did not observe foot shakes or any other visual displays usually found in continental *Podarcis*. We found that none of the UV–blue patch variables covaried with morphometric variables indicative of fighting ability or body condition in males, suggesting that this coloration does not signal individual quality. We also found very little sexual dichromatism. In particular, the UV–blue patches of females seem over-expressed and more similar to those of males than those of continental *Podarcis*. Ancestral state reconstruction reveals that the lack of sexual dimorphism in the UV–blue patches is a derived condition for *P. lilfordi gigliolii* and other *Podarcis* living on small islands. Our results thus show a pattern of reduced social signalling in *P. lilfordi gigliolii* relative to mainland *Podarcis*, with some signals being lost or under-expressed (visual displays) and others losing their signalling function (UV–blue patches). We hypothesize that these changes are attributable to the high population density of *P. lilfordi gigliolii*, which discourages territorial behaviour and promotes extreme social tolerance, making most social signals unnecessary. More work will be needed to determine whether this is a common pattern in lizards inhabiting small and densely populated islands.

ADDITIONAL KEYWORDS: animal communication – colour signals – insularity – *Podarcis* – social signals – ultraviolet – visual display.

INTRODUCTION

Islands, as isolated systems sharing some ecological characteristics with the mainland, provide a unique opportunity to test many important hypotheses in evolutionary biology (e.g. MacArthur *et al.*, 1972; Adler & Levins, 1994; Grant, 1998; Warren *et al.*, 2015). In comparison to the mainland, animals on islands often experience low predator and parasite pressures, reduced food abundance and diversity, reduced interspecific competition and/or low genetic diversity owing to stochastic processes, such as bottlenecks or founder effects (Adler & Levins, 1994; Frankham, 1997; Losos & Ricklefs, 2009; Roulin & Salamin, 2010). These ecological and genetic peculiarities might promote a suite of correlated morphological, physiological, behavioural and life-history differences between inhabitants of islands and their mainland counterparts (Adler & Levins, 1994; Losos & Ricklefs, 2009; Doutrelant *et al.*, 2016). This phenomenon, termed the 'island syndrome', includes large body sizes, small clutches, late sexual maturation, high population densities, reduced sexual dimorphism and reduced aggressiveness (Case, 1975; Adler & Levins, 1994; Rodda & Dean-Bradley, 2002; Doutrelant *et al.*, 2016; Baeckens & Van Damme, 2020; Bliard *et al.*, 2020), although in some cases the bias occurs in the opposite direction (i.e. 'reversed island syndrome';

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Raia *et al.*, 2010). These effects of insularity are mainly influenced by distance to the mainland and island size, being more pronounced on small islands than on large ones and, consequently, very large islands (> 9000 km^2) are considered as mainland (MacArthur *et al.*, 1972; Buckley & Jetz, 2007).

Most island studies have focused on changes in life histories, ecological niches and body sizes (Adler & Levins, 1994; Blondel, 2000; Novosolov *et al.*, 2013; BeVier *et al.*, 2021; Gavriilidi *et al.*, 2022), whereas few have investigated the effects of insularity on the design of animal signals (Morinay *et al.*, 2013; Doutrelant *et al.*, 2016; Bliard *et al.*, 2020). This is unfortunate because signals play a major role in processes that are central to fitness and might be affected by insularity, such as mate choice, species recognition and predator avoidance (Poulton, 1890; Burtt, 1979; Cuthill *et al.*, 2017). Chromatic (i.e. colour-based) signals, in particular, offer great potential owing to their role in sexual selection as condition-dependent signals that can inform about the quality of rivals or mates (Bradbury & Vehrencamp, 2011; Olsson *et al.*, 2013; Cuthill *et al.*, 2017). Previous studies have reported responses of chromatic traits to insularity, such as a reduction of sexual dichromatism (sexual dimorphism in colour), an increase in the complexity/diversity of colour polymorphisms and changes in luminance, but no general pattern has emerged, and several hypotheses have been proposed (Hayashi & Chiba, 2004; Doutrelant *et al.*, 2016; Bliard *et al.*, 2020). Notably, one of the most important factors to consider is predation intensity, which is generally lower on islands. A lack of predators can lead to an increase in the complexity and/or conspicuousness of a sexually selected signal owing to a relaxation of the selection pressure that would otherwise push towards cryptic or aposematic colorations (Endler, 1992; Runemark *et al.*, 2014; Doutrelant *et al.*, 2016).

Insular species also face a reduction in the intensity of sexual selection. Intersexual selection has been proposed to be less intense on islands because: (1) the benefits of mate choice are reduced if males are very similar genetically (Frankham, 1997; Doutrelant *et al.*, 2016); (2) whatever role parasites might play in the expression of a sexual signal, it is expected to decrease its intensity because parasite communities are impoverished on islands (Hamilton & Zuk, 1982); and (3) population density is high and mates are a non-limited resource (Raia *et al.*, 2010). Intrasexual selection, in contrast, is expected to vary depending on environmental conditions, resource availability and population density. If population density is low or fluctuating and the environmental conditions are unpredictable, aggressive behaviour and cannibalism are expected to occur (Pafilis *et al.*, 2009; Raia *et al.*, 2010; Novosolov *et al.*, 2013; Cooper *et al.*, 2015). However, if population density is high and the environment and resources are stable, territorial behaviours and aggressiveness are expected to decrease (Stamps & Buechner, 1985). It has long been known that insular lizards, birds and mammals in high-density populations often exhibit an apparent lack of territoriality, with overlapping home ranges, high social tolerance of intruders, subordinates and juveniles, reduced situation-specific aggression and infrequent displays (Rand *et al.*, 1975; Stamps & Buechner, 1985). Therefore, explaining the response of social signals to insularity requires paying attention to a host of selective forces potentially driving their evolution.

Lacertid lizards are a valuable group to study the evolution of chromatic signals because they often exhibit complex and striking colour patterns that combine both pigmentary and structural colours (Olsson *et al.*, 2013; Pérez i de Lanuza *et al.*, 2013a; Pérez i de Lanuza & Font, 2016), typically differing between sexes (Pérez i de Lanuza & Font, 2007; Font *et al.*, 2009; Pérez i de Lanuza *et al.*, 2013a). Many lacertids, particularly in the genus *Podarcis*, possess a cryptic brown or green dorsal surface, white, yellow or orange-red ventral coloration and conspicuous ultraviolet (UV)–blue patches located on the flanks, head and/or shoulder region (Arnold *et al.*, 2007; Pérez i de Lanuza *et al.*, 2013a, 2014). Although UV–blue patches are also present in the females of most *Podarcis* species, they are usually smaller and less abundant than in males (Pérez i de Lanuza *et al.*, 2014). It is generally assumed that this incomplete sexual dimorphism results from non-adaptive genetic correlations between the sexes (Lande, 1980; Potti & Canal, 2011; Assis *et al.*, 2021), but empirical tests in lizards are lacking. Given that lacertid visual perception extends into the near-UV range (Pérez i de Lanuza & Font, 2014; Martin *et al.*, 2015a), UV-based coloration can be relevant in a signalling context and often affects mating success [e.g. *Lacerta viridis* (Bajer *et al.*, 2011); *Lacerta agilis* (Olsson *et al.*, 2011); *Zootoca vivipara* (Badiane *et al.*, 2020); *Podarcis muralis* (Pérez i de Lanuza *et al.*, 2014; Names *et al.*, 2019)]. In particular, current evidence for a role of the ventrolateral UV–blue patches as a social signal conveying information about male fighting ability (often referred to as resource-holding potential) is compelling. In *P. muralis* and *Podarcis tiliguerta*, the size and spectral properties of the UV–blue patches are good indicators of male quality, fighting ability and reproductive success (Pérez i de Lanuza *et al.*, 2014; Martin *et al.*, 2015b; MacGregor *et al.*, 2017a; Names *et al.*, 2019; Badiane & Font, 2021). Nevertheless, many questions remain unanswered, and more research is needed to understand these chromatic signals, particularly in certain environmental conditions, such as those experienced on islands.

The ventrolateral UV–blue patches are relatively inconspicuous in a resting lizard, but they are exposed during social interactions, when males raise on their extended forelegs, with the abdomen compressed laterally, and display these colour patches, particularly in interactions with other males (Verbeek, 1972; Pérez i de Lanuza & Font, 2010, 2014). Thus, signalling by means of UV–blue patches comprises both morphological (the UV–blue patches) and behavioural (raised body display, often accompanied by sagittal trunk compression, arched back and/or throat extension) components. In addition to the raised body display, lacertid lizards have a rich repertoire of dynamic (i.e. movement-based) visual signals, including head bobs, foot shakes and tail waving (e.g. Weber, 1957; Verbeek, 1972; Edsman, 1990). Foot shakes consist of one or more up and down, roughly circular movements of the hand or the entire forelimb that can engage one or both forelegs, either sequentially or simultaneously. *Podarcis* lizards, in particular, communicate using several types of foot shakes that differ both in the context in which they are used and in their structure and the overall body posture of the displaying lizard (Font *et al.*, 2012). Type I foot shakes are broadcast (non-directed, spontaneous) displays similar to the assertion/advertisement displays of iguanid lizards (e.g. Jenssen, 1977), and type III foot shakes function as pursuit-deterrent signals directed at potential predators (Font *et al.*, 2012). Type II foot shakes, in contrast, are social signals used in interactions with conspecifics, where they function as submission/appeasement displays (Gómez *et al.*, 1993; Font & Desfilis, 2002; Pérez i de Lanuza *et al.*, 2016; Abalos *et al.*, 2020).

Lilford's wall lizard [*Podarcis lilfordi* (Günther, 1874)] is an endemic species of the Balearic Islands (western Mediterranean, Spain). In the past, *P. lilfordi* inhabited the main islands of Majorca and Minorca, but it became extinct there ~2000 years ago following the introduction of cats and other predators by man (Pérez-Mellado, 2004; Salvador, 2014a). Currently, it is found in the Cabrera archipelago and many small islands and islets around Majorca and Minorca (Pérez-Mellado, 2004; Salvador, 2014a). Up to 25 subspecies have been described, with extensive variation in size, sexual dimorphism, relative body proportions, pholidosis and coloration (Pérez-Mellado, 1989; Salvador, 2014a). Here, we focus on the subspecies *P. lilfordi gigliolii*, present only on the island of Dragonera, off the west coast of Majorca (Pérez-Mellado *et al.*, 2008; Salvador, 2014a; Fig. 1). This subspecies belongs to the basal group of *P. lilfordi* from Majorca, probably being the sister taxon of the extinct subspecies from this island and retaining traits of the original source population (Brown *et al.*, 2008; Terrasa *et al.*, 2009). *Podarcis lilfordi gigliolii* reaches high population densities (729 lizards/ha), which have been attributed to low or non-existent predation levels on Dragonera (Eisentraut, 1928; Pérez-Mellado *et al.*, 2008). Also, in contrast to mainland *Podarcis*, *P. lilfordi* lizards from Dragonera have overlapping home ranges, and aggressive displays and interactions among them are rare, with several individuals of both sexes often sharing crevices (Zawadzki, 2000).

In this study, we address three main objectives. First, we document the repertoire of visual signals of *P. lilfordi gigliolii*, including its coloration, which we characterize using reflectance spectrophotometry. Second, we examine whether the number or spectral characteristics of the ventrolateral UV–blue patches are correlated with morphological or performance traits indicative of individual quality, as in other *Podarcis*. Third, we use visual modelling to quantify conspicuousness and to establish whether different colour patches can be discriminated from each other and from the background by a lizard, and whether these colours are sexually dichromatic. Given that the original mainland stock from which *P. lilfordi* evolved from is no longer available, a direct comparison between island and continental populations to determine the consequences of insularity on the design of chromatic signals is not possible. Instead, our aim is to establish some of the effects that insularity might have on chromatic signals by comparing the UV–blue patches of *P. lilfordi gigliolii* with the two mainland *Podarcis* species for which extensive spectral data are available: *P. muralis* (Pérez i de Lanuza *et al.*, 2014; Names *et al.*, 2019) and *P. tiliguerta* (Badiane & Font, 2021). Additionally, we expect that the altered selective regime associated with insularity will affect the degree to which the two sexes diverge. To test this prediction, we conduct an ancestral character reconstruction of sexual dimorphism in the UV–blue patches across the whole genus.

MATERIAL AND METHODS

Study area and data collection

Dragonera is a small (~2.88 km^2), uninhabited coastal island with typical Mediterranean flora and few lizard predators, including some species of gulls and a few small raptors, such as the common kestrel (*Falco tinnunculus*) and Eleonora's falcon (*Falco eleonorae*) (Zawadzki, 2000; Pérez-Mellado *et al.*, 2008; Salvador, 2014). In the recent past, rats (*Rattus rattus*) were the main lizard predator, and their population density was very high on the island (Pérez-Mellado *et al.*, 2008), but currently the species is absent from the island as a result of an eradication campaign implemented in 2011 (Mayol *et al.*, 2011).

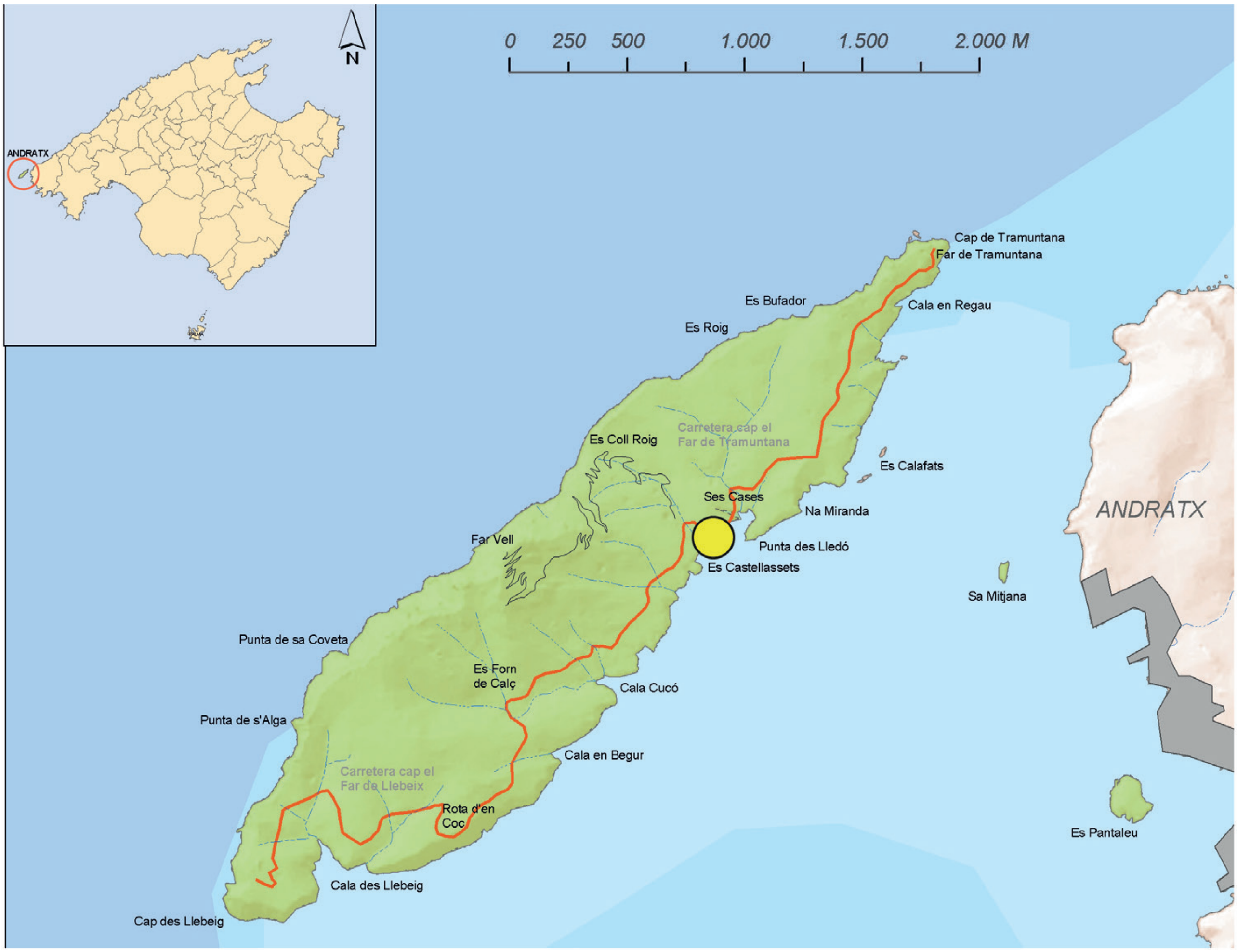

Figure 1. Map of Dragonera island, with the sampling area (yellow circle) and its location relative to Majorca. Extracted from the Balearic Islands Government website (https://www.caib.es/).

In May 2013, during the reproductive season (Zawadzki, 2000; Salvador, 2014a), we captured 116 adult lizards (74 males and 42 females) by noosing around Cala Lladó (39.59°N, 2.33°E; Fig. 1). After capture, lizards were held individually in cloth bags, where they remained before and after measurements to minimize stress. Morphometric and reflectance measurements were taken within 6–10 h of capture, after which the lizards were released back at their original capture location.

Each lizard was sexed unequivocally by head and body proportions and by the presence of active femoral pores and hemipeneal bulges found only in males. We considered only adult individuals to ensure that the lizards had fully developed coloration (Pérez i de Lanuza *et al.*, 2013b, 2014). For each lizard, we measured snout–vent length (SVL), head length (HL) and head width (HW) to the nearest 1 mm and body mass to the nearest 0.1 g. Nineteen lizards could not be weighed because they were too heavy and exceeded the maximum capacity (11.2 g) of the light-line spring scale available, but we retained them for further analyses. We also calculated a body condition index (BCI), separately for both sexes, as the residual from a least-squares linear regression of log(body mass) against log(SVL) (Green, 2001). Additionally, we measured bite force using a purpose-built bite force meter. The bite force meter was constructed from a modified Sauter FK 25 N digital force meter, with two metal plates on which each animal bites, one attached to the main body of the force meter and the other to the fixed recording rod. This same device has been used extensively by ourselves and by others to measure bite force in several *Podarcis* species (While *et al.*, 2015; MacGregor *et al.*, 2017a, b). Immediately before measuring bite force, we placed the lizards inside a plastic container, where temperature was constantly kept high, until the lizards reached a body temperature of ≥ 32 °C (body temperature of active lizards of this species is in the range 32–36 °C; Ortega *et al.*, 2014). Lizards were induced to bite by placing the plate between their open jaws, which usually causes the lizards to bite aggressively (but see below), and we retained the maximum score out of three bite force measurements. Finally, we counted the number of UV–blue patches on both sides of each lizard.

We used a combination of behaviour and focal animal sampling (Bateson & Martin, 2021) to collect data on foot shakes and other visual displays. Lizards were observed directly or through close-range binoculars (Papilio 8.5 × 21; Pentax). In the event that visual displays were produced, lizards were also filmed with a high-resolution digital camera recorder (Panasonic AG-HPX250) at a temporal resolution of 25 frames/s.

COLOUR MEASUREMENTS AND VISUAL MODELLING

Reflectance spectra were obtained with a USB-2000 portable diode-array spectrometer and a PX-2 xenon strobe light source (Ocean Optics, Dunedin, FL, USA), both connected to a probe via a bifurcated fibre-optic cable. Spectra were recorded in 0.37 nm steps and expressed as the percentage of light reflected relative to a Spectralon white diffuse reflectance standard (Labsphere). The reflectance probe was held perpendicularly at 5 mm from the lizard's skin, resulting in a reading spot of ~2 mm in diameter. For each measurement, the spectrophotometer averaged 20 spectra; integration time was set at 50 ms, and we used a data-smoothing level of ten. All measurements were taken in a darkened room to minimize interference from external light sources. Spectral analyses were restricted to the 300–700 nm range, which spans the visual spectrum perceived by diurnal lizards (Pérez i de Lanuza & Font, 2014; Martin *et al.*, 2015a; Font & Fleishman, 2019). Spectra were obtained for each lizard from the belly, throat, dorsum and the second rostral-most UV–blue patch on the right flank. Additionally, we obtained spectra of the most representative natural background found in the habitat of the lizards (i.e. limestone, $N = 7$).

Spectra were analysed in R v.4.0.3 (R Development Core Team, 2017) using the package PAVO 2 (Maia *et al.*, 2019). For colour analyses, we extracted three variables: luminance (intensity, brightness), hue and chroma (saturation; Endler, 1990; Kemp *et al.*, 2015). Luminance was calculated by summing the reflectance across the entire spectrum (i.e. $R_{300-700}$), and hue was measured as the wavelength at maximum reflectance. Chroma was calculated differently for each colour patch according to the wavelength range containing its maximum reflectance (Endler, 1990). For the UV–blue patches, we measured UV chroma (C_{UV}) by summing the reflectance across the UV range and dividing it by the luminance (i.e. $R_{300-400}/R_{300-700}$). For the ventral coloration (i.e. throat and belly) and dorsum, we measured intermediate chroma (MC) dividing the reflectance in the 400–600 nm wavelength band by the reflectance of the entire spectrum (i.e. $R_{400-600}/R_{300-700}$).

We built visual models using the receptor noise model (Vorobyev & Osorio, 1998) implemented in PAVO 2 to assess sexual dichromatism and conspicuousness. The latter was estimated by calculating chromatic and achromatic distances between different colour patches of *P. lilfordi gigliolii* and between each patch and the limestone substrate. Given that information on the visual system of *P. lilfordi* is not available, we used cone sensitivities (UVS:SWS:MWS:LWS, 367:456:497:562 nm) and cone ratios (1:1:1:4) of *P. muralis* (Martin *et al.*, 2015a). We set the Weber fraction to 0.05 (Siddiqi *et al.*, 2004) and used a standard daylight 'D65' irradiance spectrum implemented in PAVO 2. Contrasts between pairs of colours were measured in units of just noticeable differences (JNDs), where one JND is the threshold of discrimination between two colours in good illumination conditions (Vorobyev *et al.*, 2001). A JND value greater than one indicates that both colours can be discriminated, whereas colours are indistinguishable if they have a contrast value of less than one JND (Vorobyev *et al.*, 2001). However, given that 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 three JNDs (Siddiqi *et al.*, 2004; Santiago *et al.*, 2020).

STATISTICAL ANALYSES

Owing to the lack of both normality and homoscedasticity (assessed with Shapiro–Wilk and Bartlett's tests, respectively), we analysed sexual dimorphism in all morphometric variables with Wilcoxon's signed-rank test. Sexual dimorphism in the number of UV–blue patches was analysed with Welch's *t*-test, because data had a normal distribution and unequal variances (Ruxton, 2006). Before the analyses, we winsorized by sex the number of UV–blue patches with a minimum and maximum value of 5% and 95%, respectively, to reduce the effect of spurious outliers. After winsorizing, we checked that the distributions were not altered owing to this transformation. We analysed the relationship between morphometric variables and colour variables of the UV–blue patches (hue, luminance, C_{UV} and number of patches) with the *lme4* R package (Bates *et al.*, 2014). We ran linear models (LMs) with colour variables as response variables and with the following independent variables as predictors: SVL, body mass, BCI, size-corrected head length (HLcor; i.e. residuals from a regression of head length against SVL), size-corrected head width (HWcor; i.e. residuals from a regression of head width against SVL), sex as a factor, and the interactions between all quantitative predictors and sex. All morphometric variables were $\log_{10}$-transformed and standardized (z transformation) before submitting them to the linear models, in order that the residuals fitted better to a normal distribution. We then proceeded with a stepwise backward model selection that consisted of discarding the non-significant terms until the model with the lowest Akaike information criterion (AIC) was obtained.

We tested whether colour patches of *P. lilfordi gigliolii* (including both alternative ventral colours, i.e. white and orange) were sexually dichromatic to the visual system of the lizards. We used throat colour instead of belly colour because it is the most exposed to conspecifics during social interactions. Given that most methods used to analyse visual models fail to estimate the separation of colour samples owing to the multivariate nature of these data, we took a two-step approach to evaluate statistical and perceptual differences, as suggested by Maia & White (2018). In the first step, we ran a permutational multivariate analysis of variance (PERMANOVA; Anderson, 2017) procedure on the chromatic and achromatic contrast values (measured in JNDs) using the *pairwise.adonis* function from the *pairwiseAdonis* R package (Martinez Arbizu, 2020), a modified version of the *adonis* function from the *vegan* R package (Oksanen *et al.*, 2016) allowing for multilevel pairwise comparisons. We created a group variable including the following levels for pairwise comparisons: dorsum, white throat, orange throat, and UV–blue patches. We tested the assumption of multivariate homogeneity of group dispersions (variances) with the *betadisper* function, an analogue of Levene's test for multivariate variances (Anderson, 2006; Supporting Information, Table S1). For each pairwise comparison, we recorded statistical significance ($\alpha = 0.05$) using 999 permutations, a pseudo-F statistic, and R^2 as an effect size estimate. Adjusted P-values for multiple comparisons were obtained using a Bonferroni procedure. Given that statistical significance does not necessarily match the theoretical perceptual threshold of one JND above which colours can be said to be distinguishable, in the second step we used a bootstrap procedure to generate confidence intervals for the mean colour distance between the different colours. We used the *bootcoldist* function from the PAVO 2 package on the visual model described above with 1000 replicates and a 0.95 level for confidence intervals. We used the same methodology, with the multilevel pairwise comparisons and the bootstrap function, to quantify the discriminability between colour patches and the conspicuousness against the natural background. In the analysis of colour patch discrimination, we found that our group levels had unequal variances for both the chromatic and achromatic contrasts (ΔS and ΔL, respectively; Supporting Information, Table S1), but not in a way that would substantially affect our distance-based PERMANOVA procedure, because the largest group had the highest variance (Anderson & Walsh, 2013; Supporting Information, Table S2).

ANCESTRAL CHARACTER STATE RECONSTRUCTION

Given that preliminary analyses revealed a lack of sexual dichromatism in the UV–blue patches of *P. lilfordi gigliolii*, we conducted a character history reconstruction to determine the ancestral state for this trait in the genus *Podarcis*. Given that spectral data of the UV–blue patches are not available for most species, we determined the sexual dimorphism in the size and abundance of these patches using photographs of wild-caught adult lizards (ventral and lateral aspect) belonging to 24 species in the genus *Podarcis* (range, 16–116 individuals per species). We created a code with three categories of sexual dimorphism: A, neither males nor females possess UV–blue patches; B, males clearly have more and/or larger UV–blue patches than females; and C, males and females have roughly the same number and size of UV–blue patches. To determine the category for each species, we first assigned a score to every individual in the sample: 1, if the lizard did not have any UV–blue patches; 2, if the lizard had few, small and/or greenish patches; and 3, if the lizard displayed many large UV–blue patches. To distinguish between scores of 2 and 3, we used the difference between female (2) and male (3) *P. muralis* as a reference (Fig. 2). We then obtained the mean score for each sex and compared the two sexes. We considered that a species is not sexually dimorphic if males and females show similar average scores between 1 and 2 (category A) or between 2 and 3 (category C). On the contrary, we considered that a species is sexually dimorphic (category B) when male mean score is > 2 and female mean score < 2 and when the difference between the mean scores for males and females is > 0.8. Scores were assessed independently by two observers (F.G. and G.P.L.), who agreed on the categorical assignment of all 24 species. Photographs were generously provided by A. Kaliontzopoulou, except for species for which we had our own photographs. For *P. lilfordi gigliolii*, we coded the sexual dimorphism in the UV–blue patches based on our observations during sampling. We reconstructed the history of sexual dimorphism in the UV–blue patches in the genus *Podarcis* using a parsimony model in MESQUITE v.3.70 (Maddison & Maddison, 2021). We used the most recent time-calibrated *Podarcis* phylogeny (Salvi *et al.*, 2021), and we added manually *Podarcis*

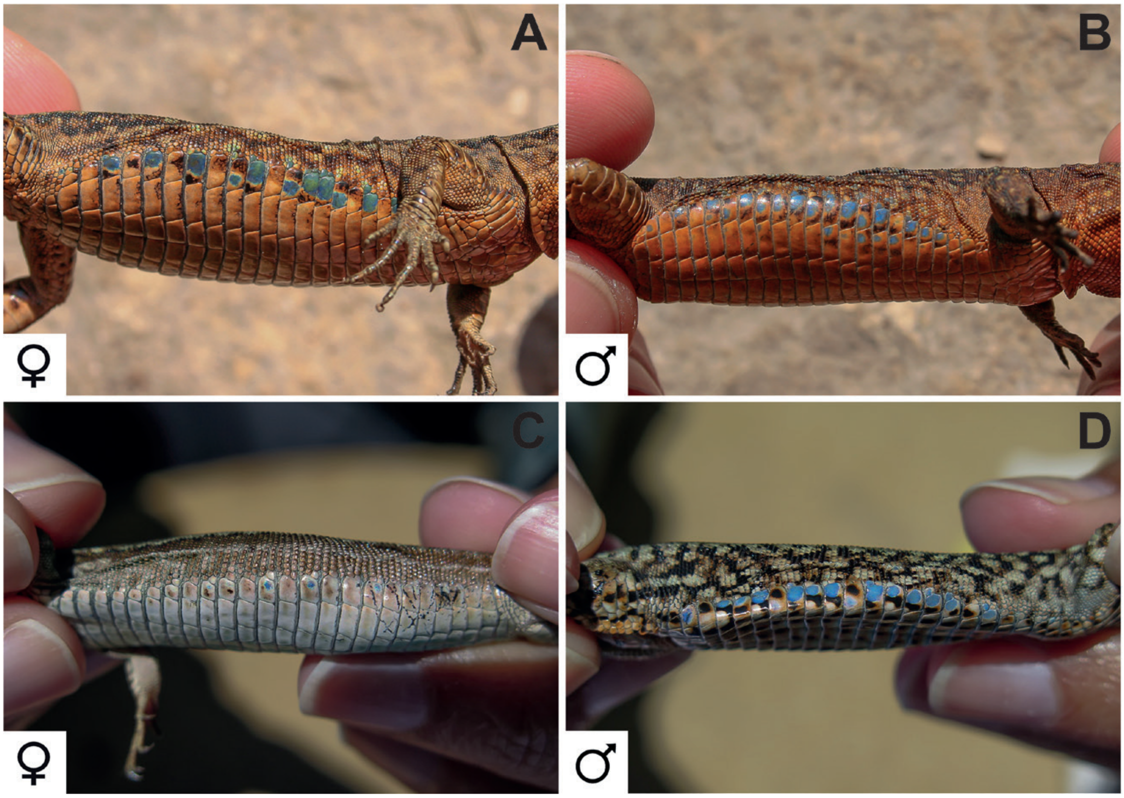

Figure 2. Representative female (A, C) and male (B, D) *Podarcis lilfordi gigliolii* (top row) and *Podarcis muralis* (bottom row) in lateral view. Note the ventrolateral ultraviolet (UV)–blue patches, which are more similar in number and size in the two sexes in *P. lilfordi gigliolii* than in *P. muralis*. According to our coding scheme for sexual dichromatism, *P. lilfordi gigliolii* was assigned a category of C, whereas *P. muralis* was assigned a category of B.

thais and *Podarcis lusitanicus* to the tree, recently elevated to species rank, based on the divergence time estimated by Kiourtsoglou *et al.* (2021) and the information provided by Caeiro-Dias *et al.* (2021), respectively. The divergence time of *P. lusitanicus* has not yet been determined accurately, but phylogenetic studies suggest that, contrary to what was previously thought, this species is more related to *Podarcis bocagei* than to *Podarcis guadarramae* (Bassitta *et al.*, 2021; Caeiro-Dias *et al.*, 2021).

RESULTS

Unexpectedly, 92 lizards (79% of the sample) refused to bite or showed an obvious lack of motivation resulting in very low bite force scores; therefore, we excluded this variable from further analyses. Additionally, UV–blue reflectance could not be measured in three females because their blue patches were too small (< 2 mm; see Badiane *et al.*, 2017). One female was excluded from analyses involving ventral coloration because her throat was a rare light blue.

At least in the part of the island where we captured lizards and made behavioural observations, lizards were very abundant, and it was frequent to see several lizards of both sexes and different age classes sharing rocks and crevices with no hint of overt aggression among them (Fig. 3). No foot shakes or any other visual displays were observed in > 4 h of observation/filming.

Unlike other *P. lilfordi* subspecies with unusual coloration (e.g. axanthism, melanism), *P. lilforfi gigliolii* exhibits the typical colour pattern of lacertid lizards (Bauwens & Castilla, 1998; Pérez i de Lanuza & Font, 2010; Salvador, 2014a). The dorsal surface is usually brown, with blackish or greenish spots. Ventrally, lizards exhibit a white and/or orange coloration, which extends over the belly and the throat, and ventrolaterally they display UV–blue patches located in some of the outer ventral scales and in the surrounding scales (Fig. 2A, B). Reflectance spectra are shown in Figure 4, and spectral variables of each colour patch are reported in Table 1.

Morphometric variables showed a strong sexual dimorphism, with males being heavier, longer and with higher BCI values and larger heads (in both length and

Figure 3. Aggregation of *Podarcis lilfordi gigliolii* in Dragonera. In this image, eight adult individuals of both sexes share a crevice, some in physical contact with each other, without any signs of overt aggression.

width) than females (Table 2). There was also sexual dimorphism ($t = 3.25$, d.f. = 92, $P < 0.001$; Welch's *t*-test) in the number of UV–blue patches (males, 16.4 ± 5.63; females, 12.6 ± 4.05; Fig. 5). Heavier lizards had UV–blue patches with higher hue (i.e. more blue biased; $F_{1,91} = 7.9$, $R^2 = 0.07$, $\beta = 0.14 \pm 0.05$, $P = 0.006$) than lighter ones, and heavier females, but not males, had a lower number of UV–blue patches [$F_{1,91} = 7.3$, $R^2 = 0.12$, β (females) $= -0.21 \pm 0.1$, P (females) $= 0.04$] than lighter females. The final models and the significance of all retained predictors are reported in the Supporting Information (Table S3). Despite a significant correlation between body mass and hue of the UV–blue patches for the overall sample, testing the sexes separately showed that this correlation was significant only in females (males, $F_{1,53} = 1.1$, $R^2 = 0.002$, $\beta = 0.9 \pm 0.85$, $P = 0.29$; females, $F_{1,56} = 10.02$, $R^2 = 0.2$, $\beta = 3.19 \pm 1.01$, $P = 0.003$; Fig. 6).

There was no sexual dichromatism in any colour patch, either chromatically or achromatically after Bonferroni correction to account for multiple testing (Table 3). The dorsum, UV–blue patches and white throat coloration of males and females probably cannot be discriminated by the lizards themselves (JNDs lower than one), either chromatically or achromatically, and the orange throat was barely discriminable between males and females (JNDs lower than three; Fig. 7A).

Statistics of the PERMANOVA procedure for the discrimination of the different colour patches are summarized in Table 4. We found that all colour patches were chromatically and achromatically discriminable from each other based on a perceptual threshold of one JND (Fig. 7C). However, using a conservative threshold of three JNDs, orange and white throats were not chromatically discriminable by lizards (Fig. 7C). Results from the discrimination analysis of different colour patches against limestone are summarized in Table 5. Chromatically, the UV–blue patches were the most conspicuous against limestone, whereas the dorsum was the most achromatically conspicuous coloration against the background (Fig. 7B).

Table 6 shows the species and character states used in the phylogenetic reconstruction. According to a parsimony model, the ancestral character for the *Podarcis* genus is the presence of sexually dimorphic UV–blue patches, with males having more and larger UV–blue patches than females (Fig. 8). This character state is exemplified by *P. muralis*, of which representative male and female individuals are pictured in Figure 2C, D. Although the results showed differences in the number of UV–blue patches between males and females in our sample (see above), *P. lilfordi* was assigned a category of C (males and females have roughly the same number and size of UV–blue patches) based on our method of visual categorization (see the comparison between *P. lilfordi gigliolii* and *P. muralis* in Fig. 2). Five independent losses of sexual dimorphism have occurred in the genus: in the clade comprising *P. bocagei* and *P. lusitanicus* and in *Podarcis hispanicus*, both sexes lack UV–blue patches, whereas in *Podarcis levendis*, *Podarcis milensis* and in the Balearic clade (*P. lilfordi* and *Podarcis pityusensis*), males and females have roughly the same number and size of UV–blue patches.

DISCUSSION

Almost all studies of behavioural changes associated with insularity in lizards have focused on antipredator behaviour, such as tameness, escape strategies and post-autotomy tail activity (Blázquez *et al.*, 1997; Márquez & Cejudo, 2000; Pafilis *et al.*, 2008; Cooper *et al.*, 2009, 2014; Runemark *et al.*, 2014). The results of these studies are consistent with the expectation of behavioural changes resulting from a relaxation of predation pressure (i.e. predator release). However, there is very little information on the effects of insularity on the design of sociosexual signals (for effects of insularity on chemical signals, see Donihue *et al.*, 2020), and most of the information we have on the evolution of these traits in lacertids is based on continental and large-island species (Pérez i de Lanuza *et al.*, 2014; Martin *et al.*, 2015b; MacGregor *et al.*, 2017a; Names *et al.*, 2019; Badiane & Font, 2021).

The costs and benefits of signalling change when animals colonize new environments, including islands. In the new environment, animals not only experience new selective regimes, but also there is often relaxed selection affecting specific behaviours. Relaxed selection often leads to the reduction or loss of costly signals that are no longer functional in the insular environment. For example, three insular

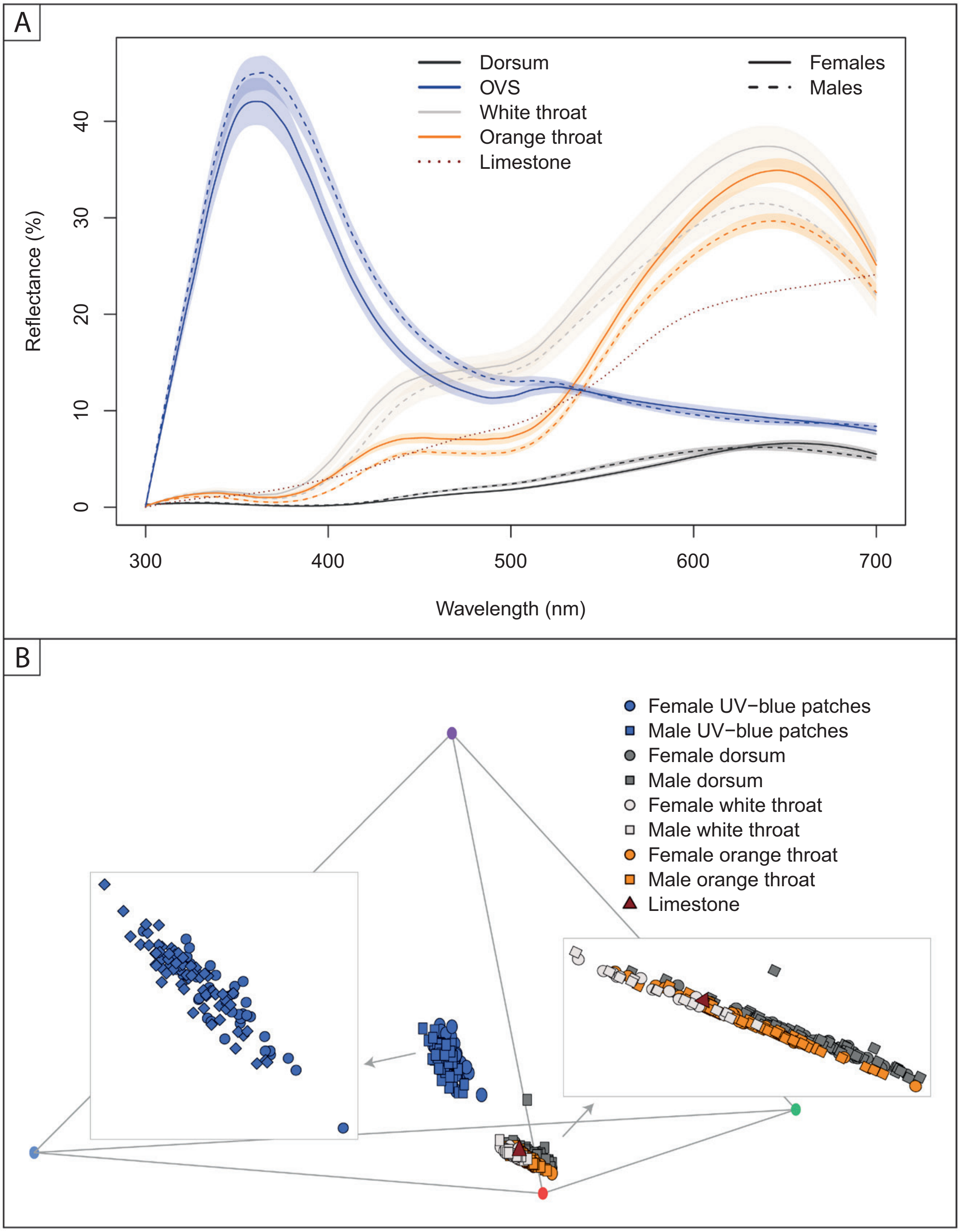

Figure 4. A, mean spectra (plain curve) and their standard errors (shaded curve) of the ultraviolet (UV)–blue patches ($N = 39$ females and $N = 74$ males), the dorsum ($N = 42$ females and $N = 74$ males) and the two throat colours: white ($N = 13$ females and $N = 13$ males) and orange ($N = 28$ females and $N = 61$ males). The mean spectrum of the most representative natural background (i.e. limestone, $N = 7$) is also shown. Abbreviation: OVS, outer ventral scales. B, representation of each individual spectrum from the different colour patches of lizards [dorsum, ultraviolet (UV)–blue patches, and throat (white, orange)] and mean spectra of the most representative natural background (i.e. limestone) in a tetrahedral colour space built for a wall lizard visual system (see details in the main text).

Table 1. Mean (±SEM) of spectral variables of each colour patch by sex

Colour patch	Sex	*N*	Hue (nm)	Luminance	Chroma
Ultraviolet–blue patches	Male	74	365 ± 8	29 101 ± 7096	0.45 ± 0.03
	Female	39	363 ± 7	27 101 ± 5444	0.44 ± 0.04
Dorsum	Male	74	631 ± 54	90 227 ± 2245	0.48 ± 0.03
	Female	42	656 ± 23	8719 ± 1888	0.46 ± 0.02
White throat	Male	13	640 ± 22	27 222 ± 3655	0.50 ± 0.03
	Female	13	644 ± 17	29 529 ± 6261	0.49 ± 0.02
Orange throat	Male	61	646 ± 16	22 561 ± 4876	0.44 ± 0.03
	Female	28	650 ± 17	26 012 ± 5505	0.44 ± 0.03
White belly	Male	7	623 ± 10	37 198 ± 3419	0.50 ± 0.02
	Female	10	630 ± 20	35 698 ± 6776	0.50 ± 0.03
Orange belly	Male	67	643 ± 17	30 213 ± 6750	0.44 ± 0.04
	Female	32	640 ± 16	32 588 ± 6874	0.46 ± 0.04

Table 2. Mean (±SEM) of morphometric variables by sex and *W*-statistic of Wilcoxon signed-rank test for sexual dimorphism

Sex	Snout–vent length (mm)	Body mass (g)	Body condition index	Head length (mm)	Head width (mm)
Males	70.1 ± 3.67	10.1 ± 1.33	0.02 ± 0.05	17.7 ± 1.03	13.2 ± 0.94
Females	63.4 ± 3.53	6.6 ± 1.09	−0.03 ± 0.05	14.8 ± 0.89	10.4 ± 0.83
W for sexual dimorphism	205	111.5	499	397	392.5

P < 0.001 for all variables.

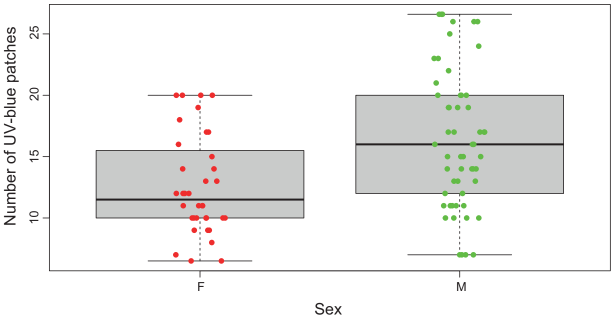

Figure 5. Boxplot of the number of ultraviolet (UV)–blue patches by sex. Values have been winsorized, with a minimum and maximum value of 5% and 95%, respectively.

species of rattlesnakes of the Gulf of California have lost the rattle, presumably owing to the absence of snake predators on the islands (Arnaud & Martins, 2019). Signal loss or reduction can take multiple forms along a continuum from genetic changes to plastic loss of expression (Lahti *et al.*, 2009). Conversely, signals that are cheap to produce or maintain or that are correlated with other traits under positive selection can be retained as relic or vestigial traits even if they no longer fulfil a signalling function (Coss, 1998; Rothstein, 2001; Rayner *et al.*, 2022).

One of the most distinctive features of *P. lilfordi gigliolii* is the absence of foot shakes (including both social and antipredator foot shakes) and other visual displays. Although the information regarding foot shakes in lacertids is largely anecdotal, at least some type of foot shake is present in most *Podarcis* species, including *P. tiliguerta* and *P. pityusensis*, two close relatives of *P. lilfordi gigliolii* (E. Font, unpublished observations). The lack of visual displays is consistent with results for other lizards living in high-density, low-predation environments (e.g. *Anolis agassizi*; Rand *et al.*, 1975) and suggests that foot shakes and other visual displays might have been lost or remain unexpressed owing to the elevated costs of territoriality and aggression in high-density populations, such as those found on Dragonera (Stamps & Buechner, 1985; Wiens, 1999; Lahti *et al.*, 2009). Loss of many male display behaviours is likewise associated with a reduction in male territoriality in horned lizards (genus *Phrynosoma*; Wiens, 2000). In support of this idea, *P. lilfordi* from Cabrera, a much larger island with a lizard density less than half that recorded on Dragonera (Pérez-Mellado *et al.*, 2008), have a foot shake repertoire similar to other *Podarcis* (E. Font, unpublished observations). However, we cannot rule out the possibility that *P. lilfordi gigliolii* individuals perform foot shakes and other visual displays at a low rate or at certain times that escaped our short-term observations.

Despite the lack of visual displays that would normally make them visible to other lizards, *P. lilfordi gigliolii* have large and conspicuous ventrolateral UV–blue patches. There is no information on the UV–blue patches of the original mainland or large-island stock from which *P. lilfordi gigliolii* evolved, but the patches of the latter are similar in number, size and spectral characteristics to those of other *Podarcis* (Pérez i de Lanuza *et al.*, 2014; Badiane & Font, 2021). This decoupling of display morphology and display behaviour seems to be relatively common in certain groups. For example, several species in the genus *Sceloporus* have lost their display coloration but retain unmodified display behaviour (Wiens, 2000). Likewise, the rattleless rattlesnakes of the Gulf of California mentioned above vibrate their tails when handled even if they do not produce any sounds (Arnaud & Martins, 2019). The situation in *P. lilfordi gigliolii* seems to be the reverse. In this case, the display behaviour has been lost or persists unexpressed, whereas the display morphology (i.e. the UV–blue patches) seems unaffected.

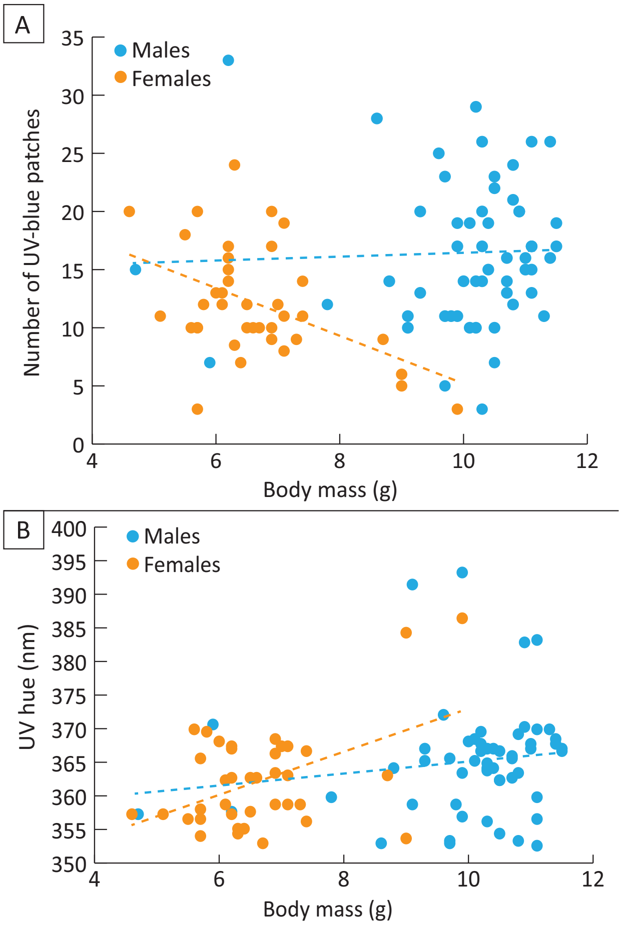

Figure 6. Correlation between body mass (in grams) and the number of ultraviolet (UV)–blue patches (A) and the hue of the UV–blue patches (in nanometres) (B) by sex.

In continental *Podarcis,* larger males have UV patches with more C_{UV} and lower hue values (i.e. more UV biased), less luminance and more total surface than smaller males (Pérez i de Lanuza *et al.*, 2014; Names *et al.*, 2019; Badiane & Font, 2021). Given that body size is a primary predictor of dominance in lizards, with larger and heavier males winning more contests than smaller and lighter ones (Carpenter, 1995; Zucker & Murray, 1996; Baird, 2013; Bohórquez-Alonso *et al.*, 2018), it has been suggested that the UV–blue patches of *Podarcis* might function to signal fighting ability (resource-holding potential) during male agonistic interactions (Pérez i de Lanuza *et al.*, 2014; Names *et al.*, 2019). This is in contrast to results obtained with *P. lilfordi gigliolii*, where the lack of an association between the number or spectral characteristics of the UV–blue patches and a range of fitness-relevant morphological traits suggests that this coloration has lost its signalling function. In our sample, body mass showed a significant association with hue and the number of patches only in females, but effect sizes were small, indicating that only a small proportion of the variance in UV–blue patch number or reflectance was influenced by body size. Another case of persistent expression of apparently

Table 3. Sexual dichromatism in different body regions of *Podaris lilfordi gigliolii*

Comparisons between sexes	Chromatic contrast, Δ*S*				Achromatic contrast, Δ*L*			
	F	R^2	*P*-value	Adjusted *P*-value	*F*	R^2	*P*-value	Adjusted *P*-value
Dorsum	0.34	0.00	0.711	1	0.48	0.00	0.538	1
Orange throat	8.24	0.09	0.003	0.084	10.48	0.11	0.002	0.056
White throat	1.30	0.05	0.275	1	1.87	0.07	0.19	1
Ultraviolet–blue patches	3.70	0.03	0.042	1	1.43	0.01	0.203	1

Results were obtained from pairwise male–female comparisons for each different colour patch with a distance-based PERMANOVA performed on the chromatic and achromatic contrasts. Pseudo-*F* statistics, R^2 as an effect size estimate, *P*-values and adjusted *P*-values (Bonferroni corrections) are shown.

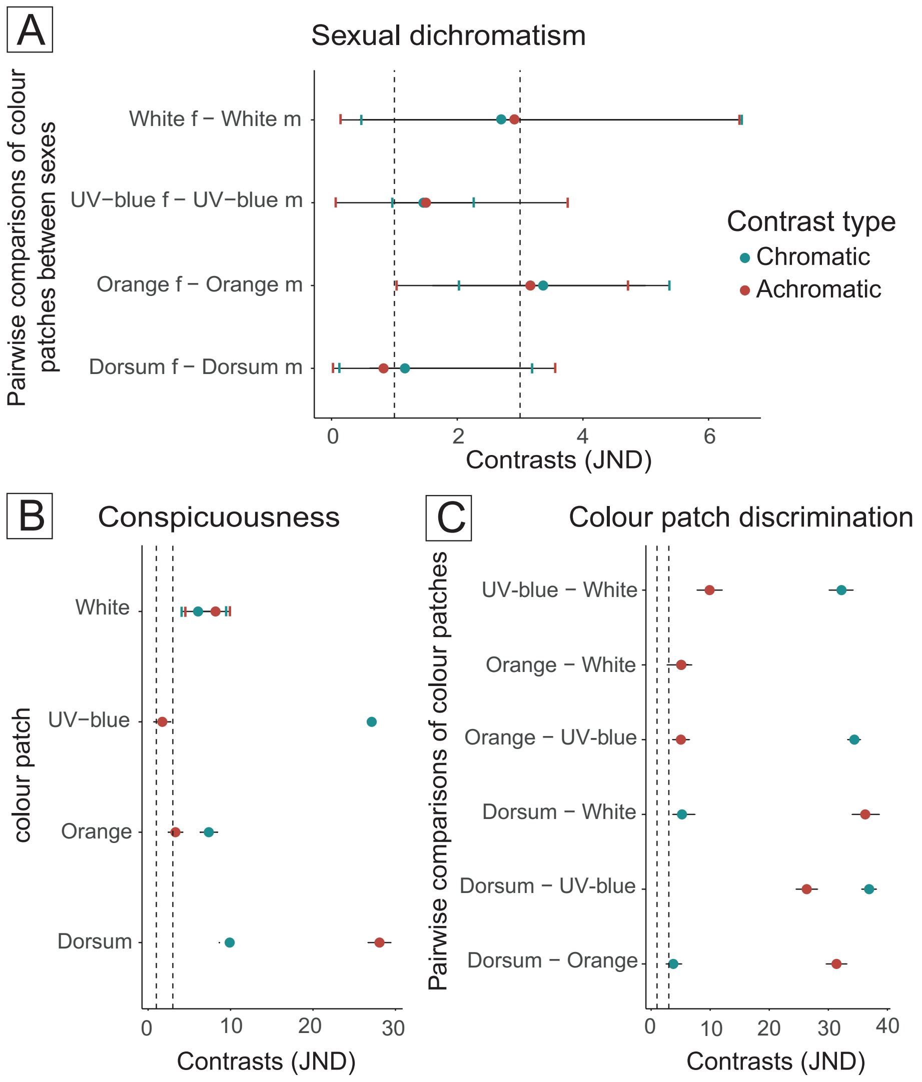

Figure 7. A, mean and 95% confidence intervals of the chromatic and achromatic contrasts between each colour patch [dorsum, ultraviolet (UV)–blue patches and throat (white or orange)] of males (m) and females (f) when viewed against the natural background. B, mean and 95% confidence intervals of the chromatic and achromatic contrasts between each colour patch [dorsum, UV–blue patches and throat (white or orange)] and the background (i.e. limestone spectra). C, mean and 95% confidence intervals of the chromatic and achromatic contrasts between each colour patch [dorsum, UV–blue patches and throat (white or orange)] when viewed against the natural background. The dashed lines at one and three just noticeable differences (JNDs) represent the discriminability thresholds.

non-adaptive UV–blue coloration was reported recently in Caucasian rock lizards of the genus *Darevskia*. Females of four parthenogenetic lineages do not show reduced or attenuated UV–blue patches relative to the females of their bisexual progenitor species, suggesting that the changes in selective regime brought about by parthenogenetic reproduction have little effect on the expression of this trait (Abramjan *et al.*, 2021). It is unclear why the conspicuous coloration should be retained when it becomes non-functional. Theory predicts that morphological traits involved in signalling should persist as vestigial traits under relaxed selection if they are not costly to produce and maintain (Rayner *et al.*, 2022). Alternatively, vestigial traits could be retained if they covary with other traits that have adaptive value under the novel selective regime (Rayner *et al.*, 2022). Unfortunately, current knowledge of the genetic and mechanistic underpinnings of UV–blue patch production does not allow us to discriminate between these hypotheses.

A striking result of the present study is the reduced sexual dichromatism observed in all the colour patches examined. This is particularly unexpected in the case of the UV–blue patches, which exhibit strong sexual

Table 4. Chromatic and achromatic contrasts between different body regions of *Podaris lilfordi gigliolii*

Pairwise comparisons	Chromatic contrast, ΔS				Achromatic contrast, ΔL			
	F	R^2	P-value	Adjusted P-value	F	R^2	P-value	Adjusted P-value
Dorsum vs. orange	10.70	0.05	0.001	0.006*	870.69	0.81	0.001	0.006*
Dorsum vs. white	9.71	0.06	0.002	0.012*	307.88	0.69	0.001	0.006*
Dorsum vs. ultraviolet–blue patches	3233.71	0.93	0.001	0.006*	717.24	0.76	0.001	0.006*
Orange vs. white	5.12	0.04	0.017	0.102	20.36	0.15	0.001	0.006*
Orange vs. ultraviolet–blue patches	4221.72	0.95	0.001	0.006*	37.62	0.16	0.001	0.006*
White vs. ultraviolet–blue patches	2180.49	0.94	0.001	0.006*	47.71	0.26	0.001	0.006*

Results were obtained from pairwise comparisons among different colour patches with a distance-based PERMANOVA performed on the chromatic and achromatic contrasts. Orange and White indicate the orange and white throats, respectively. Pseudo-F statistics, R^2 as an effect size estimate, P-values and adjusted P-values (Bonferroni corrections) are shown.
*Statistically significant ($P < 0.05$).

Table 5. Conspicuousness of the colour patches of *Podarcis lilfordi gigliolii*

Colour patch	Chromatic contrast, ΔS				Achromatic contrast, ΔL			
	F	R^2	P-value	Adjusted P-value	F	R^2	P-value	Adjusted P-value
Dorsum	8.08	0.07	0.002	0.02*	68.16	0.37	0.001	0.01*
Orange throat	8.51	0.08	0.001	0.01*	3.65	0.04	0.051	0.51
White throat	3.98	0.11	0.042	0.42	10.87	0.26	0.003	0.03*
Ultraviolet–blue patches	904.11	0.88	0.001	0.01*	0.40	0.003	0.625	1

Results were obtained from pairwise comparisons among the different colour patches against the natural background (i.e. limestone) with a distance-based PERMANOVA performed on the chromatic and achromatic contrasts. Pseudo-F statistics, R^2 as an effect size estimate, P-values and adjusted P-values (Bonferroni corrections) are shown.
*Statistically significant ($P < 0.05$).

dimorphism (male biased) in most continental *Podarcis* species. In fact, sexual dimorphism in UV coloration is a common pattern shared by many lacertid lizards, such as *Gallotia galloti* (Molina-Borja *et al.*, 2006), *Timon nevadensis* (formerly *Lacerta lepida*; Font *et al.*, 2009) and *Z. vivipara* (Martin *et al.*, 2013). In contrast, female *P. lilfordi gigliolii* are notably male-like in the number, size and spectral characteristics of their UV–blue patches. For the sake of comparison, in a mainland population of *P. muralis,* only 60% of females show some UV–blue patches, and these are small and shifted towards blue relative to those of males (Pérez i de Lanuza *et al.*, 2014). In contrast, 100% of female *P. lilfordi gigliolii* possess UV–blue patches with spectral characteristics similar to those of males. To be sure, there is some degree of sexual dimorphism in *P. lilfordi gigliolii* UV–blue coloration, in that males have more patches than females, but there is considerable overlap in the number of UV–blue patches of both sexes.

Reduced sexual dichromatism is usually considered part of the island syndrome, although data on lizards are scarce (Roulin & Salamin, 2010; Doutrelant *et al.*, 2016). Our character history reconstruction shows that the presence of sexually dimorphic UV–blue patches is the ancestral character state for the genus, with males having more and larger patches than females, although five independent losses of this condition have occurred, including one in the Balearic *Podarcis* group, which encompasses *P. lilfordi* and *P. pityusensis*. The transition from sexual dimorphism to monomorphism in continental *Podarcis* has involved the loss of the UV–blue patches in both sexes (*P. bocagei*, *P. lusitanicus* and *P. hispanicus*). In contrast, the loss of sexual dimorphism in some island species has involved females gaining male-like UV–blue coloration. In addition to *P. lilfordi* from Dragonera, *P. pityusensis* from Formentera Island (Balearic Islands), *P. levendis* from Pori Island (Greece) and *P. milensis* from Milos Island (Greece) have females with male-like UV–blue patches. Both Formentera and Pori are small, predator-free and densely populated islands (Martínez-Rica & Cirer, 1982; Salvador, 2014b; Lymberakis *et al.*, 2016). Milos is a slightly larger island and is host to several lizard predators, including birds and snakes (Pafilis *et al.*, 2005), but population density of lizards is also notably high (Lymberakis *et al.*, 2016).

Table 6. Sexual dimorphism resulting from differences in the presence/size of the ultraviolet–blue patches for the *Podarcis* species included in the phylogenetic analysis

Species	N_m	N_f	UV-bm	UV-bf	Sexual dimorphism	Locality
P. bocagei	7	9	1.57	1.00	A	Mindelo, Portugal (41.31°, –8.74°)
*P. carbonelli**	26	25	2.20	1.00	B	El Acebuche, Spain (37.05°, –6.57°)
*P. cretensis**	19	7	3.00	1.00	B	Lissos gorge, Greece (35.25°, 23.79°)
*P. erhardii**	40	37	2.90	1.35	B	Mount Parnitha, Greece (38.18°, 23.73°)
*P. filfolensis**	20	19	2.85	1.75	B	Dwerja, Malta (36.05°, 14.19°)
*P. gaigeae**	11	9	2.86	1.60	B	Palamari, Greece (38.96°, 24.51°)
*P. guadarramae**	20	14	2.05	1.07	B	Alba de Tormes, Spain (40.83°, –5.52°)
*P. hispanicus**	21	12	1.38	1.00	A	Embalse Pedrera, Spain (38.03°, –0.88°)
P. ionicus	31	33	2.97	1.50	B	Feneos, Greece (37.94°, 22.33°)
*P. levendis**	14	15	2.79	2.53	C	Pori, Greece (35.97°, 23.25°)
P. lilfordi gigliolii†	74	42	–	–	C	Dragonera, Spain (39.59°, 2.33°)
P. liolepis	27	17	2.13	1.05	B	Godella, Spain (39.51°, –0.42°)
*P. lusitanicus**	18	17	1.06	1.00	A	Gerês NP, Portugal (41.74°, –8.17°)
*P. melisellensis**	22	15	2.85	1.06	B	Socerb, Slovenia (45.59°, 13.86°)
P. milensis	41	22	2.92	2.36	C	Milos, Greece (36.73°, 24.46°)
P. muralis	32	43	2.88	1.78	B	Acs, France (42.72°, 1.83°)
P. peloponesiacus	35	39	2.94	1.46	B	Feneos, Greece (37.94°, 22.33°)
P. pityusensis	31	36	2.94	2.92	C	Sant Francesc Xavier, Spain (38.71°, 1.43°)
*P. siculus**	42	35	2.65	1.32	B	Marina di Pisa, Italy (43.62°, 10.30°)
*P. tauricus**	21	20	2.80	1.35	B	Prespes, Greece (40.81°, 21.07°)
P. thais	33	26	2.94	1.92	B	Stymphalia, Greece (37.86°, 22.46°)
*P. tiliguerta**	40	41	2.80	1.85	B	S. G. Moriani, France (42.37°, 9.47°)
P. vaucheri	20	25	2.89	1.50	B	Mischliffen, Morocco (33.41°, –5.10°)
*P. wagleriana**	17	17	2.30	1.69	B	Monte Catalfano, Italy (38.11°, 13.52°)

Abbreviations: N_m and N_f represent sample sizes per species for males and females, respectively; UV-bm and UV-bf are the mean scores for males and females, respectively (see main text for explanation). Sexual dimorphism was based on the visual categorization as follows: A, neither males nor females possess UV–blue patches (both UV-bm and UV-bf < 2); B, males clearly have more and/or larger UV–blue patches than females (UV-bm > 2 and UV-bf < 2, and the difference between the mean scores for males and females is > 0.8); and C, males and females have roughly the same number and size of UV–blue patches (both UV-bm and UV-bf > 2). The locality of the species/subspecies analysed is also indicated.
*Data obtained from pictures provided by A. Kaliontzopoulou.
†Data for *P. lilfordi giglioli* correspond to the sample used for the present study.

Recent phylogenetic studies of avian coloration have revealed that losses of sexual ornaments are more common than gains, but historical decreases of dichromatism have involved females evolving rapidly to look like males (Badyaevl & Hill, 2003; Price & Eaton, 2014). Relaxation or removal of the negative selection pressure imposed by predators might explain the over-expression of conspicuous coloration in females in the case of lizards and birds living on islands. An alternative explanation for the reduced sexual dichromatism observed in *P. lilfordi gigliolii* is that females are selected to resemble males (i.e. sexual mimicry) in order to avoid male harassment in high-density populations (Gosden & Svensson, 2009; Xu & Fincke, 2011; Falk *et al.*, 2021). Sexual mimicry of females could prevent or minimize unnecessary copulations and the associated damage, because in lacertids, as in many other reptiles, copulation involves repeated biting of the female by the male (Noble & Bradley, 1933; Verbeek, 1972). Sexual mimicry has been described in some coastal and island populations of *P. bocagei*, where some females show a green dorsal coloration similar to that of males, presumably to avoid male harassment and copulation attempts after fertilization (Galán, 2000).

Although our results point to a relationship between insularity and lack of sexual dichromatism in *Podarcis* lizards (with females over-expressing their UV–blue coloration to resemble males), an alternative explanation in light of our phylogenetic reconstruction is that dimorphic UV–blue patches were lost earlier in the Balearic clade, in the common ancestor of *P. lilfordi* and *P. pityusensis*, and the lack of sexual dimorphism in UV–blue patch and abundance is therefore unrelated to the conditions currently prevailing in Dragonera. However, this does not rule out an effect of insularity, because the loss of sexual dimorphism could still have occurred in relationship to the colonization of the Balearic

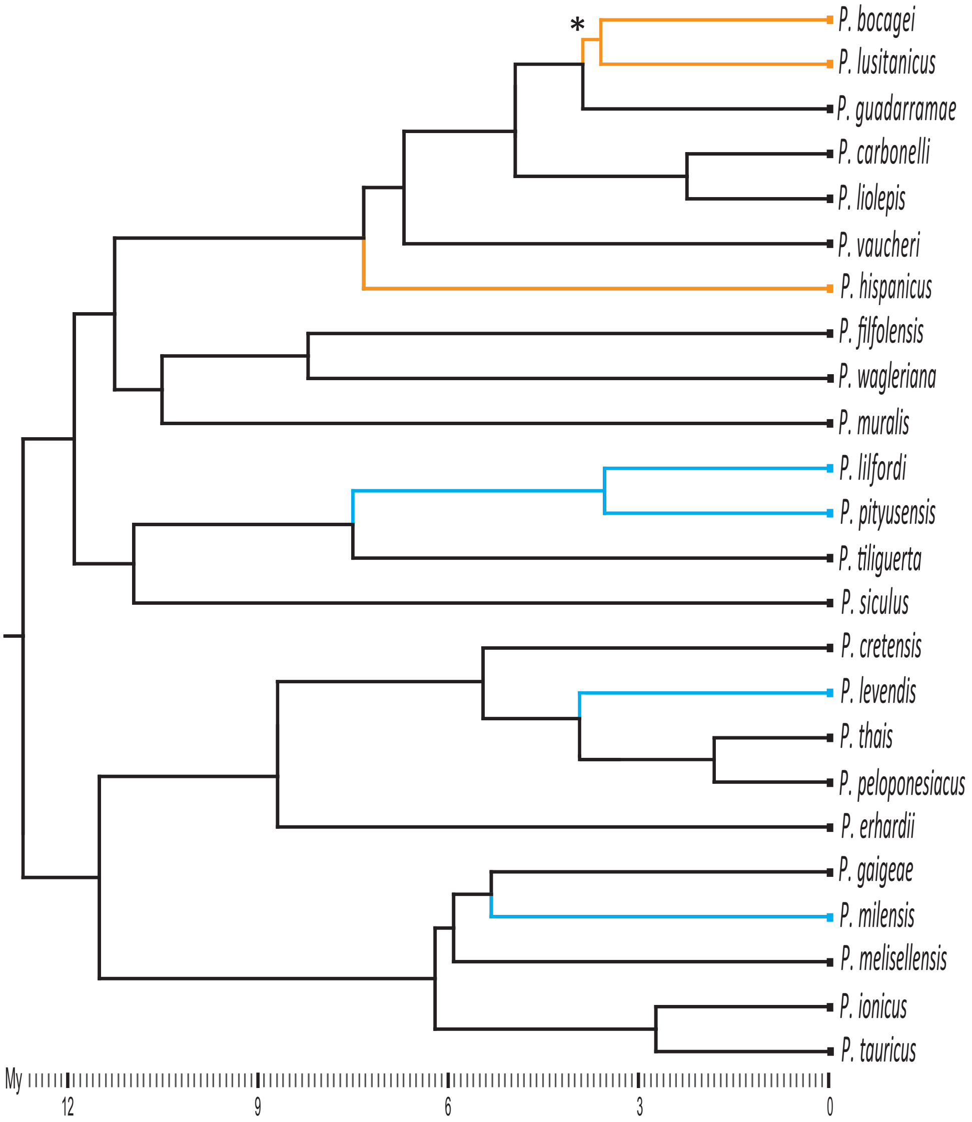

Figure 8. Historical character reconstruction of sexual dimorphism of the ultraviolet (UV)–blue patches in the genus *Podarcis* (orange, neither males nor females possess UV–blue patches; black, males clearly have more UV–blue patches and/or a larger area covered by this colour than females; blue, males and females have roughly the same number and size of UV–blue patches). *Podarcis thais* has been added to the original phylogeny, considering the time of divergence with *Podarcis peloponesiacus* (1.7 Mya). **Podarcis lusitanicus* has been added to the tree as a sister species of *Podarcis bocagei*. Abbreviation: My, millions of years. Reconstructions were performed with a parsimony model in MESQUITE v.3.7 (Maddison & Maddison, 2021) .

archipelago by the ancestor of these two species. Moreover, even if sexual dimorphism in the UV–blue patches was lost long before the colonization of Dragonera, it is possible that the peculiar conditions on this island have helped to maintain this trait in *P. lilfordi gigliolii*.

Dorsal coloration of *P. lilfordi gigliolii* also seems to be shaped by insularity conditions, because it is the second most chromatically conspicuous and the most achromatically conspicuous against the background. In contrast, dorsal coloration is the most cryptic coloration in mainland *Podarcis* (Pérez i de Lanuza & Font, 2015; Badiane & Font, 2021). This result is consistent with evidence from other *Podarcis* living on islands. For example, dorsal coloration in small-island populations of the Aegean *Podarcis gaigeae* is greener and matches their respective habitats less well than in mainland lizards (Runemark *et al.*, 2014). The increased conspicuousness and reduced local background matching again point to relaxed selection for crypsis owing to lower predation in insular environments (Doutrelant *et al.*, 2016).

In conclusion, our study demonstrates that signalling in *P. lilfordi gigliolii* differs in important ways from mainland and large-island *Podarcis*. Foot shakes (both social and antipredator) and other visual displays have been lost or remain unexpressed, whereas the UV–blue patches persist but have apparently lost their signalling function. In addition, the UV–blue patches of females are more similar to those of males than in other *Podarcis* species. These changes might arise from the relaxation of several selective pressures relating to sexual selection and predation and support a role of predator release as a driver of insular divergence. Further work is needed to assess whether this is a general trend affecting signalling in small and densely populated islands, at least in lizards.

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DATA AVAILABILITY

The data underlying this work are available on request to the corresponding author.

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article on the publisher's website:

Table S1. Multivariate homogeneity of group dispersions (variances) for the analyses of sexual dichromatism, colour patch discrimination and conspicuousness. The effect size (η^2), F value and P-value are shown.

Table S2. Tukey's test for multivariate homogeneity of group dispersions (variances) in the analysis of colour patch discrimination. The difference of means (Diff.), lower and upper intervals (Lwr. and Upr., respectively), adjusted P-values and sample size (N) are shown.

Table S3. Final models after stepwise backward selection based on the Akaike information criterion. The predictors retained (HL, head length; HW, head width; sexf, females; sexm, males; SVL, snout–vent length; W, body weight), t values, P-values and adjusted R^2 are shown.