

## RESEARCH ARTICLE

# Intrinsic climatic predictability affects ornamental coloration of adult males: Evidence for compensation among carotenoid- and melanin-based coloration

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## Abstract

1. Ornamental coloration is frequently an honest signal of quality associated with sexual selection. While changes in average environmental conditions affect carotenoid- and melanin-based coloration, no evidence exists that changes in intrinsic environmental predictability affect coloration.
2. Here we experimentally manipulated the intrinsic predictability of precipitation in semi-natural populations of common lizards *Zootoca vivipara* and tested its effect on ornamental coloration and reproduction of adult males.
3. Less predictable precipitation decreased hue of carotenoid-based coloration and the extent of melanin-based coloration. Hue was positively correlated and the extent of melanin-based coloration was negatively correlated with the male's number of confirmed mate partners.
4. Treatment effects on hue were associated with reduced, and treatment effects on the extent of melanin-based coloration with increased access to females, in line with differential effects on sexual selection.
5. Neither survival nor reproductive success of adult males significantly differed among predictability treatments, suggesting that negative effects on reproduction caused by changes in carotenoid-based coloration may have been compensated by changes in melanin-based coloration.
6. The results also showed that ornamentation, rather than reproduction and survival of adult males, was affected by less favourable conditions. Together with previous results, this suggests that coloration might be more sensitive to changes in environmental conditions than direct fitness proxies.

## KEYWORDS

carotenoid- and melanin-based coloration, climate change, compensation, intrinsic environmental predictability, mesocosms, population experiment, sexual selection

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## 1 | INTRODUCTION

In many animal species, conspicuous ornamental colours are honest signals of individual quality (Weaver et al., 2017), which are used in intrasexual and intersexual interactions (Andersson, 1994; San-Jose et al., 2014). Signal honesty frequently originates from the costs and benefits of producing and maintaining signals (e.g. physiological or socially imposed costs; Penn & Számadó, 2020), and the production and maintenance of elaborate ornaments may also be affected by trade-offs with other life-history traits (Siefferman & Hill, 2005). In line with this, studies have shown that the expression of ornamental coloration depends at least partly on environmental conditions (Kodric-Brown, 1989), suggesting that the expression and costs/benefits of ornamental coloration may be context dependent. For example, stress (Cote et al., 2006), resource availability (e.g. ingestion of pigments or lipids; San-Jose et al., 2012, 2013), parasite load (Weaver et al., 2017) and operational sex ratio (Cote et al., 2008) influence the expression of ornamental coloration (Fitze et al., 2009; San-Jose et al., 2016). However, less is known about whether and how changes in abiotic conditions lead to changes in ornamental coloration and published studies have focused mainly on how changes in average conditions (e.g. average temperature: Langkilde & Boronow, 2012; or ambient colour and light conditions: Merchant et al., 2018) affect coloration. It is frequently believed that environmental changes impose a direct cost, for example, in the production or maintenance of coloration (Weaver et al., 2017), but changes may also reflect behavioural strategies, for example, to mitigate effects on fitness-related traits (e.g. best-of-bad-job strategies; Gonzalez-Jimena & Fitze, 2012). It is therefore crucial to analyse whether colour changes are associated with changes in sexual attractiveness, competitive capacity, thermoregulation or reproductive success. Although some studies demonstrated the influence of changes in means of temperature and precipitation on ornamental traits and reproductive success (Scordato et al., 2012), to our knowledge, no single study investigated whether differences in intrinsic environmental predictability affect coloration and reproductive success.

Such evidence may not only be important to advance the understanding of colour signal evolution, but also serve to forecast climate change effects (e.g. changes in temperature, precipitation, environmental variability and environmental predictability; Stocker et al., 2013) on coloration and sexual selection. For example, decreased environmental predictability may lead to habitat change and thereby to an increase in stress (Pétavy et al., 2004), which may potentially increase the costs of producing and maintaining elaborate ornaments. Moreover, less predictable environments are predicted to negatively affect life-history traits (Ashander et al., 2016; Dewar & Richard, 2007) and population dynamics (Masó et al., 2019, 2020). Given the feedback between life-history traits and ornamentation (Siefferman & Hill, 2005), less predictable environments may also negatively affect ornamental coloration.

Here, we experimentally tested whether and how intrinsic precipitation predictability affects carotenoid- and melanin-based ornamental coloration of adult male common lizards *Zootoca vivipara*

(Lichtenstein, 1823) and whether detected effects may have fitness consequences. We manipulated intrinsic precipitation predictability, because precipitation is particularly important for the European common lizard given its high dependence on water (Dupoué et al., 2017; Lorenzon et al., 1999; Peñalver-Alcázar et al., 2016; Romero-Díaz et al., 2017). Moreover, the intrinsic predictability of rainfall has changed in the past decades and it is predicted to change in the future (Stocker et al., 2013), but very little research has tested its effect on animals. Male *Z. vivipara* exhibit carotenoid- and melanin-based coloration, both highly plastic traits (Fitze et al., 2009; San-Jose et al., 2013). In the Pyrenean populations, adult male *Z. vivipara* exhibit distinct colour morphs that behave like a locus with three alleles (orange, yellow and white) and can be classified using two colour scores (San-Jose et al., 2012, 2013; Sinervo et al., 2008), namely  $o$  and  $y$ , which account for the number of putative colour alleles ( $o$  score:  $0 = ww, wy, 1 = yo, wo, 2 = oo$ ;  $y$  score:  $0 = ww, oo, wo, 1 = wy, yo, 2 = yy$ ). Colour morphs are determined by differential carotenoid deposition (San-Jose et al., 2012, 2013) and carotenoid ingestion does not affect carotenoid deposition in the chromatophore (Fitze et al., 2009; San-Jose et al., 2013), which is in line with the genetic determination of the skin-carotenoid content and the colour morphs (Fitze et al., 2014). Nevertheless, carotenoid-based coloration is a plastic trait (San-Jose et al., 2012, 2013) that reflects the stress response (Cote et al., 2008; Fitze et al., 2009), lipid ingestion (San-Jose et al., 2012) and environmental conditions (San-Jose et al., 2013). This is because reptiles, amphibians and fish exhibit a dermal chromatophore unit that consists of contiguous cell layers containing carotenoids, iridophores and melanophores and an underlying fascia (Grether et al., 2004); and at least in *Z. vivipara* and another lizard species, components other than carotenoids are responsible for the plasticity of the carotenoid-based coloration (Lewis et al., 2017; San-Jose et al., 2013). Male *Z. vivipara* also exhibit many melanin-based black spots and melanin-based coloration is positively correlated with the immune response (Vroonen et al., 2013), body size (Vroonen et al., 2013), head size and bite force (San-Jose et al., 2017), and negatively with sprint speed (San-Jose et al., 2017).

In *Z. vivipara*, the hue of carotenoid-based coloration is linked to reproductive success (Fitze et al., 2009), whereby melanin-based coloration is positively linked with bite force (San-Jose et al., 2017), and bite force is negatively correlated with reproductive success (Huyghe et al., 2013). In this species, female mate choice has important consequences for a male's reproductive success (Fitze et al., 2010; Gonzalez-Jimena & Fitze, 2012; San-Jose et al., 2013), and male ornamental coloration affects a female's choice (Fitze et al., 2009; San-Jose et al., 2013). Changes in male ornamental coloration may thus directly affect a male's reproductive success, but their effect on reproductive success may vary in time, because male colour morphs are under frequency-dependent sexual selection (Fitze et al., 2014; San-Jose et al., 2014). Moreover, the plasticity of iridophore-based signals has only been shown in a few studies (Lewis et al., 2017; San-Jose et al., 2014; White, 2020), and the costliness of melanin-based signals is debated (Weaver et al., 2017). Thus, precise knowledge about the association between male ornamental

coloration and male reproduction success is crucial to interpret treatment effects.

To assess whether and how decreased precipitation predictability affects ornamental coloration and other fitness-related traits, intrinsic precipitation predictability was manipulated in 12 semi-natural *Z. vivipara* populations with equal male colour morph frequency. The yearly colour change of adult males was assessed over three subsequent years, to investigate the robustness of the effects. Previous studies on common lizards demonstrated that decreased precipitation predictability negatively affect life-history traits, such as growth and body condition, as well as population growth rate (Masó et al., 2019, 2020). This suggests that changes in precipitation predictability may also negatively affect ornamental coloration of *Z. vivipara*. Consequently, we predicted that decreased precipitation predictability will negatively affect (a) hue of carotenoid-based coloration and (b) melanin-based coloration, given that in previous experiments their expression was found to be plastic (Fitze et al., 2009; San-Jose et al., 2013). In addition, prior evidence on the link between coloration and sexual selection (San-Jose et al., 2014), we predicted (c) that carotenoid-based and melanin-based coloration will be significantly correlated with reproductive success. Finally, we also tested (d) whether effects on reproduction, potentially induced by colour changes in carotenoid-based and melanin-based coloration, were additive, or whether compensation may have existed. We tested this, because *Z. vivipara* males exhibit behavioural strategies that mitigate effects on reproductive success (Gonzalez-Jimena & Fitze, 2012).

## 2 | MATERIALS AND METHODS

### 2.1 | Species description

The common lizard *Zootoca vivipara* is a small lacertid widely distributed across Europe and Asia. It inhabits peat-bogs and moist heathlands. Microhabitat selection is positively related to habitat humidity (San-Jose et al., 2016) and it is a highly hydrophilic species, whose control of the hydric balance is of great importance (Lorenzon et al., 1999). Many studies demonstrated negative effects of reduced humidity on life-history traits, for example, on growth and reproduction (Lorenzon et al., 1999), and intra- and inter-age variation in vital rates is related to humidity (Romero-Diaz et al., 2017). Lizard activity depends mainly on ambient temperature, humidity, sunshine (Breedveld & Fitze, 2015; Vitt & Caldwell, 2013) and wind conditions (Ortega et al., 2017). At our field site, during late spring/summer, lizards are usually active from 7:30 a.m. onwards and on warm days they are even active after sunset. Peak activity is between 9 and 10 a.m. (sometimes until 11 a.m.) and a second activity peak exists around 6 p.m.

Ventral coloration of *Z. vivipara* exhibits a marked sexual dimorphism (Fitze et al., 2009). In *Z. vivipara louslantzi* (clade B; Horreo et al., 2018, 2019), adult females exhibit white to cream belly coloration with few black spots (Fitze et al., 2009, 2014). Adult

males exhibit six discrete colour morphs (see Introduction; Fitze et al., 2014; San-Jose et al., 2013) and the ventral coloration also consists of many melanin-based black spots. Carotenoid-based throat and upper belly coloration are highly correlated (Vroonen et al., 2013) and visible to conspecifics when exhibiting push-ups (Martin et al., 2013). During moult, lizards shed the transparent uppermost skin layers. When the layers of the epidermis start to separate (just before lizards start to shed the skin), the lizards' coloration becomes temporally duller and paler (e.g. Department of Natural Resources, 2018).

### 2.2 | Experimental design

#### 2.2.1 | Environmental procedures

To test how differences in environmental predictability affect male ornamental coloration and reproductive traits, 12 age-structured *Z. vivipara louslantzi* populations were established in independent enclosures containing natural vegetation and located at the Research Station 'El Boalar' (Jaca, Spain; for details see Romero-Diaz et al., 2017; San-Jose et al., 2014). The intrinsic environmental predictability was manipulated at the enclosure level over 4 years (2012–2015). Six enclosures were exposed to more and another six to less predictable precipitation, by supplementing precipitation with 4 sprinklers per enclosure, one in each corner, ensuring homogeneous precipitation. In our experimental populations, on March 15th sunrise is at 7:14 a.m., earliest sunrise is at 5:25 a.m., and on October 15th it is at 7:16 a.m. (all time specifications provided in this article refer to winter time). In the more predictable treatment, supplemental precipitation was provided every day, at 9.00 a.m. and at 6.00 p.m. (i.e. 14 supplemental precipitation events per 7 days, each providing the same amount of precipitation). In the less predictable treatment, 14 supplemental precipitation events were randomly distributed among 7 days between 9.00 a.m. and 7.00 p.m. Populations were irrigated from around emergence from hibernation of the lizards (March 15th) until most of the lizards were back in hibernation (around October 15th). In both treatments, the duration of each precipitation event was 5 min and corresponded to 2.6 mm of precipitation. The humidity of the enclosures without irrigation is below the common lizard's natural humidity requirements, allowing for manipulation within the species' natural range. The humidity regime (natural +supplemental precipitation) corresponded to the lowest 10–15th percentile of humidity found in the nuclei of three natural populations of the Pyrenees (Peñalver-Alcázar et al., 2016; Romero-Diaz et al., 2017), which exhibit high lizard densities. Permutation entropy (calculated based on natural plus supplemental precipitation; for calculation details, see supporting information Appendix S1) was larger in the less (0.86) and smaller in the more predictable treatment (0.77), showing that precipitation was less predictable in the less predictable treatment. In summary, only intrinsic precipitation predictability differed among treatments, and no differences existed in the amount of precipitation among treatments and enclosures.

## 2.2.2 | Release and captures

Lizards used for this experiment were captured from natural populations located in Aragón and Navarra, and they belong to the North-East Spain subclade, B4 and to the subspecies *Zootoca vivipara lousilantzi* (Horreo et al., 2018). The capture and handling of lizards were conducted under the license provided by the Gobierno de Aragón (LC/ehv 24/2010/105 and 106) and Gobierno de Navarra. The conducted study complies with the Spanish laws and the Association for the Study of Animal Behaviour/Animal Behaviour Society guidelines for the treatment of animals in behavioural research, and the study did not require ethical approval.

In July of each experimental year, lizards were released in an unfamiliar enclosure, that is, not in the enclosure where they or their mother have been captured previously. In 2013 and 2014, half of the recaptured lizards of each sex and age class were released in the same predictability treatment, while the other half was released in the other predictability treatment. All lizards were individually marked by toe-clipping and in each experimental year, the same number of adults and yearlings, and a similar number of juveniles was released in each enclosure (Appendix S2). No significant differences existed among treatments in the number ( $F_{1,10} = 1.033$ ;  $p = 0.317$ ) and sex-ratio ( $F_{1,10} = 0.005$ ;  $p = 0.940$ ) of the released juveniles. Lizards were randomly attributed to enclosures and no significant differences existed among treatment levels in SVL, body condition and adult male colour morph frequency (all  $p \geq 0.2$ ). Lizards hibernated in the enclosures and in spring, after the mating season (approximately end of May), all surviving lizards were recaptured and brought to the laboratory. Thereafter, all individuals were kept in individual terrariums until release following the protocol used by San-Jose et al. (2016). Recapture of all surviving individuals was assured by searching a given enclosure for lizards until 5 days passed since the last lizard had been seen and recaptured in this enclosure. At recapture, there existed no significant differences in colour morph frequency among treatment levels, year and their interaction was not significant either ( $p > 0.2$ ). Each year, at the beginning and at the end of the experiment, SVL (accuracy: 1 mm) and body mass (accuracy: 1 mg) were measured and standardized photographs of all adult males were taken (San-Jose et al., 2012).

## 2.3 | Colour analyses

To obtain standardized photos, adult males were gently placed into a dark box filled with foam material and a photographic filter lens (Hoya UV-filter, Kenko Tokina Co., Ltd., Tokyo, Japan) was slid over the lizard to immobilize it and to guarantee that the distance between the object and the objective was exactly the same for all photos. Standard colour squares (white, green, red, blue and yellow) were located on each lens side to detect potential failures of the flashes (for more details, see San-Jose et al., 2012). The dark box was placed in a fixed position inside a larger opaque camera box. The distance between the box and the digital camera (Nikon D70S, 6.10 megapixels,

with a 105 mm f/2.8 Nikkor objective, Nikon Corporation, Tokyo, Japan) was set at 40 cm. Illumination was provided by two flashes (Nikon SB-600, Nikon Corporation) positioned on each side of the camera box at an angle of 13° relative to the optical axis. Illumination settings were manually set to ensure that each photo received the exactly same amount of light (Fitze & Richner, 2002).

Of each photo, coloration was measured with ADOBE PHOTOSHOP CS6 (Adobe Systems, Inc). First, blackness and the extent of the melanin-based coloration were measured. To this end, the belly (from anal plate to gular scales) was divided into three thirds (anterior, central and posterior third), each of them consisting of the same number of inner longitudinal scales ( $\pm 1$  scale). The three thirds were divided in the middle of the two inner longitudinal scale lines (right, left side), resulting in six regions. In each lizard, five spots were selected in three regions (left anterior, right central and left posterior third). The selected spots were evenly distributed within regions (two spots on the exterior and three on the interior longitudinal line). Each colour photo was then transformed to grey scale, an area of 5 × 5 pixels was selected in the centre and close to the border of each selected spot, and average brightness (%) of each area was measured using the average filter implemented in Photoshop. Thereafter, average brightness per lizard (average of the 30 measurements: 3 regions × 5 spots per regions × 2 measures per spot) and blackness (BL) were calculated, the latter as '100—mean brightness', where 100% reflects completely black and 0% completely white (San-Jose et al., 2013, 2017). To measure the extent (E) of the black belly coloration (i.e. the proportion of black surface of a lizard's belly), the two inner and exterior longitudinal lines were selected and within this selection the surface of the black spots was determined by selecting all pixels exhibiting a lizard's average spot brightness  $\pm 30\%$ , using the 'Colour range' tool implemented in Photoshop. The number of the selected black pixels was divided by the number of pixels of the initially selected belly surface, yielding the proportion of black belly coloration.

Second, carotenoid-based coloration was measured on the third scale from the collar scales, on the third scale from the anal scale, and on the scale being in the middle of the two measurements on both, the left and right inner longitudinal line. In the middle of each selected scale a square of 8 × 8 pixels was placed that did not include black spots, and average hue (H), saturation (S) and brightness (B) were measured using the average filter implemented in Photoshop. Average hue, saturation and brightness were calculated per lizard (average of the 6 measurements) and used for further analyses. In the range of the coloration exhibited by *Zootoca vivipara*, higher H values indicate less orange, that is, yellower coloration, higher S values correspond to purer coloration, and higher B indicates brighter and more intense coloration (Fitze et al., 2009). All colour measures were derived from the photographs by DVS, who did not participate in the field work and who was unaware of the lizard's treatment.

Before taking photos, we examined each lizard belly for signs of moulting, that is, for duller and paler skin parts, which usually first appear on the breast or close to the anal scale (Breedveld & Fitze, 2016).

## 2.4 | Paternity analyses

Paternity analyses based on five polymorphic microsatellite DNA loci (Lv-3-19, Lv-4-72, Lv-4-alpha, Lv-4X and Lv-4-115; Horreo et al., 2017) were run to measure male reproductive success. To this end, DNA from tissue samples of stillborn and alive juveniles and all eggs was extracted using a BioSprint 96 DNA Blood Kit (Qiagen, Hilden, Germany). The methods used for polymerase chain reaction and determination of allelic size have been previously described (Horreo et al., 2017). The genetic profile of all mothers and of all potential fathers was known. Paternity assessment was performed manually by first assigning the alleles inherited from the mother. Thereafter, the father was searched among all putative fathers, by determining the male whose genotype matched with the remaining alleles. This assignment was then verified using Cervus v.3.0 (Marshall et al., 1998). In cases where the genotype of two fathers matched with the remaining juvenile alleles, paternity was confirmed by analysing two additional loci (Lv-1-139 and Lv-2-145; Horreo et al., 2017). This procedure led to unique paternity attribution in all offspring, without any mismatch between the fathers and the offspring's genotype. Thereafter, we decomposed annual male reproduction into the following statistically independent multiplicative fitness components (i.e. per year): reproductive success (juveniles produced: '1'; no juveniles produced: '0'), number of confirmed mate partners (number of females of whose clutch the male fertilized at least one egg) and average number of juveniles sired per mate partner (total number of juveniles sired by a given male/number of confirmed mate partners).

## 2.5 | Measures and statistical analysis

Treatment effects on carotenoid-based (H, S, B) and melanin-based coloration (BL, E), and reproductive parameters (reproductive success, number of confirmed mate partners and average number of sired juveniles) were analysed using mixed models (lmer and glmer from the package lme4; Bates et al., 2014) and the data available from the public repository digital.csic.es: <http://hthedl.handle.net/10261/259670> (Masó et al., 2022). Linear mixed models with Gaussian error distribution were applied to analyse coloration, generalized mixed models with binomial error distribution to analyse reproductive success, and generalized mixed models with Poisson error distribution for number of confirmed mate partners and average number of sired juveniles. In all the analyses, treatment and year were modelled as fixed factors and enclosure as random factor. Analyses of coloration consisted of two measures per individual: coloration at the beginning of the experiment (initial measures) and coloration at the end of the experiment (final measures), and therefore, the statistical model additionally included time as a fixed factor and 'animal ID' as random factor. In these models, a significant interaction between treatment and time indicates that treatment affected the colour change measured over the course of

a year. To account for moult, during which coloration becomes duller and paler (Department of Natural Resources, 2018), a factor moult was included in the model (0: moulting; 1: not moulting). Additionally, SVL and body condition were added as covariates, as well as their interaction with treatment and time. Non-significant interactions are not presented in the tables. Body condition corresponds to the residuals of a linear regression of body mass on SVL. Including an individuals' colour morph in these analyses (for details see Fitze et al., 2014) did not qualitatively change the results on carotenoid-based coloration shown in Table 1, and no significant colour morph  $\times$  treatment, colour morph  $\times$  year, and colour morph  $\times$  treatment  $\times$  year interactions existed (all  $p > 0.1$ , see Appendix S3), the latter showing that treatment effects were not morph specific. Therefore, male colour morph is not included in the analyses presented in the main manuscript. Analyses on reproductive traits additionally included the colour parameters measured during the reproductive period, SVL and body condition as covariates, the former to test for an association between coloration and reproduction. To account for potential effects of moult on coloration, a linear model with moult as fixed factor was previously run, and the residuals were extracted and used as variates.

Model selection started with the full model that included all parameters and all possible interactions, and the final model was obtained using backward elimination. For all tests, the significance level was set at  $\alpha = 0.05$  (two-tailed test). All assumptions of the applied models (e.g. for linear models: normality and heteroscedasticity of the residuals) were tested and if they were not met, transformations were applied. If after transformation heteroscedasticity still existed, weighted least square regressions were ran. Overdispersion existed in none of the non-Gaussian models. For significant factors containing more than two levels, post-hoc Tukey's HSD tests accounting for multiple testing were run. All analyses were run using R 3.5.0 (R Core Team, 2018).

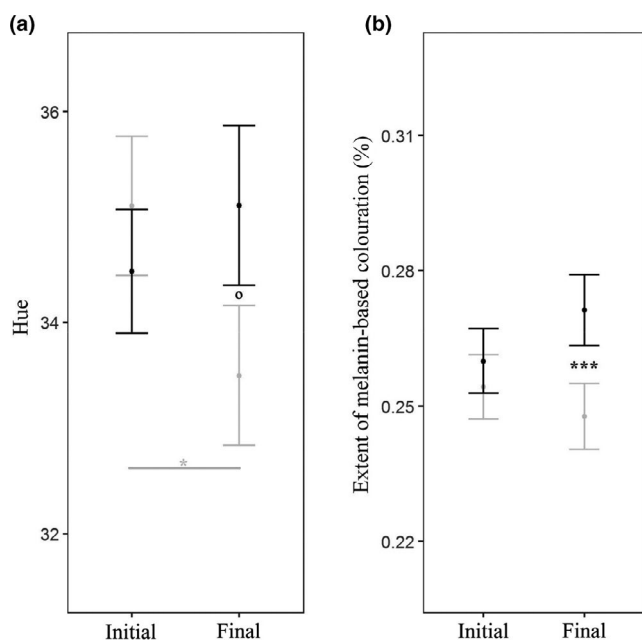
## 3 | RESULTS

### 3.1 | Carotenoid- and melanin-based ventral coloration

There was a significant interaction between time and treatment on hue of carotenoid-based coloration (Table 1; Figure 1a) and on the extent of melanin-based coloration (Table 1; Figure 1b). Post-hoc contrasts showed that, in the less predictable treatment, final hue was significantly lower than initial hue ( $p = 0.029$ ), that is, coloration became more orange, and no significant differences existed in the more predictable treatment ( $p = 0.401$ ). There were no significant differences among treatment levels in initial measures ( $p = 0.403$ ) and there was a tendency in final measures (Figure 1a). No significant treatment differences existed in initial measures of the extent of melanin-based coloration ( $p > 0.104$ ), and final measures were significantly larger in the more predictable than the less predictable

**TABLE 1** Minimum adequate models of carotenoid- and melanin-based coloration. Shown are test statistics and *p*-values. Significant parameters are bold and non-significant parameters removed from the initial model are denoted as ‘–’. The following abbreviations were used: BC, body condition; SVL, snout-to-vent length; *trt*, treatment; H, hue; S, saturation; B, brightness; E, extent of melanin-based coloration; BL, blackness of melanin-based coloration. The sample size was 373

Parameter	<i>df</i>	Carotenoid-based						Melanin-based			
		H		S		B		BL		E	
		$\chi^2$	<i>p</i>	$\chi^2$	<i>p</i>	$\chi^2$	<i>p</i>	$\chi^2$	<i>p</i>	$\chi^2$	<i>p</i>
Moult	1	<b>5.540</b>	<b>0.019</b>	<b>28.126</b>	<b>&lt;0.001</b>	<b>8.286</b>	<b>0.004</b>	<b>41.944</b>	<b>&lt;0.001</b>	0.179	0.672
<i>trt</i>	1	0.224	0.322	–	–	–	–	–	–	<b>5.211</b>	<b>0.022</b>
Time	1	0.981	0.322	<b>28.525</b>	<b>&lt;0.001</b>	<b>13.112</b>	<b>&lt;0.001</b>	<b>26.381</b>	<b>&lt;0.001</b>	0.079	0.779
Year	2	–	–	<b>27.990</b>	<b>&lt;0.001</b>	<b>14.111</b>	<b>0.004</b>	<b>23.721</b>	<b>&lt;0.001</b>	0.907	0.635
<i>trt</i> × time	1	<b>4.465</b>	<b>0.035</b>	–	–	–	–	–	–	<b>4.14</b>	<b>0.042</b>
<i>trt</i> × year	2	–	–	–	–	–	–	–	–	<b>6.493</b>	<b>0.039</b>
time × year	2	–	–	<b>11.006</b>	<b>0.004</b>	<b>12.467</b>	<b>0.002</b>	<b>32.232</b>	<b>&lt;0.001</b>	–	–
<i>trt</i> × time × year	2	–	–	–	–	–	–	–	–	–	–
Covariates											
SVL	1	<b>12.249</b>	<b>&lt;0.001</b>	0.183	0.672	2.982	0.084	0.196	0.658	2.395	0.122
BC	1	1.639	0.200	0.319	0.592	0.151	0.698	0.142	0.707	3.673	0.055



**FIGURE 1** Treatment effects (black: more predictable precipitation; grey: less predictable precipitation) on hue of carotenoid-based coloration (a) and the extent of melanin-based coloration (b). Predicted means  $\pm$  SE per treatment and time (Initial and Final measures) are shown. Horizontal lines indicate significant post-hoc contrasts:  $^{\circ}p = 0.069$ ;  $^*p < 0.05$ ;  $^{***}p < 0.001$

treatment (Figure 1b). All other colour parameters (S, B, BL) were not significantly affected by treatment (Table 1).

Saturation and brightness of carotenoid-based and blackness of melanin-based coloration were as well affected by a significant interaction between year and time (Table 1; Appendix S4), showing

that coloration changed within the same year independent of the treatment, and that the slopes of these changes significantly differed between years. There existed a significant interaction between treatment and year on the extent of melanin-based coloration, showing that the magnitude of the treatment effect depended on the year (note: the treatment  $\times$  year interaction on initial measures was highly non-significant:  $\chi^2 = 0.02$ ,  $p = 0.991$ , thus the significant interaction stems from the treatment-induced intra-annual colour change). Moult negatively affected saturation (not moulting =  $57.628 \pm 1.616$ ; moulting =  $49.287 \pm 2.019$ ), brightness (not moulting =  $50.676 \pm 0.390$ ; moulting =  $49.061 \pm 0.546$ ) and blackness (not moulting =  $85.205 \pm 0.287$ ; moulting =  $82.577 \pm 0.423$ ), and positively affected hue (not moulting =  $34.231 \pm 0.489$ ; moulting =  $35.932 \pm 0.739$ ; Table 1). Hue was significantly and positively correlated with SVL (Table 1) and all other colour parameters were not significantly correlated with SVL or body condition (Table 1). Moreover, their interactions with treatment were not significant (all  $p > 0.05$ ).

Male colour morphs significantly differed in H, S and B (Appendix S3). In both colour scores, H, S and B significantly increased with an increasing number of putative colour alleles (Appendix S5), as predicted by the optical differentiability of the male colour morphs (San-Jose et al., 2014; Sinervo et al., 2008).

### 3.2 | Reproductive traits

Precipitation predictability, alone or in interaction with year or the covariates, did not significantly affect reproduction (all  $p > 0.05$ ; Table 2). There existed significant differences among years in

**TABLE 2** Treatment effects on male reproductive traits. Minimum adequate models of reproductive success (RS), number of confirmed mate partners (NM) and average number of juveniles sired per mate partner ( $\phi$ NJ). Shown are test statistics based on standardized variables after backward elimination. Significant parameters are bold. Non-significant parameters removed from the initial model are denoted as '–'. The following abbreviations were used: *trt*, treatment; BC, body condition; SVL, snout-to-vent length; H, hue; S, saturation; B, brightness; E, extent of melanin-based coloration; BL, blackness of melanin-based coloration. Covariates describing coloration correspond to the residuals extracted from the linear model with moult as fixed factor (see Section 2)

Parameter	RS			NM				$\phi$ NJ					
	df	$\chi^2$	<i>p</i>	$\chi^2$	<i>p</i>	$\beta$	SE	$\chi^2$	<i>p</i>	$\beta$	SE		
<i>trt</i>	1	–	–	–	–	–	–	–	–	–	–		
Time	1	–	–	–	–	–	–	–	–	–	–		
Year	2	<b>7.173</b>	<b>0.028</b>	<b>19.137</b>	<b>&lt;0.001</b>	–	–	–	–	–	–		
	df	$\chi^2$	<i>p</i>	$\beta$	SE	$\chi^2$	<i>p</i>	$\beta$	SE	$\chi^2$	<i>p</i>	$\beta$	SE
<b>Covariates</b>													
SVL	1	1.753	0.185	–	–	<b>5.073</b>	<b>0.024</b>	<b>0.259</b>	<b>0.115</b>	0.588	0.443	–	–
BC	1	0.116	0.733	–	–	0.283	0.595	–	–	0.414	0.520	–	–
<b>Carotenoid</b>													
S	1	0.199	0.655	–	–	0.001	0.970	–	–	0.318	0.573	–	–
H	1	0.249	0.134	–	–	<b>4.851</b>	<b>0.028</b>	<b>0.231</b>	<b>0.105</b>	0.743	0.389	–	–
B	1	1.755	0.185	–	–	0.175	0.676	–	–	0.270	0.604	–	–
<b>Melanin</b>													
E	1	2.678	0.102	–	–	<b>6.982</b>	<b>0.008</b>	<b>–0.305</b>	<b>0.115</b>	0.415	0.520	–	–
BL	1	1.680	0.195	–	–	0.558	0.455	–	–	<b>5.501</b>	<b>0.019</b>	<b>4.051</b>	<b>1.727</b>

reproductive success and number of confirmed mate partners ( $p < 0.05$ ; Table 2). Post-hoc contrasts showed that reproductive success was significantly higher in 2014 compared to 2013 ( $p = 0.023$ ), and in 2012 it was intermediate. The number of confirmed mate partners was significantly higher in 2014 than in 2012 and 2013 (all  $p < 0.05$ ), and no differences existed between 2012 and 2013.

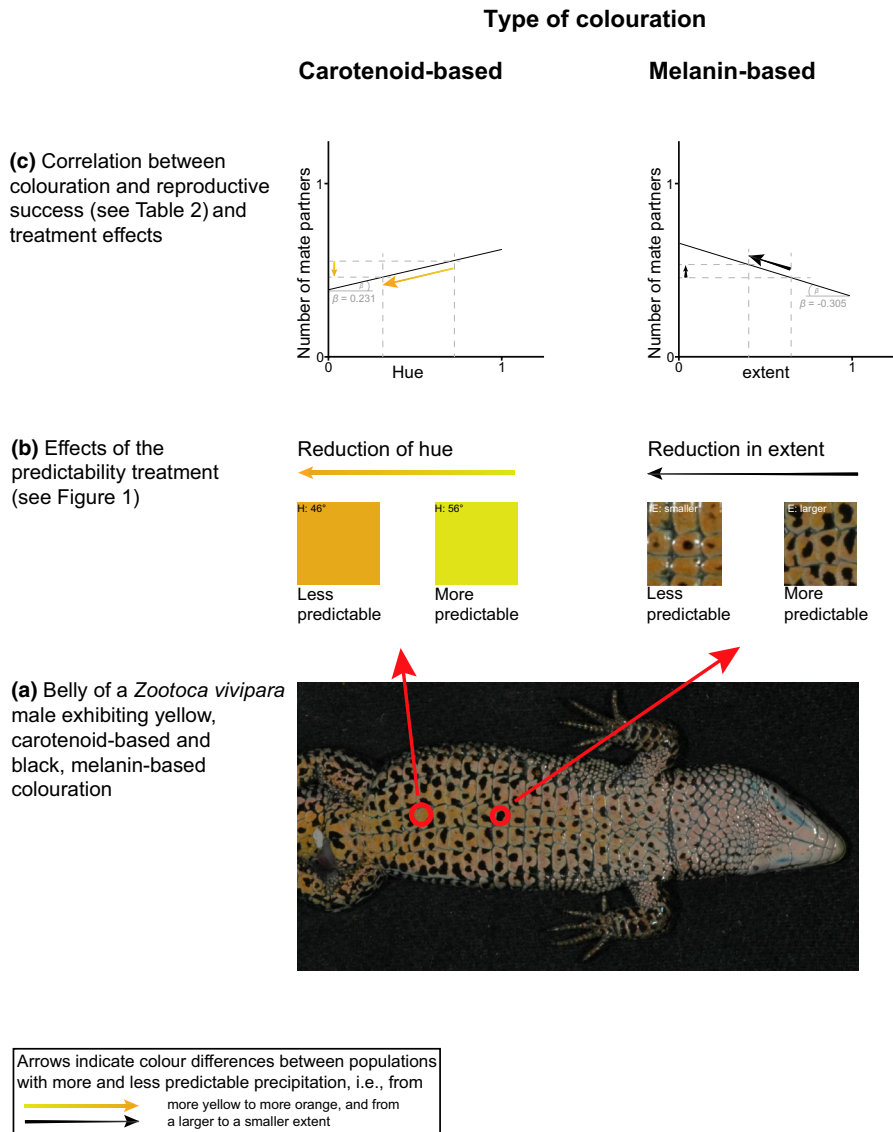
The number of confirmed mate partners was significantly and positively correlated with hue and SVL ( $p < 0.05$ ; Table 2), and it was significantly and negatively correlated with the extent of melanin-based coloration ( $p < 0.05$ ; Table 2). The average number of sired juveniles was positively correlated with blackness (Table 2). For both number of confirmed mate partners and average number of sired juveniles, no significant correlations existed with other colour parameters or body condition (all  $p > 0.05$ ; Table 2). In contrast, reproductive success was not significantly correlated with any of the covariates ( $p > 0.05$ ; Table 2).

## 4 | DISCUSSION

Many animal ornaments are honest signals of individual quality, and their expression depends on biotic (Cote et al., 2008; Kodric-Brown, 1989; San-Jose et al., 2013) and abiotic environmental conditions (Langkilde & Boronow, 2012; Merchant et al., 2018). While effects of changes in average temperature, ambient colour and light conditions on colour expression have been demonstrated, it is unclear whether and how predictability of abiotic conditions affect

ornamental coloration. The present study experimentally tested whether differences in intrinsic precipitation predictability affect carotenoid- and melanin-based ornamental coloration of adult males using the common lizard as a model species. Less predictable precipitation led to more orange hues of carotenoid-based coloration and to a reduced extent of melanin-based coloration (Figures 1 and 2), which is in line with the previously observed plasticity of both traits (Fitze et al., 2009) and with our predictions that melanin-based coloration and hue of carotenoid-based coloration will be affected by precipitation predictability (predictions 1 and 2). These findings, as well as within and across seasonal changes (significant time, year and year  $\times$  time effects in Table 1 and Appendix S4), agree with the plasticity of both traits. The treatment-induced changes further suggest that both ornaments are plastic honest signals (Weaver et al., 2017). The absence of treatment effects on saturation and brightness of carotenoid-based coloration is in line with the absence of treatment effects on both traits described in previous studies (Fitze et al., 2009). The absence of treatment effects on blackness (Table 1) indicates that the extent, but not the density of melanins, was modified, suggesting that the observed change was not due to re-distribution of existing melanins, but rather to removal and addition of melanin pigments.

To understand whether the observed changes may reflect behavioural strategies, their relationship with fitness proxies is crucial (Weaver et al., 2017). The hue of carotenoid-based coloration and SVL were positively correlated with the number of confirmed mate partners (i.e. the yellower the males' coloration was, the more mate



**FIGURE 2** Schematic summary of treatment effects on different types of coloration and how they affect reproductive success. From bottom to top, (a) location of the different types of coloration on a lizard's belly; (b) schematic treatment effects on both types of coloration; and (c) coloration between coloration and reproductive success. In (c), arrows indicate the direction of the observed treatment effect on coloration and its effect on reproductive success. For comparability among types of coloration, variables are standardized

partners they had; Table 2; Figure 2). The latter finding is in line with previous studies showing that body size positively predicts the number of mates (Fitze & Le Galliard, 2008) and the former is in line with our prediction, that coloration is linked with components of male reproductive success. The extent of melanin-based coloration was negatively correlated with the number of confirmed mate partners (Table 2; Figure 2), that is, with the most important determinant of male reproductive success (Fitze & Le Galliard, 2008). Blackness of melanin-based coloration was positively correlated with the average number of sired juveniles (Table 2).

The hue-decrease (change to more orange hues) was associated with less predictable precipitation, and also with a lower number of mate partners (Tables 1 and 2; Figure 2). This finding is in line with negative effects of reduced intrinsic precipitation predictability on growth and body size observed in yearlings (Masó et al., 2019). The extent of melanin-based coloration decreased under less predictable precipitation and it increased under more predictable precipitation. There was a negative correlation between the extent of melanin-based coloration and the number of mate partners (Table 2). A

decrease in the extent thus led to more and an increase of the extent led to less mate partners (Figure 2). This negative association is at first sight counter-intuitive, since under benign conditions (more predictable precipitation), males increased the extent of melanin-based coloration, but had a disadvantage in sexual selection (Figure 1b). In this species, the extent of melanin-based coloration is positively associated with the immune response (Vroonen et al., 2013) and bite force capacity (San-Jose et al., 2017), suggesting that males exhibiting a larger extent may be of better quality and thus they should have higher rather than lower reproductive success. However, while an increased immune response is beneficial (Vroonen et al., 2013), increased bite force capacity might be at the same time an advantage and a disadvantage for common lizard males. Advantages may arise because stronger bites allow to better immobilize and coerce females to copulate (Fitze et al., 2010; Huyghe et al., 2013), potentially leading to reduced female reluctance. However in *Z. vivipara*, female choice has important consequences for a male's reproductive success (Fitze et al., 2010; Gonzalez-Jimena & Fitze, 2012; San-Jose et al., 2013), and females may avoid mating with males exhibiting



high bite force, because male aggression towards females can have fatal consequences: it increases the risk to get injured during copulation, overrides female mating preferences, reduces a female's reproductive success and can lead to female death (Fitze et al., 2005; Le Galliard et al., 2005). Thus, avoiding males that exhibit high bite force may increase a female's short-term and life-time reproductive success and previous results showed that males with higher bite force were less likely to copulate than males with lower bite force (Huyghe et al., 2013). The results on melanin-based coloration thus suggest that in the more predictable treatment, traits unrelated to reproductive success may have improved (e.g. immune defence; Vroonen et al., 2013) at the expense of reproduction.

Since the slopes of the correlations between the number of mate partners and the hue of the carotenoid-based coloration, and between the number of mate partners and the extent of the melanin-based coloration were of similar magnitude (see  $\beta$ s in Table 2; Figure 2), it is possible that the effect of the hue change on the number of mate partners was cancelled out by the change in the extent of melanin-based coloration. This is in line with no significant treatment effects on reproductive parameters (Table 2; note that in models without covariates, treatment was not significant either) and it shows that treatment effects on one colour trait may have been compensated by treatment effects on another colour trait, in line with our prediction (see prediction 4). This suggests that adult males may have compensated the effects on carotenoid-based coloration by changing melanin-based coloration (Figure 2), which is in line with best-of-bad job strategies of male common lizards (Gonzalez-Jimena & Fitze, 2012) and with life-history theory predicting a trade-off for self-maintenance (Stearns, 1992). Evidence for compensation among ornamental traits is to our knowledge rare. However, most species exhibit several ornamental traits (Brooks & Coulldridge, 1999; Girard et al., 2015), suggesting that compensation among ornamental traits may not be restricted to *Z. vivipara*. But to detect compensation, several ornaments need to be measured at the same time and pertinent analyses need to be conducted. Analysing only a few ornaments can lead to a lack of information (Chaine & Lyon, 2015) and it can hinder the detection of compensation, which can lead to wrong conclusions.

In conclusion, to our knowledge, this is the first study to experimentally demonstrate that individual coloration responds to differences in environmental predictability and not only to the frequently studied changes in environmental means. Negative effects on carotenoid-based coloration may have been compensated by effects on melanin-based coloration, resulting in no treatment effects on fitness proxies and parameters linked to population dynamics. This is in line with previous studies pointing to the absence of treatment effects on survival, reproduction and growth of adult males (Masó et al., 2019), which contrasts to theory predicting negative effects of decreased environmental predictability on life-history traits (Ashander et al., 2016; Dewar & Richard, 2007). This shows that ornamentation is more sensitive to environmental changes than fitness proxies and parameters directly linked with population extinction, and suggests that ornamental coloration may be used to

early detect adverse conditions in lizards and as well in a wide range of other animal species (Camplani et al., 1999; Galvan et al., 2011; Marasco & Costantini, 2016).

## COMPETING INTEREST

The author(s) declare no competing interests.

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## AUTHORS' CONTRIBUTIONS

Patrick S. Fitze and Guillem Masó conceived the ideas and designed the methodology; Guillem Masó collected and analysed the data with the help of Diego Vicente-Sastre and under the supervision of Patrick S. Fitze; Guillem Masó and Patrick S. Fitze wrote the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

## DATA AVAILABILITY STATEMENT

The data used in this article are deposited in a public institutional repository (digital.csic.es) and can be accessed using the following link <https://digital.csic.es/handle/10261/259670>.

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## SUPPORTING INFORMATION

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