

# Long-Term Decrease in Coloration: A Consequence of Climate Change?

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Submitted March 30, 2021; Accepted January 6, 2022; Electronically published May 11, 2022

Online enhancements: supplemental PDF. Dryad data: <https://doi.org/10.5061/dryad.w6m905qr9>.

**ABSTRACT:** Climate change has been shown to affect fitness-related traits in a wide range of taxa; for instance, warming leads to phenological advancements in many plant and animal species. The influence of climate change on social and secondary sexual traits, which are associated with fitness because of their role as quality signals, is, however, unknown. Here, we use more than 5,800 observations collected on two Mediterranean blue tit subspecies (*Cyanistes caeruleus caeruleus* and *Cyanistes caeruleus ogliastrae*) to explore whether blue crown and yellow breast patch colorations have changed over the past 15 years. Our data suggest that coloration has become duller and less chromatic in both sexes. In addition, in the Corsican *C.c. ogliastrae*, but not in the mainland *C.c. caeruleus*, the decrease is associated with an increase in temperature at molt. Quantitative genetic analyses do not reveal any microevolutionary change in the color traits over the study period, strongly suggesting that the observed change over time was caused by a plastic response to the environmental conditions. Overall, this study suggests that ornamental colorations could become less conspicuous because of warming, revealing climate change effects on sexual and social ornaments and calling for further research on the proximate mechanisms behind these effects.

**Keywords:** ornaments, heritability, predicted breeding values, phenotypic plasticity, blue tit, global warming.

## Introduction

Environmental conditions play a key role in modulating the life cycles of organisms (Stenseth et al. 2002). As a con-

sequence, in many taxa, trait expression changes as a result of environmental heterogeneity, especially in relation to current rapid climate change (plants [Peñuelas et al. 2002; McDowell et al. 2020], fish [Crozier and Hutchings 2014; Asch et al. 2019], mammals [Réale et al. 2003; Boutin and Lane 2014], and insects [Pureswaran et al. 2018; Kellermann and van Heerwaarden 2019]). One of the most commonly reported responses regards plant and animal phenology (Parmesan 2007; Hällfors et al. 2020), whereby many species are advancing their breeding periods as a consequence of global warming (Hällfors et al. 2020). By contrast, less attention has been given to the impacts of climate change on other fitness-related traits, such as social or secondary sexual traits.

Ornaments have evolved to signal individual quality to mates or competitors, determining mating opportunities and/or the outcome of intrasexual interactions (Andersson 1994); however, whether climate change influences the expression and contemporary evolution of ornaments is unclear (Svensson 2019). Yet a reduction in ornament intensity and variance can reduce their signaling potential and the strength of sexual selection acting on them (Cockburn et al. 2008), something that can compromise the adaptive capabilities of a population (Gómez-Llano et al. 2021).

An ornament's reliability is often associated with its cost and/or condition dependence (Pomiankowski 1987; Cotton et al. 2004), and as a consequence, ornament expression is expected to be sensitive to variation in environmental conditions (Breckels and Neff 2013; López-Idiáquez et al. 2016b). In male guppies (*Poecilia reticulata*), for instance, experiments have revealed that their orange ornament hue is highest for a water temperature of 28°C while lower at colder and warmer temperatures (Breckels and Neff 2013). Furthermore, the environment can also modulate the relative costs

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and benefits associated with ornament expression (Vergara et al. 2012). For example, in lions (*Panthera leo*) mane length and darkness, which are secondary sexual traits, have temperature-dependent costs, as the individuals with longer and darker manes suffer from reduced sperm quality and lower ability to obtain food at high temperatures (West and Packer 2002; Patterson et al. 2006). Thus, given the current rapid global warming, the costs associated with the production and maintenance of ornaments could be expected to change, and at least in warmer areas, climate change could constrain the expression of secondary sexual traits.

In birds and in other taxa, the expression of conspicuous colored patches is usually driven by sexual and/or social selection (Stuart-Fox and Ord 2004; Dale et al. 2015). Plumage coloration can be produced by different mechanisms: the deposition of pigments, such as carotenoids or melanin, the microstructure of the feather, or a combination of both (Hill and McGraw 2006). Because of their different developmental mechanisms, each type of coloration may respond differently to environmental variation. On the one hand, carotenoid-based traits are linked to factors such as diet, stress, or parasite prevalence, and their signaling role is traded off with antioxidant and immune functions; thus, they are expected to be highly sensitive to the environmental variation (Hill et al. 2002; Mougeot et al. 2010). On the other hand, structural colorations are less costly to produce (Prum et al. 2009), and their expression constraints may be more indirectly linked to the environment (e.g., feather development time; Griggio et al. 2009); thus, they are expected to be less reactive to environmental variation (Prum 2006; Janas et al. 2020). However, all colorations present some degree of environmental dependence and can be driven by the interannual variation in climatic conditions (e.g., for birds; melanin [Jensen et al. 2006], carotenoids [Reudink et al. 2015], structural [Masello et al. 2008]). In general, we can expect coloration to become duller and less chromatic as a result of climate change, since warmer temperatures have been negatively associated with body condition (McLean et al. 2018) and increased infection risk by parasites like haemosporidians (Garamszegi 2011) that can negatively affect coloration (del Cerro et al. 2009). However, it is also important to consider that the strength and direction of the consequences of climate change on ornamental colorations may be different between colors and populations, as climate change effects differ across geographic areas (IPCC 2018).

To the best of our knowledge, only four long-term studies have explored the potential influence of climate change on the expression of ornamental colorations: two focusing on the size of an achromatic patch in migratory bird species (Scordato et al. 2012; Evans and Gustafsson 2017), one on the intensity of the carotenoid-based coloration in a seden-

tary bird species (Laczi et al. 2020), and another on the degree of melanization in dragonflies (Moore et al. 2021). The first found no variation on the achromatic white wing bar size of Hume's warblers (*Phylloscopus humei*) in the Himalayas over 25 years, despite a mean 2°C increase in the study area (Scordato et al. 2012). Two found negative associations with climate change. The size of the achromatic white forehead patch in collared flycatchers (*Ficedula albicollis*) breeding in Sweden decreased, hypothetically as a consequence of the estimated 1.5°C rise over a 34-year period (Evans and Gustafsson 2017). Also, warming led to a decrease in the degree of melanization in 10 dragonfly species across North America between 2005 and 2019 (Moore et al. 2021). The fourth study, on the contrary, described an increase in the yellow chest coloration over 8 years in a Hungarian great tit (*Parus major*) population due to the increase in temperature and decrease in precipitation (Laczi et al. 2020). To date, nothing is known about how climate change affects the intensity of other types of colorations, such as structural colors, which despite being understudied, play an important role as condition-dependent signals in different taxa such as birds, reptiles, or arachnids (White 2020). Furthermore, from the aforementioned studies, only one reported a microevolutionary response (using estimated breeding values) of the ornamental colors to the environmental change (Evans and Gustafsson 2017). Still, identifying whether changes at the phenotypic level occur through microevolution or are the product of phenotypic plasticity is crucial to understand the consequences of climate change, as only microevolution can ensure the adaptation to continued environmental change (van Buskirk and Steiner 2009; Duputié et al. 2015).

Here, we explored the effects of climate change on two coloration types of male and female blue tits (*Cyanistes caeruleus*). We used 15 years of data collected in two subspecies, *C.c. caeruleus* on the French Mediterranean mainland and *C.c. ogliastroae* in Corsica near the south edge of the species distribution. Specifically, we studied the ultraviolet (UV) blue coloration of the crown (structural coloration) and the yellow coloration of the breast patch (carotenoid-based coloration), both renewed annually during molt in summer. These two colorations are condition dependent in both sexes in our populations (Doutrelant et al. 2012) and may play a role as signals in social and sexual contexts (Hunt et al. 1999; Sheldon et al. 1999; Alonso-Alvarez et al. 2004; Limbourg et al. 2013; Midamegbe et al. 2013; Doutrelant et al. 2020; but see Parker 2013). Our specific objectives were to determine whether (i) blue tit ornamental colorations showed a temporal trend in their expression, (ii) temperature and precipitation have changed over the study period, (iii) the temporal variation observed in trait expression was explained by the variation in temperature and precipitation, and (iv) the change shown at the phenotypic

level was due to microevolution, by exploring the temporal trends in trait breeding values. Given the expected negative impacts of warming and droughts on bird body condition and health for species living in hot and dry conditions (Garamszegi 2011; McLean et al. 2018; McKechnie and Wolf 2019), we predicted that if temperature is increasing and/or precipitation is decreasing in the study area, we would find a decline in blue tit ornamental colorations owing to their condition dependence (Doutrelant et al. 2012). In addition, given that it has been shown that blue tit coloration is heritable both in our populations (Charmantier et al. 2017) and in other populations (Hadfield et al. 2006; Drobniak et al. 2013), we evaluated the extent to which a genetic change contributes to the change described at the phenotypic level.

## Methods

### *Study Area and General Procedures*

This study was conducted between 2005 and 2019 in two Mediterranean areas equipped with nest boxes. The first area is located in La Rouvière forest (D-Rouvière) in the vicinity of Montpellier (subspecies *caeruleus*). The second is located on the island of Corsica (subspecies *ogliastrae*) and includes three different study sites in northwest Corsica (D-Muro, E-Muro, and E-Pirio; Charmantier et al. 2016). Blue tits were captured when nestlings were 9 days old. At that time, each bird was ringed with a uniquely numbered metal ring, and six blue feathers from the crown and eight yellow feathers from the chest were collected to assess the coloration using spectrophotometry in the lab. The captures and the sampling of the feathers were done following a standardized protocol, mostly by permanent staff and doctoral students (88% of the captures). We computed chromatic and achromatic color variables using AVICOL version 2 or the R package pavo (Gomez 2006; Maia et al. 2019). Specifically, for the blue crown coloration, we computed UV chroma and brightness, and for the yellow breast patch coloration, we computed yellow chroma and brightness, following precedent studies (Andersson et al. 1998; Doutrelant et al. 2008, 2012; Fargevielle et al. 2017; see supplementary material 1 (SM-1) in the supplemental PDF for further details on how the feathers were sampled and measured and how color was extracted). Blue tits undergo one molt per year. First, the postjuvenile molt, which is limited to the head, body, and a variable number of flight feathers, takes place in summer at approximately 2 months of age (Shirihai and Svensson 2018; Stenning 2018). Then as adults the complete postbreeding molt in which blue tits renew all of their feathers occurs mainly between mid-June and mid-September (Shirihai and Svensson 2018).

### *Climatic Variables*

Daily values of mean temperature (i.e., average between the maximum and the minimum temperatures of the day) and precipitation between 2004 and 2018 were obtained from the French national meteorological service. Following Bonamour et al. (2019), we used weather information from the stations of Saint Martin de Londres on the mainland (about 24 km from D-Rouvière) and Calvi in Corsica (9–19 km to the Corsican study sites). Temperatures from the meteorological stations were highly correlated with the local temperatures at each study site (for further information, see Bonamour et al. 2019). With this information, we computed two variables for each population: the average temperature during molt (average temperature between June 1 and September 30 in the previous year) and average precipitation during molt (i.e., across the same period). The time interval between June and September in the previous year was selected to capture the climatic conditions experienced by the blue tits during molting.

### *Statistical Analyses*

*Temporal Trends in Coloration.* To test for a change in the colored traits over time, we fitted a series of linear mixed models (LMMs) with a normal distribution of errors, one for each of the four color components in the two subspecies separately. These models included the colored traits as dependent variables and year (as a continuous variable) as an explanatory term scaled to a mean of zero and standard deviation of unity. In addition, sex and its interaction with year were included as covariates. Individual identity, year (as a categorical variable), and site (in the Corsican models) were included as random factors to account for the nonindependence of data within sites, years, and individuals.

*Temporal Trends in Climatic Variables.* The temporal trends in the climatic proxies (average temperature and precipitation during molt) for the period 2004–2018 were analyzed separately for each population. We fitted a linear model with a normal distribution of errors that included the climatic indexes as dependent variables and year (as a continuous variable) as an explanatory term.

*Association between the Colored Traits and the Climatic Variables.* We fitted LMMs with a normal distribution of errors to analyze the association between the colorations and the climatic proxies in the two subspecies separately. We included the colored traits as dependent variables in separate models and average temperature and precipitation during molt as explanatory terms. Sex and its interaction with the climatic variables were also included to control for possible sex-dependent responses. Year (as

a continuous variable) was included as a covariate in the D-Rouvière models but not in the Corsican models, as it was collinear with the climatic variables (variance inflation factor  $> 3$ ; Zuur et al. 2010; see table S2.1). All models included year (as a categorical variable), individual identity, and site (in the Corsican models) as random factors. Predictors were scaled to a mean of zero and standard deviation of unity.

**Quantitative Genetics Analyses.** In each population, we fitted a univariate animal model with Gaussian errors for each colored trait and sex to estimate the heritability and predicted individual breeding values for each trait. We included year (as a continuous variable) and site (in the Corsican models) as fixed effects. The random effects decomposed the phenotypic variance ( $V_P$ ) into four components, namely, additive genetic variance ( $V_A$ ), permanent-environment variance ( $V_{PE}$ ; estimated using the repeated observations of the individuals in different years), variance associated with measurement year ( $V_{YR}$ ), and residual variance ( $V_R$ ). The  $V_A$  was estimated by incorporating a relatedness matrix based on a social pedigree of our population. Extrapair paternity occurs in our populations (average of 18.4% extrapair young found between 2000 and 2003; Charmantier and Blondel 2003), which may lead to heritability underestimated by up to 17% (Charmantier and Réale 2005). For those individuals with unidentified parents a dummy code was assigned to represent the missing parent so that the sibship information was retained. We used the `prunePed` function of the `MCMCglmm` package (Hadfield 2010) to retain only the informative individuals in each analysis. The different pruned pedigrees used in the analysis had between 1,129 and 1,864 observations and a maximum pedigree depth of 16 generations (see SM-3 for further information on the pedigrees used). These models were run with the `MCMCglmm` package with a total of 2,500,000 iterations, including a burn-in period of 500,000 iterations and a thinning interval of 2,000 iterations. For random effects, we used parameter-expanded priors ( $V = 1, \nu = 1, \alpha\mu = 0, \alpha V = 1,000$ ). We also fitted additional models using alternative priors that showed that the quantitative genetic estimates were robust (for further information, see SM-4). Calculations of the quantitative genetic estimates were done on the Markov chain Monte Carlo posterior distributions to propagate the uncertainty in parameter estimates (Evans and Gustafsson 2017; Bonnet et al. 2019). In all models, autocorrelation values were lower than 0.1, and effective sample size was at least 1,000. We also checked that models satisfied convergence criteria according to the Heidelberg and Welsh (1981) convergence diagnostic. To estimate the temporal trends in breeding values, we fitted for each trait a linear regression of the best linear unbiased predictors (BLUPs) for the additive genetic individual

effect against the individual mean value of its breeding years, as previously done in Bonnet et al. (2019). To account for the uncertainty around BLUP estimations (Hadfield et al. 2010), we used their full posterior distribution to estimate the time trend. For each of the 1,000 interactions, we ran the regression of BLUPs against the individual mean values of the breeding year, and then the overall time trend was estimated by the posterior distribution of these 1,000 slopes. We used individual mean value of year rather than hatching year, as it reflects when the individual was contributing to the temporal trends as a breeder and because it allows including individuals for which hatching year is unknown. Using a less conservative approach (namely, not including year as continuous fixed effect) yields similar results (see table S5.1). Maternal effects were not considered in the animal models, something that led to a slight overestimation (mean: 0.011, range: 0.004–0.027) of the heritabilities (for further details, see SM-6).

Mixed models were run with the packages `lmerTest` (Kuznetsova et al. 2017) or `MCMCglmm` (Hadfield 2010) in R (ver. 3.6.3; R Core Team 2019). We computed the conditional  $R^2$  ( $R^2_{\text{cond}}$ ), which represents the percentage of total variance explained by both the fixed effects and the random effects, and the marginal  $R^2$  ( $R^2_{\text{mar}}$ ), which represents the percentage of total variance explained by the fixed effects only (Nakagawa and Schielzeth 2013), using the package `MuMIn` (Barton 2019). Finally, variance inflation factors were estimated using the package `usdm` (Babak 2015) to estimate the collinearity between the explanatory variables. Including age (1 year old vs.  $\geq 2$  years old) did not change the obtained results (see table S7.1–S7.4). Data used in this study have been deposited in the Dryad Digital Depository (<https://doi.org/10.5061/dryad.w6m905qr9>; López-Idiáquez et al. 2022).

## Results

### Coloration across Years

**Blue crown.** In both Corsica and D-Rouvière we found a significant year-by-sex interaction showing a decrease in the UV chroma with time (table 1; fig. 1) that was slightly stronger in males (Corsica:  $-0.019 \pm 0.005$ ,  $F_{1,13.05} = 14.63$ ,  $P = .002$ ; D-Rouvière:  $-0.012 \pm 0.005$ ,  $F_{1,13.00} = 5.238$ ,  $P = .039$ ) than in females (Corsica:  $-0.015 \pm 0.004$ ,  $F_{1,13.07} = 10.05$ ,  $P = .007$ ; D-Rouvière:  $-0.008 \pm 0.004$ ,  $F_{1,13.17} = 4.528$ ,  $P = .052$ ). In both models the fixed effects explained approximately 35% of the variance ( $R^2_{\text{mar}}$ ), and around 70% was explained by the combined fixed and random effects ( $R^2_{\text{cond}}$ ; table 1). Regarding brightness, while no significant change over time was found in Corsica, it significantly decreased in both sexes in D-Rouvière (table 1; fig. 1;  $R^2_{\text{mar}} = 0.148$ ,  $R^2_{\text{cond}} = 0.502$ ).

**Table 1:** Linear temporal trends for blue crown and yellow breast patch colorations of the blue tits in Corsica and D-Rouvière

Fixed effect	Corsica				D-Rouvière			
	Estimate	SE	<i>F</i>	<i>P</i>	Estimate	SE	<i>F</i>	<i>P</i>
Blue crown ultraviolet chroma								
Year	<b>-.019</b>	<b>.004</b>	$F_{1,13.03} = 12.524$	<b>.003</b>	<b>-.011</b>	<b>.004</b>	$F_{1,13.03} = 5.038$	<b>.042</b>
Sex(fem)	<b>-.035</b>	<b>.0008</b>	$F_{1,2,213.7} = 1,614.7$	<b>&lt;.001</b>	<b>-.038</b>	<b>.001</b>	$F_{1,1,169.4} = 1,024.9$	<b>&lt;.001</b>
Year × sex(fem)	<b>.004</b>	<b>.0008</b>	$F_{1,2,790.5} = 23.383$	<b>&lt;.001</b>	<b>.002</b>	<b>.001</b>	$F_{1,1,407.8} = 3.927$	<b>.047</b>
$R^2$	$R^2_{\text{cond}} = .740; R^2_{\text{mar}} = .365$				$R^2_{\text{cond}} = .696; R^2_{\text{mar}} = .338$			
Blue crown brightness								
Year	<b>-.756</b>	<b>.586</b>	$F_{1,13.06} = 1.287$	<b>.276</b>	<b>-1.557</b>	<b>.701</b>	$F_{1,13.01} = 5.670$	<b>.033</b>
Sex(fem)	<b>-2.378</b>	<b>.118</b>	$F_{1,2,125.6} = 399.71$	<b>&lt;.001</b>	<b>-2.332</b>	<b>.189</b>	$F_{1,1,097.0} = 150.75$	<b>&lt;.001</b>
Year × sex(fem)	.190	.117	$F_{1,2,774.0} = 2.653$	.103	-.195	.187	$F_{1,1,337.7} = 1.093$	.295
$R^2$	$R^2_{\text{cond}} = .431; R^2_{\text{mar}} = .094$				$R^2_{\text{cond}} = .502; R^2_{\text{mar}} = .148$			
Yellow breast patch chroma								
Year	<b>-.051</b>	<b>.018</b>	$F_{1,13.15} = 12.673$	<b>.003</b>	-.040	.021	$F_{1,13.07} = 3.412$	.087
Sex(fem)	<b>-.068</b>	<b>.004</b>	$F_{1,2,074.8} = 277.11$	<b>&lt;.001</b>	<b>-.012</b>	<b>.006</b>	$F_{1,1,015.5} = 4.100$	<b>.043</b>
Year × sex(fem)	<b>.020</b>	<b>.004</b>	$F_{1,2,731.1} = 25.071$	<b>&lt;.001</b>	.001	.006	$F_{1,1,248.6} = .101$	.750
$R^2$	$R^2_{\text{cond}} = .385; R^2_{\text{mar}} = .138$				$R^2_{\text{cond}} = .472; R^2_{\text{mar}} = .062$			
Yellow breast patch brightness								
Year	<b>-1.294</b>	<b>.310</b>	$F_{1,13.11} = 21.860$	<b>&lt;.001</b>	<b>-1.481</b>	<b>.480</b>	$F_{1,13.09} = 9.706$	<b>.008</b>
Sex(fem)	<b>.627</b>	<b>.090</b>	$F_{1,1,904.7} = 48.007$	<b>&lt;.001</b>	.503	.127	$F_{1,935.33} = 15.581$	<b>&lt;.001</b>
Year × sex(fem)	<b>-.286</b>	<b>.089</b>	$F_{1,2,600.6} = 10.271$	<b>.001</b>	-.004	.126	$F_{1,1,169.5} = .001$	.971
$R^2$	$R^2_{\text{cond}} = .391; R^2_{\text{mar}} = .199$				$R^2_{\text{cond}} = .507; R^2_{\text{mar}} = .169$			

Note: Significant ( $P < .05$ ) variables are in bold.  $R^2_{\text{cond}}$  represents the variance explained by both the fixed effects and the random effects included in the model.  $R^2_{\text{mar}}$  represents the variance explained by the fixed factors alone. Blue crown ultraviolet chroma and brightness number of observations: Corsica = 3,867; D-Rouvière = 2,068. Yellow breast patch chroma and brightness number of observations: Corsica = 3,890; D-Rouvière = 2,007.

*Yellow breast patch.* In Corsica we found a significant year-by-sex interaction ( $R^2_{\text{mar}} = 0.145$ ,  $R^2_{\text{cond}} = 0.368$ ; table 1; fig. 1) showing that chroma decreased with time with a stronger effect in males ( $-0.052 \pm 0.012$ ,  $F_{1,13.29} = 17.57$ ,  $P = .001$ ) than in females ( $-0.030 \pm 0.012$ ,  $F_{1,13.07} = 6.213$ ,  $P = .026$ ). In D-Rouvière a marginal negative association was found between chroma and year ( $P = .087$ ). Regarding brightness, in Corsica a significant interaction between year and sex was found (table 1; fig. 1;  $R^2_{\text{mar}} = 0.199$ ,  $R^2_{\text{cond}} = 0.391$ ). In both sexes, brightness decreased with year (males:  $-1.288 \pm 0.320$ ,  $F_{1,13.17} = 16.175$ ,  $P = .001$ ; females:  $-1.597 \pm 0.310$ ,  $F_{1,13.20} = 26.497$ ,  $P < .001$ ). In D-Rouvière brightness decreased with time with no interaction between year and sex ( $R^2_{\text{mar}} = 0.169$ ,  $R^2_{\text{cond}} = 0.507$ ; table 1; fig. 1; see table S8.1 and S8.3 for further details).

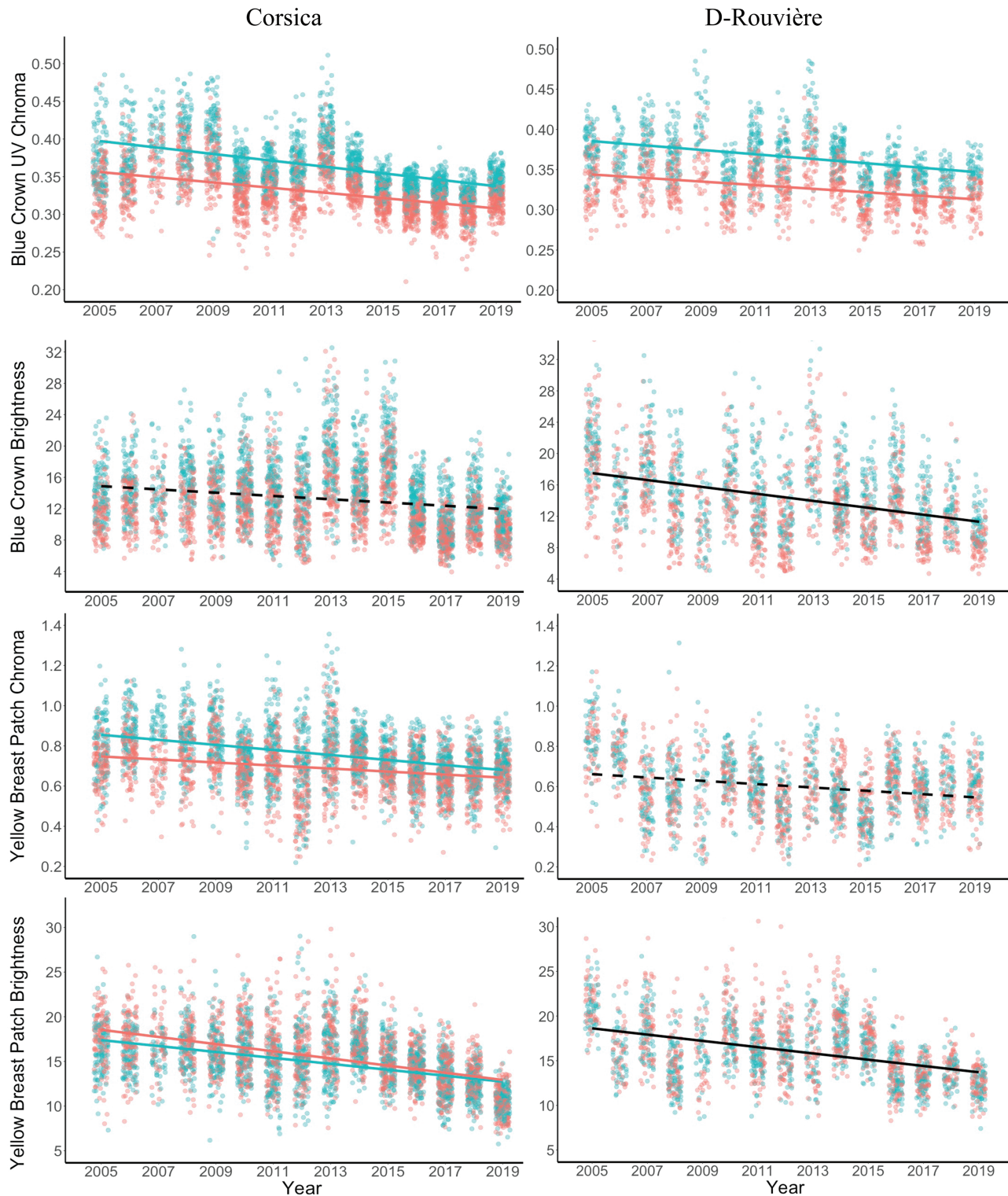
#### *Climate across Years*

In Corsica we found a significant increase in average temperature ( $1.23^\circ\text{C}$ ;  $0.080 \pm 0.024$ ,  $F_{1,13} = 10.782$ ,  $P = .005$ ) and decrease in average precipitation ( $-0.64$  mm;  $-0.068 \pm 0.021$ ,  $F_{1,13} = 10.306$ ,  $P = .006$ ) during molt across the

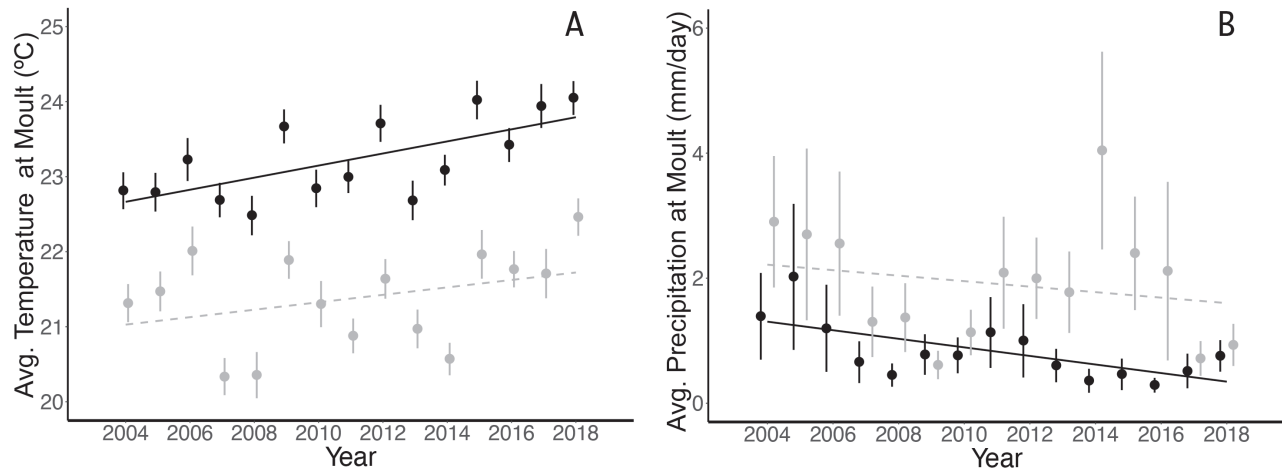
past 15 years (fig. 2). In D-Rouvière, while the two climatic variables showed trajectories similar to those in Corsica, there was no significant change over time either in average temperature ( $0.049 \pm 0.037$ ,  $F_{1,13} = 1.777$ ,  $P = .205$ ) or in precipitation ( $-0.043 \pm 0.056$ ,  $F_{1,13} = 0.601$ ,  $P = .452$ ) during molt (fig. 2).

#### *Association between the Colored Traits and the Climatic Variables*

*Blue crown.* In Corsica for the UV chroma, we found weak but significant interactions between sex and both average temperature and precipitation during molting, suggesting sex-dependent negative associations with temperature and positive associations with precipitation ( $R^2_{\text{mar}} = 0.308$ ,  $R^2_{\text{cond}} = 0.750$ ; table 2). When each sex is analyzed separately, the negative associations between UV chroma and average temperature during molt were only marginally significant in males ( $-0.012 \pm 0.006$ ,  $F_{1,11.93} = 3.781$ ,  $P = .075$ ; fig. 3) and females ( $-0.010 \pm 0.005$ ,  $F_{1,11.93} = 3.180$ ,  $P = .099$ ; fig. 3). Within each sex separately, no significant associations between average precipitation during molt and UV chroma in males ( $0.007 \pm 0.006$ ,  $F_{1,11.97} = 1.715$ ,



**Figure 1:** Linear decrease in male and female blue crown and yellow breast patch colorations in blue tits of Corsica and D-Rouvière across time. Blue dots represent males, and red dots represent females. The lines show the predicted slope values (table 1). Black lines show the directional changes in color across time when the associations were not sex dependent. Blue and red lines show the directional change in color across time for males and females, respectively, when the trajectories were sex dependent. Dashed lines represent nonsignificant associations. A jitter was added to visualize overlapping data points. UV = ultraviolet.



**Figure 2:** Change in average temperature (A) and precipitation (B) during molting over the study period. Black dots and solid lines represent the Corsican population, and gray dots and dashed lines represent the D-Rouvière population. Only the Corsican associations are significant.

$P = .214$ ) or females ( $0.005 \pm 0.005$ ,  $F_{1,11.98} = 0.930$ ,  $P = .353$ ) appeared. In D-Rouvière we found no significant associations between the UV chroma and the climatic variables (table 2). For brightness, our results also showed no significant associations with the average temperature in Corsica but a marginal positive association in D-Rouvière (see fig. S9.1). No significant associations were found between brightness and average precipitation during molt (table 2).

**Yellow breast patch.** In Corsica we found that yellow chroma was negatively associated with average temperature and positively associated with precipitation during molt (table 2) and that these associations differed between males and females ( $R^2_{\text{mar}} = 0.133$ ,  $R^2_{\text{cond}} = 0.395$ ; table 2; fig. 3). When we analyzed the interactions in each sex separately, in males we found that yellow chroma decreased with higher temperatures ( $-0.038 \pm 0.014$ ,  $F_{1,11.82} = 6.827$ ,  $P = .022$ ) and that it increased when precipitation was more abundant ( $0.025 \pm 0.013$ ,  $F_{1,12.04} = 3.452$ ,  $P = .087$ ), although the latter relationship was marginally significant. In females yellow chroma also decreased with higher temperatures but with a shallower slope than in males ( $-0.025 \pm 0.013$ ,  $F_{1,11.96} = 3.416$ ,  $P = .089$ ). In females no significant relationship was found between chroma and average precipitation during molting ( $0.009 \pm 0.013$ ,  $F_{1,12.14} = 0.516$ ,  $P = .486$ ; fig. 3). In D-Rouvière a sex-dependent association between chroma and both average temperature and precipitation during molting was also found. Sex-specific analyses revealed a marginal positive association between average temperature at molt in males ( $0.054 \pm 0.024$ ,  $F_{1,10.98} = 4.749$ ,  $P = .052$ ) and females ( $0.037 \pm 0.020$ ,  $F_{1,11.04} = 3.436$ ,  $P = .090$ ; see SM-8, fig. S1). No significant associations were found

for the association between chroma and average precipitation in males ( $-0.011 \pm 0.024$ ,  $F_{1,10.98} = 0.232$ ,  $P = .639$ ) or females ( $0.006 \pm 0.019$ ,  $F_{1,10.97} = 0.011$ ,  $P = .745$ ). Last, in Corsica, for brightness our results showed a negative association with average temperature during molting in both males and females and a significant interaction between average precipitation during molting and sex ( $R^2_{\text{mar}} = 0.163$ ,  $R^2_{\text{cond}} = 0.412$ ; table 2). After analyzing each sex separately, we found no significant associations between yellow brightness and precipitation during molting in males ( $0.553 \pm 0.442$ ,  $F_{1,13.10} = 1.564$ ,  $P = .232$ ) or females ( $0.873 \pm 0.468$ ,  $F_{1,13.083} = 3.477$ ,  $P = .084$ ). No significant associations were found for yellow brightness in D-Rouvière (see table S8.2 and S8.4 for further details).

#### Quantitative Genetic Analyses

We found low to moderate heritabilities for the colored traits in our studied populations, ranging from 0.026 to 0.167 in Corsica and from 0.029 to 0.173 in D-Rouvière (table 3). Consistent environmental differences across individuals (permanent environment) accounted for a small fraction of the total phenotypic variance (for Corsica, range: 0.6%–5.1%, average: 2.6%; for D-Rouvière, range: 1.6%–6.6%, average: 4.2%) that was explained mostly by year (for Corsica, range: 15.0%–43.8%, average: 28.1%; for D-Rouvière, range: 28.5%–46.0%, average: 37.0%; for more information on each random factor variance, see table S10.1–S10.6). Regarding the temporal trends in breeding values, most of the posterior mode estimates were negative, yet in all of them the 95% credible interval included zero (table 4); hence, there was no evidence for a

**Table 2:** Associations between the four color components and the average temperature (avg temp) and average precipitation (avg prec) during molting in Corsica and D-Rouvière

Fixed effect	Corsica				D-Rouvière			
	Estimate	SE	<i>F</i>	<i>P</i>	Estimate	SE	<i>F</i>	<i>P</i>
Blue crown ultraviolet chroma								
Avg temp	-.012	.006	$F_{1,12.0} = 3.537$	.084	-.003	.005	$F_{1,10.98} = .306$	.590
Avg prec	.007	.005	$F_{1,12.0} = 1.343$	.268	-.003	.005	$F_{1,10.98} = .493$	.496
Sex(fem)	<b>-.035</b>	<b>.0008</b>	$F_{1,2,205.4} = 1,609.5$	<b>&lt;.001</b>	<b>-.038</b>	<b>.001</b>	$F_{1,1,185.9} = 1,030.5$	<b>&lt;.001</b>
Year	...	...	...	...	-.010	.005	$F_{1,11.02} = 3.688$	.081
Avg temp × sex(fem)	<b>.001</b>	<b>.0007</b>	$F_{1,3,704.5} = 4.927$	<b>.026</b>	.001	.001	$F_{1,1,986.0} = 1.696$	.192
Avg prec × sex(fem)	<b>-.002</b>	<b>.0008</b>	$F_{1,3,838.0} = 10.46$	<b>.001</b>	.0005	.001	$F_{1,2,039.3} = .261$	.609
$R^2$	$R^2_{\text{cond}} = .750; R^2_{\text{mar}} = .308$				$R^2_{\text{cond}} = .709; R^2_{\text{mar}} = .338$			
Blue crown brightness								
Avg temp	-.765	.661	$F_{1,12.0} = 1.010$	.334	1.414	.670	$F_{1,10.97} = 4.811$	.051
Avg prec	.039	.615	$F_{1,12.0} = .008$	.927	.763	.661	$F_{1,10.95} = 1.260$	.285
Sex(fem)	<b>-2.379</b>	<b>.118</b>	$F_{1,2,118.3} = 400.85$	<b>&lt;.001</b>	<b>-2.325</b>	<b>.189</b>	$F_{1,1,108.0} = 149.87$	<b>&lt;.001</b>
Year	...	...	...	...	<b>-2.015</b>	<b>.666</b>	$F_{1,10.99} = 9.144$	<b>.011</b>
Avg temp × sex(fem)	.206	.117	$F_{1,3,833.5} = 3.109$	.077	.084	.181	$F_{1,2,036.1} = .218$	.640
Avg prec × sex(fem)	.035	.118	$F_{1,3,789.7} = .089$	.765	-.057	.183	$F_{1,2,045.9} = .098$	.753
$R^2$	$R^2_{\text{cond}} = .444; R^2_{\text{mar}} = .094$				$R^2_{\text{cond}} = .511; R^2_{\text{mar}} = .218$			
Yellow breast patch chroma								
Avg temp	<b>-.038</b>	<b>.013</b>	$F_{1,12.0} = 5.532$	<b>.036</b>	.052	.022	$F_{1,11.01} = 4.272$	.063
Avg prec	.025	.012	$F_{1,12.1} = 1.918$	.191	-.011	.021	$F_{1,10.99} = .009$	.922
Sex(fem)	<b>-.068</b>	<b>.004</b>	$F_{1,2,070.1} = 276.90$	<b>&lt;.001</b>	<b>-.012</b>	<b>.006</b>	$F_{1,1,022.9} = 3.979$	<b>.046</b>
Year	...	...	...	...	<b>-.055</b>	<b>.021</b>	$F_{1,11.07} = 6.725$	<b>.024</b>
Avg temp × sex(fem)	<b>.013</b>	<b>.004</b>	$F_{1,3,850.4} = 10.590$	<b>.001</b>	<b>-.012</b>	<b>.005</b>	$F_{1,1,964.2} = 4.398$	<b>.036</b>
Avg prec × sex(fem)	<b>-.015</b>	<b>.004</b>	$F_{1,3,816.5} = 13.514$	<b>&lt;.001</b>	<b>.018</b>	<b>.005</b>	$F_{1,1,989.0} = 9.713$	<b>.001</b>
$R^2$	$R^2_{\text{cond}} = .395; R^2_{\text{mar}} = .133$				$R^2_{\text{cond}} = .492; R^2_{\text{mar}} = .137$			
Yellow breast patch brightness								
Avg temp	<b>-1.050</b>	<b>.408</b>	$F_{1,12.0} = 7.654$	<b>.017</b>	.154	.562	$F_{1,11.03} = .055$	.817
Avg prec	.310	.380	$F_{1,12.1} = 1.389$	.261	.577	.545	$F_{1,11.01} = .874$	.369
Sex(fem)	<b>.625</b>	<b>.090</b>	$F_{1,1,898.2} = 47.904$	<b>&lt;.001</b>	<b>.501</b>	<b>.127</b>	$F_{1,1,941.90} = 15.501$	<b>&lt;.001</b>
Year	...	...	...	...	<b>-1.426</b>	<b>.536</b>	$F_{1,11.05} = 7.062$	<b>.022</b>
Avg temp × sex(fem)	<b>-.143</b>	.089	$F_{1,3,858.7} = 2.560$	.109	-.044	.124	$F_{1,1,982.5} = .128$	.719
Avg prec × sex(fem)	<b>.269</b>	<b>.090</b>	$F_{1,3,797.1} = 8.899$	<b>.002</b>	-.142	.125	$F_{1,1,975.4} = 1.290$	.256
$R^2$	$R^2_{\text{cond}} = .412; R^2_{\text{mar}} = .163$				$R^2_{\text{cond}} = .524; R^2_{\text{mar}} = .172$			

Note: Significant ( $P < .05$ ) variables are in bold.  $R^2_{\text{cond}}$  represents the variance explained by both the fixed effects and the random effects included in the model.  $R^2_{\text{mar}}$  represents the variance explained by the fixed factors alone. Blue crown ultraviolet chroma and brightness number of observations: Corsica = 3,867; D-Rouvière = 2,068. Yellow breast patch chroma and brightness number of observations: Corsica = 3,890; D-Rouvière = 2,007.

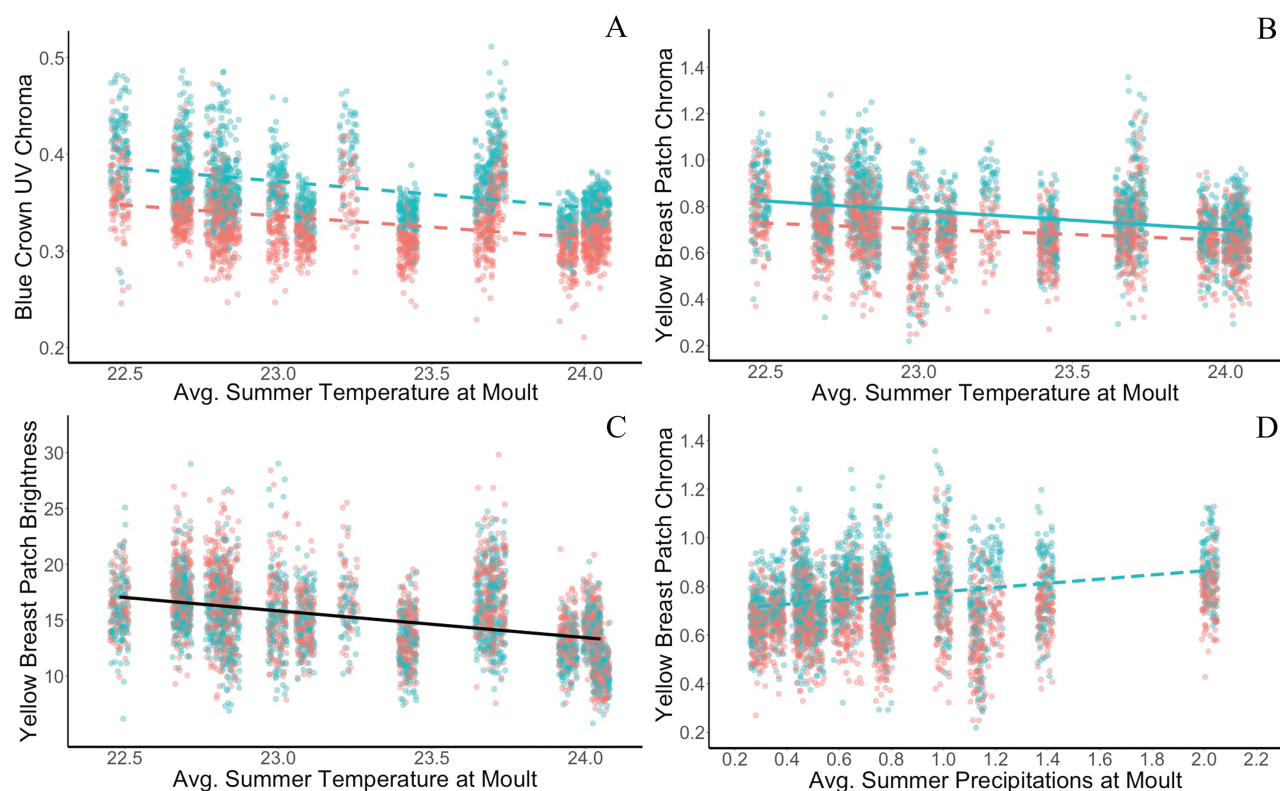
temporal trend in breeding values for any of the traits/areas (see fig. S11.1, S11.2).

### Discussion

Our longitudinal 15-year data set including more than 5,800 color ornament measures shows that the yellow breast patch and blue crown colorations of male and female Mediterranean blue tits have become duller and less chromatic throughout the years (decrease from 9% to 23%; see table S12.1). Over the same period, we de-

tected an increase in temperature and a decrease in precipitation, mainly in Corsica. Associating the climatic variation with coloration shows that color changes were partly associated with changes in temperature and precipitation during molting, particularly in the more southern Corsican population. Last, we found that the temporal trends described at the phenotypic level were not aligned with a change at the genetic level, evidencing that the described change did not represent a microevolutionary response but rather originated from plasticity. Overall, these results suggest an impact of climate change





**Figure 3:** In Corsica blue crown ultraviolet (UV) chroma (A) and yellow breast patch chroma (B) and brightness (C) decreased with increased average temperature during molting (see table 2). In addition, yellow breast patch chroma (D) increased with higher average precipitation during molting. Blue dots and lines represent males, and red dots and lines represent females. Black lines represent the associations when there was no interaction with sex. Solid lines represent significant results, and dashed lines represent marginally significant relationships. A jitter was added to visualize overlapping data points.

on the visual communication system of the blue tits. Given the potential role of these traits in social and sexual selection and the importance of mate choice for adaptation (Whitlock and Agrawal 2009; Gómez-Llano et al. 2021), our results raise the question of whether this reduction could affect species' abilities to react to climate change.

#### *Temporal Trends and Association with the Climatic Proxies*

The studies exploring the association between coloration and climatic variables have traditionally focused on melanin-based traits in several taxa (e.g., Gloger rule or thermal melanism hypothesis; Delhey 2017), including birds (Fargallo et al. 2018; Delhey et al. 2019), reptiles (Martínez-Freiría et al. 2020), and insects (Zeuss et al. 2014; Clusella-Trullas and Nielsen 2020). Still, most of this work has not explored the impact of climate change on ornamental colorations, despite their importance for fitness because of their role as signals in different intra- and intersexual contexts (Kodric-Brown 1985; Stuart-Fox and Ord 2004; Girard et al. 2015; López-Idiáquez et al. 2016a). The evidence available, how-

ever, has shown that the expression of achromatic and melanin-based ornaments can be driven by climate change (Evans and Gustafsson 2017; Moore et al. 2021). Here, our results suggest that rapid climate change can in addition impact both structural colorations and carotenoid-based colorations (the other two major coloration types) in the blue tits from Corsica. However, it should be noted that collinearity exists between year and climate, and caution is needed: other environmental factors might cause this association as well, calling for further studies to confirm it.

In our study warmer and drier summers in Corsica led to a reduced chromaticity of the UV blue crown coloration. This result is in line with a previous study in the burrowing parrot (*Cyanoliseus patagonus*) showing that feathers grown in drier years displayed less bright structural colors (Masello et al. 2008). While unraveling the physiological processes behind these associations will require specific studies, a potential driver could be a reduction in food availability or quality during hot and dry summers (Both 2010), an effect that would fit with the results of a meta-analysis including information on birds, insects, reptiles,

**Table 3:** Heritability ( $V_A/V_P$ ) and 95% credible intervals (CIs) obtained from the animal models of each colored trait in each sex and population

	Males		Females	
	$h^2$	95% CI	$h^2$	95% CI
Corsica:				
Blue crown ultraviolet chroma	.167	.088 to .237	.161	.086 to .233
Blue crown brightness	.029	<.001 to .070	.053	<.001 to .103
Yellow breast patch chroma	.074	<.001 to .143	.026	<.001 to .074
Yellow breast patch brightness	.078	<.001 to .134	.034	<.001 to .079
D-Rouvière:				
Blue crown ultraviolet chroma	.058	<.001 to .128	.173	.063 to .266
Blue crown brightness	.068	<.001 to .135	.073	<.001 to .132
Yellow breast patch chroma	.110	.016 to .193	.080	<.001 to .151
Yellow breast patch brightness	.039	<.001 to .097	.029	<.001 to .088

Note:  $V_A$  = additive genetic variance;  $V_P$  = phenotypic variance.

and arachnids and supporting the condition dependence of structural colorations (White 2020). Furthermore, brood size manipulation experiments in wild blue tits and eastern bluebirds (*Sialia sialis*) also seem to support this idea, suggesting that food limitations can constrain the expression of the offspring's blue UV colorations (Jacot and Kempenaers 2007; Siefferman and Hill 2007), although this association was not always found in captivity or in adults (McGraw et al. 2002; Peters et al. 2011). Besides, a nonexclusive alternative could be that hot and dry summers lead to an increased occurrence of energetically costly behaviors that allow heat dissipation (du Plessis et al. 2012; Pattinson et al. 2020; McKechnie et al. 2021). While experimental studies are needed to clarify the mechanism behind the association of climate and structural coloration, our results seem to support the suspected (Jacot and Kempenaers 2007; Siefferman and Hill 2007; Doutrelant et al. 2012), but debated (Prum 2006) and not often demonstrated, environmental sensitivity of structural colorations (Masello et al. 2008).

Regarding the influence of climate on carotenoid-based traits, the information available is more abundant but is

also mixed. A recent comparative analysis has shown that in nine Australian bird species the individuals living in warmer areas had more saturated carotenoid colorations than those living in colder ones, while the opposite pattern (less saturation in warmer areas) was found in three species (Prasetya et al. 2020). Besides, in guppies an experimental study showed a nonlinear association between their orange coloration hue and temperature, with enhanced colorations at intermediate temperatures (Breckels and Neff 2013). Finally, two long-term studies have explored the associations between climate and the carotenoid-based colorations, showing that while higher temperature and lower precipitation at molt led to a reduction in the red tail coloration of the American redstart (*Setophaga ruticilla*) in Canada (Reudink et al. 2015), they, by contrast, enhanced the yellow chest coloration in Hungarian great tits (Laczi et al. 2020). In both studies the reported patterns were ascribed to variations in food availability, suggesting a potential opposite effect of climate on food availability or quality depending on the study area. Here, we found that temperature was negatively correlated with yellow breast

**Table 4:** Posterior mode estimates and 95% credible intervals (CIs) of the linear regression of the best linear unbiased predictors obtained from the animal models against the mean year

	Males		Females	
	Estimate	95% CI	Estimate	95% CI
Corsica:				
Blue crown ultraviolet chroma	-.0014	-.0043 to .0012	-.0002	-.0036 to .0010
Blue crown brightness	.0107	-.2155 to .1548	-.0012	-.2429 to .1255
Yellow breast patch chroma	-.00005	-.0100 to .0060	-.00002	-.0043 to .0044
Yellow breast patch brightness	.0043	-.1738 to .1791	-.0004	-.1306 to .099
D-Rouvière:				
Blue crown ultraviolet chroma	-.00003	-.0003 to .0023	-.0010	-.0055 to .0019
Blue crown brightness	-.00009	-.6115 to .3825	.0332	-.5408 to .2943
Yellow breast patch chroma	-.0011	-.0208 to .0180	-.0007	-.0156 to .0125
Yellow breast patch brightness	-.0012	-.1591 to .3134	.0009	-.1935 to .2288

patch chroma and brightness and that there was a marginal positive association between precipitation and yellow breast patch chroma in males. Therefore, our results for the yellow breast patch coloration strongly differ from those found by Laczi et al. (2020) in great tits. Mediterranean areas undergo hotter and drier summers compared with Hungary, so we hypothesize that this lack of consistency may be because Mediterranean birds face a reduction in food availability during molt or other heat-related costs (du Plessis et al. 2012; Gardner et al. 2016; Pattinson et al. 2020; McKechnie et al. 2021) not faced by the Hungarian birds. If true, the impacts of warming on ornamental traits could be more severe in warmer areas within a species distribution. Further comparison across more species will in the future allow determining whether the documented variation between species and study areas is a common phenomenon.

Finally, our results agree with those previously published reporting negative effects of climate change on ornamental traits (Svensson 2019; Moore et al. 2021; but see Møller and Szép 2005). It is interesting to highlight, however, that most of the published evidence comes from a small number of species, mostly birds (Svensson 2019). Considering that the consequences of climate change may differ depending on the species and their particular constraints (e.g., ectotherms may be differently affected than endotherms; Aragón et al. 2010), studies encompassing different taxa are needed to grasp a general understanding of the consequences of climate change on ornamental traits.

#### *Quantitative Genetics of the Blue Tit Colorations*

On the basis of a social pedigree across 16 generations including all birds with color measures, quantitative genetic models report that the blue and yellow colorations of the blue tits present low to moderate heritabilities, concordant with estimates previously published in this species. Repeatabilities were also low, suggesting that the studied traits are highly dynamic. The low repeatability, along with the fact that year accounted for much of the phenotypic variance, points out that environmental conditions play an important role as drivers of the expression of the blue and yellow colors in the blue tit in agreement with our results, suggesting that climate influences their coloration.

Despite low to moderate heritabilities, the existence of additive genetic variance on the blue tit colorations raised the possibility that the trends described at the phenotypic level were caused by a change at the genetic level. However, no significant temporal trends in the breeding values were detected for any of the studied traits, either in males or in females in Corsica or D-Rouvière. While such analyses on breeding value trends are fundamental to test for evidence of microevolution, they are scarcely conducted because of

the lack of appropriate data and the complexity to account for uncertainty around breeding value estimation (Hadfield et al. 2010). For this reason, it still remains virtually unknown whether climate change is leading to a change at the genetic level in ornamental traits. So far, only one study has explored this issue, showing a reduction in the breeding values for the forehead patch of the collared flycatcher (Evans and Gustafsson 2017). Interestingly, our results contrast with these, as we did not find a change at the genetic level. This difference may be explained by higher heritability for the sizes of melanin/white color patches, ranging from 0.35 to 0.79 (in species such as pied and collared flycatchers, garter snakes [*Thamnophis sirtalis*], or guppies; Qvarnström 1999; Brooks and Endler 2001; Hegyi et al. 2002; Westphal and Morgan 2010; Potti and Canal 2011; Evans and Gustafsson 2017), compared with heritabilities of structural or carotenoid-based traits, ranging from 0.02 to 0.25 (e.g., in blue and great tits and guppies; Brooks and Endler 2001; Hadfield et al. 2006; Evans and Sheldon 2012; Drobniak et al. 2013; Charmantier et al. 2017). Because of this low heritability, the maximum expected evolutionary response could be small, and we may lack power to detect it. In any case, the nonsignificance of the temporal trends in breeding values strongly suggests that the documented phenotypic decline over time is caused by a plastic response to the environmental conditions.

#### *Differences in the Climatic Effects for *ogliastrae* and *caeruleus* Subspecies*

Previous studies have reported that the strength and direction of the responses to climate change can be population dependent, with, for example, stronger phenological responses at higher latitudes (Parmesan 2007) or near the edge of a species range (Sheth and Angert 2016). Furthermore, climate-dependent selection can lead to population differences in coloration. For instance, in northern and central Italy, wall lizards (*Podarcis muralis*) display more conspicuous green and black colorations in hotter and drier environments (Miñano et al. 2021). Here, we found that while three of the four studied color components (blue crown UV chroma and yellow breast patch brightness and chroma) were negatively associated with temperature during molt in Corsica, in D-Rouvière two of them (blue crown brightness and yellow breast patch chroma) showed marginal positive associations with temperature, suggesting a differential response to warming in the two populations. This difference could be explained by the fact that the effect of climate change on temperature and rain was more marked in Corsica (*ogliastrae* subspecies) than in D-Rouvière (*caeruleus* subspecies). In line with this, a study in the same populations showed that warming in spring was associated with the timing of laying of the blue tits in Corsica but not in

D-Rouvière (Bonamour et al. 2019). This difference could also be explained because climate in Corsica is hotter and drier when compared with climate in D-Rouvière, and thus it is likely that Corsican blue tits are closer to their thermal limits. If the latter is true, the rise in temperature could have different effects in Corsica and D-Rouvière, given that latitude is not expected to have a large impact on the heat resistance of endotherms (Araújo et al. 2013). For instance, in *Drosophila* the association between heat resistance and latitude (Kimura 2004) or temperature across their distribution range is weak (Kellermann et al. 2012). From a more mechanistic perspective, the differences in the temperature dependence among our two populations could be caused by higher humidity in D-Rouvière than in Corsica. Studies in fruit flies have shown that the effects of temperature may be mitigated in more humid regions (i.e., where the loss of water may be less important; Kellermann et al. 2012). Whether this is happening in birds needs to be confirmed, but it highlights the important role that precipitation may play as a driver of selection (Siepielski et al. 2017) and modulator of the effects of other environmental variables on ornamental and other types of traits.

The lack of association between blue tit colors and climate in D-Rouvière, however, leaves one question open: why is there a decrease in coloration in this population? Several hypotheses can be formulated. For instance, blue tit color changes over time may not be directly generated by climate but by other factors that also change with time and that have an impact on coloration, such as habitat structure (Medina et al. 2017), parasite prevalence (Janas et al. 2018), or food availability that may have decreased because of the increase in the use of pesticides (Møller et al. 2021). Alternatively, it is also possible that our climate windows and variables were more efficient at capturing the variability in temperature and precipitation in Corsica than in D-Rouvière, where other variables and windows may be more relevant. However, although we could not point to the exact environmental variable, the described changes in color are nonetheless plastic, as we could not detect a change in the breeding values.

#### *Sex Differences in the Temporal and Climatic Trends*

We found sex-dependent associations in both populations, with overall stronger trends in males than in females, suggesting a higher environmental sensitivity of male coloration. This finding opens exciting perspectives to explore the mechanisms explaining this sex-specific pattern. Male blue tits face stronger intersexual selection than female blue tits (Doutrelant et al. 2020), and thus it is possible that they invest more in ornamentation than females. This could explain why it has been described in Swedish blue tits that males start molting earlier than females, even when there

are still young in the nest (Svensson and Nilsen 1997). As a consequence of this higher investment in ornamentation, warming or changes in precipitation regimes could have a stronger impact on male coloration via their influences on male body condition or on parasite prevalence. Alternatively, because of sex-specific investment and sex-specific resulting costs (Fitzpatrick et al. 1995), female condition may be more sensitive to the costs inherent to reproduction, such as egg production (Doutrelant et al. 2012), than to those imposed by climate at molt, and thus the climatic effects occurring at molting time may be milder in this sex.

#### *Potential Consequences of the Documented Reduction in Coloration*

Whether sexual selection facilitates or hinders the adaptation to novel environmental conditions is still debated (Candolin and Heuschele 2008). On the one hand, sexual selection could promote adaptation, for instance, by favoring higher-quality individuals (Hamilton and Zuk 1982; Whitlock and Agrawal 2009; Gómez-Llano et al. 2021). On the other hand, sexual selection might have detrimental demographic consequences, for example, by favoring the presence of costly traits whose expression negatively influences the viability of the individuals (Long et al. 2009). Here, our data suggest a reduction in the coloration of the blue tits over time (mean reduction of 15.51%; see table S12.1) and a reduction in the variance of some of the studied traits (e.g., blue UV and yellow chroma in Corsica and blue UV chroma in D-Rouvière; see SM-13). Given the potential role of the blue tit coloration as a secondary sexual trait, our results may be evidencing a decrease in the signaling potential of its color ornaments. For example, if there is not enough variance among males, females will not be able to discern between high-quality individuals and low-quality individuals. Such effect has been found in the superb fairy wren (*Malurus cyaneus*), whereby males cannot acquire their breeding plumage in time when dry summers occur, resulting in weaker sexual selection (Cockburn et al. 2008). The importance of such loss of signaling potential is highlighted by a recent experiment in *Drosophila melanogaster* concluding that mating regimes with strong sexual selection led to increased female fitness when compared with regimes lacking sexual selection under a warming scenario (Gómez-Llano et al. 2021). If blue tits are experiencing a decreasing strength in sexual selection for color ornaments, this could hence result in a reduced capacity for these populations to adapt to the new conditions imposed by climate change. Further studies are needed to explore this more deeply, ideally including other signaling traits present in this species, because if females cannot rely on color during mate choice,

selection could favor alternative signaling systems, such as male song.

### Conclusions

Our data suggest that in the past 15 years there has been a general decrease in the coloration of blue tits breeding in two Mediterranean populations. In Corsica, where climate has become warmer and drier across the study period, the changes in coloration were related to changes in temperature at molt, suggesting a connection with climate change. Also, our results discard the presence of a microevolutionary change in blue tit coloration over the past 15 years. On the basis of this evidence, future research should aim at analyzing the link between climate and ornaments in other bird species and taxa, elucidating the mechanisms linking climate to the observed phenotypic change and the consequences of the reported trends for sexual selection and adaptation to climate change.

### Acknowledgments

We thank all of the researchers involved in the long-term monitoring of the blue tit populations, in particular, Denis Réale, Philippe Perret, Jacques Blondel, Samuel Caro, and Marcel Lambrechts as well as Annick Lucas, Pablo Giovannini, and Samuel Perret from the plateforme des Programmes à Long Terme. We thank Doris Gomez for all of her expertise on color measurement. We recognize the help of all the students and field assistants involved in capturing the blue tits throughout the years and those that participated in measuring the coloration, in particular, Emeline Mourocq and Afiwa Midamegbe. We thank the Office National des forêts, the Association pour l'étude écologique du Maquis, the mayors of Manso and Montarnaud for allowing us to work on E-Pirio and D-Rouvière, and the landowners of D-Muro and E-Muro for their permission to work on their properties. The comments from J. Lau, E. Svensson, and three anonymous reviewers greatly improved the previous versions of this work. The long-term monitoring was supported by the Observatoire de Recherche Méditerranéen de l'Environnement; several Agence Nationale de la Recherche (ANR) grants to A.C., C.D., and C.T. (in particular, ANR-09-JCJC-0050, ANR-12-ADAP-0006-02-PEPS); the Languedoc-Rousillon region *chercheur d'avenir* grant to C.D.; and the European Research Council 2013-StG-337365-SHE to A.C. D.L.-I. was funded by a postdoctoral grant from the Basque Country government (POS-2019-1-0026).

### Statement of Authorship

D.L.-I., C.T., A.G., A.C., and C.D. conceptualized the study; A.C., C.T., and C.D. acquired funding; C.D. and A.G. de-

veloped the color-measuring method; C.d.F., A.F., A.C., C.D., and A.G. collected data and performed fieldwork; A.F., M.d.R., and C.D. measured color and curated the data set; D.L.-I. and C.T. analyzed the data; D.L.-I. wrote the manuscript; C.T., A.G., A.F., A.C., and C.D. commented on and edited the manuscript.

### Data and Code Availability

Data and code underlying this article have been deposited in the Dryad Digital Repository (<https://doi.org/10.5061/dryad.w6m905qr9>; López-Idiáquez et al. 2022)

### Literature Cited

- Alonso-Alvarez, C., C. Doutrelant, and G. Sorci. 2004. Ultraviolet reflectance affects male-male interactions in the blue tit (*Parus caeruleus ultramarinus*). *Behavioral Ecology* 15:805–809.
- Andersson, M. 1994. *Sexual selection*. Princeton University Press, Princeton, NJ.
- Andersson, S., J. Örnborg, and M. Andersson. 1998. Ultraviolet sexual dimorphism and assortative mating in blue tits. *Proceedings of the Royal Society B* 265:445–450.
- Aragón, P., M. A. Rodríguez, M. A. Olalla-Tárraga, and J. M. Lobo. 2010. Predicted impact of climate change on threatened terrestrial vertebrates in central Spain highlights differences between endotherms and ectotherms: climate-change impact on threatened vertebrates. *Animal Conservation* 13:363–373.
- Araújo, M. B., F. Ferri-Yáñez, F. Bozinovic, P. A. Marquet, F. Valladares, and S. L. Chown. 2013. Heat freezes niche evolution. *Ecology Letters* 16:1206–1219.
- Asch, R. G., C. A. Stock, and J. L. Sarmiento. 2019. Climate change impacts on mismatches between phytoplankton blooms and fish spawning phenology. *Global Change Biology* 25:2544–2559.
- Babak, N. 2015. usdm: uncertainty analysis for species distribution models. R package version 1.1–15. <https://CRAN.R-project.org/package=usdm>.
- Barton, K. 2019. MuMIn: multi-model inference. R package version 1.43.15. <https://CRAN.R-project.org/package=MUMIN>.
- Bonamour, S., L.-M. Chevin, A. Charmantier, and C. Teplitsky. 2019. Phenotypic plasticity in response to climate change: the importance of cue variation. *Philosophical Transactions of the Royal Society B* 374:20180178.
- Bonnet, T., M. B. Morrissey, A. Morris, S. Morris, T. H. Clutton-Brock, J. M. Pemberton, and L. E. B. Kruuk. 2019. The role of selection and evolution in changing parturition date in a red deer population. *PLoS Biology* 17:e3000493.
- Both, C. 2010. Food availability, mistiming, and climatic change. Pages 129–147 in A. P. Møller, W. Fiedler, and P. Berthold, eds. *Effects of climate change on birds*. Oxford University Press, Oxford.
- Boutin, S., and J. E. Lane. 2014. Climate change and mammals: evolutionary versus plastic responses. *Evolutionary Applications* 7:29–41.
- Breckels, R. D., and B. D. Neff. 2013. The effects of elevated temperature on the sexual traits, immunology and survivorship of a tropical ectotherm. *Journal of Experimental Biology* 216:2658–2664.
- Brooks, R., and J. A. Endler. 2001. Female guppies agree to differ: phenotypic and genetic variation in mate-choice behaviour and the consequences for sexual selection. *Evolution* 55:1644–1655.

- Candolin, U., and J. Heuschele. 2008. Is sexual selection beneficial during adaptation to environmental change? *Trends in Ecology and Evolution* 23:446–452.
- Charmantier, A., and J. Blondel. 2003. A contrast in extra-pair paternity levels on mainland and island populations of Mediterranean blue tits. *Ethology* 109:351–363.
- Charmantier, A., C. Doutrelant, G. Dubuc-Messier, A. Fargevielle, and M. Szulkin. 2016. Mediterranean blue tits as a case study of local adaptation. *Evolutionary Applications* 9:135–152.
- Charmantier, A., and D. Réale. 2005. How do misassigned paternities affect the estimation of heritability in the wild? *Molecular Ecology* 14:2839–2850.
- Charmantier, A., M. E. Wolak, A. Grégoire, A. Fargevielle, and C. Doutrelant. 2017. Colour ornamentation in the blue tit: quantitative genetic (co)variances across sexes. *Heredity* 118:125–134.
- Clusella-Trullas, S., and M. Nielsen. 2020. The evolution of insect body coloration under changing climates. *Current Opinion in Insect Science* 41:25–32.
- Cockburn, A., H. L. Osmond, and M. C. Double. 2008. Swingin' in the rain: condition dependence and sexual selection in a capricious world. *Proceedings of the Royal Society B* 275:605–612.
- Cotton, S., K. Fowler, and A. Pomiankowski. 2004. Do sexual ornaments demonstrate heightened condition-dependent expression as predicted by the handicap hypothesis? *Proceedings of the Royal Society B* 271:771–783.
- Crozier, L. G., and J. A. Hutchings. 2014. Plastic and evolutionary responses to climate change in fish. *Evolutionary Applications* 7:68–87.
- Dale, J., C. J. Dey, K. Delhey, B. Kempenaers, and M. Valcu. 2015. The effects of life history and sexual selection on male and female plumage coloration. *Nature* 527:367–370.
- del Cerro, S., S. Merino, J. Martínez-de la Puente, E. Lobato, R. Ruiz-de-Castañeda, J. Rivero-de Aguilar, J. Martínez, J. Morales, G. Tomás, and J. Moreno. 2009. Carotenoid-based plumage coloration is associated with blood parasite richness and stress protein levels in blue tits (*Cyanistes caeruleus*). *Oecologia* 162:825–835.
- Delhey, K. 2017. Gloger's rule. *Current Biology* 27:R689–R691.
- Delhey, K., J. Dale, M. Valcu, and B. Kempenaers. 2019. Reconciling ecogeographical rules: rainfall and temperature predict global colour variation in the largest bird radiation. *Ecology Letters* 22:726–736.
- Doutrelant, C., A. Fargevielle, and A. Grégoire. 2020. Evolution of female coloration: what have we learned from birds in general and blue tits in particular. *Advances in the Study of Behavior* 52:123–202.
- Doutrelant, C., A. Grégoire, N. Grnac, D. Gomez, M. M. Lambrechts, and P. Perret. 2008. Female coloration indicates female reproductive capacity in blue tits. *Journal of Evolutionary Biology* 21:226–233.
- Doutrelant, C., A. Grégoire, A. Midamegbe, M. Lambrechts, and P. Perret. 2012. Female plumage coloration is sensitive to the cost of reproduction: an experiment in blue tits. *Journal of Animal Ecology* 81:87–96.
- Drobnik, S. M., D. Wiejaczka, A. Arct, A. Dubiec, L. Gustafsson, and M. Cichoń. 2013. Low cross-sex genetic correlation in carotenoid-based plumage traits in the blue tit nestlings (*Cyanistes caeruleus*). *PLoS ONE* 8:e69786.
- du Plessis, K. L., R. O. Martin, P. A. R. Hockey, S. J. Cunningham, and A. R. Ridley. 2012. The costs of keeping cool in a warming world: implications of high temperatures for foraging, thermoregulation and body condition of an arid-zone bird. *Global Change Biology* 18:3063–3070.
- Duputié, A., A. Rutschmann, O. Ronce, and I. Chuine. 2015. Phenological plasticity will not help all species adapt to climate change. *Global Change Biology* 21:3062–3073.
- Evans, S. R., and L. Gustafsson. 2017. Climate change upends selection on ornamentation in a wild bird. *Nature Ecology and Evolution* 1:39.
- Evans, S. R., and B. C. Sheldon. 2012. Quantitative genetics of a carotenoid-based color: heritability and persistent natal environmental effects in the great tit. *American Naturalist* 179:79–94.
- Fargallo, J. A., F. Martínez, K. Wakamatsu, D. Serrano, and G. Blanco. 2018. Sex-dependent expression and fitness consequences of sunlight-derived color phenotypes. *American Naturalist* 191:726–743.
- Fargevielle, A., A. Grégoire, A. Charmantier, M. Del Rey Granada, and C. Doutrelant. 2017. Assortative mating by colored ornaments in blue tits: space and time matter. *Ecology and Evolution* 7:2069–2078.
- Fitzpatrick, S., A. Berglund, and G. Rosenqvist. 1995. Ornaments or offspring: costs to reproductive success restrict sexual selection processes. *Biological Journal of the Linnean Society* 55:251–260.
- Garamszegi, L. Z. 2011. Climate change increases the risk of malaria in birds. *Global Change Biology* 17:1751–1759.
- Gardner, J. L., T. Amano, W. J. Sutherland, M. Clayton, and A. Peters. 2016. Individual and demographic consequences of reduced body condition following repeated exposure to high temperatures. *Ecology* 97:786–795.
- Girard, M. B., D. O. Elias, and M. M. Kasumovic. 2015. Female preference for multi-modal courtship: multiple signals are important for male mating success in peacock spiders. *Proceedings of the Royal Society B* 282:20152222.
- Gomez, D. 2006. AVICOL, a program to analyse spectrometric data. <http://sites.google.com/site/avicolprogram/>.
- Gómez-Llano, M., E. Scott, and E. I. Svensson. 2021. The importance of pre- and postcopulatory sexual selection promoting adaptation to increasing temperatures. *Current Zoology* 67:321–327.
- Griggio, M., L. Serra, D. Licheri, C. Campomori, and A. Pilastro. 2009. Moulting speed affects structural feather ornaments in the blue tit. *Journal of Evolutionary Biology* 22:782–792.
- Hadfield, J. D. 2010. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R package. *Journal of Statistical Software* 33:1–22.
- Hadfield, J. D., M. D. Burgess, A. Lord, A. B. Phillimore, S. M. Clegg, and I. P. F. Owens. 2006. Direct versus indirect sexual selection: genetic basis of colour, size and recruitment in a wild bird. *Proceedings of the Royal Society B* 273:1347–1353.
- Hadfield, J. D., A. J. Wilson, D. Garant, B. C. Sheldon, and L. E. B. Kruuk. 2010. The misuse of BLUP in ecology and evolution. *American Naturalist* 175:116–125.
- Hällfors, M. H., L. H. Antão, M. Itter, A. Lehtikoinen, T. Lindholm, T. Roslin, and M. Saastamoinen. 2020. Shifts in timing and duration of breeding for 73 boreal bird species over four decades. *Proceedings of the National Academy of Sciences of the USA* 13:201913579.
- Hamilton, W. D., and M. Zuk. 1982. Heritable true fitness and bright birds: a role for parasites? *Science* 218:384–387.
- Hegy, G., J. Török, and L. Tóth. 2002. Qualitative population divergence in proximate determination of a sexually selected trait in the collared flycatcher. *Journal of Evolutionary Biology* 15:710–719.
- Heidelberger, P., and P. D. Welch. 1981. A spectral method for confidence interval generation and run length control in simulations. *Communications of the ACM* 24:233–245.

- Hill, G. E., C. Y. Inouye, and R. Montgomerie. 2002. Dietary carotenoids predict plumage coloration in wild house finches. *Proceedings of the Royal Society B* 269:1119–1124.
- Hill, G. E., and K. J. McGraw, eds. 2006. *Bird coloration: mechanisms and measurements*. Harvard University Press, Cambridge, MA.
- Hunt, S., I. Cuthill, A. Bennett, and R. Griffiths. 1999. Preferences for ultraviolet partners in the blue tit. *Animal Behaviour* 58:809–815.
- IPCC (Intergovernmental Panel on Climate Change). 2018. *Global warming of 1.5°C*. Intergovernmental Panel on Climate Change, Geneva.
- Jacot, A., and B. Kempnaers. 2007. Effects of nestling condition on UV plumage traits in blue tits: an experimental approach. *Behavioral Ecology* 18:34–40.
- Janas, K., A. Latkiewicz, A. Parnell, D. Lutyk, J. Barczyk, M. D. Shawkey, L. Gustafsson, M. Cichon, and S. M. Drobniak. 2020. Differential effects of early growth conditions on colour-producing nanostructures revealed through small angle X-ray scattering (SAXS) and electron microscopy. *Journal of Experimental Biology* 223:jeb.228387.
- Janas, K., E. Podmokla, D. Lutyk, A. Dubiec, L. Gustafsson, M. Cichon, and S. Drobniak. 2018. Influence of haemosporidian infection status on structural and carotenoid-based colouration in the blue tit *Cyanistes caeruleus*. *Journal of Avian Biology* 49:e01840.
- Jensen, H., T. Svorkmo-Lundberg, T. H. Ringsby, and B.-E. Saether. 2006. Environmental influence and cohort effects in a sexual ornament in the house sparrow, *Passer domesticus*. *Oikos* 114:212–224.
- Kellermann, V., J. Overgaard, A. A. Hoffmann, C. Flojgaard, J.-C. Svenning, and V. Loeschcke. 2012. Upper thermal limits of *Drosophila* are linked to species distributions and strongly constrained phylogenetically. *Proceedings of the National Academy of Sciences of the USA* 109:16228–16233.
- Kellermann, V., and B. van Heerwaarden. 2019. Terrestrial insects and climate change: adaptive responses in key traits. *Physiological Entomology* 44:99–115.
- Kimura, M. T. 2004. Cold and heat tolerance of drosophilid flies with reference to their latitudinal distributions. *Oecologia* 140:442–449.
- Kodric-Brown, A. 1985. Female preference and sexual selection for male coloration in the guppy (*Poecilia reticulata*). *Behavioral Ecology and Sociobiology* 17:199–205.
- Kuznetsova, A., P. B. Brockhoff, and R. H. B. Christensen. 2017. lmerTest: test for random and fixed effects for linear mixed effect models (lmer objects of lme4 package). *Journal of Statistical Software* 82:1–26.
- Laczi, M., G. Hegyi, G. Nagy, R. Pongrácz, and J. Török. 2020. Yellow plumage colour of great tits *Parus major* correlates with changing temperature and precipitation. *Ibis* 162:232–237.
- Limbou, T., A. C. Mateman, and C. M. Lessells. 2013. Parental care and UV coloration in blue tits: opposite correlations in males and females between provisioning rate and mate's coloration. *Journal of Avian Biology* 44:17–26.
- Long, T. A. F., A. Pischedda, A. D. Stewart, and W. R. Rice. 2009. A cost of sexual attractiveness to high-fitness females. *PLoS Biology* 7:e1000254.
- López-Idiáquez, D., C. Teplitsky, A. Grégoire, A. Fargevielle, M. del Rey, C. de Franceschi, A. Charmantier, et al. 2022. Data from: Long-term decrease in coloration: a consequence of climate change? *American Naturalist*, Dryad Digital Repository, <https://doi.org/10.5061/dryad.w6m905qr9>.
- López-Idiáquez, D., P. Vergara, J. A. Fargallo, and J. Martínez-Padilla. 2016a. Female plumage coloration signals status to conspecifics. *Animal Behaviour* 121:101–106.
- . 2016b. Old males reduce melanin-pigmented traits and increase reproductive outcome under worse environmental conditions in common kestrels. *Ecology and Evolution* 6:1224–1235.
- Maia, R., H. Gruson, J. A. Endler, and T. E. White. 2019. pavo 2: new tools for the spectral and spatial analysis of colour in R. *Methods in Ecology and Evolution* 10:1097–1107.
- Martínez-Freiría, F., K. S. Toyama, I. Freitas, and A. Kaliontzopoulou. 2020. Thermal melanism explains macroevolutionary variation of dorsal pigmentation in Eurasian vipers. *Scientific Reports* 10:16122.
- Masello, J. F., T. Lubjuhn, and P. Quillfeldt. 2008. Is the structural and psittacofulvin-based coloration of wild burrowing parrots *Cyanoliseus patagonus* condition dependent? *Journal of Avian Biology* 39:653–662.
- McDowell, N. G., C. D. Allen, K. Anderson-Teixeira, B. H. Aukema, B. Bond-Lamberty, L. Chini, J. S. Clark, et al. 2020. Pervasive shifts in forest dynamics in a changing world. *Science* 368:eaaz9463.
- McGraw, K. J., E. A. Mackillop, J. Dale, and M. E. Hauber. 2002. Different colors reveal different information: how nutritional stress affects the expression of melanin- and structurally based ornamental plumage. *Journal of Experimental Biology* 205:3747–3755.
- McKechnie, A. E., A. R. Gerson, and B. O. Wolf. 2021. Thermoregulation in desert birds: scaling and phylogenetic variation in heat tolerance and evaporative cooling. *Journal of Experimental Biology* 224:jeb229211.
- McKechnie, A. E., and B. O. Wolf. 2019. The physiology of heat tolerance in small endotherms. *Physiology* 34:302–313.
- McLean, N., H. P. van der Jeugd, and M. van de Pol. 2018. High intraspecific variation in avian body condition responses to climate limits generalisation across species. *PLoS ONE* 13:e0192401.
- Medina, I., K. Delhey, A. Peters, K. E. Cain, M. L. Hall, R. A. Mulder, and N. E. Langmore. 2017. Habitat structure is linked to the evolution of plumage colour in female, but not male, fairy-wrens. *BMC Evolutionary Biology* 17:1–9.
- Midamegbe, A., A. Grégoire, V. Staszewski, P. Perret, M. M. Lambrechts, T. Boulonier, and C. Doutrelant. 2013. Female blue tits with brighter yellow chests transfer more carotenoids to their eggs after an immune challenge. *Oecologia* 173:387–397.
- Miñano, M. R., G. M. While, W. Yang, C. P. Burridge, R. Sacchi, M. Zuffi, S. Scali, D. Salvi and T. Uller. 2021. Climate shapes the geographic distribution and introgressive spread of color ornamentation in common wall lizards. *American Naturalist* 198:379–393.
- Møller, A. P., D. Czeszczewik, E. Flensted-Jensen, J. Erritzøe, I. Krams, K. Laursen, W. Liang, and W. Walankiewicz. 2021. Abundance of insects and aerial insectivorous birds in relation to pesticide and fertilizer use. *Avian Research* 12:43.
- Møller, A. P., and T. Szép. 2005. Rapid evolutionary change in a secondary sexual character linked to climatic change. *Journal of Evolutionary Biology* 18:481–495.
- Moore, M. P., K. Hersch, C. Sricharoen, S. Lee, C. Reice, P. Rice, S. Kronick, K. A. Medley, and K. D. Fowler-Finn. 2021. Sex-specific ornament evolution is a consistent feature of climatic adaptation across space and time in dragonflies. *Proceedings of the National Academy of Sciences of the USA* 118:e2101458118.
- Mougeot, F., J. Martínez-Padilla, G. R. Bortolotti, L. M. I. Webster, and S. B. Pieltney. 2010. Physiological stress links parasites to carotenoid-based colour signals. *Journal of Evolutionary Biology* 23:643–650.

- Nakagawa, S., and H. Schielzeth. 2013. A general and simple method for obtaining  $R^2$  from generalized linear mixed-effects models. *Methods in Ecology and Evolution* 4:133–142.
- Parker, T. H. 2013. What do we really know about the signalling role of plumage colour in blue tits? a case study of impediments to progress in evolutionary biology. *Biological Reviews* 88:511–536.
- Parmesan, C. 2007. Influences of species, latitudes and methodologies on estimates of phenological response to global warming. *Global Change Biology* 13:1860–1872.
- Patterson, B. D., R. W. Kays, S. M. Kasiki, and V. M. Sebestyen. 2006. Developmental effects of climate on the lion's mane (*Panthera leo*). *Journal of Mammalogy* 87:193–200.
- Pattinson, N. B., M. L. Thompson, M. Griego, G. Russell, N. J. Mitchell, R. O. Martin, B. O. Wolf, et al. 2020. Heat dissipation behaviour of birds in seasonally hot arid-zones: are there global patterns? *Journal of Avian Biology* 51:e02350.
- Peñuelas, J., I. Filella, and P. Comas. 2002. Changed plant and animal life cycles from 1952 to 2000 in the Mediterranean region. *Global Change Biology* 8:531–544.
- Peters, A., R. H. J. M. Kurvers, M. L. Roberts, and K. Delhey. 2011. No evidence for general condition-dependence of structural plumage colour in blue tits: an experiment. *Journal of Evolutionary Biology* 24:976–987.
- Pomiankowski, A. 1987. Sexual selection: the handicap principle does work—sometimes. *Proceedings of the Royal Society B* 231:123–145.
- Potti, J., and D. Canal. 2011. Heritability and genetic correlation between the sexes in a songbird sexual ornament. *Heredity* 106:945–954.
- Prasetya, A. M., A. Peters, and K. Delhey. 2020. Carotenoid-based plumage colour saturation increases with temperature in Australian passerines. *Journal of Biogeography* 47:2671–2683.
- Prum, R. O. 2006. Anatomy, physics, and evolution of structural colours. Pages 295–353 in G. E. Hill and K. J. McGraw, eds. *Bird coloration: mechanisms and measurements*. Vol. 1. Harvard University Press, Cambridge, MA.
- Prum, R. O., E. R. Dufresne, T. Quinn, and K. Waters. 2009. Development of colour-producing  $\beta$ -keratin nanostructures in avian feather barbs. *Journal of the Royal Society Interface* 6:S253–S265.
- Pureswaran, D. S., A. Roques, and A. Battisti. 2018. Forest insects and climate change. *Current Forestry Reports* 4:35–50.
- Qvarnström, A. 1999. Genotype-by-environment interactions in the determination of the size of a secondary sexual character in the collared flycatcher (*Ficedula albicollis*). *Evolution* 53:1564–1572.
- R Core Team. 2019. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna.
- Réale, D., A. G. McAdam, S. Boutin, and D. Berteaux. 2003. Genetic and plastic responses of a northern mammal to climate change. *Proceedings of the Royal Society B* 270:591–596.
- Reudink, M. W., A. E. McKellar, K. L. D. Marini, S. L. McArthur, P. P. Marra, and L. M. Ratcliffe. 2015. Inter-annual variation in American redstart (*Setophaga ruticilla*) plumage colour is associated with rainfall and temperature during moult: an 11-year study. *Oecologia* 178:161–173.
- Scordato, E. S. C., A. L. Bontrager, and T. D. Price. 2012. Cross-generational effects of climate change on expression of a sexually selected trait. *Current Biology* 22:78–82.
- Sheldon, B. C., S. Andersson, S. C. Griffith, and J. Örnberg. 1999. Ultraviolet colour variation influences blue tit sex ratios. *Nature* 492:874–877.
- Sheth, S. N., and A. L. Angert. 2016. Artificial selection reveals high genetic variation in phenology at the trailing edge of a species range. *American Naturalist* 187:182–193.
- Shirihai, H., and L. Svensson. 2018. *Handbook of the western Palearctic birds*. A & C Black, London.
- Siefferman, L., and G. E. Hill. 2007. The effect of rearing environment on blue structural coloration of eastern bluebirds (*Sialia sialis*). *Behavioral Ecology and Sociobiology* 61:1839–1846.
- Siepielski, A. M., M. B. Morrissey, M. Buoro, S. M. Carlson, C. M. Caruso, S. M. Clegg, T. Coulson, et al. 2017. Precipitation drives global variation in natural selection. *Science* 355:959–962.
- Stenning, M. J. 2018. *The blue tit*. Poyser, London.
- Stenseth, N. C., A. Mysterud, G. Ottersen, J. W. Hurrell, K.-S. Chan, and M. Lima. 2002. Ecological effects of climate fluctuations. *Science* 297:1292–1296.
- Stuart-Fox, D. M., and T. J. Ord. 2004. Sexual selection, natural selection and the evolution of dimorphic coloration and ornamentation in agamid lizards. *Proceedings of the Royal Society B* 271:2249–2255.
- Svensson, E. I. 2019. Eco-evolutionary dynamics of sexual selection and sexual conflict. *Functional Ecology* 33:60–72.
- Svensson, E., and J. A. Nilsen. 1997. The trade-off between molt and parental care: a sexual conflict in the blue tit? *Behavioral Ecology* 8:92–98.
- Van Buskirk, J., and U. K. Steiner. 2009. The fitness costs of developmental canalization and plasticity. *Journal of Evolutionary Biology* 22:852–860.
- Vergara, P., J. Martinez-Padilla, F. Mougeot, F. Leckie, and S. M. Redpath. 2012. Environmental heterogeneity influences the reliability of secondary sexual traits as condition indicators. *Journal of Evolutionary Biology* 25:20–28.
- West, P. M., and C. Packer. 2002. Sexual selection, temperature, and the lion's mane. *Science* 297:1339–1343.
- Westphal, M. F., and T. J. Morgan. 2010. Quantitative genetics of pigmentation development in 2 populations of the common garter snake, *Thamnophis sirtalis*. *Journal of Heredity* 101:573–580.
- White, T. E. 2020. Structural colours reflect individual quality: a meta-analysis. *Biology Letters* 16:20200001.
- Whitlock, M. C., and A. F. Agrawal. 2009. Purging the genome with sexual selection: reducing mutation load through sexual selection on males. *Evolution* 63:569–582.
- Zeuss, D., R. Brandl, M. Brändle, C. Rahbek, and S. Brunzel. 2014. Global warming favours light-coloured insects in Europe. *Nature Communications* 5:3874.
- Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. *Methods in Ecology and Evolution* 1:3–14.

### References Cited Only in the Online Enhancements

- Isaksson, C., J. Örnberg, M. Prager, and S. Andersson. 2008. Sex and age differences in reflectance and biochemistry of carotenoid-based colour variation in the great tit *Parus major*. *Biological Journal of the Linnean Society* 95:758–765.
- Morrissey, M. B., and A. J. Wilson. 2010. pedantics: an R package for pedigree-based genetic simulation and pedigree manipulation, characterization and viewing. *Molecular Ecology Resources* 10: 711–719.

Associate Editor: Erik Svensson  
Editor: Jennifer A. Lau