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ORIGINAL ARTICLE

Colour ornamentation in the blue tit: quantitative genetic (co)variances across sexes

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Although secondary sexual traits are commonly more developed in males than females, in many animal species females also display elaborate ornaments or weaponry. Indirect selection on correlated traits in males and/or direct sexual or social selection in females are hypothesized to drive the evolution and maintenance of female ornaments. Yet, the relative roles of these evolutionary processes remain unidentified, because little is known about the genetic correlation that might exist between the ornaments of both sexes, and few estimates of sex-specific autosomal or sex-linked genetic variances are available. In this study, we used two wild blue tit populations with 9 years of measurements on two colour ornaments: one structurally based (blue crown) and one carotenoid based (yellow chest). We found significant autosomal heritability for the chromatic part of the structurally based colouration in both sexes, whereas carotenoid chroma was heritable only in males, and the achromatic part of both colour patches was mostly non heritable. Power limitations, which are probably common among most data sets collected so far in wild populations, prevented estimation of sex-linked genetic variance. Bivariate analyses revealed very strong cross-sex genetic correlations in all heritable traits, although the strength of these correlations was not related to the level of sexual dimorphism. In total, our results suggest that males and females share a majority of their genetic variation underlying colour ornamentation, and hence the evolution of these sex-specific traits may depend greatly on correlated responses to selection in the opposite sex.
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INTRODUCTION

Since Darwin's development of sexual selection theory (Darwin, 1871), theoretical and empirical work has greatly progressed towards explaining the mechanisms responsible for the evolution and maintenance of exaggerated male ornaments and weaponry (see, for example, Andersson, 1994; Savalli, 2001). Although secondary sexual characters are commonly more developed in males than females, in many animal species females also display elaborate ornaments (for example, conspicuous colours) or weaponry. After ignoring the issue for decades, evolutionary biologists have struggled to explain the evolution and maintenance of secondary sexual characteristics that are also exaggerated in females (Amundsen, 2000; Lebas, 2006; Clutton-Brock, 2007; Kraaijeveld *et al.*, 2007; Tobias *et al.*, 2012). Two nonexclusive hypotheses have been suggested as explanations for the evolution and maintenance of female ornaments: (1) indirect selection for elaborate female traits through direct selection on correlated male traits (*correlated response hypothesis*) (Lande, 1980; Price, 1996) and (2) direct selection on female traits occurring through either female–female competition for mates (Dijkstra *et al.*, 2008), male mate choice (Griggio *et al.*, 2005; Byrne and Rice, 2006) or social competition for ecological resources (Heinsohn *et al.*, 2005). Although each of these hypotheses has received some empirical support, there is currently no consensus about whether one plays a prevailing role, even within a given taxonomic group such as birds. A recent comparative analysis on 6000 species of passerines concluded that both female and male plumage colourations are more extravagant in larger species and in tropical species (Dale *et al.*, 2015). Yet, the strength of sexual selection has antagonistic effects in the two sexes as it increases male colouration while decreasing female colouration (Dale *et al.*, 2015), supporting the possibility of independent evolution as suggested by previous studies (Amundsen, 2000). The work by Dale *et al.* (2015) also confirms that the general focus on male ornamentation has limited our understanding of the evolution of colour ornaments in both sexes.

Even though the presence of strong cross-sex genetic covariances is a crucial assumption underlying the correlated response hypothesis, sex-specific estimates of key quantitative genetic (co)variances underlying secondary sexual traits that are expressed in both sexes have been conspicuously scarce in the empirical literature (but see Price and Burley, 1993; Price, 1996; Chenoweth and Blows, 2003; Roulin and Jensen, 2015). In particular, studies on the role of ornamentation have largely focussed on sexually dimorphic species while neglecting species with low or no sexual dimorphism (see reviews in Kraaijeveld *et al.*, 2007; Poissant *et al.*, 2010). In the absence of further investigation into the heritability of sexual ornaments/weapons and their cross-sex genetic covariance, no generality can be drawn from the present empirical data regarding the importance of the hypotheses cited above. For example, in the review of Poissant *et al.* (2010), only 14 out of 549 estimations of cross-sex genetic correlations concerned ornaments or weaponry and the strength of these correlations varied substantially

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across taxa and across trait types (for example, between morphological traits and traits linked to communication).

In addition, theory for the evolution of sexual dimorphism also predicts that the degree of phenotypic difference between the sexes should be negatively associated with the cross-sex additive genetic covariance (and, to a certain extent, the cross-sex additive genetic correlation), and positively associated with the amount of sex-linked genetic variance (Fairbairn and Roff, 2006). Evidence supporting these predictions is presently very limited (Dean and Mank, 2014). Quantitative genetic analyses in natural populations based on long-term observations of individual phenotypes and relatedness (pedigrees) could offer a means to estimate sex-linked genetic variance. However, the large majority of studies in wild populations estimate additive genetic (co)variances while assuming only autosomal inheritance (Charmantier *et al.*, 2014). Recent investigations on colour variation have revealed Z-linked genetic variance in the collared flycatcher *Ficedulla albicollis* (explaining 40% of total phenotypic variance in wing patch size; Husby *et al.*, 2013), the barn owl *Tyto alba* (30% of variance in eumelanic spot diameter; Larsen *et al.*, 2014) and W-linked genetic variance in the zebra finch *Taeniopygia guttata* (2.6% of variance in beak colouration; Evans *et al.*, 2014). In many other cases however, investigations show no evidence for sex-linked genetic variance in colour ornamentation (for example, the Florida scrub-jay *Aphelocoma coerulescens*; Tringali *et al.*, 2015). Overall, contributions of sex-linked genetic variance to phenotypic variance in sexually selected and morphological traits measured in pedigreed populations is usually weak, yet it is commonly acknowledged that this could be because of low power to distinguish autosomal from sex-linked genetic variance (Husby *et al.*, 2013). It is indeed currently unclear whether wild population pedigrees used for quantitative genetic analyses confer sufficient power to disentangle autosomal additive genetic variance from other components of genetic variance (Wolak and Keller, 2014), as power analyses are not performed in these studies.

Colouration is often a sexually and/or socially selected trait that can signal individual quality and identity, as well as signal species identity, enhance crypsis, provide thermoregulatory benefits and protect against bacteria (Hill and McGraw, 2006), and is therefore central to an animal's fitness. However, to date, we know very little on the heritability of colouration (Svensson and Wong, 2011) or the genetic correlation that might exist between the sexes (Kraaijeveld *et al.*, 2007; Roulin and Ducrest, 2013). Comparative analyses have shown that colouration can evolve conjointly or separately in the two sexes (Amundsen, 2000; Dale *et al.*, 2015), but quantitative genetic studies of colouration are required to determine the main factors driving the observed sex-specific evolutionary patterns.

Although blue tits can appear sexually monomorphic to a human eye, spectrophotometry analyses have shown that blue tits from the subspecies *Cyanistes caeruleus caeruleus* are sexually dichromatic in the ultraviolet (UV) blue of the crown patch but monomorphic in their yellow carotenoid-based chest colouration (Andersson *et al.*, 1998; Hunt *et al.*, 1998; Doutrelant *et al.*, 2008). Both male and female UV blue colouration influences intrasexual interactions (see, for example, Alonso-Alvarez *et al.*, 2004; Rémy *et al.*, 2010; but see Vedder *et al.*, 2008), mutual mate choice (Hunt *et al.*, 1999) and mate reproductive investments (see, for example, Sheldon *et al.*, 1999; Limbourg *et al.*, 2004; Kingma *et al.*, 2009; but see Dreiss *et al.*, 2006 for males and Limbourg *et al.*, 2013 for females). In addition, male and female UV blue and yellow adult colouration is condition dependent (Doutrelant *et al.*, 2012; but see Peters *et al.*, 2011) and can be linked to parental investment or success (see, for example, Garcia-Navas *et al.*, 2012; Midamegbe *et al.*, 2013) and to parasite levels (del Cerro *et al.*, 2010). Overall, all these studies suggest that both UV blue and yellow colouration can be sexually selected in both sexes, yet Parker and colleagues (Parker *et al.*, 2011; Parker, 2013) have recently challenged this view. Parker *et al.* (2011) found weak but contrasted evidence of fecundity selection on colouration for both sexes over 3 years. Following a meta-analysis that considered all previous studies with the same strength, regardless of the pertinence and robustness of their methodology, Parker (2013) further concluded that the sexual and/or social functions of blue and yellow colouration in blue tits remains to be demonstrated. This debate highlights the need for more studies on the colour patches in this species, and the examination of the cross-sex genetic correlation is an essential step to advance our understanding of the evolution in ornaments in both sexes. Despite many documented and proposed selective advantages to colour ornaments in blue tits, only three quantitative genetic studies have been conducted on colouration in this species (Johnsen *et al.*, 2003; Hadfield *et al.*, 2006a, 2007; Drobniak *et al.*, 2013), showing low autosomal heritability for both types of colourations. Furthermore, the indirect selection hypothesis remains untested as there are no estimates to date of cross-sex additive genetic covariance.

We used 9 years of colour measures in long-term monitored blue tits located in a Mediterranean mainland population (subspecies *C. c. caeruleus*) and on the island of Corsica (subspecies *C. c. ogliastrae*) to investigate the sex-specific and cross-sex additive genetic (co)variances underlying colour ornamentation traits that show a gradient of sexual dimorphism, and have been suggested to be involved in intra- or inter-sexual selection. Colour features were measured in one structurally based (blue crown) and one carotenoid-based (yellow chest) ornament.

In the context of improving our understanding of the evolution and maintenance of sexual ornaments and the importance of genetic correlations in the evolution of female ornaments, our aims were originally threefold:

(1) Assessing whether there is autosomal and/or sex-linked genetic variation for colour ornamentation in the blue tit;
(2) Measuring the strength of cross-sex genetic covariances, with the particular aim to evaluate whether female ornament evolution could be driven by such covariances;
(3) Testing the theoretical predictions that the degree of sexual dimorphism is negatively associated with the cross-sex additive genetic covariance and positively associated with the amount of sex-linked genetic variance (Fairbairn and Roff, 2006; Poissant *et al.*, 2010).

MATERIALS AND METHODS

Sampling procedure and colour measurement

Blue tits have been monitored in the Rouvière forest (mainland France) since 1991 and at two localities in Corsica since 1976 (Pirio) and 1994 (Muro). Details on these study sites can be found in (Blondel *et al.* (2006) and Charmantier *et al.* (2016). Blue tits from Corsica belong to a different subspecies from blue tits found in the French Mediterranean mainland. The distance between Muro and Pirio in Corsica is 25 km. In order to improve our power for quantitative genetic models, individuals from these two valleys were pooled in one common Corsican data set. Supplementary Information A2 provides statistical justification for this choice based on a test for equality of additive genetic variances between the two populations.

Each year, breeding parents were captured in nest boxes between April and June. A small proportion of individuals were caught before the breeding period in January–March (in 2008–2009 and 2011–2013, $n = 577$ or 15.9% of

measures). Each bird was equipped with a uniquely numbered metal ring provided by the Museum National d'Histoire Naturelle in Paris, six blue feathers were collected from the bird's blue crown and eight yellow feathers from the yellow chest to allow colour measurements in the lab. Bird sex and age were determined based on the capture–recapture database or on the colour of wing coverts for unringed birds. Chicks were ringed after 9 days of age that allowed building social pedigrees for each population. Genotyping of parents and offspring in 2000–2003 has shown that up to 29.3% (annual range: 18.2–29.3%, Charmantier *et al.*, 2004) of chicks were the result of extra-pair matings in Corsica, and 18.2% (annual range: 11.5–18.2%, Charmantier and Perret, 2004) on the mainland. The social pedigree used in this study was corrected for extra pair paternities only for chicks born in 2000–2003 in both populations. In these years, molecular genetic data allowed to identify 53% of extra-pair sires, whereas nonidentified genetic fathers were attributed a dummy identity. The Corsican pruned pedigree included 1507 individuals over 14 generations and the mainland pedigree 1233 individuals over 12 generations.

Feather colouration was measured in laboratory conditions, using a spectrometer (AVASPEC-2048, Avantes BV, Apeldoorn, Netherlands) and a deuterium-halogen light source (AVALIGHT-DH-S lamp, Avantes BV) covering the range 300–700 nm (Doutrelant *et al.*, 2008, 2012) and kept at a constant angle of 90° from the feathers. For each bird and colour patch (crown and chest), we computed the mean of six reflectance spectra taken on two sets of three blue and four yellow feathers (Doutrelant *et al.*, 2008, 2012). We used the software Avicol v2 (Gomez, 2006) to compute chromatic and achromatic colour variables based on the shape of the spectra (Andersson *et al.*, 1998; Doutrelant *et al.*, 2008), following previous studies on blue tits in our populations (see, for example, Doutrelant *et al.*, 2008, 2012) and others (see, for example, Alonso-Alvarez *et al.*, 2004; but see Parker *et al.*, 2011). For the UV blue crown colouration, we computed one achromatic variable: blue brightness (area under the reflectance curve divided by the width of the interval 300–700 nm); and two chromatic variables: blue hue (wavelength at maximal reflectance) and blue UV chroma (proportion of the total reflectance falling in the range 300–400 nm). Lower values of hue and higher values of UV chroma mean that the signal is stronger in the UV. For the yellow chest colouration, in addition to yellow brightness, we computed yellow chroma as $(R_{700}-R_{450})/R_{700}$. Higher values of yellow chroma are linked to higher carotenoid contents in the plumage (Isaksson *et al.*, 2008). We have shown previously that our measures of these five colour traits using a spectrometer are highly repeatable (see, for example, Doutrelant *et al.*, 2008, 2012; Midamegbe *et al.*, 2013), suggesting acceptable measurement error. Figure 1 displays average spectra for blue crown and yellow chest measures in 2011.

The complete data set included 3629 observations with at least one colour parameter measured ($n=1659$ in Rouvière (mainland), $n=1035$ observations in Muro (Corsica) and $n=935$ in Pirio (Corsica)) for a total of 2177 birds (see Table 1 for detailed sampling efforts on males and females). Supplementary Figure S1 presents the distribution of each colour parameter in Rouvière and in Corsica and Supplementary Table S1 shows the phenotypic correlation between each pair of traits in the mainland and the Corsican populations (Supplementary Information). As Supplementary Table S1 illustrates, among the five classically used and biologically relevant measures of colouration, some are phenotypically correlated yet Spearman rank's correlation did not exceed 0.672 in absolute value. The strongest phenotypic correlation was between blue UV chroma and blue hue (Spearman rank's correlation ranging from −0.476 to −0.672). All other trait combinations showed correlations of absolute value less than 0.4.

Sexual dimorphism

For each trait in both data sets, we measured the degree of sexual dimorphism in colour ornamentation by calculating a standardized effect size: Cohen's *d*, and its associated standard error (equations 10 and 16 in Nakagawa and Cuthill, 2007). Cohen's *d* effect size is a dimensionless statistic; a value of 0.2 would typically be suggestive of small sexual dimorphism, whereas a value of 0.8 would be interpreted as revealing strong sexual dimorphism.

Quantitative genetics

Exploring fixed effects. Previous to conducting quantitative genetic models, we conducted linear mixed models to explore the contribution of fixed effects (year of measure, year of birth, period of measurement and individual age) to the various colour parameters in both data sets. For all traits, only year of

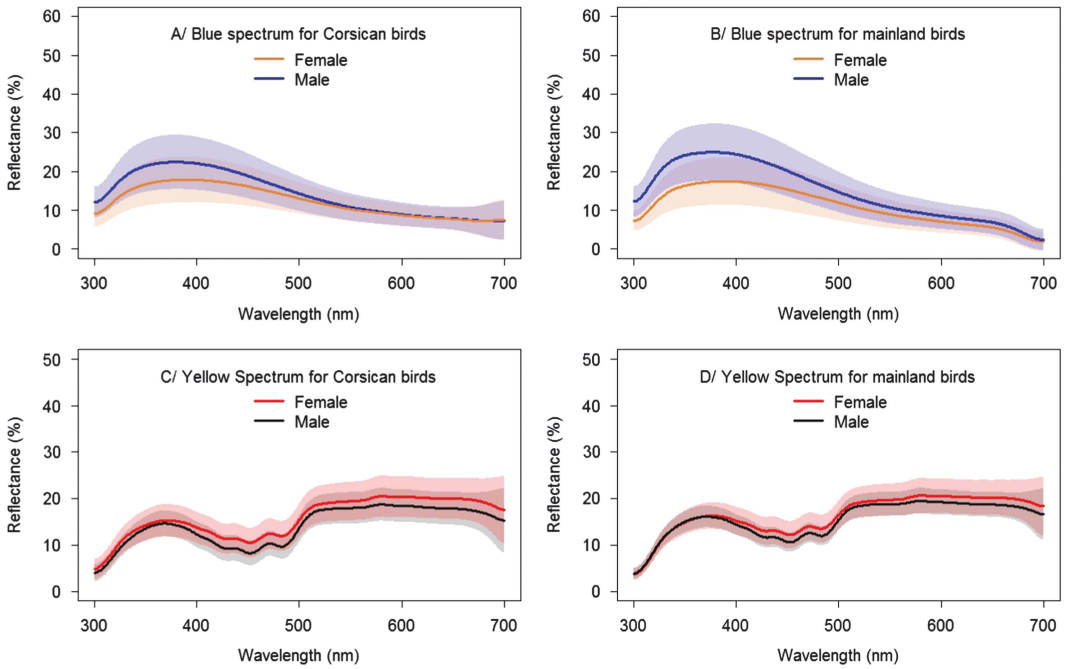

Figure 1 Average UV blue crown spectra for male (blue) and female (orange) blue tits sampled in 2011 (**a**) in Corsica and (**b**) on the mainland. Average yellow chest spectra for male (black) and female (red) blue tits sampled in 2011 (**c**) in Corsica and (**d**) on the mainland. Thick lines represent mean spectra and shaded areas associated s.d. values. Plots were realized using the R package 'pavo' (www.rafaelmaia.net/r-packages/pavo).

Table 1 Sampling effort and mean values (with associated s.d. values) for colour traits measured in blue tit males and females in Rouvière (mainland) and in Corsica between 2005 and 2013

	Blue brightness	*Blue hue*	*Blue UV chroma*	*Yellow brightness*	*Yellow chroma*
Corsica, males					
Nb measures	882	882	882	870	958
Mean (s.d.)	15.6 (4.8)	375.1 (11.7)	0.39 (0.04)	16.1 (3.7)	0.80 (0.18)
Corsica, females					
Nb measures	865	865	865	825	930
Mean (s.d.)	12.9 (4.3)	383.3 (12.2)	0.35 (0.04)	16.8 (3.6)	0.70 (0.16)
Rouvière, males					
Nb measures	810	810	810	769	769
Mean (s.d.)	16.6 (5.2)	376.5 (11.3)	0.38 (0.03)	17.0 (3.5)	0.63 (0.17)
Rouvière, females					
Nb measures	840	840	840	801	801
Mean (s.d.)	14.2 (5.4)	388.1 (11.3)	0.34 (0.03)	17.3 (3.9)	0.61 (0.17)

Abbreviation: UV, ultraviolet.
Hue is in nm.

measure was retained in all models as a categorical fixed effect (see details in Supplementary Information A1).

Univariate animal models. Genetic (co)variances, heritabilities and genetic correlations were estimated using restricted maximum-likelihood (REML) estimation procedures implemented in the software ASReml v3.0 (Gilmour *et al.*, 2009). For each data set and colour measure, we first implemented a sex-specific univariate 'animal model' that combined the phenotypic measures for a given sex with the pedigree information to partition the phenotypic variance into an additive genetic variance (V_A), a variance due to permanent environment effects (V_{PE}, based on repeated observations of individuals) and a residual variance (V_R), while controlling for annual fluctuations using year as a single fixed effect. In such a model the phenotypic value of an individual i is written as:

$$y_i = \mu + YEAR + a_i + PE_i + \varepsilon_i \quad (1)$$

The additive genetic effect on individual i (a_i), was assumed to be normally distributed with mean of zero and variance of V_A. The permanent environment effect (PE_i) and residual errors (ε_i) were also assumed to be normally distributed, with zero means and variances V_{PE} and V_R. Residual errors were assumed to be uncorrelated within individuals across measurements. In the Corsican model, a genetic group determined the Muro/Pirio origin for each bird.

The additive genetic variance estimates were tested against a null hypothesis of zero by carrying out likelihood ratio tests, where minus two times the difference in log likelihood between a model including the variance and a model without it was tested against the χ^2 distribution with one degree of freedom.

Bivariate animal models and cross-sex additive genetic variance. In order to estimate the cross-sex additive genetic covariance for each colour measurement, we expanded Equation 1 to a bivariate model where the phenotypic values of males (m_i) and of females (f_i) are explained by fixed (year of measure) and random effects (as previously, additive genetic, permanent environment and residual effects):

$$\begin{aligned} m_i &= \mu_m + YEAR_m + a_{mi} + PE_{mi} + \varepsilon_{mi} \\ f_i &= \mu_f + YEAR_f + a_{fi} + PE_{fi} + \varepsilon_{fi} \end{aligned} \quad (2)$$

This bivariate animal model provides sex-specific estimations of additive genetic variances (V_{A_m}, V_{A_f}), permanent environment variances (V_{PE_m}, V_{PE_f}) and residual variances (V_{R_m}, V_{R_f}). In this model, each character is sex specific and cannot be measured in males and females simultaneously, and hence this model cannot fit any between-individual (permanent environment) or within-individual (residual) covariance. However, it can fit a cross-sex additive genetic covariance ($COV_{A_{m,f}}$) from which we estimate the cross-sex additive genetic correlation:

$$r_{A_{m,f}} = \frac{COV_{A_{m,f}}}{\sqrt{V_{A_m} \times V_{A_f}}} \quad (3)$$

A bivariate animal model was fitted for each colour trait in each population, with a genetic group specified for Muro and Pirio individuals in the case of the Corsican data set. The additive genetic covariance estimates were tested against a null hypothesis of zero by carrying out a likelihood ratio test using the χ^2 distribution with one degree of freedom. In order to test for a genotype × sex interaction, which occurs when a given genotype has different phenotypic expressions in males versus females, we compared the original model with a model where $V_{A_m} = V_{A_f} = COV_{A_{m,f}}$ using likelihood ratio tests and the χ^2 distribution with two degrees of freedom. To allow comparisons between traits and populations, we also report sex-specific coefficients of additive genetic variance CV_{A_m} and CV_{A_f} (Houle, 1992) in which the square root of the additive genetic variance is scaled by the trait mean:

$$CV_A = 100 \times \sqrt{V_A}/\overline{X} \quad (4)$$

Including a Z-linked genetic variance. We conducted power analyses to determine the ability of the animal model to estimate sex-chromosomal and autosomal additive genetic variance given our blue tit pedigrees and data structures. Specifically, our goal was to determine whether we could detect Z-chromosome-linked additive genetic variance (V_Z) in the blue tit colouration data. Our general approach was to use Monte Carlo simulation to reassign individual phenotypes with known (that is, simulated) sources of trait covariation in the population and then use animal models with each simulated data set to test the null hypothesis that Z-chromosomal additive genetic (co) variances were equal to zero. Over many replicate simulations, the proportion of significant P-values ($P<0.05$) obtained from our null hypothesis tests reflect the power (the probability of rejecting the null hypothesis when it is false) of the animal model to estimate V_Z. We note that this does not determine the power of the animal model to provide unbiased estimates of autosomal (V_A) and sex-linked (V_Z) additive genetic variances (Supplementary Information).

We simulated random effects underlying observed phenotypes similar to those modeled for the observed data (Equation 2): additive genetic (autosomal and Z-linked), permanent environment and residual effects (Supplementary Information A3). We used 27 unique combinations of autosomal additive genetic, permanent environment and residual variances along with cross-sex autosomal and sex-linked additive genetic correlations (Supplementary

Table S2). Within each of these unique combinations, the *Z*-linked additive genetic variance was set to one of seven values: $\sigma_{Z\text{-male}}^2 = 1$, 10, 30, 50, 60, 70 or 90 to assess the power at each level.

For each of the above parameter combinations, in each of the two data sets (Corsica and Rouvière), we simulated phenotypes for every individual (Supplementary Equation S1 in Supplementary Information) a total of 1000 different times. We used R (R Core Team, 2014) and the R package nadiv (Wolak, 2012) to simulate each of the above effects (Supplementary Information A3). We used the model of sex-chromosomal additive genetic variance of Fernando and Grossman (1990) that assumes no global sex chromosomal dosage compensation or recombination between the Z and W chromosomes.

Simulated phenotypes were analysed with an animal model implemented in the ASReml R package (v3.0, Butler *et al.*, 2009). Models were conducted with and without the Z-linked additive genetic (co)variance terms, and minus two times the difference in these model log likelihoods was used to calculate a likelihood ratio test statistic. Probabilities of obtaining a difference in log likelihoods were assigned assuming an asymptotically χ^2 distributed test statistic with three degrees of freedom. For a given set of parameters, we used the proportion of *P*-values <0.05 as an estimate of power. Full details are available in the Supplementary Information A3.

RESULTS

Additive genetic (co)variances and heritabilities

As detailed in Table 2, the bivariate animal models revealed that the chromatic part of the crown colouration (blue UV chroma and hue) was overall heritable (except for 2 of the 8 estimated colour parameters: male hue and female UV chroma in Corsica) with heritability estimates ranging from 0.07 to 0.19 in Corsica (0.73–4.06 for CV_A) and from 0.18 to 0.23 in Rouvière (1.10–3.98 for CV_A). In contrast, the achromatic part of the crown colouration (brightness) was heritable for both sexes (with heritabilities of 0.18 and 0.10 for males and females) in Corsica but not heritable for both sexes in the mainland Rouvière population (although CV_As were high), suggesting it is more sensitive to nongenetic variation than chromatic parameters. Similarly, the achromatic part of the yellow colouration was nonheritable in both sexes and populations, whereas the chromatic part was significantly heritable in males (heritabilities of 0.13 and 0.25 in Corsica and the mainland), but not in females.

Differences in model log likelihoods where sex-specific additive genetic variances—V_{A_m} and V_{A_f}—were unconstrained or constrained to be equal indicated genotype by sex interactions only in two cases: in Corsica for blue hue ($P=0.003$) and blue UV chroma ($P<0.0001$). Estimated $\mathrm{COV}_{A_{m,f}}$ (Table 2) for all blue measures and for Corsican yellow chroma were large and significantly greater than zero. $\mathrm{COV}_{A_{m,f}}$ was not significantly different from zero for yellow chroma in Rouvière, yet this is most likely explained by the very small V_{A_f} that prevents a correct estimation of the covariance.

Power analysis for sex-linked genetic variance

Overall, the power simulations revealed low power to estimate Z-linked additive genetic variance in our two data sets (see partial results in Figure 2 and Supplementary Information A3). Using a common rule of thumb for power, the Corsican data only achieve a minimum level of desired power (80%) when the Z-linked between-sex additive genetic correlation is one (bottom row, Supplementary Figure S2a), Z-linked additive genetic variance is very high (>70) and autosomal additive genetic variance is two. The animal model combined with the Rouvière population structure (Supplementary Figure S2b) achieves 80% power under less restrictive conditions, although this still requires Z-linked additive genetic variance to comprise at least 50% of total phenotypic variance (that is, $h^2_{\text{Z-linked}} > 0.5$).

Sexual colour dimorphism

All colour traits displayed some sexual dimorphism, apart from yellow brightness in the Rouvière population (Figure 3, all paired one-sided Student's *t*-tests with $P<0.016$ except for yellow brightness in the Rouvière: $P=0.061$), with males being more colourful than females for both ornaments, with brighter blue and slightly brighter yellow.

DISCUSSION

Autosomal and sex-linked genetic variation for colour ornamentation in the blue tit

Autosomal genetic variation. Our quantitative genetic analyses reveal higher heritabilities for the crown blue UV colour than previously estimated (Hadfield *et al.*, 2006a), confirm that the chromatic part of yellow colouration can be heritable in males (Evans and Sheldon, 2012) and reveal a lower heritability for yellow chroma in females than males.

Table 2 Heritability of colour features in male and female blue tits (h^2_m and h^2_f) and cross-sex additive genetic covariances ($COV_{A_{m,f}}$) and correlations ($r_{A_{m,f}}$) estimated using bivariate animal models (with s.e. values)

	nb obs	V_{Am}	CV_{A_m}	h^2_m	V_{A_f}	CV_{A_f}	h^2_f	$COV_{A_{m,f}}$	$r_{A_{m,f}}$
Corsica									
Blue brightness	1795	**3.73 (1.02)**	12.34	**0.18 (0.05)**	**1.59 (0.76)**	9.81	**0.10 (0.05)**	**2.37 (1.30)**	0.97 (0.54)
Blue hue	1795	7.48 (4.98)	0.73	0.07 (0.04)	**13.59 (6.18)**	0.96	**0.11 (0.05)**	**10.06 (7.98)**	1.00 (0.87)
Blue UV chroma	1795	**2.5E10^{-4} (5.3E10^{-5})**	4.06	**0.19 (0.06)**	1.2E10^{-4} (1.2E10^{-4})	3.10	0.14 (0.14)	**1.710^{-4} (7.9E10^{-5})**	0.99 (0.68)
Yellow brightness	1772	0.95 (0.61)	6.05	0.07 (0.05)	0.73 (0.60)	5.07	0.06 (0.05)		
Yellow chroma	1957	**3.6E10^{-3} (1.2E10^{-3})**	7.56	**0.13 (0.04)**	3.6E10^{-3} (2.7E10^{-3})	8.51	0.15 (0.11)	**3.6E10^{-3} (1.7E10^{-3})**	1.00 (0.63)
Rouvière									
Blue brightness	1650	1.35 (1.05)	7.01	0.06 (0.05)	1.33 (1.27)	8.15	0.07 (0.07)		
Blue hue	1650	**17.24 (7.48)**	1.10	**0.18 (0.07)**	**21.37 (5.58)**	1.19	**0.20 (0.05)**	**19.04 (5.65)**	0.99 (0.28)
Blue UV chroma	1650	**1.6E10^{-4} (5.7E10^{-5})**	3.31	**0.19 (0.07)**	**1.9E10^{-4} (4.3E10^{-5})**	3.98	**0.23 (0.05)**	**1.6E10^{-4} (4.5E10^{-5})**	0.94 (0.25)
Yellow brightness	1570	0.74 (0.38)	5.07	0.09 (0.04)	0.75 (0.93)	5.00	0.07 (0.08)		
Yellow chroma	1570	**4.9E10^{-3} (1.9E10^{-3})**	11.16	**0.25 (0.10)**	3.6E10^{-3} (2.0E10^{-3})	9.91	0.16 (0.09)	9.3E10^{-4} (1.4E10^{-3})	0.22 (0.33)

Abbreviation: nb obs, number of measures for each trait; UV, ultraviolet.
The cross-sex additive genetic correlation is presented only for cases where at least one sex-specific additive genetic variance (V_{A_m}, V_{A_f}) was significant. All significant results ($P<0.05$) are in bold.
Significance of $r_{A_{m,f}}$ was not assessed.

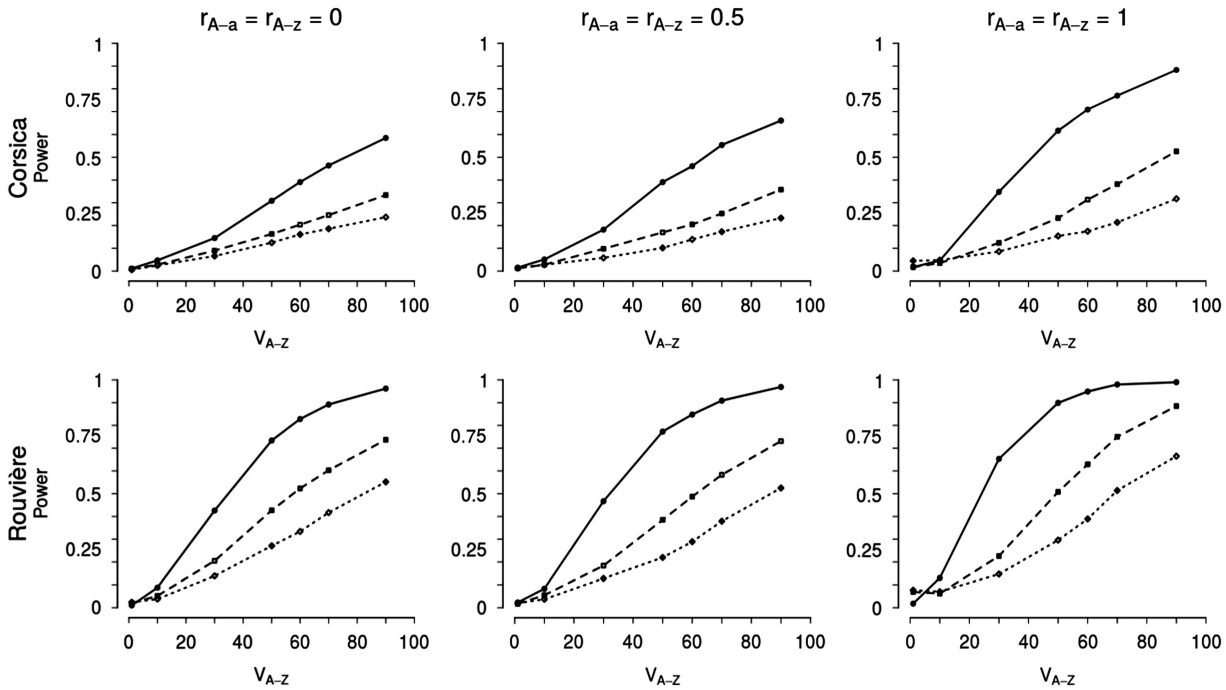

Figure 2 Power to estimate Z-chromosomal additive genetic variance in the Corsican (top row) and Rouvière (bottom row) populations. Between-sex additive genetic autosomal (r_{A-a}) and Z-chromosomal (r_{A-z}) correlations vary from zero to one. Power is calculated as the proportion of simulations for which the model with Z-chromosomal additive genetic (co)variances fitted significantly better than a model without. Power was assessed at seven values of Z-chromosomal additive genetic variance (values along the x axes) and three values of autosomal additive genetic variance (V_{A-a}; solid = 2, dashed = 50, and dotted = 100 lines).

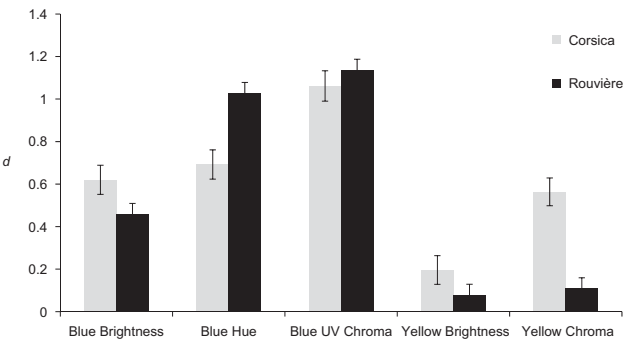

Figure 3 Sexual dimorphism (Cohen's *d)* on five colour traits in blue tits from Corsica (grey) and from the mainland (population of Rouvière, black). Bars represent s.e. values. See Table 1 for sample sizes and main text for statistics.

Blue UV colouration depends on the microstructure of the plumage (Prum, 2006), whereas yellow colouration is influenced by carotenoid contents (Partali *et al.*, 1987) and by microstructure (Shawkey and Hill, 2005). Food is the sole source of carotenoids for blue tits as animals cannot synthesize them. Hence, stronger environmental dependence is expected in carotenoid-based colouration compared with the structurally based colouration. This prediction is upheld by our results for females, but not so much for males where there is no strong contrast between heritabilities for carotenoid-based and structurally based colouration.

The fact that male yellow chroma is as heritable as the UV blue colouration in both populations, and displays high CV_{A_m}, is very interesting. As yellow chroma is related to carotenoid content in the feathers, more chromatic individuals are often depicted as having higher foraging capacities and/or higher parasite resistance (see, for example, del Cerro *et al.*, 2010). Our results suggest that more chromatic males have male offspring that are more chromatic themselves. This could be interpreted as more chromatic males having higher abilities at finding food and/or at parasite resistance, and that their male offspring inherit these aptitudes, either genetically or nongenetically. Indeed, although the additive genetic variance is estimated here based on a variety of relatedness types, the animal model cannot always decipher accurately between genetic versus shared environmental or social resemblance between relatives when the large majority of individuals in the pedigree are siblings or parent–offspring (Wolak and Keller, 2014). A male-specific social rather than genetic inheritance of yellow chroma, for example, mediated by paternal care, could explain why this trait is less heritable in females (although note that CV_As are of similar magnitude). As females disperse longer distances than males in the Blue tit (Matthysen *et al.*, 2005), males sharing microhabitats could possibly lead to a male-specific nongenetic inheritance pattern. Such sex-specific environmental covariance between relatives needs to be investigated in future work, ideally using experimental approaches to isolate genetic and environmental effects. In any case, such father–son resemblance in yellow chroma makes it a good candidate for a sexually selected trait to optimize both direct and indirect benefits for females.

The moderate but significant heritabilities presented here are consistent with previous estimates in colour patches of blue tits (Hadfield and Owens, 2006) and great tits (Evans and Sheldon, 2012), yet they are much smaller than heritabilities associated with the sizes of melanin and white colour patches in other species (ranging from 0.28 to 0.90, see, for example, Saino *et al.*, 2013; Hubbard *et al.*, 2015;

Roulin and Jensen, 2015). Melanin and white patches have previously been suggested to be influenced by an individual's condition (Gustafsson *et al.*, 1995; Griffith, 2000), including long-lasting effects of early environments (Roulin, 2016). However, our recent understanding on the genetic determinism for melanism (Theron *et al.*, 2001; Ducrest *et al.*, 2008), as well as the comparison with our present results suggest that variation in black and white ornaments may be less susceptible to body condition than structural and carotenoid-based colourations. In particular, we found that additive genetic variance explains only a small proportion of total variation in the achromatic part of yellow chest colouration, consistent with findings in other blue and great tit populations (Hadfield and Owens, 2006; Hadfield *et al.*, 2006b; Drobniak *et al.*, 2013). These results suggest that most variation in this aspect of colouration is likely attributable to environmental sources, including individual condition. Differences in condition dependence across colouration signals have been demonstrated experimentally using drug or nutritional treatments (McGraw *et al.*, 2002; Hill *et al.*, 2009). Two comparative analyses have also revealed that sexual dichromatism (used as a proxy of sexual selection) is more intense for carotenoid-based or structurally based colouration than for melanin-based colouration (Badyaev and Hill, 2000; Taysom *et al.*, 2011).

Our variance partitioning in the blue UV crown colour reveals some striking differences between the two blue tit subspecies (for example, heritable blue brightness in Corsica only), although the absence of other comparable studies prevents any generalization. In addition, we found higher heritabilities overall than Hadfield *et al.* (2006a), thereby illustrating that the genetic determinism of colouration can vary across populations and requires further quantitative genetic investigations of colouration both within and across species (see review in Mundy, 2006).

Sex-linked genetic variation. Although it is now clear that many genes underlying sexual dimorphism are not sex linked (Badyaev, 2002) and that sex linkage is not a requirement for sexual dimorphism (Fairbairn and Roff, 2006; Dean and Mank, 2014; Roulin and Jensen, 2015), there is accumulating evidence for sex linkage of genes underlying sexually dimorphic traits, especially with the increasing accessibility of genetic mapping in nonmodel organisms (Charlesworth and Mank, 2010; Huang and Rabosky, 2015). Recent evidence suggests that Z-linked genetic variance can explain as much as 40% of the total phenotypic variation in colour ornaments of birds (see Introduction and Husby *et al.*, 2013). However, the statistical power to estimate Z-linked additive genetic variance in our two data sets was very low (see partial results in Figure 2 and Supplementary Information A3). Although we found more power in Rouvière than the Corsican populations (possibly because of a higher pedigree connectedness), it is unlikely, however, that an animal model using data collected from either population would have enough power to detect Z-linked additive genetic variance. Only when the simulated autosomal additive genetic variance was at its lowest value and the simulated Z-chromosomal additive genetic variance was among its highest values would conventional rules of thumb deem there to be sufficient power (that is, power $>80\%$) to calculate Z-chromosomal additive genetic variance. Although empirical estimates of sex-chromosomal additive genetic variance are few, it seems an unlikely condition to find such high sex-chromosomal heritability almost at the exclusion of autosomal heritability. Overall, these simulations revealed that we could not test the hypotheses involving sex-linked genetic variation, and that most if not all previously published results on sex-linked genetic variance suffered from similar lack of power. This is a worrying report that calls for further simulations to determine the structure and size of pedigree and data required to estimate sex-linked genetic variance.

Cross-sex genetic covariances and female ornamentation

In the animal kingdom, dimorphic traits under sexual selection have been shown to be associated with a whole range of cross-sex genetic correlations : from low (for example, in *Drosophila serrata*; Chenoweth and Blows, 2003) to very strong correlations (for example, in the red deer *Cervus elaphus*; Pavitt *et al.*, 2014). The sparse and contrasted results prevent from drawing general conclusions on the link between genetic covariances across sexes and the evolution of sexual traits. In our study, estimated cross-sex additive genetic correlation—$r_{A_{m,f}}$—were high (close to one), even in cases where the trait was not significantly heritable in one sex (for example, blue hue and yellow chroma in Corsica, see Table 2 for details). To our knowledge, only one other study explored $r_{A_{m,f}}$ for blue structural colours (in Florida scrub-jays, Tringali *et al.*, 2015), with similar results of very strong cross-sex genetic correlations. These results validate the fundamental assumption underlying the correlated response hypothesis (Lande, 1980). They suggest that evolution of female crown colouration could be drastically constrained by indirect selection acting on males.

Analogous conclusions can be drawn from estimates of $r_{A_{m,f}}$ in carotenoid-based ornaments: the evolution of colouration in one sex is likely to have a strong influence on the colouration in the other sex. However, we found large variability in our estimates, with $r_{A_{m,f}}$ of yellow chest chroma ranging from 0.22 in Rouvière to 1 in Corsica. The few estimates of cross-sex genetic correlations for carotenoid-based colour traits so far in the literature show a similarly large range of values for $r_{A_{m,f}}$. High additive genetic correlation was found for beak redness in the zebra finch ($r_{A_{m,f}} = 0.926$; Schielzeth *et al.*, 2012) but a study of yellow brightness, saturation and hue in blue tit nestlings showed $r_{A_{m,f}}$ ranging from -0.13 to 0.19 with very large confidence intervals (Drobniak *et al.*, 2013). These very divergent results call for further investigations on cross-sex genetic correlations in carotenoid-based ornaments in a wider range of species and populations. New genomic tools might also soon allow the identification of genomic regions involved in colour variation in both males and females, thereby revealing whether the same genes influence plumage colouration in both sexes (Roulin and Ducrest, 2013; Kraaijeveld, 2014; Huang and Rabosky, 2015).

Our quantitative genetic analyses used social pedigrees that were only partially corrected for extra-pair paternity. Hence, additive genetic variances and heritabilities in Table 2 could be underestimated, although as said above they were overall larger than reported in previous studies (Charmantier and Réale, 2005). Unfortunately, little is known on how errors in paternity assignment due to extra-pair reproduction can affect the estimation of genetic covariances and sex-linked genetic variance (Reid, 2014). A study combining data on extra-pair occurrence and parental colour is planned for our study populations so that we may quantify to what extent missassigned paternity will bias quantitative genetic (co)variance estimates.

Linking the degree of sexual dimorphism to cross-sex additive genetic covariance

In accordance with previous studies in this species (Andersson *et al.*, 1998; Hunt *et al.*, 1998; Delhey and Peters, 2008; Doutrelant *et al.*, 2008) blue characteristics were all highly dimorphic, with the strongest dimorphism expressed in the blue UV chroma, whereas yellow characteristics showed small or moderate dimorphism. Interestingly, Corsican subspecies of blue tits were significantly more dimorphic for yellow chroma than mainland birds (two-sided Student's

t-test, $P = 4 \times 10^{-8}$), whereas the reverse was true for blue hue (two-sided *t*-test, $P = 0.0001$). Although sexual dimorphism in yellow is usually considered very small for this species and possibly below the detectable level for birds (Delhey *et al.*, 2010), strong dichromatism has been reported once before, in central Spain (Garcia-Navas *et al.*, 2012). Our personal observations across the *ultramarinus* complex (C Doutrelant and G Sorci, unpublished data) suggest that the yellow sexual dimorphism might be a characteristic of blue tits in the southern part of the species distribution. These observations limited to the southern edge of the distribution could be explained by differences in selective forces acting on this ornament. Southern blue tit populations are subject to more drastic food limitation than northern ones. Comparative selection analyses would confirm whether these increased environmental constraints result in different selection pressures acting on male and/or female yellow colouration, in particular on yellow chroma, as it is directly linked to the carotenoid content of the feather, and is heritable.

Homologous characters in the two sexes, such as blue crown colour and yellow chest colour in blue tits, are presumably controlled, at least in the early evolution of these traits, by very similar sets of genes, leading to strong cross-sex genetic covariance. As any dimorphic character, these traits are likely to be under antagonistic selection in males and females (Rice, 1984) that, combined with a strong cross-sex genetic covariance, would create an intralocus sexual conflict (Lande, 1980; Bonduriansky and Rowe, 2005; Poissant *et al.*, 2010). This leads to the classic prediction that the degree of sexual dimorphism should be inversely correlated with the level of $\mathrm{COV_{A_{m,f}}}$ (Fairbairn and Roff, 2006) and of $\mathrm{r_{A_{m,f}}}$ (Lande, 1980; Bonduriansky and Rowe, 2005). The negative relationship between the cross-sex additive genetic covariance and the magnitude of sexual dimorphism is generally upheld over a range of trait types and across a variety of animal and plant species (Fairbairn and Roff, 2006; Bonduriansky, 2007; Poissant *et al.*, 2010). However, studies on the role of ornamentation in sexual selection have largely focussed on conspicuously sexually dimorphic species, neglecting species with low or no sexual dimorphism (see reviews in Kraaijeveld *et al.*, 2007; Poissant *et al.*, 2010). Estimating cross-sex genetic covariances for weakly dimorphic or nondimorphic species/traits is now a necessary stepping stone in our understanding of the evolution of sexual dimorphism (Lande, 1980). In our blue tit study, this prediction was not validated when comparing the five colour traits with varying degrees of dimorphism. Indeed, the most dimorphic traits (blue UV chroma and blue UV hue) displayed strong $COV_{A_{m,f}}$ in both data sets, with $r_{A_{m,f}}$ close to 1, and the only nonsignificant $COV_{A_{m,f}}$ was found in one of the least dimorphic traits (yellow chroma). These results imply that the evolution of sexual dimorphism in this species was not facilitated by low intersexual genetic covariance, suggesting other mechanisms should be considered.

First, the observed sexual dimorphism in colour could be driven by environmental differences rather than genetic ones, with a greater sensitivity of one sex to environmental variation. For instance, it has been shown in insects that sex-specific phenotypic plasticity can generate variation in sexual size dimorphism (Stillwell *et al.*, 2010). Differences in plasticity between males and females should lead to consistent differences in sex-specific heritabilities for similar levels of CV_A (Houle, 1992), but this is not a general result witnessed across the focal traits in Table 2. Second, genes linked to sex chromosomes could explain the sexual dimorphism over and above the autosomal genetic (co)variances estimated here, although we could not estimate such sex-linked genetic variance. Third, cross-sex genetic covariances may have changed over the course of the evolution of sexual dimorphism. Meagher (1992) has suggested that during the evolution of sexual dimorphism, loci that show sex-specific expression should be strongly selected for and should become fixed, thereby no longer contributing to the additive genetic variance. This could explain how $COV_{A_{m,f}}$ could be temporarily low or negative during the evolution of dimorphism, but then large and positive once the sex-specific loci are fixed.

An important limitation of our study is that we could not adopt a truly multivariate approach where genetic covariances between suites of traits within and between the sexes might provide a different view on the genetic constraints for the evolution of sexual dimorphism. Indeed, the evolutionary trajectory of a given sex-specific character can be constrained or facilitated by selection acting on the variance displayed by the same trait expressed in the other sex, but also by positive or negative genetic correlations with other traits within and between both sexes (Blows and Hoffmann, 2005; Poissant *et al.*, 2010). For this reason, future studies will need to integrate cross-sex genetic covariances across traits with multivariate selection analyses (Lande, 1980; Chenoweth *et al.*, 2010) in order to fully uncover how sexual antagonistic selection and intralocus sexual conflicts can promote or constrain the evolution of divergent male and female traits (Wyman *et al.*, 2013). Such an approach has been adopted recently in a study of a laboratory population of *Drosophila melanogaster* (Ingleby *et al.*, 2014) and also in a natural population of barn owl (Roulin and Jensen, 2015). Yet, model complexity combined with data availability still largely prevent such multivariate analyses in many natural populations.

CONCLUSION

Overall, this study brought three major advancements in our understanding of the evolution of colour ornamentation and sexual dimorphism. First, the present analyses demonstrated heritability for UV colouration (in both sexes) and yellow colouration (in males), a major requirement for the evolution of colour through sexual or social selection. Second, our simulations revealed the low power of animal models to estimate sex-linked additive genetic variance in wild populations, thereby hampering our ability to test a major hypothesis for the evolution of sexual dimorphism. Third, in the current debate on the evolution of female ornaments, the present results suggest that cross-sex genetic correlations can be very high in colour traits across varying degrees of dimorphism. A fine-scale analysis of sex-specific forces of natural, social and sexual selection is now required to determine the role of indirect (selection acting on males) and direct selection for the evolution of female ornaments. Future genomic studies should be used to determine whether the same genes underlie colouration in males and females.

DATA ARCHIVING

Phenotypic and pedigree data sets available from the Dryad Digital Repository: http://dx.doi.org/10.5061/dryad.gp384. The raw data will be embargoed for 5 years, but could be made available during this period upon request to the authors.

CONFLICT OF INTEREST

The authors declare no conflict of interest.

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