

Female plumage coloration is sensitive to the cost of reproduction. An experiment in blue tits

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Summary

1. A growing number of studies suggest that female ornaments are linked to maternal quality and influence male mate choice. These findings challenge the traditional male-biased view of sexual selection and the hypothesis that female ornaments are the outcome of a genetic correlation with male ornaments. To further test the hypothesis that female traits have a function, it is now essential to investigate their honesty and to determine how signalling and reproduction interact in females. If female traits are honest indicators of quality, then they are likely to have a specific signalling function.

2. We investigated whether carry-over effects of reproduction might ensure the honesty of plumage colour signalling of a bird species with conspicuous UV-blue and yellow coloration, the blue tit *Cyanistes caeruleus*. Reproductive effort was manipulated by removing clutches, thereby forcing both sexes to reproduce twice and to raise chicks later in the breeding season when food is less abundant. In the year following this manipulation, we investigated the change in plumage in experimental and control males and females. The change was measured in the two putative feather ornaments, the UV-blue cap and the yellow breast, and another feather trait probably less likely to be sexually selected: the wing length. We also tested whether higher-quality females had their coloration less affected by the experiment.

3. We found that control but not manipulated males and females increased their signal towards UV. In addition, in the manipulated group, females that were able to lay more eggs had their UV-blue coloration less affected by the treatment. For yellow coloration, we found that manipulated yearlings but not manipulated adults decreased their yellow chroma in comparison with control. Lastly, our results show that the condition of the manipulated females tended to be positively correlated with yellow chroma.

4. These results show that the trade-offs between reproduction and signalling can ensure the honesty of conspicuous plumage traits in female and male blue tits. In addition, they suggest that female traits have the potential to evolve under sexual selection in this and other bird species.

Key-words: bird, carotenoid-based colour, condition dependence, cost of reproduction, handicap principle, structural coloration

Introduction

It is well known that females have conspicuous traits such as antlers and coloured patches. By contrast, major questions remain on why and how conspicuous female traits are maintained (Clutton-Brock 2007, 2009). A common explanation, rooted in an asymmetric concept of sexual selection (sexy males and choosy females), is that female traits emerge as by-products of sexual selection on male traits (e.g. Lande 1980; Kraaijeveld, Kraaijeveld-Smit & Komdeur 2007). The alternative to this hypothesis is that female traits themselves serve as secondary sexual or social signals (Amundsen 2000;

Kraaijeveld, Kraaijeveld-Smit & Komdeur 2007). In agreement with the hypothesis that female traits are used in signalling, both correlational (e.g. Boulet *et al.* 2010; Huchard *et al.* 2010) and experimental studies (e.g. Doutrelant *et al.* 2008; Roulin *et al.* 2000; Siefferman & Hill 2005a; Smiseth & Amundsen 2000) indicate that female traits are linked to reproductive performance and female quality. In addition, experiments have reported male mate choice (Kraaijeveld, Kraaijeveld-Smit & Komdeur 2007) and a role of female ornament in female–female competition (Griggio, Zanollo & Hoi 2010; Midamegbe *et al.* 2011; Murphy *et al.* 2009). An important step now to further test the hypothesis that female traits have a function is to demonstrate that they are honest indicators of female quality.

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One of the main mechanisms hypothesized to ensure the honesty of signals is condition dependence (Grafen 1990; Iwasa & Pomiankowski 1999; Zahavi 1975). Condition dependence suggests that signals have to be costly so that only good-quality individuals can present exaggerated sexual ornaments, armaments or displays and be viable afterward (i.e. be fecund and survive). However, potential fecundity costs of investment in signals have been proposed as a mechanism preventing the evolution of these traits under sexual selection in females (Chenoweth *et al.* 2007; Fitzpatrick, Berglund & Rosenqvist 1995; Morales, Velando & Torres 2009 but see Doutrelant *et al.* 2008; Simmons & Emlen 2008). Indeed, the fitness of females is often mainly determined by fecundity, rather than by mating success as in males (Trivers 1972), and energy trade-offs might prevent females from investing simultaneously too much energy in signalling and in reproduction (Kelly & Alonzo 2009; Kokko 1998).

Life-history trade-offs provide an especially interesting framework to test mechanisms maintaining the honesty of signals (Badyaev & Qvarnstrom 2002; Hoglund & Sheldon 1998). As a consequence of carry-over effects (Harrison *et al.* 2011), secondary sexual traits are predicted to affect and be affected by investments in other costly life-history traits linked to maintenance and reproduction (Griffith 2000; Gustafsson, Qvarnstrom & Sheldon 1995; Siefferman & Hill 2005b). To reveal trade-offs between traits, manipulations are required (Van Noordwijk & De Jong 1986).

We manipulated the costs of reproduction in a bird, the blue tit *Cyanistes caeruleus*, where both sexes are brightly coloured with a slightly dimorphic UV-blue coloration on the cap and a monomorphic carotenoid-based yellow coloration on the chest (Hunt *et al.* 1998). UV-blue and yellow colorations are hypothesized to be sexually selected in both sexes (e.g. Delhey & Peters 2008; Doutrelant *et al.* 2008; Griffith *et al.* 2003; Midamegbe *et al.* 2011). We increased reproductive cost by removing the whole clutch and nest material shortly after clutch completion. This manipulation forced blue tits to breed twice and later in the season. Breeding later in the season is costly as fewer prey are available to rear the chicks (Lambrechts *et al.* 1997; Thomas *et al.* 2001) and is supposed to have carry-over effects on condition during moult (Nilsson & Svensson 1996; Sanz 1999), which is also a costly process (Cyr, Wikelski & Romero 2008) consecutive to reproduction in most temperate species. In the year following our experiment, we investigated the change in the characteristics of three plumage traits: the UV-blue coloration, the yellow coloration and in a trait more constrained by natural selection, the wing length. We compared these changes with the ones observed in a control group in both males and females. We measured male plumage traits because males are less ambiguously suspected to be sexually selected than females and thus can serve to position the results obtained on females. We measured wing length because it is a trait renewed and grown during the same moulting period as coloration but predicted to be less sensitive to condition if not sexually selected (Cotton, Fowler & Pomiankowski 2004; Siitari *et al.* 2007; but see Johnstone, Rands & Evans 2009).

If female blue tit coloration is sensitive to reproduction, we made two predictions. First, we predicted that the change in coloration will be different for the manipulated and the control birds in both males and females. Secondly, based on the condition dependence hypothesis, we predicted that lower quality females will be more affected by the increased cost of reproduction than better quality females.

Materials and methods

BIOLOGICAL MODEL

The blue tit is a socially monogamous passerine with bi-parental care. All blue tits renew their wing feathers during moult, and blue tits older than 1 year undergo a complete post-breeding moult (Ginn & Melville 1983), which is expected to be sensitive to reproductive cost (Nilsson & Svensson 1996; Sanz 1999).

UV-blue coloration depends on the microstructure of the plumage in many species (Prum 2006). In tits, yellow coloration is influenced by carotenoid contents (Partali *et al.* 1987) and probably also by microstructure (Shawkey & Hill 2005) and melanin (Isaksson *et al.* 2008). In blue tits, many studies have been conducted showing that male UV-blue coloration influenced male–male interactions (Alonso-Alvarez, Doutrelant & Sorci 2004; Rémy *et al.* 2010; Vedder *et al.* 2009) and was linked to female reproductive decisions and investments in this species (Delhey *et al.* 2003; Griffith *et al.* 2003; Johnsen *et al.* 2005; Kingma *et al.* 2009; Limbourg *et al.* 2004; Sheldon *et al.* 1999 but see Dreiss *et al.* 2006). Male yellow coloration was linked to male parental investment (Senar, Figuerola & Pascual 2002) and to parasite levels (del Cerro *et al.* 2010; infected birds being less chromatic). Female yellow coloration was linked to fecundity and recruitment (Doutrelant *et al.* 2008) and female UV-blue coloration influenced female–female aggressiveness (Midamegbe *et al.* 2011). Lastly, the UV component of coloration affected male and female mate choice (Hunt *et al.* 1999) and increased with age, with individuals displaying stronger UV coloration as they get older (Delhey & Kempenaers 2006).

EXPERIMENT

Our experiment lasted 4 years. It was conducted in a broad-leaved deciduous oak *Quercus humilis* forest near Montpellier (la Rouvière). Manipulated and control males and females had their coloration and wing length measured in the first year of the experiment (2005 or 2007) and the year after (2006 or 2008). All birds were captured in the nest boxes when their chicks were 9 days old. At each capture, birds were sexed based on the presence/absence of a brood patch. Breeders' age (yearling vs. adult) was determined through the colour of their wing covert (Svensson 1992). Wing size was measured with a ruler to the nearest 0.5 mm. Eight UV-blue cap and eight yellow collar feathers were collected for later colour measurements in the laboratory (see section Colour Measurement), a method consistent with direct measurements on individuals (Quesada & Senar 2006).

Manipulated birds had their whole clutch and nest material removed 2–4 days after the completion of the clutch for the manipulated group. Before removing the clutches, we captured the breeding birds with mist nets to identify them individually (based on their ring number). In 2005 and 2007, we had a total of 76 manipulated breeding boxes and 76 controls. None of the control pairs was affected by predation, and thus, none produced more than one clutch.

About 80% of the manipulated birds laid a second time. The females that did not re-lay were never recaptured in the following

years. The females that did and did not re-lay had similar phenotypic reproductive, morphologic and colour traits [see Data S1 and S2 (Supporting information) for details]. The replacement clutch was laid on average 20.6 days (std = 2.99; min = 14, max = 29) after the beginning of the first one, and the size of the first and replacement clutch was correlated ($R = 0.26$, $P = 0.04$).

The year after the manipulation, an average of 30% of the control and 34% of the manipulated birds were recaptured. The manipulation did not affect the proportion of individuals that were recaptured breeding the following year, and this proportion was not related to their coloration, laying date or clutch size (all $P > 0.50$). Only year replicate (i.e. 2005–2006 vs. 2007–2008: $F_{1,56} = 5.77$, $P = 0.01$), age ($F_{1,56} = 2.57$, $P = 0.11$) and wing length ($F_{1,56} = 2.84$, $P = 0.09$) were negatively linked to return rate.

Overall, 99 individuals [25 control and 30 manipulated females and 22 control and 22 manipulated males, see Data S1 and S2 (Supporting information) for details on age] were captured during two consecutive years. No individual was manipulated twice. We had blue and yellow feathers for 86 and 85 of the 99 individuals, reducing our sample size to 86 and 85 for these colour variables.

COLOUR MEASUREMENTS

To measure feather coloration, we used a spectrometer [see Data S1 and S2 (Supporting information) for details]. We used AVICOL SOFTWARE v2 (Gomez 2009) to compute colour variables based on the shape of the spectra (Andersson, Örnberg & Andersson 1998; Andersson *et al.* 2002; Doutrelant *et al.* 2008). For UV-blue coloration, we computed brightness (area under the curve divided by the width of the interval 300–700 nm); hue (wavelength at maximal reflectance); and UV chroma (proportion of the total reflectance falling in the range 300–400 nm). Because UV chroma was significantly correlated with brightness ($R_{\text{brightness-uvchroma}} = 0.24$, $P = 0.002$) and hue ($R_{\text{uvchroma-hue}} = -0.77$, $P < 10^{-4}$), we did not keep them in the main statistical analyses [the results on UV chroma are, however, presented for information in the Data S1 and S2 (Supporting information)]. Brightness and hue were not significantly correlated ($R_{\text{brightness-hue}} = 0.07$, $P = 0.39$) and were included in the statistical analyses. A lower value of hue means that the signal is stronger in UV. For yellow coloration, in addition to brightness, we computed yellow chroma as $(R_{700} - R_{450})/R_{700}$. The two variables were not correlated ($R_{\text{brightness-yellow chroma}} = -0.08$, $P = 0.28$) and were used in the statistical analyses.

STATISTICS

Two series of statistical models were conducted.

1. In a first series, we investigated the prediction that our experiment leads to a different change in coloration in control and manipulated birds. Five plumage traits were analysed: UV-blue brightness and hue; yellow brightness and chroma; and wing length. Our five dependent variables were the values of these plumage traits the year after the manipulation minus the year of the manipulation. The explanatory factors common to these five analyses were 'treatment' (manipulated or control birds), 'sex', 'age' (adult vs. yearling the year of the manipulation), 'replicate' (manipulation performed in 2005–2006 or 2007–2008) and the triple interaction 'age \times treatment \times sex'. A GLMM was run with 'nest' (equivalent to 'pair identity') as a random factor. In parallel, we checked whether the results remained the same when our dependent variable was the 'plumage coloration after treat-

ment' and when the 'plumage coloration before treatment' was a covariate. This was the case. We also tested whether birds had different coloration the year after the treatment. Again this was the case [see Data S1 and S2 (Supporting information)].

2. In a second series of analyses, we investigated the prediction of the condition dependence hypothesis, which states that individual attributes (e.g. quality, condition) should affect the association between signals and costs: better individuals being predicted to have their signals less affected by an experimental cost than lower ones. We used five proxies of female quality/condition: (i) 'female age' (yearling vs. adult); (ii) 'female tarsus length' (which is assumed to reflect both environmental conditions at the nest and genetic quality in tits; Merilä & Fry 1998); and (iii) 'female body mass' (which associated with tarsus length is supposed to be an estimate of condition: Garcia-Berthou 2001). In addition, we used (iv) 'laying date before the manipulation' and (v) 'total clutch size' (the sum of the first and the replacement clutches in the year of the experiment), two parameters that indicate maternal quality. They are repeatable, heritable (Auld & Charmantier 2011; Nussey *et al.* 2005; Pettifor, Perrins & McCleery 2001; Postma & van Noordwijk 2005; Sheldon, Kruuk & Merilä 2003) and sensitive to condition (Marzal *et al.* 2005). In our sample, as predicted, if clutch size and laying date are indicators of maternal quality, the total clutch size laid in the first year and clutch size in the second year are correlated (manipulated females: $R = 0.53$, $P = 0.0083$). Also the clutch size and laying date of the clutches produced in the first and second year are correlated (manipulated and control females: $R = 0.48$, $P = 0.0002$ for 'clutch size'; $R = 0.57$, $P < 10^{-4}$ for 'laying date').

For these analyses, the dependent variables in our GLMs were the change in female plumage coloration that appeared to be significantly affected by our experiment in the series of analyses (i) above. The explanatory factors were the five female attributes mentioned above ('age', 'body mass', 'tarsus length', 'laying date' and 'total clutch size') and 'delay in laying a replacement clutch'. In addition, 'replicate' (2005–2006 and 2007–2008) and the interactions between 'tarsus length and total clutch size' and 'body mass and total clutch size' were included. Because 'laying date' varies between years, it was standardized and reduced in the analyses (i.e. it was calculated as laying date minus average laying date divided by standard deviation). In parallel, we checked whether the results of these analyses remained the same if we tested the effect of the 'number of eggs laid in the first clutch' instead of the 'total clutch size'. This was the case.

We always started our GLMMs and GLMs by including all the explanatory variables in the full model and then running backward selection procedures with Type III errors in SAS v9 (SAS Institute Inc., Cary, NC, USA). All tests are two-tailed. The P values, estimates, SE and 95% CI of the significant factors are those obtained in the minimal model after backward deletion. The details of non-significant factors are given in the Data S1 and S2 (Supporting information).

Results

CHANGE IN COLORATION AND WING LENGTH IN BOTH SEXES IN RELATION TO THE EXPERIMENT

UV-blue coloration

The treatment affected the UV-blue coloration of the cap. In both sexes, the change in hue was stronger in control birds

Table 1. Effect of sex and treatment on the change in hue of the UV-blue cap in both males and females

Explanatory variables	d.f.	<i>F</i>	<i>P</i>	Estimate ± SE	95% CI
Kept in the minimal model					
Treatment	1,30	6.1	0.019	-4.9 ± 1.97	-8.91, -0.85
Excluded from the model					
Treatment × sex × age	1,23	1.08	0.30	-8.2 ± 7.87	-24.46, 8.08
Treatment × sex	1,24	0.01	0.92	-0.4 ± 3.81	-8.26, 7.49
Treatment × age	1,25	0.53	0.47	-2.9 ± 3.97	11.29, 4.86
Sex × age	1,26	0.64	0.44	-3.1 ± 3.87	-11.07, 4.85
Age	1,27	0.03	0.86	-0.3 ± 1.97	-4.39, 3.70
Sex	1,28	0.12	0.73	0.6 ± 1.84	-3.13, 4.43
Replicate	1,29	1.24	0.27	-2.1 ± 1.91	-6.04, 1.77

Table 2. Change in coloration and wing length for both males and females. Average and standard deviation are given. Hue is in nm, brightness in percentage, wing length in cm

		UV-blue coloration		Yellow coloration		Wing length
		Hue	Brightness	Chroma	Brightness	
Females	Control	-5.4 ± 9.57	-3.0 ± 5.59	0.00 ± 0.167	-8.0 ± 3.44	0.5 ± 1.18
	Manipulated	-0.9 ± 8.80	-4.9 ± 4.16	-0.03 ± 0.196	-7.5 ± 4.31	0.9 ± 1.17
Males	Control	-6.1 ± 9.20	-5.4 ± 5.81	-0.01 ± 0.158	-7.4 ± 2.76	0.9 ± 1.31
	Manipulated	-1.8 ± 6.48	-3.6 ± 4.84	-0.09 ± 0.167	-5.3 ± 3.97	0.7 ± 1.41

than in manipulated birds: control birds increased their cap coloration towards UV, while manipulated birds did not (Tables 1 and 2, Fig. 1). The brightness of the UV-blue cap was not affected by the treatment alone or in interaction with age or sex ['treatment': $P = 0.56$; 'sex × treatment': $P = 0.14$, Table 2; 'sex × treatment × age': $P = 0.82$; 'age × treatment' see Data S1 and S2 (Supporting information) for details].

Yellow coloration

The treatment affected the coloration of the yellow chest. We found that the interaction between the age at manipulation

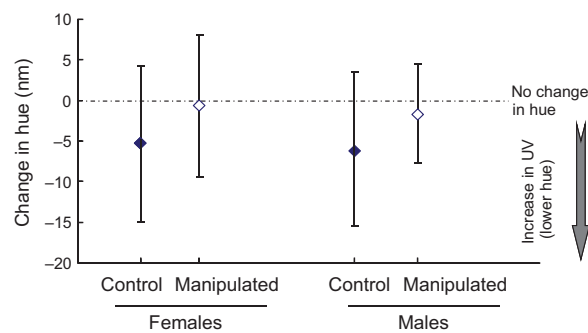


Fig. 1. Change in the hue of the UV-blue cap for control and manipulated males and females. Control but not manipulated birds increased their signal towards UV, i.e. their hue decreased towards lower wavelengths. The change = $\text{hue}_{y+1} - \text{hue}_y$ (y = year of manipulation). Dots and error bars correspond to average and standard deviation, respectively.

and the treatment had a significant effect on the change in yellow chroma (minimal model: 'treatment × age': $F_{1,28} = 4.62$, $P = 0.04$, est ± SE: 0.16 ± 0.073 , 95% CI: $-0.30, -0.007$; 'treatment': $F_{1,27} = 0.74$, $P = 0.39$, est ± SE: 0.1 ± 0.04 , 95% CI: $-0.016, 0.21$; 'age': $F_{1,27} = 0.03$, $P = 0.87$, est ± SE: 0.08 ± 0.052 , 95% CI: $-0.016, 0.20$). Yearlings, but not adults, presented a stronger decrease in yellow chroma in the manipulated than the control group (Fig. 2, Table 2, Tukey post hoc test: 'control vs.

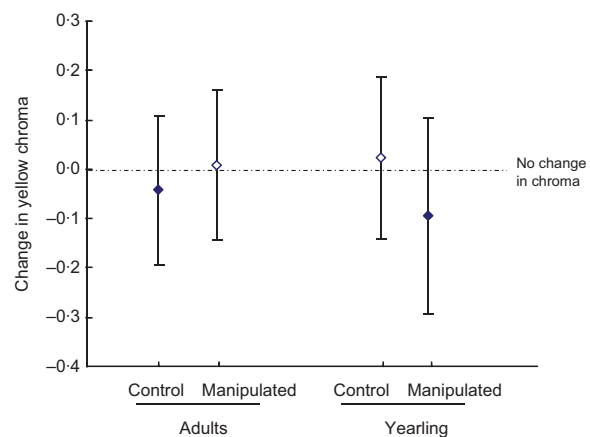


Fig. 2. Change in the yellow chroma of the chest in relation to age and treatment. Manipulated yearlings presented a stronger decrease in yellow chroma than control. By contrast, manipulated and control adults presented similar change (see Results section). The change = $\text{Chroma}_{y+1} - \text{chroma}_y$ (y = year of manipulation). Dots and error bars correspond to average and standard deviation, respectively.

Table 3. Effect of treatment and maternal quality on the change in UV-blue hue in the manipulated females. Results of a GLM model after backward deletion

Explanatory variables	d.f.	<i>F</i>	<i>P</i>	Estimate ± SE	95% CI
Kept in the minimal model					
Clutch size	1,22	7.06	0.01	-2.1 ± 0.82	-3.88, -0.48
Excluded from the model					
Body mass × clutch size	1,14	0.09	0.77	-0.5 ± 1.64	-4.01, 3.04
Tarsus × clutch size	1,15	0.29	0.59	-2.0 ± 3.66	-9.80, 5.82
Age	1,16	0.06	0.81	1.1 ± 4.65	-8.74, 10.99
Replicate	1,17	0.26	0.61	1.9 ± 3.85	-6.18, 10.09
Tarsus	1,18	0.35	0.56	-3.2 ± 5.42	-14.7, 8.21
Body mass	1,19	0.17	0.68	1.3 ± 3.18	-5.32, 7.99
Laying date	1,20	0.11	0.74	-0.7 ± 2.10	-5.07, 3.70
Delay	1,21	2.11	0.16	1.0 ± 0.71	-0.45, 2.51

manipulated adults' $P = 0.43$; 'control vs. manipulated yearling' $P = 0.02$). This effect was similar on the yellow chroma of both sexes ['sex × treatment × age' $P = 0.44$; 'sex × treatment' $P = 0.42$, Table 2, see Data S1 and S2 (Supporting information) for details]. None of the tested variables affected significantly the variation in yellow brightness. The outcome of the experiment was similar on the yellow brightness of males and females whatever their age ['treatment × sex': $P = 0.19$; Table 2; 'sex × treatment × age': $P = 0.90$; 'treatment × age': $P = 0.13$; 'treatment': $P = 0.29$, see Data S1 and S2 (Supporting information) for details].

Wing length

The treatment did not affect significantly the change in wing length ('treatment': $P = 0.76$; 'sex × treatment × age' $P = 0.66$; 'treatment × sex': $P = 0.13$; Table 2; 'treatment × age': $P = 0.91$).

CHANGE IN THE COLOUR VARIABLES AFFECTED BY OUR MANIPULATION IN RELATION TO FEMALE QUALITY

The change in the hue of the UV-blue cap in manipulated females was negatively correlated with the total number of eggs they were able to lay (Table 3, Fig. 3). This shows that the manipulated females able to produce a higher number of

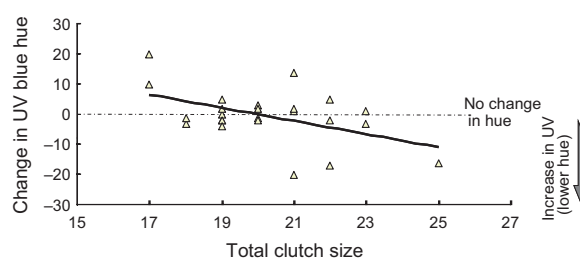


Fig. 3. Change in the hue of the UV-blue cap in relation to egg number in the manipulated group showing that the females that laid more eggs had an increased UV-blue signal afterwards (i.e. a lower hue). The change = $\text{hue}_{y+1} - \text{hue}_y$ (y = year of manipulation).

eggs increased more their signals towards UV afterwards (i.e. shorter wavelengths) than the females that laid fewer eggs. We did not detect any significant effect of 'laying date', 'delay to re-lay', 'body condition', 'age' and 'tarsus length' on the change in the UV-blue hue (Table 3).

The change in yellow chroma was only marginally significantly related to body condition at the end of the laying period ($P = 0.10$, Table 4). Estimates indicated that females in better condition tended to have a higher increase in yellow chroma afterwards (Fig. 4). None of the other variables tested significantly influenced the change in yellow chroma (all $P > 0.50$).

Table 4. Effect of treatment and maternal quality on the change in yellow chroma in the manipulated females. Results of a GLM model after backward deletion

Explanatory variables	d.f.	<i>F</i>	<i>P</i>	Estimate ± SE	95% CI
Body mass × clutch size	1,14	0.45	0.51	0.02 ± 0.038	-0.05, 0.11
Tarsus × clutch size	1,15	0.22	0.64	-0.04 ± 0.086	-0.23, 0.14
Clutch size	1,16	0.14	0.71	0.01 ± 0.026	-0.04, 0.06
Replicate	1,17	0.16	0.69	0.04 ± 0.091	-0.16, 0.23
Laying date	1,18	0.15	0.69	-0.02 ± 0.023	-0.06, 0.03
Age	1,19	0.26	0.61	-0.05 ± 0.098	-0.26, 0.16
Delay	1,20	0.16	0.69	-0.007 ± 0.0179	-0.04, 0.03
Body mass	1,23	2.92	0.10	0.10 ± 0.057	-0.02, 0.22
Tarsus	1,24	2.14	0.15	-0.14 ± 0.098	-0.35, 0.06

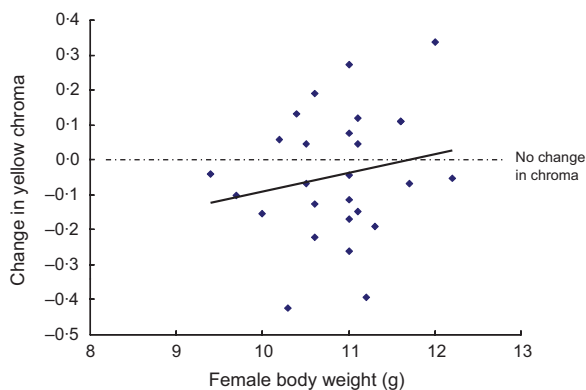


Fig. 4. Change in the yellow chroma of the yellow chest in relation to the body mass of the manipulated females showing that females in better condition tended to have a higher increase in yellow chroma afterwards. The change = $\text{Chroma}_{y+1} - \text{chroma}_y$ (y = year of manipulation).

Discussion

We investigated whether honesty of female coloration can be ensured by carry-over effects of reproduction on signalling. We manipulated reproductive costs and, as predicted if female coloration is condition dependent, we found that female coloration changed differently in control and manipulated groups and that this change varied according to the quality estimates of the females in the manipulated group. More precisely, our results first showed that control but not manipulated females increased their signal towards UV (i.e. their hue decreased towards lower wavelengths). This change in control birds was expected as the UV signal increases with age in blue tits (Delhey *et al.* 2006). Similar results were found for males suggesting similar condition dependence in both sexes. Secondly, our results showed that females that were able to lay more eggs in the manipulated group were also more able to shift their coloration towards UV afterwards suggesting that better quality females are able to invest in both reproduction and ornaments. For yellow coloration, we found in both sexes that yearlings had their yellow chroma more affected by our experiment than adults. In addition, in the manipulated group, the change in yellow chroma tended to be positively correlated with female body mass. No effect of our manipulation was detected on wing length.

EFFECT OF INCREASED REPRODUCTIVE EFFORT ON UV-BLUE COLORATION

Our experiment mimics a natural situation where nest predated birds would have to re-lay and would suffer from both a delay in moulting and an increased reproductive cost. It affected UV-blue coloration afterwards, confirming recent results obtained on other species showing that both stress during moulting and moult speed affect structural signals (Hill, Doucet & Buchholz 2005; McGraw *et al.* 2002; Siefferman & Hill 2005a; Siitari *et al.* 2007). In our

experiment, it is difficult to separate the effects of the delay from the effect of the increased cost of reproduction. In an experiment, Griggio *et al.* (2009) accelerated moult speed in blue tits by exposing them to a rapidly decreasing photoperiod. They found that manipulated birds grew crown UV-blue feathers with strongly reduced UV reflectance (and thus presented a reduced brightness, hue and UV chroma). In our experiment, two results are in favour of a stronger effect of an increased reproductive cost than of an increased moult speed. First, the explanatory variable 'delay to re-lay a replacement clutch' was never found to influence the change in coloration. Secondly, as predicted under the condition dependence hypothesis, variables linked to quality (age, body mass and female laying capacity) influenced the change in coloration.

Previous studies (Prum 2006; Shawkey *et al.* 2005, 2003) reported a correlation between the nanostructure and the coloration of the feather. In consequence, at the proximate level, the link between structural coloration and our experiment can be explained by a change in the nanostructure of the feather. In particular, UV-blue coloration is caused by coherent scattering of light within the medullary spongy layer of feather barbs. Lower value of hue seems to be associated with lower distance between scattering elements (i.e. keratin rods and air spaces) in the spongy layer and by thicker spongy layer (Shawkey *et al.* 2005).

In the manipulated group, we found that the females that were able to invest more in reproduction (i.e. those that had a higher laying capacity) also present stronger UV coloration afterwards. This suggests that better quality mothers are more able to support the cost of reproduction than others and that this is mirrored in their UV plumage. This result is both predicted by trade-off theory (Van Noordwijk & De Jong 1986) and condition-dependent theory (Grafen 1990; Iwasa & Pomiankowski 1999; Zahavi 1975). Females that lay smaller clutches may be females in low condition (for instance, they may have more parasites: Dufva 1996) or have a lower genetic quality.

Three additional factors other than the cost of reproduction could have influenced the differences observed between control and manipulated birds. First, in blue tits, UV coloration has been shown to change with time during the season (Delhey *et al.* 2006; Ornborg *et al.* 2002). In our experiment, as in the vast majority of the studies, bird coloration is measured at the end of the reproductive season. Consequently, our results could be affected by this seasonal change if the feathers of the birds that suffered from reproductive costs deteriorate faster than the ones of control birds. While we cannot dismiss this hypothesis, previous studies suggested that the rank of the individuals is conserved despite this seasonal change (Delhey *et al.* 2006), meaning that individuals with stronger UV coloration at the beginning of the season present stronger UV coloration at the end of the season. In addition, in our sample, the hue of the manipulated individuals during the laying period was similar before and after the manipulation ($N = 26$ individuals captured twice during laying: paired t test $P = 0.52$) meaning that the results we

obtained in the feeding period (no increase in UV coloration with age in the manipulated birds) would be identical earlier in the season when mate choice decisions occur.

Another parameter that could have affected our results is that manipulated birds have been measured after control birds in the first year because of our experimental delay of reproduction and that this time difference would have directly impacted the results. We can dismiss this possibility because we did not detect any difference in the hue of the two groups in the years of the manipulation ($F_{1,84} = 0.03$, $P = 0.85$ av \pm ste = 388.4 ± 1.45 for control females vs. 388.0 ± 1.67 for manipulated females) but detected a higher hue (i.e. a lower UV signal) of the manipulated birds in the years after manipulations (Data S1 and S2, Supporting information).

A last parameter that could have biased our results is that our experiment caused different patterns of dispersal in the manipulated and control groups or have led a greater proportion of better quality individual to disperse from the manipulated group (Boulinier *et al.* 1997). This hypothesis seems unlikely for two reasons. First, the manipulated and the control birds had similar return rates and so our manipulation did not result in more dispersal (30% of the control and 34% of the manipulated birds were recaptured breeding again). Secondly, the phenotypes of the individuals that were recaptured seemed equivalent in both groups as both presented an equivalent distribution of their phenotypic trait in the year of the experiment [morphology, colour, reproduction, see Data S1 and S2 (Supporting information)].

COMPARISON OF THE EFFECT OF THE MANIPULATION ON COLORATION AND WING LENGTH IN BOTH SEXES

The comparison of condition dependence between female and male traits has only been performed in species where female traits are known not to be sexually selected (e.g. Burley, Price & Zann 1992; David *et al.* 2000). In these studies, female traits were used as a negative control to prove heightened condition dependence of male traits. Here, we found a similar effect of our manipulation on both sexes. This similar effect suggests that female and male colorations present similar sensitivity to the cost of reproduction in blue tits. Hence, colorations could evolve under sexual selection in both sexes, which is in agreement with previous findings in this species (e.g. Delhey *et al.* 2003; Doutrelant *et al.* 2008; Hunt *et al.* 1999; Limbourg *et al.* 2004; Midamegbe *et al.* 2011; Sheldon *et al.* 1999).

An alternative explanation, however, is that male plumage is more condition dependent than female plumage because in our experiment, males incurred lower reproductive costs than females, which have to produce a second clutch in addition to feeding young later in the season. While it is difficult to dismiss this explanation, it may not be the case, because it is currently recognized that producing and maintaining sperm production and high levels of testosterone is costly for males (Dewsbury 1982; Helfenstein *et al.* 2009) and because our manipulation increased these needs for males. Another expla-

nation against a similar sensitivity of male and female plumage coloration to costs of reproduction would be that males invest less in late reproduction than females. Without more detailed data on the feeding rate of both sexes, we cannot dismiss this hypothesis.

In males, the influence of reproductive investment on coloration was investigated experimentally in males for the UV-blue coloration of eastern bluebirds *Sialis sialis* (Siefferman & Hill 2005b), the white coloration of collared flycatchers *Ficedula albicollis* (Gustafsson, Qvarnstrom & Sheldon 1995), and the melanin-based coloration of house sparrows *Passer domesticus* (Griffith 2000). These three studies manipulated the number of nestlings and found an effect of reproductive investment on the expression of male plumage coloration in the following year. In our study, the same effect was found for both sexes, and in addition, we found that a control trait, wing length, was not affected by our manipulation. As the wing feathers grow during the same period as the coloured feathers, this result suggests that, as expected by the condition dependence hypothesis, colour traits may be more sensitive to condition than other phenotypic traits (Cotton, Fowler & Pomiankowski 2004).

EFFECT OF OUR MANIPULATION ON YELLOW COLORATION

The analyses conducted on both sexes showed that yearlings, but not adults, presented a decrease in yellow chroma when manipulated. In addition, the analyses conducted on the manipulated females showed that females in lower condition tended to present a higher decrease in yellow coloration afterwards. These suggest that yellow coloration is condition dependent and has the potential to be sexually selected in this species. Yellow chroma is expected to be directly related to the carotenoid content of the feathers (e.g. Shawkey *et al.* 2006). The immune response and detoxification function have been shown by other studies to be affected by the cost of reproduction (Knowles, Nakagawa & Sheldon 2009) and are supposed to deeply influence signal expression through the common utilization of carotenoids (Faivre *et al.* 2003; Lozano 1994; Møller *et al.* 2000; Olson & Owens 1998; von Schantz *et al.* 1999). Hence, the decreased yellow chroma of manipulated yearling birds found here could mean that the cost of reproduction affected more the physiological responses of yearlings than of adults, a result that has been found by other studies notably in blue tits (Stjernman, Raberg & Nilsson 2004).

Conclusion

Studies investigating condition dependence of different ornaments within a single experiment are rare (e.g. Hill, Hood & Huggins 2009; McGraw *et al.* 2002; Scheuber, Jacot & Brinkhof 2003) but are needed to better evaluate the hypotheses behind multiple ornamentation (Møller & Pomiankowski 1993). The results we found for UV-blue and yellow colorations are in agreement with the hypothesis that both colorations

tions are sensitive to reproductive costs and could therefore honestly signal condition in this species. The different relationships obtained with quality estimated for yellow and UV-blue colorations, however, suggest that UV-blue coloration is more directly sensitive to the cost of reproduction than yellow coloration. Yellow coloration might be more sensitive to other factors affected by reproductive cost such as immunity.

More generally, our results lead us to conclude that the trade-offs between reproduction and signalling are one mechanism that can ensure the honesty of plumage traits. Plumage traits are formed after the breeding season, and thus, our study suggests that when female ornaments are produced outside the breeding season, trade-offs between investing energy in fecundity and ornaments may promote rather than impede the evolution of female ornaments under sexual selection. It could be suggested that condition dependence in female ornaments could exist as a result of a condition dependence in male ornaments. However, the results presented here in combination with other results suggesting the occurrence of male mate choice (Hunt *et al.* 1999), female–female competition (Midamegbe *et al.* 2011) and links between female ornaments and female quality (Doutrelant *et al.* 2008) provide strong evidence that female ornaments are sexually selected in this species and may be so in other species.

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Supporting Information

Additional Supporting Information may be found in the online version of this article.

Data S1. Material and method.

Data S2. Results.

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