Female coloration indicates female reproductive capacity in blue tits

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Abstract

It is poorly understood whether female morphological and behavioural traits can be used as 'signals'. In particular, experimental tests of the hypothesis that female ornaments reflect quality are scarce. Here, we experimentally examine whether female plumage coloration might signal maternal quality in the blue tit, *Cyanistes caeruleus* by forcing half of the females breeding in our population to produce a replacement clutch. Using statistical models that controlled for the effects of male coloration, and the effects of age and condition of both parents, we found that carotenoid-based female coloration was positively linked to key proxies of bird lifetime reproductive success: clutch size, fledgling success and recruitment. Importantly, the relationships between maternal yellow carotenoid coloration and both clutch size and recruitment were stronger in the experimental group than in the control group, indicating that breeding females with higher values of yellow coloration were better able to handle the cost of producing a second clutch. Finally, UV-blue female coloration was positively linked to female survival and marginally linked to laying date. Taken together, these results show for the first time in a natural population that female coloration can indicate individual and maternal quality under natural and adverse reproductive conditions. They highlight the potential for the evolution of female ornamental traits through sexual selection.

Introduction

Females often exhibit conspicuous traits such as brightly coloured feathers or elaborate songs (Amundsen, 2000). However, the evolution and function of such traits remains poorly understood. In males, the evolution of ornaments has been extensively investigated and is closely linked to sexual selection (Andersson, 1994). In females, it is classically thought that conspicuous traits evolved because male and female traits are genetically correlated (Lande, 1980). However, female–female competition for resources and/or male mate choice may also drive the evolution of female ornaments (Amundsen,

2000; Lebas, 2006). Males may obtain fitness benefits through their choice of females if there is variation in female reproductive or genetic quality associated with monogamy and/or with cost of reproduction for males (e.g. through biparental care or cost of sperm production) (e.g. Burley, 1977; Simmons & Parker, 1996; Pizzari et al., 2003; Simmons & Kvarnemo, 2006). The view that sexual selection could also operate on females received support from theoretical (Chenoweth et al., 2006; Servedio & Lande, 2006), comparative (Wiens, 2001; Kolm et al., 2007) and empirical male choice studies (Hill, 1993; Jones & Hunter, 1993; Amundsen et al., 1997; Amundsen & Forsgren, 2001; Jones et al., 2001; Griggio et al., 2005; Torres & Velando, 2005). By contrast, the type of information conveyed by female signals has been investigated by surprisingly few studies.

The meaning of female traits has to be determined to evaluate which fitness benefits males can get by choosing

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conspicuous females. This question has been mostly tackled by correlative studies that found both positive and negative relationships between female coloration and proxies of phenotypic quality (reproductive success, feeding rate, degree of parasitic infection, immunocompetence, age, body condition or survival, e.g. Amundsen, 2000; Vercken *et al.*, 2007). By contrast, only few experimental studies have been conducted. In birds, two cross-fostering experiments have shown that melanin-based female coloration might reflect heritable resistance to parasites in barn owls, *Tyto alba* (Roulin *et al.*, 2000, 2001) and one experimental manipulation of food intake during moult has shown that female UV-blue coloration might be condition dependent in eastern bluebirds, *Sialia sialis* (Siefferman & Hill, 2005). On the other hand, one mate removal experiment has suggested that more colourful UV-blue females do not provide better parental care in bluethroats, *Luscinia s. svecica* (Smiseth & Amundsen, 2000). More experiments are thus needed before drawing any conclusions about the adaptive significance of female coloration. In particular, given that females usually incur a larger cost of reproduction and provide more parental care than males, experiments testing the link between female coloration and female reproductive quality would be especially relevant, but are largely missing.

Here, we experimentally investigate the hypothesis that female coloration indicates breeding capacity in the blue tit, *Cyanistes caeruleus* (former *Parus caeruleus)*. The blue tit is a socially monomagous species with biparental care. Blue tits are slightly sexually dimorphic birds with females presenting a decreased coloration in the UV-blue cap (Andersson *et al.*, 1998; Hunt *et al.*, 1998) but not in the yellow chest (Hunt *et al.*, 1998). Several studies on blue tit male coloration suggest that it has an important signalling function in the context of sexual selection (Sheldon *et al.*, 1999; Delhey *et al.*, 2003; Griffith *et al.*, 2003; Alonso-Alvarez *et al.*, 2004; Johnsen *et al.*, 2005; Hadfield *et al.*, 2006). By contrast, to date, it is unknown whether female coloration has a signalling function in this species.

We tested here whether female coloration signals female capacity to breed successfully in normal and adverse conditions. As egg laying and incubation are costly for females (Visser & Lessells, 2001; Hanssen *et al.*, 2005; de Heij *et al.*, 2006), we experimentally increased the cost of reproduction for breeding females by removing their first clutches and thereby forcing females to produce a replacement clutch. This experiment mimics natural events as nest predation is common in natural populations. Under the hypothesis that female coloration indicates female quality, we expected positive relationships between female coloration and fitness components (laying date, clutch size, fledgling success, recruitment and survival). We also expected an interaction between female coloration and treatment if female quality is important to reproduce successfully under adverse con-

ditions, but has a weak effect on reproductive success in good or normal reproductive conditions (i.e. when there are enough resources to allow bad quality females to reproduce successfully).

Method

Breeding and morphometric parameters

Breeding parameters (onset of egg laying, clutch size and fledgling success, i.e. number of fledglings divided by the number of eggs) were collected through routine inspection of nest boxes (Blondel *et al.*, 2006). The study population is located near Montpellier, south of France (43°40′N, 03°40′E) in a broad-leaved deciduous forest of downy oaks where nest boxes were erected in 1991 (see Dias & Blondel, 1996). Parents were captured at nest boxes after their chicks were 9 days old. Adult body mass and tarsus length were measured to the nearest 0.1 g and 0.01 mm respectively. Breeding birds were sexed based on the presence/absence of a brood patch. Breeders' age (yearling vs. adult) was determined through the colour of the wing coverts (Svensson, 1992). When possible, age was also obtained from the data collected since 1992. The experiment was conducted in 2005. In 2006, we recaptured all the breeding blue tits in our population to estimate breeders' return rate and local recruitment of offspring.

Control and experimental group

Eighty pairs bred in the study populations in 2005. We artificially increased the cost of reproduction for 37 females by removing the whole clutch and nest material after about 5 days of incubation (the experimental group) and used 43 unmanipulated pairs as controls. Experimental birds were captured and ringed on the day we removed their clutch to get their identity. Thirty-four of the 37 experimental females initiated a new reproductive attempt.

Colour measurements

Adult coloration was measured on feathers taken from parents at the beginning of the chick rearing period. We collected six UV-blue cap feathers and six yellow collar feathers. Colour was measured with an AVASPEC-2048 spectrometer (Avantes, NL), a deuterium-halogen light source (AVALIGHT-DH-S lamp, Avantes, NL) covering the range 300–700 nm and a 200-μm fibre optic probe. All measurements were taken perpendicular to the feather surface using the probe mount with a back rubber cap to exclude ambient light. The probe was held at a fixed distance of 2 mm from the feather surface. We generated reflectance data relative to a white standard (WS1 ocean optics) and the dark current (black felt background). For each bird and position (collar or cap),
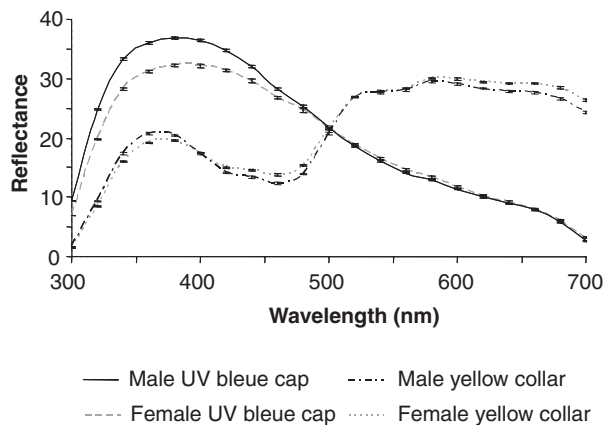
Fig. 1 Average and standard error reflectance for male and female UV-blue cap and yellow collar.

we computed the mean of six reflectance spectra taken on two sets of three feathers (Fig. 1). Each measurement was taken at a different point of the feathers. These six measurements allowed us to estimate repeatabilities (Lessells & Boag, 1987) that account in this case, both for errors of measurement due to device and for colour spatial variability within the feathers.

Colour variables

Colour spectra information was extracted using Avicol software v2 (Gomez, 2007). For both colour patches, brightness was taken as the mean reflectance over the range 300–700 nm (computed as the area under the curve divided by the width of the interval 300–700 nm; e.g. Andersson *et al.*, 2007; Doucet *et al.*, 2005; Delhey *et al.*, 2006) to include the whole range of bird sensitivity. UV chroma is the proportion of the total reflectance falling in the range 300–400 nm. Hue and chroma are computed based on the shape of reflectance spectra (e.g. Andersson *et al.*, 1998; Delhey *et al.*, 2003; Griffith *et al.*, 2003; Korsten *et al.*, 2006). For UV-blue coloration, we computed hue as the wavelength at maximal reflectance, and chroma as the difference between maximal and minimal reflectance divided by the average reflectance. For yellow coloration, we computed chroma as $(R_{700} - R_{450})/R_{700}$, as this should directly indicate the influence of carotenoids, which maximally absorb around 450 nm (Andersson *et al.*, 2002). We did not compute hue parameters because of the double peaked nature of these carotenoid-based spectra (Johnsen *et al.*, 2003). All our measurements were significantly repeatable with values of $P < 10^{-4}$ (UV-blue cap: brightness, repeatability (R) =0.81; hue, R = 0.58; UV chroma, R = 0.75; choma, R = 0.72; yellow collar: brightness, R = 0.56; UV chroma, R = 0.67; chroma, R = 0.60).

We examined and detected significant correlations between the four colour variables computed above (all parameters correlated two by two with $P < 10^{-4}$ for UV-blue coloration). To avoid entering redundant variables into the statistical tests and the resulting colinearity in the analyses of general linear models (GLM), we run a PCA for UV-blue and yellow colours separately (Sheldon *et al.*, 1999; Siefferman & Hill, 2005).

For each PCA, we kept the first two principal components (the sum of the first two components explained 85% of the variation in UV-blue coloration and 74% of the variation in yellow coloration). In both analyses, PC1 described chromatic aspects, whereas PC2 described achromatic aspects of the colour. More precisely for UV-blue coloration, the first component ($PC_{blue}1$) received strong loadings from hue, UV chroma and chroma (-0.50, 0.56 and 0.54 respectively), whereas the second component ($PC_{blue}2$) received strong loading from brightness (0.86). Higher scores of $PC_{blue}1$ thus corresponded to feathers presenting more short-wave peak, more UV and more chroma; higher scores of $PC_{blue}2$ corresponded to brighter feathers. The first component for carotenoid-based coloration ($PC_{yellow}1$) received strong loadings from UV chroma and chroma (-0.63 and 0.67 respectively, an individual with higher score of $PC_{yellow}1$ thus presented less UV and more chroma). The second axe $PC_{yellow}2$ received strong loading from brightness (0.90).

Statistical methods

Experimental data were analysed through GLMs. To estimate whether female coloration indicates breeding capacity in normal and adverse conditions, we investigated whether measurements of reproductive success varied with female coloration in control and experimental groups and whether there was a significant interaction between colour variables and the treatment.

The dependent variables used to estimate the reproductive success were laying date (before the manipulation), clutch size (after treatment), fledgling success and local recruitment. In the full statistical models, we included the following explanatory variables: treatment (control vs. experimental group), coloration ($PC_{blue}1$; $PC_{blue}2$; $PC_{yellow}1$; $PC_{yellow}2$), age, tarsus length and body mass of both breeding males and breeding females. We also included in these GLMs, the two-way interactions between coloration and treatment and coloration and age (also for both sexes). Body mass was always included in association with tarsus length in a type III model to estimate body condition (Garcia-Berthou, 2001; Green, 2001).

Female local survival was analysed in relation to female phenotype (coloration, age, body condition, tarsus length, laying date before manipulation, clutch size) and treatment. We also included in these analyses the interactions between female age and female coloration, and the interactions between female coloration and treatment.

We always started GLMs by including all the explanatory variables in the full model and then run backward selection procedures with type III errors in sas v8 (SAS Institute Inc., Cary, NC, USA). We specified normal distribution for laying date, Poisson distribution for clutch size and binomial distribution for fledgling success, local recruitment and local survival. Over-dispersion was corrected when necessary. Only factors with a value of $P < 0.1$ are presented in the tables. We presented slope estimates in each table. In logistic regressions, slope estimates can be used to calculate odd ratios which are common measures of the size of an effect, they also indicate whether the effect is positive or negative. Sample sizes varied between 68 and 77 nests because in nine cases age or body weight or coloration were not taken. We run all the analyses twice using 'age' as a dichotomous factor (adult vs. yearling; $N = 75$) or as a continuous variable (exact age, $N = 49$). Because the results obtained were identical, we presented only the results obtained with age in classes (adult vs. yearling).

Results

Laying date

None of the explanatory variables significantly explained the variation in laying date. Only female UV-blue coloration ($PC_{blue}1^{female}$) marginally explained some of the variation in laying date ($F_{1,62} = 3.7$, $P = 0.058$, estimate ± SE = −0.89 ± 0.46). Breeding females with hue shifted towards shorter wavelengths and higher UV chroma tended to lay earlier.

Clutch size

The variation in clutch size was significantly explained by the interaction between treatment (experimental vs. control) and female yellow coloration ($PC_{yellow}2^{female}$, Table 1). The estimates indicated that clutch size increased with female yellow coloration (brightness) in

Fig. 2 Clutch size increased with yellow coloration ($PC_{yellow}2^{Female}$) in the experimental group where the cost of reproduction is increased but not in the control group. Females with higher $PC_{yellow}2$ score are brighter. Simple regression lines are shown to indicate the trends in the data.

the experimental group, whereas that was not the case in the control group (Fig. 2).

Fledgling success

Maternal yellow coloration, treatment and paternal body condition significantly explained the variation in fledgling success (Table 2). Breeding females presenting a yellow collar with less UV and more chroma (higher value of $PC_{yellow}1^{female}$) had higher fledgling success. Breeding males that were in lower body condition during the nestlings' feeding period fledged more young. Exper-

Table 1 Factors affecting the variation in clutch size ($N = 71$).

Clutch size	Est ± SE	χ_1^2	P
$PC_{yellow}2^{Female}$	0.1 ± 0.04	1.43	0.2320
Treatment (control > experimental group)	0.2 ± 0.04	21.56	<0.0001
$PC_{yellow}2^{Female}$* treatment	Control: −0.05 experimental: 0.1	10.49	0.0012

Est ± SE refers to estimate ± standard error. $PC_{yellow}2^{Female}$ corresponds to the second PC for yellow collar coloration. Females with higher score of $PC_{yellow}2$ are brighter. The table corresponds to the final model after backward selection excluding explanatory variables with a value of $P > 0.1$ (see *Method* section for information on the full model). Clutch size for the experimental group corresponds to clutch size after we removed the first clutch.
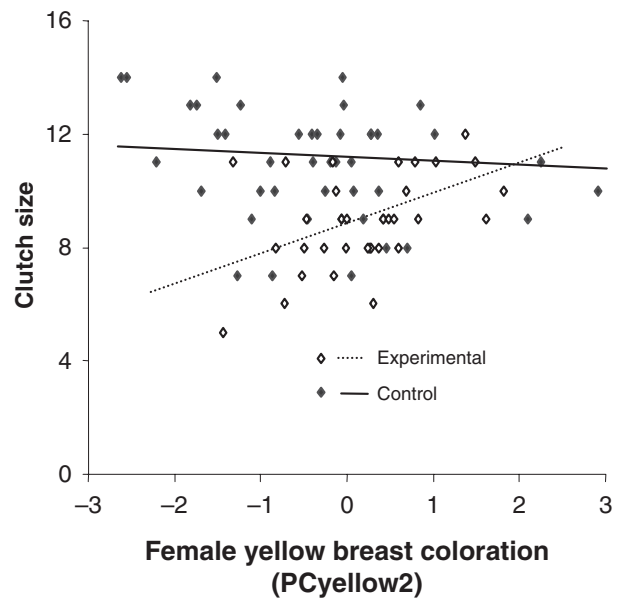
Table 2 Factors affecting the variation in fledgling success ($N = 68$).

Fledgling success	Est ± SE	χ_1^2	P
$PC_{yellow}1^{Female}$	0.22 ± 0.08	7.22	0.0072
Treatment (control > experimental group)	0.78 ± 0.23	11.89	0.0006
Male body mass	−0.66 ± 0.22	9.06	0.0026
Male tarsus length	0.16 ± 0.31	0.27	0.6038

Male tarsus length is kept to estimate male body condition. Est ± SE refers to estimate ± standard error. $PC_{yellow}1^{Female}$ corresponds to the first PC axis for yellow collar coloration. Females with higher score of $PC_{yellow}1$ present less UV and more chroma. The table corresponds to the final model after backward selection excluding explanatory variables with a value of $P > 0.1$ (see *Method* section for information on the full model).

imental nests had lower fledgling success than control nests.

Local probability of recruiting at least one chick

The probability of recruiting locally at least one young was significantly affected by the treatment, maternal yellow coloration ($PC_{yellow}2^{female}$), maternal body condition and maternal age. Estimates showed that adult females and females in lower body condition at the end of the reproductive season had a higher probability of recruiting young (Table 3). The probability of recruiting at least one was also marginally explained by the interaction between maternal yellow coloration ($PC_{yellow}2^{female}$) and treatment. This showed that recruitment was positively correlated with maternal yellow brightness ($PC_{yellow}2^{female}$) in the experimental group, whereas the tendency was the same but the slope was much lower in the control group (Table 3).

Local female survival

Younger, early-laying and brighter UV-blue cap breeding females ($PC_{blue}2^{female}$) had a higher probability to be found breeding again the following season (Table 4).

Discussion

We experimentally forced half of the females breeding in a blue tit population to produce a replacement clutch to test whether female coloration might signal reproductive quality. We assessed the link between female coloration and key proxies of bird lifetime reproductive success (laying date, clutch size, local recruitment and adult local survival) in control and experimental groups. In analyses controlling for male coloration, age and condition of both parents, we found that carotenoid-based female colora-

Table 3 Factors affecting the variation in the probability of locally recruiting at least one chick.

Recruitment	Est ± SE	χ_1^2	P
$PC_{yellow}2^{Female}$	1.8 ± 0.78	8.32	0.0039
Treatment (control > experimental group)	1.53 ± 0.77	4.76	0.0291
Female age (Adults > yearlings)	1.6 ± 0.69	6.26	0.0124
Female body mass	−1.7 ± 0.65	9.22	0.0024
Female tarsus	1.06 ± 0.86	1.67	0.1969
Treatment *$PC_{yellow}2^{Female}$	Control: 0.35 experimental: 1.80	3.62	0.057

$N = 69$, 23 pairs recruited at least one chick and 46 did not recruit any. Est ± SE refers to estimate ± standard errors. $PC_{yellow}2^{Female}$ corresponds to the second PC axis for yellow collar coloration. Females with higher score of $PC_{yellow}2$ are brighter. The table presented above corresponds to the final model after backward selection excluding explanatory variables with a value of $P > 0.1$ (see *Method* section for information on the full model).

Table 4 Factors affecting the variation in the probability of being recaptured as breeder in the following season ($N = 77$, 22 of 77 females were recaptured).

Female 'survival'	Est ± SE	χ_1^2	P
$PC_{blue}2^{Female}$	0.97 ± 0.45	5.59	0.0181
Female age (adults < yearling)	−3.1 ± 0.9	16.61	<.0001
Laying date before manipulation	−0.18 ± 0.07	6.58	0.0103

Est ± SE refers to estimate ± standard errors. $PC_{blue}2^{Female}$ corresponds to the second PC axis for UV-blue cap coloration. Females with higher score of $PC_{blue}2$ are brighter. The table corresponds to the final model after backward selection excluding explanatory variables with a value of $P > 0.1$ (see *Method* section for information on the full model).

tion was positively linked to reproductive success (clutch size, fledgling success and local recruitment). Importantly, for both clutch size and local recruitment, the positive associations with maternal yellow coloration were stronger in the experimental group than in the control group. Lastly, UV-blue female coloration was positively linked to female local survival and marginally positively linked to laying date. These results show that, in blue tits, conspicuous female colours reflect individual and maternal quality and suggest that, in this species, males could improve their lifetime reproductive success if they choose a mate based on its coloration. Our result lastly suggests that female coloration might be an especially informative signal under adverse reproductive environmental conditions.

The link between carotenoid-based female coloration and reproductive success could also be due to territorial quality if individuals feed in the same place during moult and breeding. In disagreement with this hypothesis, blue tits seem to move around during the moulting period and only be territorial from autumn to spring (Perrins, 1979). Moreover, also in disagreement with this hypothesis, the correlations between the carotenoid-based coloration of both male and female inside a pair were not statistically significant ($N = 66$ pairs, $P > 0.20$ for all PC). Thus, at this stage, we suggest that female colours should contain information on individual quality independent of the characteristics of the local breeding territory.

Interestingly, our analyses did not reveal any effect of male coloration on reproductive success. This suggests either that male coloration does not indicate direct benefits in blue tits or that all males, whatever their quality, were able to be good fathers because the environmental conditions were good in 2005. We cannot distinguish between these two explanations because our experiment was not designed to test the link between male coloration and male quality. Our experiment imposed a much higher reproductive cost on females than on males, as females had to rebuild the nest, re-lay, re-incubate and feed later in the season, whereas males only had to feed later in the season. Furthermore, the 2005 season presented good reproductive conditions for

birds in the south of France as indicated by the average offspring body mass and tarsus length that was higher in 2005 than in other years of the study (1991–2006; M.M. Lambrechts, C. Doutrelant, P. Perret, unpublished data). The same good year effect might explain why the manipulation did not affect adult survival contrary to what has been found is Sweden and Spain with clutch removal experiments on blue tits (Nilsson & Svensson, 1996; Sanz, 1999).

Our study indicates that yellow and UV-blue plumage coloration is linked to different aspects of female fitness. This absence of redundancy is expected if we consider that these two colorations are produced through different mechanisms. Yellow coloration in blue tits is due to carotenoids (Partali *et al.*, 1987), and carotenoid-based coloration should reflect foraging efficiency and/or current condition due to the simultaneous demand for signalling and investment in immunity or detoxification (Lozano, 1994; Olson & Owens, 1998; von Schantz *et al.*, 1999; Moller *et al.*, 2000). In agreement with these functions, our results suggest that yellow plumage reflects the female's capacity to reproduce successfully under adverse reproductive conditions. By contrast, UV-blue coloration is a structural coloration which results from the size and arrangement of nanostructural elements within the medullary 'spongy layer' of feather barbs (Prum *et al.*, 1998, 2003). UV coloration is probably a condition-dependent signal reflecting individual quality, as suggested by experimental (McGraw *et al.*, 2002; Siefferman & Hill, 2005) and nonexperimental approaches (Keyser & Hill, 2000; Doucet & Montgomerie, 2003; Johnsen *et al.*, 2003). Our findings are in agreement with this hypothesis, as UV-blue female coloration is linked to early laying date and high local survival.

In conclusion, our results provide the first experimental evidence that female coloration might indicate maternal and individual quality in a natural population. They also point out that female coloration can be an especially informative character for males for use in mate choice under adverse reproductive environmental conditions. These results, together with the several other studies that found that males prefer more conspicuous females in mate choice experiments, lead us to conclude that sexual selection in females is an under-appreciated evolutionary force that deserves further attention.

Acknowledgments

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