

Offspring plumage colouration as a condition-dependent signal in the blue tit

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September 29, 2022

Abstract

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Offspring plumage colouration as a condition-dependent signal in the blue tit

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Running head: Offspring colour and condition-dependence

Abstract

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Keywords : nestling colouration, quality, honest signalling, condition dependence, UV colouration, sex differences, carotenoids

Introduction

Colouration is ubiquitous in nature and plays a significant role in communication between different species (e.g., in the context of pollination, competition for resources and predator-prey interactions) or between individuals of the same species (e.g., in the context of mating and parental care) (Cuthill et al. 2017; Endler & Mappes 2017; Postema et al. 2022). The most colourful taxa in the animal kingdom are coral fishes, tropical frogs, certain groups of insects, and birds, and those species have historically received most attention in studies about the role of colouration in animal communication.

To understand the great variation in colour expression between individuals of the same species, evolutionary biologists have mainly focused on sexual selection processes. Colourful traits are here seen as handicaps that seem not to increase longevity or fecundity, so they are potentially not favoured by natural selection. Conspicuous colourful patches - displayed mainly by males - would rather allow to attract mates or to bully potential competitors (Andersson 1994). Hence, colourful ornaments are thought to function as signals of quality to reliably inform conspecifics about, for example, condition (Hill 2011), immune status (Rodríguez-Ruiz et al. 2020) or parasitic burden (Megía-Palma et al. 2016). Honesty in signalling traits is achieved through associated costs to produce and maintain them (Andersson 1994). Taken together, a significant number of studies have proven the role of colouration in a sexual selection context, which implies that these studies were performed with sexually mature individuals.

However, there are conspicuous colourful traits that are also expressed in sexually non-mature or even in newborn individuals. In these cases, colouration is displayed in a non-sexual selection context (West-Eberhard 1983). These traits could have evolved as by-products of selection acting on colouration in adults, at least when both offspring and adults display the same traits (similar to the evolution of female ornaments that can be explained through correlated selection on these traits in males; Amundsen 2000). However, offspring colouration may have important signalling functions in itself like, for example, in intra-family interactions (Lyon et al. 1994; Parker et al. 2002). The expression of structural ornaments such as plumage colouration requires a substantial investment of resources such as carotenoids, and thus they can inform parents and other family members (like siblings and breeding helpers) about individual quality (Caro et al. 2016). Like in a sexual selection context, honesty can be achieved if the offspring pay a cost for displaying or maintaining such signalling traits, which prevents cheating (handicap principle). Therefore, nestling colouration has the potential to evolve as a condition-dependent signal to which other family members respond (honest signalling models, Godfray 1991, 1995, Laidre & Johnstone 2013; Fromhage & Henshaw 2021).

A good model system to study whether adult-like colouration shows similar patterns of condition-dependence in the offspring is the carotenoid-based colouration of the yellow breast plumage of blue tits (*Cyanistes caeruleus*). Blue tit adults exhibit both UV/blue crown feathers and yellow breast feathers. In adults, it is well established that UV/blue colouration functions as a sexual signal that reflects condition (Delhey et al. 2006) and shapes the parental investment of mates (Limbourg et al. 20013a; 2013b). Similarly, yellow breast feathers reliably reflect aspects of individual quality like parasite burden (del Cerro et al. 2010), parental capacity (García-Navas et al. 2012) and laying performance (Midamegbe et al. 2013). Furthermore, the UV chroma of adult breast plumage functions as a signal in parental interactions during offspring care (García-

Campa et al. 2022). Here, partners of UV-reduced individuals (either males or females) increased their parental investment during offspring provisioning, perhaps to compensate for the apparent lower condition of their mates (García-Campa et al. 2022). Blue tit nestlings do not exhibit the UV/blue crown colouration, but there is some evidence that two colour parameters of the yellow breast plumage, carotenoid chroma (Johnsen et al. 2003) and UV chroma (Jacot & Kempenaers 2006; Morales & Velando 2018), co-vary with nestling body mass. Moreover, family members rely on nestling UV chroma to adjust their decision rules over parental investment. Concretely, nestlings with experimentally blocked UV colour beg more during feeding rates and in sib-sib competitive interactions (Morales & Velando 2018). In addition, when resources are limited, parents favour chicks with higher UV chroma, thus, presumably those of high quality (Morales & Velando 2018; García-Campa et al. 2021). It is possible that the different components of colouration reveal different aspects of individual quality (Candolin 2004), as they involve different dimensions of avian colour perception (Jacot & Kempenaers 2006): reflectance in the ultraviolet region of the spectrum (UV chroma), carotenoid-based reflectance (carotenoid chroma) and total reflectance (brightness). Hence, in order to understand the signalling function of yellow breast plumage colouration in blue tit nestlings, it is valuable to investigate the different colour components as well as their relationships.

In this study, we first explored the associations between UV-chroma, carotenoid chroma and total brightness of blue tit nestling yellow breast feathers. Then, we investigated the relationship of each of the three colour components with body mass in three consecutive breeding seasons. We hypothesised that only individuals in good condition (i.e., nestlings with higher body mass) would be able to achieve, in particular, a higher reflectance in the ultraviolet region of the spectrum, as this has been experimentally demonstrated previously (Morales & Velando 2018). Furthermore, as multiple chicks per nest were measured, we tested whether any effect of body mass on colouration was due to an among-nest or a within-nest effect, which, to our knowledge, has not been explored to date. The within-nest effect allows testing whether chick colouration varies according to within brood differences in body mass, reflecting condition-dependence at the nest level. The among-nest effect in turn would show whether the correlation of body mass and colouration is due to, for instance, genetic effects, parental quality effects, or other (common) environmental effects at the nest level. If nestling yellow plumage functions as a signal in intra-family interactions, we expect a within-nest effect of body mass on colouration, since this would allow other family members to assess individual quality relative to other siblings in the nest. The interaction between the within and the among-nest effect then again would allow testing whether the strength of condition-dependence is influenced by brood identity. Decomposing how genetic and environmental effects contribute to condition dependence is of significant relevance for our understanding of the signalling function of colouration (Hooper & Bonduriansky 2022).

Material and methods

General methods

The study was carried out in the locality of Miraflores de la Sierra, Madrid, central Spain (40°48'N, 03deg47'W) throughout the breeding seasons of 2017, 2018 and 2019. We studied a blue tit population breeding in nest-boxes in a deciduous forest, mainly dominated by Pyrenean oak (*Quercus pyrenaica*). At the beginning of the breeding season, we started visiting nest-boxes every week to record the onset of nest construction. Then, we checked them every 2-3 days to record laying and hatching dates (hatching day = day 0). On days 11 (in 2019) or 12 (in 2017 and 2018), that is, once blue tit nestlings had developed yellow breast feathers (Peters et al. 2007), we measured feather colouration and body mass (see a detailed explanation in *Colour measurements* below). Blue tit nestlings exhibit yellow breast feathers, which they moult about two months after fledging, during the post-juvenile moult (Cramp & Perrins 1993). This trait reflects light both in the longwave band of the reflectance spectrum (yellow to red wavelengths between 550 and 700 nm) and in the ultraviolet (UV) region (Shawkey & Hill 2005).

Colour measurements

We measured breast plumage colouration with a portable spectrophotometer (Jazz, OceanOptics(c)). For each nestling, we took three consecutive measurements relative to a white standard and perpendicular to the

feather surface, using an external probe fitted with a plastic cylinder to standardize the measuring distance and exclude ambient light. We then obtained the reflectance spectra between 320-700 nm using CLR program v 1.1 (Montgomerie 2009). We excluded the first part of the spectrum (300-320 nm) in order to avoid noisy reflectance values.

We then calculated three objective colour parameters: i) total brightness (i.e., average reflectance between 320 and 700 nm; adapted from Jacot & Kempenaers 2007), ii) UV chroma (i.e., reflectance in the UV wave-band region of the spectrum divided by the total reflectance of the spectrum in the avian visual range ($R_{320-400}/R_{320-700}$); adapted from Johnsen et al 2003) and iii) carotenoid chroma (i.e., an estimation of the carotenoid content of yellow breast feathers $(R_{700}-R_{450})/R_{700}$), since carotenoids highly absorb in 450 nm; Shawkey and Hill 2005). For each colour parameter, we then calculated the mean of the three consecutive colour measurements sampled per nestling.

We measured the plumage colouration of 1837 nestlings ($n_{2017} = 672$; $n_{2018} = 639$; $n_{2019} = 526$) of which 945 were males and 892 females. Due to the experiments performed in parallel studies, colour measurements were taken at the age of 12 days in 2017 and 2018, and 11 days in 2019. On the day of colour measurement, we also weighted each nestling to the nearest 0.01 g with an electronic Pesola spring balance.

In 2017, we provided blue tit females with extra lutein pigment prior to and during egg laying (for details, see Garcia-Campa et al. 2020). However, nestlings of lutein supplemented mothers did not differ in colouration from control nestlings (one-way ANOVA test; total brightness: $F_{1,670} = 2.13$; $P = 0.15$; UV chroma: $F_{1,669} = 0.29$; $P = 0.59$; carotenoid chroma: $F_{1,670} = 0.02$; $P = 0.89$). In the 2018 season, we reduced the yellow UV chroma of one blue tit parent (indistinctly males and females) at the nest on the second week of nestling age (Garcia-Campa et al. 2022). Nonetheless, parental UV chroma did not have an effect on offspring colour parameters (one-way ANOVA test; total brightness: $F_{1,521} = 0.61$; $P = 0.44$; UV chroma: $F_{1,521} = 1.20$; $P = 0.28$; carotenoid chroma: $F_{1,521} = 0.78$; $P = 0.38$). Additionally, in 2017 and 2018, we cross-fostered full clutches among nests at the end of incubation. Thus, among-nest differences in the relationship between colour and condition could be partly explained by the rearing effects of the foster nest.

Statistical analyses

We used R 4.1.0 (R Core Team 2020) for statistical analyses. First, to explore how the colour parameters were inter-related, we performed correlations between UV chroma, carotenoid chroma and brightness both at the individual level and at the nest level (the latter using mean values of colour parameters). Second, we fitted three linear mixed models with a normal distribution of errors using the `lmer` function in the “*lme4*” package (Bates et al. 2015) to determine the relationships between body mass and each of the three colour parameters. The models included as fixed effects the average body mass of the brood (= among-nest effect), the deviation from the average body mass of the brood (= within-nest effect), and their interaction. We included in addition year (2017, 2018 and 2019), nestling sex, brood size, and the interactions between year and nestling sex, average body mass and year, average body mass and brood size, and nestling sex with the deviation from the average body mass. Backward elimination for non-significant interactions ($\alpha = 0.05$) was used to build the minimal models. We also included nest ID as a random intercept, and the interaction between nest ID and the deviation from the average body mass (= within-nest effect) as a random slope.

Results

Associations between colour parameters

At the individual level, yellow UV chroma of nestlings was positively correlated with yellow brightness ($r = 0.34$; $P < 0.001$; $n = 1834$), and negatively with carotenoid chroma ($r = -0.54$; $P < 0.001$; $n = 1835$). In contrast, there was no relationship between carotenoid chroma and brightness ($r = -0.010$; $P = 0.70$; $n = 1834$).

When running the correlations of colour parameters at the nest level, mean yellow UV chroma was positively correlated with mean yellow brightness ($r = 0.54$; $P < 0.001$; $n = 234$; Figure 1a), and negatively with

carotenoid chroma ($r = -0.52$; $P < 0.001$; $n = 234$; Fig. 1b). Moreover, the relationship between carotenoid chroma and brightness was slightly significant and negative ($r = -0.14$; $P = 0.030$; $n = 234$; Fig. 1c).

Condition-dependence

We found a significant among-nest effect of body mass on yellow UV chroma ($F_{2,220.78} = 57.57$; $P < 0.001$; Table 1). Broods in which the average nestling mass was higher had higher levels of UV chroma than broods with on average lower nestling body mass (Fig. 2a). However, we did not find a significant within-nest effect of body mass on UV chroma ($F_{1,205.99} = 1.76$; $P = 0.19$), so that nestlings with lower than average body mass in their brood did not have lower UV chroma than their siblings (Fig. 3a; see also Fig. S3). Yellow UV chroma was significantly affected by the interaction between year and nestling sex ($F_{2,1553.2} = 5.10$; $P = 0.0062$; Fig. S1). UV chroma was higher in females than in males in all the seasons (all Post-Hoc tests: $P < 0.001$). In females, UV chroma was higher in 2017 than in the other two years and it did not differ between 2018 and 2019 ($P = 0.23$). The same effect was found for males, but, unlike females, the difference between 2018 and 2019 was almost significant ($P = 0.051$). The rest of the interactions were not significant (all $P > 0.11$).

We did not find among-nest ($F_{1,225.43} = 0.22$; $P = 0.64$) or within-nest effects ($F_{1,1161.01} = 1.98$; $P = 0.16$) of body mass on carotenoid chroma (Table 1; Fig. 2b and 2c; see also Fig. S4). Carotenoid chroma significantly differed among years ($F_{2,218.77} = 8.99$; $P = 0.002$) and sexes ($F_{1,1642.67} = 73.39$; $P < 0.001$), being higher in 2017 than in the other two years (Post-hoc tests: $P < 0.001$), and being higher in males than in females. However, there was not a significant interaction effect between year and sex. The rest of the interactions were also not significant (all $P > 0.63$).

Interestingly, we found significant both among-nest ($F_{1,227.51} = 5.05$; $P = 0.026$) and within-nest effects ($F_{1,1410.24} = 22.74$; $P < 0.001$) of body mass on yellow brightness (Table 1). Thus, broods with higher than average body mass displayed brighter yellow colourations (Fig. 2c), and those nestlings with a higher body mass relative to the average body mass of their brood displayed brighter yellow colouration than their siblings (Fig. 3c; see also Fig. S5). Yellow brightness was significantly affected by the interaction between year and nestling sex ($F_{2,1622.30} = 6.23$; $P = 0.0020$; Fig. S2). Yellow brightness was higher for male nestlings than for female nestlings in years 2017 and 2019, while there was not a significant difference in 2018 (Post-Hoc test: $P = 0.28$; Fig. S2). All other interactions were not significantly different (all $P > 0.30$).

Discussion

We hypothesized that offspring and adults not only display similar colourful traits but that these traits might also have a correlated signalling value across life-history stages. Indeed, as has already been suggested (Johnsen et al. 2003; Jacot & Kempenaers 2006; Morales & Velando 2018), we found that certain colour components of nestling yellow breast feathers reflected body mass in the 3-year period. This pattern was particularly relevant for UV chroma and total brightness. Hence, these traits could act as condition-dependent signals beyond a sexual selection framework, around which most previous work has focussed (e.g., Senar et al. 2002; Hidalgo-García 2006; Doutrelant et al. 2008, 2012; Ferns and Hinsley 2008; del Cerro et al. 2010; García-Navas et al. 2012; Midamegbe et al. 2013; Ferrer et al. 2015). Furthermore, our approach allowed us to explore the potential of the three colour components as quality signals both within nests and among nests contexts.

Associations between colour parameters

We found a negative association between carotenoid chroma and UV chroma of yellow breast feathers, in line with previous results in other study populations (Johnsen et al. 2003; 2005). This negative association may be due to the fact that higher amounts of carotenoid pigments in the feathers partly conceal feather structures, which results in lower UV reflectance. However, this does not imply that an increase in one of these two colour parameters inevitably leads to a reduction in the other (Jacot & Kempenaers 2007). Indeed, each colour parameter results from a combination of metabolic pathways (pigment-based and structural colouration; Hill 2006): while carotenoids are acquired from food and deposited in the feathers, UV reflectance is produced

by an entirely different mechanism related to feather synthesis and it relies on the precise organization of the network of barb and barbules. Moreover, we found that yellow brightness was strongly and positively associated with UV chroma, but not with carotenoid chroma. Hence, the overall reflectance of yellow breast colouration indicates to a large extent the reflectance in the UV region of the spectrum. This is particularly relevant in our model system, since UV colouration is more easily perceived by cavity-nesting birds than carotenoid-based reflectance (Hunt et al. 2003; Avilés et al. 2006; Wiebe and Slagsvold 2009; Wgrzyn et al. 2011).

Condition-dependence: nestling colour as an honest signal of quality

While the colour expression of the nestlings' yellow breast feathers showed condition-dependency, this effect differed for the three colour parameters under study. Furthermore, the contribution of among-nest effects (which encompass a combination of genetic effects, parental quality effects or other common environmental effects) and within-nest effects (reflecting the relative differences in body mass among all the nestlings raised in the same brood) also varied between the colour parameters.

We found a significant among-nest effect of body mass on yellow UV chroma. Broods with higher mean body mass also had higher mean UV chroma. This effect was independent of brood size. Interestingly, UV chroma could reflect genetic quality (Charmantier et al. 2017) or parental rearing capacity (Senar et al. 2002), which we cannot separate in our study. However, we did not find differences in UV chroma between nestlings of the same brood (within-nest effect). This suggests that, at the intra-brood level, family members might not use UV chroma as a reliable signal of body mass. This was unexpected since we have experimentally demonstrated in the study population that chicks with reduced UV chroma gain less body mass (Morales & Velando 2018), and that this trait is used as a signal during intra-family interactions (Morales & Velando 2018; García-Campa et al. 2021; A. García-Antón, J. García-Campa, W. Müller and J. Morales unpublished data).

In addition, our findings show that there were among-nest effects of nestling body mass on yellow brightness. Unlike UV chroma, it is less likely that brightness functions as a signal of genetic quality, since it shows low heritability (Charmantier et al. 2017). However, it may reflect parental quality effects or other (common) environmental effects. Surprisingly, there were neither among- nor within-nest effects of nestling body mass on carotenoid chroma, in contrast to a number of previous studies supporting that this colour component is condition-dependent in nestling blue tits (Johnsen et al. 2003; 2005; Jacot and Kempenaers 2007, Delhey et al. 2006; 2010). One possibility is that differences in the calculation of carotenoid chroma used across studies ($(R_{UV\ peak} - R_{450})/R_{UV\ peak}$ see in Bleiweiss 2004; Jacot and Kempenaers 2007; and $R_{300-400}/R_{300-700}$ see in Johnsen et al. 2005) explains this inconsistency. Besides, since this colour parameter is strongly dependent on dietary carotenoid availability, it might contain a strong environmental component, which is, however, not captured at the nest level.

Differences between the sexes

We also found a consistent effect of nestling sex on the three colour parameters analysed, in accordance with previous studies (Johnsen et al. 2003; 2005; Jacot and Kempenaers 2007). Females expressed higher mean values for yellow UV chroma than males, whereas we detected the opposite pattern for carotenoid chroma and brightness (even though UV chroma and brightness are strongly and positively associated). While the blue tit was one of the first species in which a sexual dimorphism in crown UV-based plumage colour was documented, this has not been found in adult yellow breast feathers (Hunt et al. 1998). It is somehow puzzling that the latter trait is dimorphic only in nestlings and juveniles- since yellow body feathers are moulted a few months after fledging (Schoppe 1977; Cramp and Perrins 1993). Thus, parents could potentially rely on both carotenoid-chroma and total brightness to discriminate offspring sex while adjusting their feeding strategies. Indeed, in other study populations, blue tit males and females receive different food items (García-Navas et al. 2014) or the total amount of investment (Dickens and Hartley 2007). In addition, fledging yellow plumage could play a signalling role in family flocks that are formed immediately after fledging (Stenning 2017), and during social interactions within flocks (Tschirren et al. 2005). These sex-specific patterns clearly need

further study.

Conclusions

We show that yellow breast feathers could function as a condition-dependent signalling trait in nestling blue tits, given the observed associations with body mass. While total brightness and UV chroma (but not carotenoid chroma) seem to reflect genetic or other common environmental effects (=among-nest effects), total brightness could also act as an honest signal during intra-family interactions (=within-nest effect). Intriguingly, plumage colour was a sexually dimorphic trait in nestlings, in contrast to the situation in adults. This is somewhat counterintuitive as the forces of sexual selection are supposed to be greater in adults. This urges further studies to identify possible diverging selective pressures for males and females in the nestling and post-fledgling periods.

Acknowledgements

We would like to thank Sonia González-Braojos and Alicia Rodríguez-Juncá for help during fieldwork, and Emilio García Juárez for labwork analyses. We also thank Daniel Díaz and Alejandra Mira (from the Centro de Gestión del Parque Regional de la Cuenca Alta del Río Manzanares) for logistic support. The study was financed by the Ministerio de Economía y Competitividad MINECO, Spain (project grants CGL2016-79390-P and PID2019-106032GB-I00 to J. Morales) funded by MCIN/AEI/<https://doi.org/10.13039/501100011033> and by “ERDF A way of making Europe”. JG-C was supported by Grant BES-2017-079750 and JM by a Ramón y Cajal contract RYC-2014-15145 funded by MCIN/AEI/ <https://doi.org/10.13039/501100011033> and “ESF Investing in your future”.

Author Contributions : JM, WM and JGC conceived and designed the study. JGC, JM, SGB and ARJ performed the fieldwork. EGJ and ARJ performed laboratory analyses. JGC, JM, WM analysed the data. JGC, JM and WM wrote the manuscript.

Disclosure statement: Authors declare that they have no conflict of interest.

Data Accessibility:

García-Campa, Jorge; Müller, Wendt; Morales, Judith (2022): Offspring plumage colouration as a condition-dependent signal in the blue tit. figshare. Dataset.<https://doi.org/10.6084/m9.figshare.21221015.v1>

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- Table 1.** Final mixed models exploring the condition-dependence of colour parameters. We included nest ID as a random intercept and the interaction between nest ID and the deviation from the average body mass of the brood (= within-nest effect) as a random slope. Reference levels are “2017” for year effects and “males” for sex effects.

	UV chroma	Brightness	Carotenoid chroma
Intercept	<i>coef.</i> = 139.50 ± 10.26	<i>coef.</i> = 21210 ± 2237	<i>coef.</i> = 615.20 ± 34.01
Within-nest effect of body mass	<i>coef.</i> = 0.55 ± 0.41 $F_{1,205.99} = 1.76$ $P = 0.18$	<i>coef.</i> = 493.90 ± 111.30 $F_{1,1410.24} = 22.74$ $P < 0.001$	<i>coef.</i> = 2.60 ± 1.84 $F_{1,1161.01} = 1.98$ $P = 0.16$
Among-nest effect of body mass	<i>coef.</i> = 2.72 ± 0.95 $F_{1,223.29} = 8.29$ $P = 0.0044$	<i>coef.</i> = 450 ± 205.90 $F_{1,227.51} = 5.05$ $P = 0.026$	<i>coef.</i> = -1.45 ± 3.13 $F_{1,225.43} = 0.22$ $P = 0.64$
Year (2017)	<i>coef.</i> = 11.67 ± 1.09 $F_{2,220.78} = 57.57$ $P < 0.001$	<i>coef.</i> = 3282 ± 236.10 $F_{1,222.38} = 98.07$ $P < 0.001$	<i>coef.</i> = -14.69 ± 3.59 $F_{1,218.77} = 8.99$ $P < 0.001$
Nestling sex (Males)	<i>coef.</i> = -2.31 ± 0.22 $F_{1,1579.93} = 106.98$ $P < 0.001$	<i>coef.</i> = 352.30 ± 71.88 $F_{1,1627.15} = 23.34$ $P < 0.001$	<i>coef.</i> = 10.24 ± 1.20 $F_{1,1642.67} = 73.39$ $P < 0.001$
Brood size	<i>coef.</i> = 0.70 ± 0.38 $F_{1,231.04} = 3.39$ $P = 0.067$	<i>coef.</i> = 6.96 ± 83.51 $F_{1,240.12} = 0.009$ $P = 0.92$	<i>coef.</i> = -0.31 ± 1.27 $F_{1,237.84} = 0.059$ $P = 0.81$
Year * Nestling sex	<i>coef.</i> = -0.87 ± 0.30 $F_{2,1553.22} = 5.10$ $P = 0.0062$	<i>coef.</i> = 321.80 ± 94.4 $F_{1,1622.30} = 6.23$ $P = 0.0020$	

Figures

(In an additional file)



