

Egg Colour Covaries with Female Expression of a Male Ornament in the Spotless Starling (*Sturnus unicolor*)

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Abstract

The sexually selected egg colour hypothesis (SSECH) proposes that egg colouration is as a post-mating sexually selected signal of female phenotypic quality, maintained by a higher allocation of paternal care. Similarly, some female traits can reflect genetic quality or condition and males could use this information in mate choice or in modulating parental investment. In our study, we examined the correlation of individual variation in egg colouration with female expression of a male ornament and how male feeding covaried with these two female traits in the spotless starling, in which egg colour varies widely between clutches and where both sexes possess showy throat feathers that are age dependent and that may signal individual quality. According to the SSECH, high-quality females (females with longer throat feathers) are expected to lay more colourful eggs than low-quality females and males should modify their feeding behaviour accordingly. By means of a principal component analysis, we found that most of the variation in egg colouration was due to brightness differences, and in a lower proportion to chromatic variation. Chromatic variation reflected a ultraviolet (UV) vs. greenness trade-off and was positively associated with throat feather length: females with larger throat feathers laid eggs with higher UV and lower green reflectance. However, egg brightness was not related to female feather length, as the SSECH would predict. Male feedings were positively related to female throat feather length and negatively related to chromatic variation, meaning that males contributed more to nests of females with long throat feathers who laid eggs with higher UV and lower green reflectance. In conclusion, our data provide mixed support for the SSECH: although egg chromatic variation was related to female expression of a male ornament and male parental care, we found no evidence that egg brightness was involved in these processes.

Introduction

Egg colouration varies widely between and within species. Traditional adaptive explanations for this variation have focused on mimetism, crypsis and physical properties of pigments such as filtering solar radiation or strengthening eggshell (see review in Underwood & Sealy 2002). However, it has been

recently proposed that some types of egg colouration could have evolved as signals of female genetic quality or condition directed to their mates (i.e. the sexually selected egg colour hypothesis, SSECH; Moreno & Osorno 2003). If male parental care varies with female quality, it would pay high-quality females to signal it and thus induce a higher allocation of paternal care. The hypothesis assumes that

showy egg colouration is costly, and that only high-quality females can afford such signals. This limitation is proposed to come about because some eggshell pigments also have an antioxidant function, especially the blue–green pigment biliverdin (McDonagh 2001; Kaur et al. 2003), and females may face a trade-off between using them in colouration or in fighting oxidative stress.

According to this hypothesis, variation in egg colour should be more important in species where male contribution differs between nests and offspring survival is affected by male parental care (Moreno & Osorno 2003). At the intraspecific level, positive correlations between egg colour, female quality and male parental effort should be expected (Moreno & Osorno 2003). Indeed, recent studies in the pied flycatcher (*Ficedula hypoleuca*) have shown that egg colour is positively related to male parental care (Morales et al. 2004), the amount of maternal antibodies in the yolk (Morales et al. 2006), female quality as measured by body condition (Moreno et al. 2006) and immunocompetence (Moreno et al. 2005). Similarly, in the Eastern bluebird (*Sialia sialis*), a correlation between egg colour and female age has been found (Siefferman & Hill 2005).

As female ornaments are often a drabber or smaller version of the same traits in males, they have been traditionally considered as the unavoidable result of genetic correlation coupled with strong sexual selection for ornaments in the male sex (Lande 1980). However, there is increasing evidence that female ornamentation can reflect phenotypic or genetic quality and that males can use this information for choosing females or modulating their parental investment (for a review see Amundsen 2000). Under this scenario, ornamentation in females could evolve as an honest signal in the same way as male ornaments. Evidence for this relationship comes from correlative studies in several species of birds where the expression of female ornaments has been found to be related to female condition, parasite resistance or offspring viability (Potti & Merino 1996; Roulin et al. 2001; Velando et al. 2001; Jawor et al. 2004). Experimental work has demonstrated that female ornaments are favoured by male choice in the budgerigar *Melopsittacus undulatus*, in the blue-footed booby *Sula nebouxii*, and in the rock sparrow *Petronia petronia* (Arnold et al. 2002; Griggio et al. 2005; Torres & Velando 2005). Furthermore, a recent study in the rock sparrow has found that males modify their parental care in response to experimental manipulation of female ornament size (Pilastro et al. 2003).

Female ornaments may signal age and age-related features, often resulting in assortative mating with respect to these ornaments (Komdeur et al. 2005). Mutual mate preferences are expected in species with biparental care (Burley 1986) and there is evidence in some species that males do show active choice of females (Monaghan et al. 1996; Jones et al. 2001). As age may indicate greater parental ability and females of many species show condition and age-dependent ornaments (Savalli 1995; Siefferman & Hill 2005), males are expected to prefer more ornamented, older females. For example, in the European starling *Sturnus vulgaris* the length of female throat feathers is related to age: older females have longer throat feathers than younger females (Svensson 1992; Komdeur et al. 2005), and assortative mating with respect to these ornaments does occur (Komdeur et al. 2005).

In this study, we addressed individual variation in egg colouration in the polygynous spotless starling *Sturnus unicolor* and examined its relationship with female expression of a male ornament such as throat feather length and with male parental contribution. If egg colouration is a signal of maternal investment, high-quality females would be expected to lay more colourful eggs than low-quality females and males should modify their feeding behaviour accordingly. The spotless starling is a suitable species to test the SSECH because biparental care occurs and polygyny could allow the males to compare the clutches of their different mates and assign paternal care accordingly. Male and female spotless starlings possess showy throat feathers that are 41% longer in males than in females, while other morphological traits differ by less than 5% (Aparicio et al. 2001). Male throat-feather length and mating success are positively correlated in this species (Aparicio et al. 2001), suggesting that this trait is under sexual selection in males.

Methods

Field Site and Nest Monitoring

The study was conducted in a nest box colony in Soto del Real, near Madrid, in central Spain, from Mar. to Jul. 2004. The colony consisted of 150 nest boxes distributed in a deciduous mixed woodland of oak (*Quercus rotundifolia*) and ash (*Fraxinus angustifolius*). Nest boxes were visited every day to determine the beginning of laying (from Apr. 13 to Jun. 6), the final clutch size ($\bar{x} \pm SD 4.57 \pm 0.69$) and the exact hatching date of the first chicks in the brood. There is a

moderate hatching asynchrony in this species (interval of 1–2 d), and our hatching dates refer to the earliest hatching chicks in the clutch. All nests were monitored periodically and nestlings were ringed, measured and weighed at 14 d of age.

Adults were captured inside the nest boxes before laying or shortly after hatching, and marked with a metallic number ring and a unique combination of coloured plastic rings. We were able to catch 78 females and biometric data were recorded from them. Also from each bird three feathers were randomly collected from the central region of the throat. Removal of feathers was performed by pulling them near the base. Feathers were kept in plastic bags until length measurements were performed with a digital calliper to the nearest 0.01 mm. We calculated the mean length of the three feathers, and this measure was found to be highly repeatable (intraclass coefficient of correlation = 0.94, $n = 24$, $p < 0.001$).

Egg Colour and Egg Size

At the end of laying, the egg colour of 325 eggs belonging to 114 clutches was measured using a Minolta spectrophotometer CM-2600d, which covered reflectance in the human visible spectrum and a segment of the ultraviolet (UV) range (360–740 nm). Spectral data were truncated at 700 nm as this is the upper limit of the visible range of birds (Endler & Mielke 2005). The data output consisted of 35 reflectance values in steps of 10 nm. A reference calibration with a standard white was taken prior to the colour measurements according to the apparatus specifications. Measurements of egg length and width were taken with a digital calliper to the nearest 0.01 mm. Egg volume was calculated by the formula: $0.45 \times \text{length} \times \text{width}^2$ (Worth 1940): average = $6211.45 \pm 528.20 \text{ mm}^3$.

In a preliminary assessment of colour variation between clutches, we found that variation in egg colour and volume was far greater between clutches than within clutches (PC1: $F_{9,54} = 8.97$, $p < 0.000$; PC2: $F_{9,54} = 14.95$, $p < 0.000$; volume: $F_{9,54} = 3.13$, $p < 0.005$). Therefore, in the rest of the nests we measured colour and volume in the first egg laid, representative of the whole clutch, thus avoiding unnecessary disturbance to the nest. Because intra-specific nest parasitism during the laying period is common in this species (Calvo et al. 2000), parasitic eggs were excluded from the analysis when detected. We assumed that a nest had been parasitized when two new eggs were found in a nest on a given day

(as starlings lay one egg per day) or when a single egg differed markedly in appearance from the other eggs in a clutch. This criteria used for detecting parasitic eggs has been employed in another study in the European starling (Pilz et al. 2005).

Female Quality

We estimated female quality by measuring female throat feathers length. To confirm that length of the female throat feathers is an index of quality, we performed two different analyses in our study population. First, we found age dependence of throat feather length, which increased from 1 yr to the next (paired t-test on birds recorded in two consecutive years: $t = -5.34$, $p < 0.000$, $n = 50$). Second, we found that female throat feather length was related to reproductive success as measured by fledgling number ($r = 0.21$, $p = 0.03$, $n = 108$).

Behavioural Observations

When chicks were 5 or 6 d old, feeding frequencies were recorded by focal observations in 22 nests. From 08:30 to 10:30 hours observations were made from hides situated 30 m from the nests using binoculars and a telescope. Once a first visit from an adult was observed, we continued to observe the nest for 30 additional minutes. Adults were identified from colour ring combinations.

Statistics

Egg colouration was described by means of a principal component analysis (PCA) performed on the reflectance data. This method allows an objective description of the colour spectra, reducing a large number of correlated variables into a few orthogonal variables which summarize most of the variation (Cuthill et al. 1999; Cherry & Bennett 2001). Colorimetric variables are expected to reflect pigment concentration; for instance, shell chroma has been found to predict concentration of biliverdin eggshell of pied flycatchers (Moreno et al. 2006). Our own data shows that in the spotless starling biliverdin is negatively related to PC1: Pearson's $r = -0.61$, $n = 80$, $p < 0.01$; López-Rull I., Miksik I., Gil D., unpubl. data).

To test for a correlation between egg colour and male feeding behaviour, male feeding contribution was estimated as brood provisioning (number of visits) by the male by unit time. In the analysis, we used a multiple linear regression including as

covariates laying date, the number of nestlings in the brood at the day we recorded male feedings, female feeding contribution and female throat feather length, as well as biologically significant meaningful interactions. Variables were transformed when necessary to approach normal distributions (logarithmic transformation for male feedings and arcsine transformation for female feedings; after transformations variables were normally distributed). All statistical analyses were performed with SPSS v.12.

Results

The mean peak reflectance (50%) of 325 starling eggs was found at 510 nm (Fig. 1). In the PCA, the first two principal components explain together 98.89% of the variance in the spectra (Fig. 2). The first principal component (PC1) describes the variance in mean reflectance, it is flat throughout the spectrum of wavelengths and consequently represents brightness. Although most of the variance is explained by PC1 (91.98%; eigenvalue 32.19), the second principal component PC2 explains additional significant proportion of the variance (6.92%; eigenvalue 2.42) and shows variation in spectral shape thus measuring aspects of the egg's chromatic variation (hue and saturation). As PC1 scores are positively associated with lightness, we expect them to be negatively associated with the amount of pigments present in the egg (i.e. biliverdin). By contrast, PC2 could be described as a bipolar component measuring UV and red vs. greenness: high scores in PC2 are mainly characterized by low UV wavelengths (approx. 360 nm), strong green wavelengths

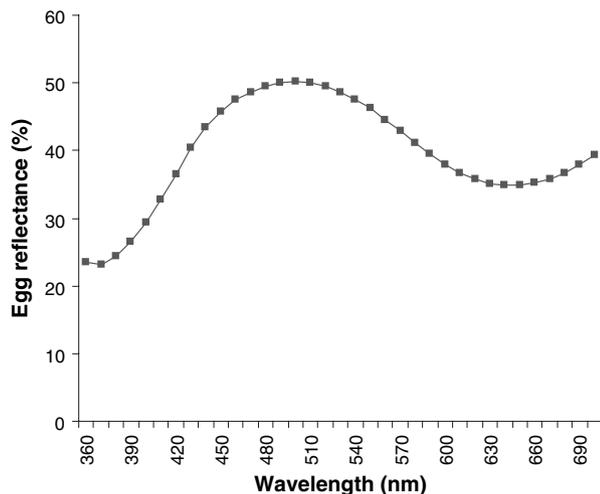


Fig. 1: Mean reflectance spectrum of spotless starling eggs.

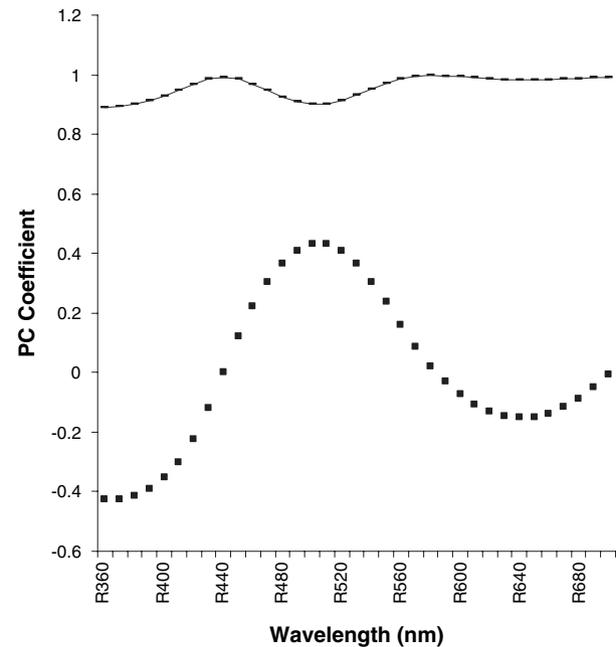


Fig. 2: Principal components as a function of wavelength. PC1 is flat and positive all over the spectrum and consequently represents colour brightness (thin line), whereas PC2 can be seen as measure of the relative contribution of chroma, particularly the near UV and the red vs. the blue–green range (dotted line).

(approx. 550 nm), and relatively low red wavelengths (approx. 660 nm). In the rest of the paper, we will refer to PC1 as brightness and to PC2 as chromatic variation.

We related egg colour of clutches to reproductive variables that could affect colour, like laying date, clutch size and volume. Egg colour was not correlated with egg volume or clutch size, neither in brightness (volume: $r = 0.03$, $p = 0.78$, $n = 114$ clutches; clutch size: $r = -0.18$, $p = 0.16$) nor in chromatic variation (volume: $r = 0.07$, $p = 0.45$, $n = 114$ clutches; clutch size: $r = -0.13$, $p = 0.34$). However, egg brightness showed a negative association with laying date (PC1: $r = -0.20$, $p = 0.03$, $n = 114$ clutches), indicating earlier clutches were characterized by brighter eggs. This association was not found for chromatic variation (PC2: $r = 0.13$, $p = 0.17$, $n = 114$ clutches).

Neither brightness nor volume were correlated with female throat feather length (PC1: $r = -0.02$, $p = 0.83$, $n = 78$; volume: $r = 0.09$, $p = 0.42$, $n = 78$). However, egg chromatic variation (PC2) was negatively associated with throat feather length ($r = -0.23$, $p = 0.04$, $n = 78$, Fig. 3), indicating that females with larger throat feathers laid eggs with relatively higher UV and red reflectance, and lower

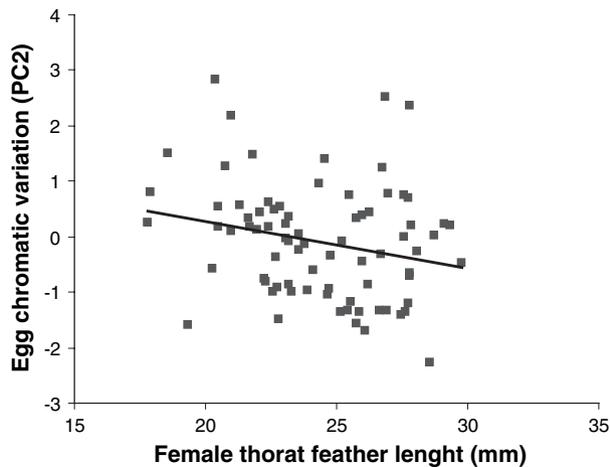


Fig. 3: Mean within clutch egg PC2 in relation to female throat feather length. Females with longer feathers laid eggs that had relatively stronger UV and weaker blue–green reflectance than females with shorter feathers.

green reflectance. Female throat feather length showed no correlation with laying date ($r = -0.15$, $p = 0.18$, $n = 78$).

We tested whether egg colour (PC1 and PC2) had an effect on male feeding contribution. The initial full model included laying date, number of nestlings in the brood, PC1, PC2, female throat feather length and the biologically meaningful interactions of these variables. Non-significant terms were removed (all $p > 0.11$). In the final model of a backward regression, the only variables that were not excluded and had a significant relationship with male feeding contribution were PC2, female feather length, and the interaction between them (overall regression: $F_{4,17} = 23.35$, $p < 0.001$, $R^2 = 0.84$; PC2: $\beta = 0.94$, $t = 5.95$, $p < 0.01$; female feather length: $\beta = 0.004$, $t = 6.72$, $p < 0.01$; Fig. 4; interaction: $\beta = -0.004$, $t = -6.64$, $p < 0.01$). Males fed more intensively in nests where eggs with relatively low PC2 values had been laid, and when mated to females with relatively long feathers. The significant interaction between female feather length and PC2 showed that the effect of either variable on male feeding increased disproportionately with respect to each other: e.g. the effect of eggs with low PC2 on male feeding contribution was relatively larger when these had been laid by females with relatively long throat feathers.

Discussion

If egg colouration is a signal of maternal investment, high-quality females would be expected to lay more

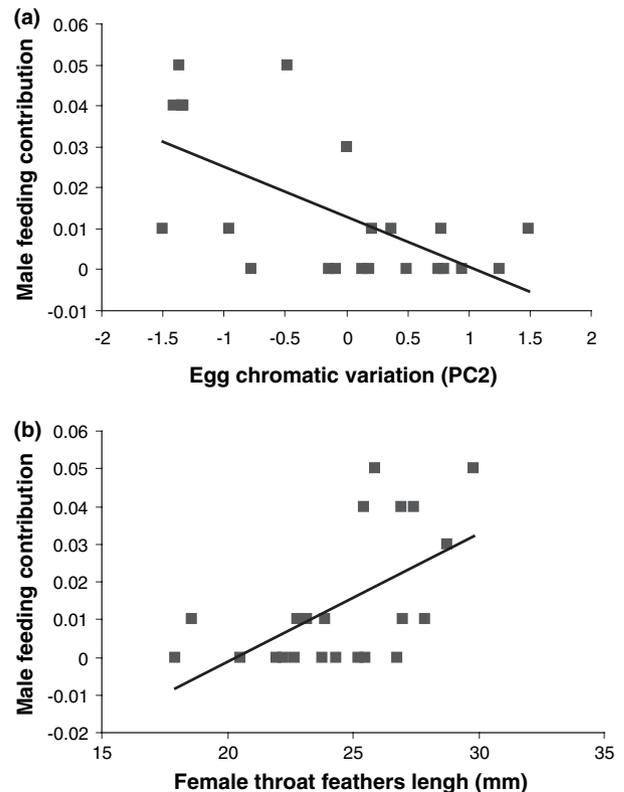


Fig. 4: Male feeding contribution in relation to (a) mean within clutch egg PC2 and (b) the length of female throat feathers. Males contributed more to nests in which eggs reflecting stronger UV and weaker blue–green wavelengths had been laid, and when paired to females with longer throat feathers.

colourful eggs than low-quality females. If this is so, interfemale variation in egg colouration is also expected. We found that interclutch variation in egg colour was greater than intraclutch variation, suggesting that there is potential for female quality to play a role in egg colour investment.

We found that most of the variation in egg colouration in the spotless starling was due to brightness differences (PC1), and in a lower proportion to chromatic variation (PC2). According to the SSECH (Moreno & Osorno 2003), female allocation of biliverdin pigment to eggs could reflect their antioxidant capacity and only females in good condition would be able to afford such investment. The mean peak reflectance of starling corresponds to the blue–green sector of the human visible spectrum and matches the maximum peak of reflectance of the pigment biliverdin (Falchuk et al. 2002). Because PC1 scores are positively associated with lightness and thus negatively with the amount of pigmentation (López-Rull I., Miksik I., Gil D., unpubl. data),

we would expect females with long throat feathers to lay darker eggs (i.e. low PC1 scores) than females with short throat feathers; however, PC1 was not related to this female trait. This result does not support the assumption of the trade-off between biliverdin and immunocompetence suggesting that this mechanism may not work in starlings.

We found that egg chromatic variation was associated with female throat feather length: females with longer throat feathers laid eggs with more UV, more red and less green than females with shorter throat feathers. Similarly, Moreno et al. (2005) found that female condition was associated with the chromatic PC of the reflectance spectra in pied flycatchers, indicating a shift away of intermediate wavelengths and toward the UV part of the spectrum in eggs of females in good condition in that species. As PC2 has no association with the amount of pigmentation in the egg (López Rull I., Miksik I., Gil D., unpubl. data), it is difficult to speculate on the constraints that may underline this colouration; however, it is possible that some aspects of eggshell structure may be playing a role in the maintenance of this variable as a quality indicator.

The fact that the major colour component which varies with female ornamentation is only visible within the bird's visibility range adds to the increasing evidence showing that many bird species use UV wavelengths in numerous processes, such as mate choice (Andersson & Amundsen 1997; Bennett et al. 1997; Hunt et al. 1997), foraging (Church et al. 1998) and parasite egg discrimination (Avilés et al. 2006).

Because UV radiation contributes strongly to conspicuousness against dark backgrounds (Endler 1993) and the intensity of brightness inside nest boxes is 16–32 times lower than outside, it is likely that UV colouration would create a strong contrast against the darkness of the nest providing a highly salient stimulus (Hunt et al. 1997; Heeb et al. 2003; Jourdie et al. 2004; Veiga & Polo 2005; Avilés et al. 2006). In this sense, our data suggest that females with longer throat feathers are emphasising the visual contrast of their eggs against the nest background. This is particularly interesting given the high prevalence of brood parasitism in this species (Calvo et al. 2000). The evolution of distinctive and condition-dependent egg colouration of individual females could facilitate discrimination of eggs from those laid by a brood parasite (Davies & Brooke 1988; Møller & Petrie 1991). In fact, a recent study (Avilés et al. 2006) in the spotless starling has found that eggs from which UV reflectance had been experimentally

blocked were less likely to be retrieved to the nest-cup than control eggs, suggesting that egg colouration enhances egg detectability by parents in dark nests.

Because the length of throat feathers is correlated with age in the spotless starling, and condition is expected to increase with age, our results may either indicate that egg colour changes longitudinally as the female ages; or alternatively that females that lay eggs with low PC2 scores are less likely to survive. In the absence of longitudinal data, we cannot distinguish between these two possibilities (Endler 1986) but nevertheless they both point to the same positive relationship between egg colour and female quality.

Contrary to our expectations, male feeding contribution was not explained by PC1, indicating that male parental care was not associated with the amount of biliverdin in the eggs. Similarly, a recent study (Krist & Grim 2007) found no evidence for increased parental effort with increasing egg colour saturation, suggesting that males can possibly assess offspring's reproductive value according to some more direct and informative cues. For instance, in our study we found that female throat feather length explained male feeding contribution. Taken together, these results may indicate that males contributed more feedings to nestlings from females with larger throat feathers, which laid eggs with higher UV and red reflectance and lower green reflectance. Moreover, the interaction of egg chromatic variation and throat feather length implies that the effect of each of these variables on male feeding behaviour is multiplicative of each other (e.g. the effect of low PC2 in male feedings is the largest when males are paired with females with long throat feathers). The relationship between male contribution and female feather length is to be expected from a pattern of differential allocation, by which individuals of species with biparental care adjust their parental investment according to their mate attractiveness (Burley 1986). However, as assortative mating with respect to age could be expected, our data do not allow us to distinguish between these possibilities.

Summarizing, our data provides mixed support for the SSECH: although female quality and male parental care were not related to the egg characteristic that is dependent on the amount of egg biliverdin, spotless starling females lay eggs with a colour pattern that correlates with the length of their throat feathers and males seem to modulate their parental investment in relation to it. It would seem that egg chromatic variation may function as a signal that

females can use to indicate their age and quality in this species. However, experimental studies relating female physiological condition to egg colouration are needed in this species to understand the meaning of these individual egg colour differences.

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