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Ultraviolet reflectance in a melanin-based plumage trait is heritable

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ABSTRACT

Question: Is ultraviolet (UV) reflectance of melanin-based plumage ornaments heritable?

Data studied: We considered the barn owl (*Tyto alba*), a species that varies continuously from white to reddish-brown, a pheomelanin-based trait.

Methods: To perform a partial cross-fostering experiment, we exchanged one to three hatchlings between 16 pairs of nests with a similar hatching date. This experiment allocated hatchlings randomly among rearing environments. Forty-nine days later, we collected three feathers per individual to measure UV reflectance.

Conclusions: The cross-fostering experiment showed that, independently of human-visible coloration, variation in UV reflectance is significantly sensitive to origin-related factors.

Keywords: colour polymorphism, heritability, melanin, plumage coloration, sex determination, structural coloration, *Tyto alba*, ultraviolet reflectance.

INTRODUCTION

In many bird species, plumage coloration provides information on phenotypic and genetic quality, and hence is an important criterion in mate choice decisions. Variation in coloration can be due either to the deposition of different amounts or types of pigments in growing feathers, or to variation in feather microstructure (Finger and Burkhardt, 1994; Keyser and Hill, 1999). Pigments, such as melanins and carotenoids, are responsible for coloration in the human-visible part of the spectrum between 400 and 720 nm (Keyser and Hill, 1999), and ultraviolet (UV) coloration between 320 and 400 nm can be produced either by colour pigments or by microstructures of the feathers (Andersson, 1996; Prum *et al*., 1999). A feather trait can therefore be viewed as a combination of pigmented and structural coloration (Osorio and Ham, 2002). For this reason, studies on the adaptive function of plumage coloration should take into account the entire spectrum of wavelengths between 320 and 720 nm, including the UV part (Cuthill *et al*., 1999). This is particularly important in birds because individuals have UV-sensitive retinal cones (Chen and Goldsmith, 1986) and hence UV vision. Not surprisingly, UV coloration has been

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shown to play a role in mate choice decisions and hence in avian sexual selection (see review in Pearn *et al.*, 2003).

Because of differences in composition, pigmented and structural components of plumage coloration may be differentially sensitive to origin-related (i.e. genetic and pre-hatching maternal effects) and environmental factors. A plumage reflecting both in human-visible and UV wavelengths may therefore convey multiple information about phenotypic and genotypic quality. For this reason, it is crucial to examine which factors modulate the expression of human-visible coloration and UV coloration of the same trait. Pigmented traits have been well studied, with melanin-based coloration usually under strong genetic control (Roulin and Dijkstra, 2003; see review in Roulin, 2004a) and carotenoid-based coloration being strongly influenced by the environment, since animals cannot synthesize carotenoids *de novo* and thereby have to obtain these pigments from the diet (Olson and Owens, 1998). Although the factors influencing the expression of human-visible coloration have been examined experimentally in a number of species, little attention has been paid to the factors controlling the expression of UV coloration.

Andersson (1996) has suggested that the small sizes of the structures producing UV coloration should make them easily perturbed by diet or other environmental factors, implying that the expression of UV coloration may be condition-dependent. Several behavioural studies have shown that males that reflect the most in UV are preferentially chosen by females and are more dominant in social interactions (see Alonso-Alvarez *et al.*, 2004 and references therein). These studies may be taken as preliminary evidence that UV coloration signals individual quality. Moreover, two studies have reported significant correlations between aspects of individual condition and UV coloration, further supporting the hypothesis of condition-dependent expression (Keyser and Hill, 1999; Johnsen *et al.*, 2003). A heritable basis for this trait has also been suggested by the significant relationship between UV coloration of feathers collected on extra-pair offspring and on their biological father (Johnsen *et al.*, 2003). Although these studies are interesting, there is still no experimental evidence that UV coloration is heritable.

This work would be greatly facilitated if hatchlings could be swapped between nests and if they had already developed a fully mature plumage that could be kept at least until the first breeding attempt. A cross-fostering experiment is a useful design to estimate the effect of origin-related factors, most likely attributable to genetics or to pre-hatching maternal effects, by comparing UV coloration of siblings raised in different environments. This design also allows an evaluation of the impact of the rearing environment by comparing the UV coloration of unrelated nest-mates. In this context, the barn owl is appropriate because nestlings already display reddish-brown to whitish coloration, a pheomelanin-based trait that is kept until maturity with birds moulting not before the second year of age (Roulin, 1999). Although both sexes can display any coloration, females are on average darker than males (Roulin and Dijkstra, 2003). Furthermore, within broods there is a pronounced age hierarchy resulting from hatching asynchrony with eggs hatching every 2½ days. This property provides an indirect opportunity to test for condition-dependent effects of producing UV coloration because first-hatched individuals eat more food and are less parasitized (Roulin *et al.*, 2003; Roulin, in press), ensuring that they are in better condition than their later-hatched siblings. Cross-fostering experiments have already shown that variation in human-visible coloration is highly heritable (Roulin and Dijkstra, 2003). In this paper, our aim is to perform a similar study on UV coloration to determine whether this trait is also sensitive to origin-related factors independently of human-visible coloration (i.e. whether variation in UV

coloration among similarly coloured individuals can be accounted for by origin-related factors).

METHODS

Experimental design

Fieldwork was carried out in 2004 in western Switzerland where barn owls breed in nest-boxes installed on the external wall of barns. To compare the UV coloration of siblings raised in different nests and of unrelated nestlings raised in the same nest, we performed partial cross-fostering experiments. One to three hatchlings aged 3 ± 2 days were exchanged between 16 pairs of nests with a similar hatching date (Spearman correlation: $r_S = 0.97$, $n = 16$, $P < 0.0001$). Similarly aged nestlings were swapped to avoid altering the within-brood age hierarchy. In this way, 74 hatchlings were successfully raised by their biological parents in the 'nest of origin' and 52 by foster parents in a 'nest of rearing'. Within pairs of nests, foster and biological parents did not resemble each other with respect to flank coloration (Pearson correlation on mean flank coloration of female and male partners: $r = -0.06$, $n = 16$, $P = 0.83$).

Feather collection and assessment of plumage coloration

When nestlings were 49 ± 4 days of age, one of the authors (A.R.) recorded plumage coloration on one flank after reliable comparison with eight colour chips, ranging from I for reddish-brown to VIII for white [referred to as 'flank coloration' (Roulin and Dijkstra, 2003)]. On the same day, three feathers of similar size were collected on one flank. To prevent damage to feather microstructures, they were cautiously cut at the base of their rachis with a pinch and scissors, and stored in an envelope. At the end of the field season, we randomly mixed all envelopes to ensure that the order of measuring spectral reflectance of feathers was random with respect to the nests of origin and of rearing.

Spectral reflectance of the collected feathers was measured with an Ocean Optics spectrophotometer (USB2000 Miniature Fibre Optic Spectrometer) and a PX-2 pulsed xenon lamp (Ocean Optics). The measurement probe consists of a bifurcated fibre-optic. Illumination from the lamp is transmitted to a 3 mm^2 area of plumage, and light reflecting from this surface is transferred back to the spectrophotometer. The probe was applied directly on the feathers at 45° by using a metallic sheath. Illumination was conducted in a direction parallel to the rachis from the proximal end of the feather.

For each bird, the three feathers were superposed and stuck with adhesive tape at the basis of their rachis on black paper to eliminate stray reflection from the background. All measurements were done in the same room under the same light conditions. Before each measurement, white (WS-1 Diffuse Reflectance Standard) and black standard references were calibrated to avoid errors associated with drifts of the light source and sensor. For each individual, reflectance was measured at five equidistant locations (top, basis and in between) at the right side of the rachis. Reflectance was recorded in 0.38 nm steps and quantified with brightness measurements, which corresponds to the sum of each reflectance value between 320 and 400 nm [UV coloration (Andersson, 1999)] and between 400 and 720 nm [human-visible coloration (Cuthill *et al.*, 1999)]. Reliability of the method was estimated in two different ways. First, for ten individuals we measured reflectance on the right and left side of the rachis

on two different days. Ultraviolet coloration measured on the right and left sides was not significant (paired *t*-test: $t_9 = 1.22$, $P = 0.25$). The same applies to human-visible coloration ($t_9 = 1.15$, $P = 0.28$). Second, reflectance was measured at one location (mid-point of the superposed feathers) on one day, and at the four other locations on another day. The four measures (numbered I to IV from the top to the base of the feather) taken on the same day were significantly repeatable within individuals for UV coloration (two-way ANOVA with 'individual' as a first independent variable: $F_{125,375} = 5.25$, $P < 0.0001$, and as a second independent variable 'measures numbered I to IV': $F_{3,375} = 523.77$, $P < 0.0001$) and human-visible coloration (individual: $F_{125,375} = 2.13$, $P < 0.0001$; measures: $F_{3,375} = 1078{,}14$, $P < 0.0001$). Within individuals the mean value of the four measures taken on the same day was significantly associated with the measure taken on another day for both UV coloration ('individual': $F_{125,125} = 7.25$, $P < 0.0001$; day: $F_{1,125} = 20.85$, $P < 0.0001$) and human-visible coloration (individual: $F_{125,122} = 3.39$, $P < 0.0001$; day: $F_{1,122} = 12.71$, $P = 0.0005$). The significant effect of the factor 'day' indicates that different feather parts reflect to different extents. For each individual, we averaged the five measurements before performing the statistical analyses.

Sex determination of nestlings

We used a novel method to identify the sex of nestlings. Blood samples (50 μl) were taken from the brachial vein and stored at −20°C in 100 μl storage EDTA-buffer. Genomic DNA was prepared from 40 μl of blood-EDTA using the Wizard Genomic DNA Isolation Kit (Catalys AG). Segments of the *SPINDLIN*-gene located on the sexual chromosomes W and Z were PCR-amplified using primers SPIN375-fw (5′-CTTGAAGTCCTTCCAGAC-3′), SPINWI2-rev (5′-CATTTAGATTATCTGCCATGT-3′) and SPINZI2-rev (5′-TGACTAGTAACATTGAAGTG-3′). The PCR conditions were as follows: 1 × PCR buffer (Qiagen), 3.5 mM $MgCl_2$, 200 μM dNTPs, 500 nM SPIN375-fw, 250 nM each SPINWI2-rev and SPINZI2-rev, and 0.2 units of TAQ DNA polymerase (Qiagen). Between 50 and 250 ng of genomic DNA was amplified after an initial denaturing at 94°C for 2 min, followed by 40 cycles of 94°C for 30 s, 50°C for 30 s and 72°C for 30 s. The program was completed by a final run at 72°C for 5 min. The PCR products were separated by electrophoresis in a 2% agarose gel stained with ethidium bromide. Males (ZZ) produced a single band at 140 bp, and females (WZ) an additional band at 90 bp. We validated the method by identifying nine males and nine females previously sexed by breeding behaviour. This method, which is based on small amplified products, is especially useful with low content/quality samples, and allows reliable sex identification in a wide range of raptors and owls (data not shown).

Statistical procedure

To test for origin-related, environmental and condition-dependent effects on UV coloration, we carried out a mixed-model nested ANCOVA. The main effect was the pair of cross-foster nests (random factor), and the nests of origin and rearing were nested in the pair of cross-foster nests (random factors). The sex of the nestlings and their position in the within-brood age hierarchy (1 for first-hatched chick, 2 for the second-hatched, 3 for the third-hatched, and so on) were entered as fixed factors in the analyses. Since our aim was to determine whether similarly coloured individuals differed in UV coloration because their origin was

different or because they were raised in different environments, human-visible coloration was added as a covariate in the model. In most studies, researchers use the index 'UV-chroma' (proportion of total reflectance occurring from 300 to 400 nm) to assess the extent to which individuals reflect in the UV part of the spectrum. We did not use this index because a low value, for example, can be due either to a low reflectance in the UV part of the spectrum or to a pronounced reflectance in the human-visible part of the spectrum. For this reason, we preferred to enter 'UV coloration' as the dependent variable (this variable was normally distributed) and 'human-visible coloration' as an independent variable rather than to enter 'UV-chroma' as the dependent variable. Two-tailed statistical analyses were performed with the software JMP (Sall and Lehman, 1996), and P-values less than 0.05 were considered significant.

RESULTS

To illustrate reflectance between differently coloured birds, we calculated mean reflectance curves of reddish-brown (flank coloration I to III), intermediate (V) and white individuals (VII and VIII) (Fig. 1). The mixed-model nested ANCOVA (Table 1) showed that the nest of origin explained a significant part of the variation in UV coloration (Fig. 2) and lighter coloured individuals reflected more in the UV part of the spectrum (Fig. 3). In the same model, males reflected more in the UV part of the spectrum than females (Fig. 3). The factors 'nest of rearing' and 'rank in within-brood age hierarchy' did not account for any significant amount of the variation in UV coloration. This indicates that we could not detect any effect of environmental factors associated with the nest of rearing and of body condition on the expression of UV coloration. The interaction between the nest of origin and of rearing was not significant ($P = 0.82$), and hence we removed it from the model.

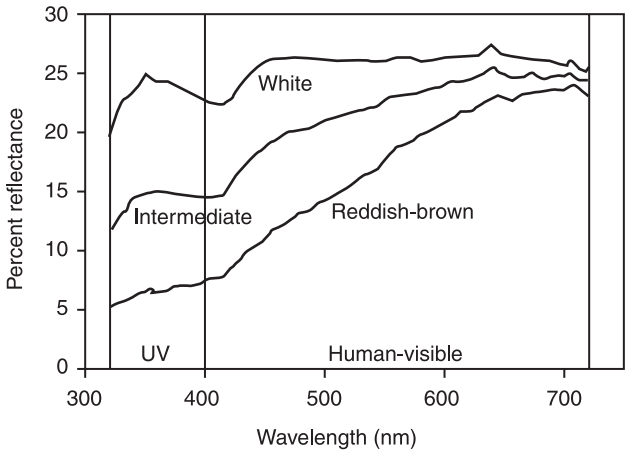

Fig. 1. Mean reflectance spectra in reddish-brown (colour score I to III; mean value of ten individuals), intermediate (V; eight individuals) and white nestling barn owls (VII to VIII; 13 individuals).

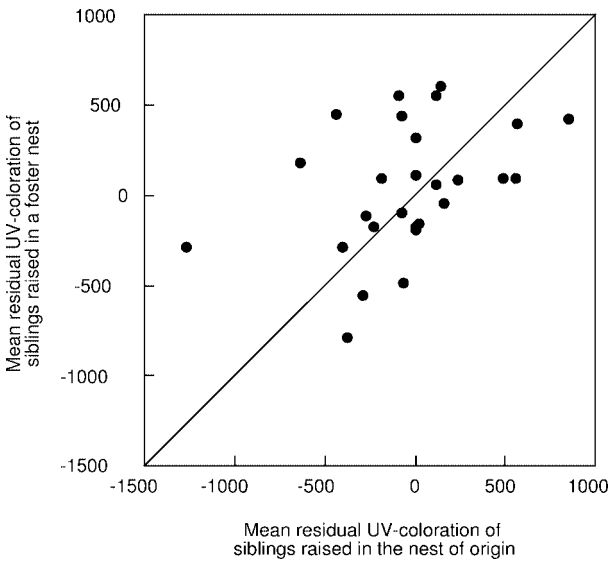

Fig. 2. Relationship between mean residual UV coloration of siblings raised in the nest of origin and mean residual UV coloration of their siblings raised in a foster nest ($r = 0.40$, $n = 27$, $P = 0.040$). Residual UV coloration was extracted from the mixed-model ANCOVA presented in Table 1 after having removed the factor 'nest of origin'. Data points on the diagonal represent nests for which origin-related variation in UV coloration of siblings raised in the nests of origin and of rearing is the same.

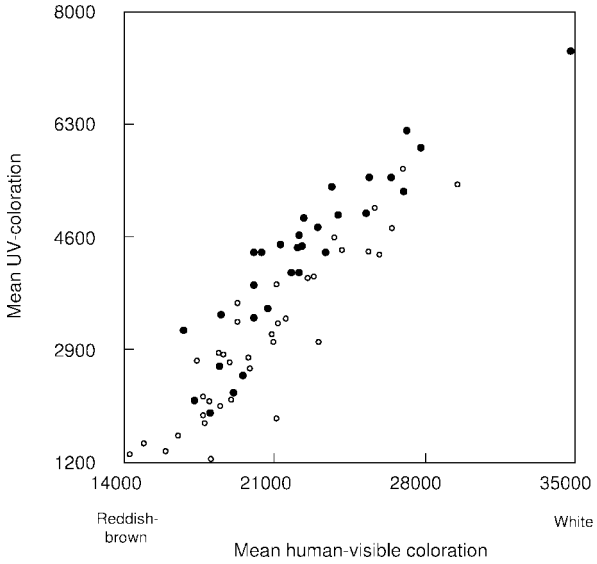

Fig. 3. Relationship between UV coloration and human-visible coloration. Solid circles represent the mean values of male siblings and open circles the mean values of female siblings.

Table 1. Mixed-model nested ANCOVA on UV coloration

Source of variation	d.f.	SS	MS	*F*-ratio	*P*-value
Pair of cross-foster nests	15	7648289	509886	0.79	0.67
Nest of origin (pair of cross-foster nests)	**16**	**12020000**	**751099**	**2.28**	**0.009**
Nest of rearing (pair of cross-foster nests)	15	3225089	215006	0.65	0.82
Sex	**1**	**11660000**	**11660000**	**35.42**	**<0.0001**
Rank in the within-brood age hierarchy	1	185948	185948	0.57	0.45
Human-visible coloration	**1**	**57200000**	**57200000**	**173.80**	**<0.0001**
Error	76	25010242	329082		

Note: The term 'pair of cross-foster nests' is the main effect, while 'nest of origin' and 'nest of rearing' are nested in the main effect as indicated by the parentheses. 'Sex' is a factor, and 'rank in the within-brood age hierarchy' and 'human-visible coloration' are the two covariates. Significant values ($P < 0.05$) are shown in **bold-face**.

DISCUSSION

The present study provides the first experimental evidence of a significant effect of origin-related factors on UV coloration. As can be seen in Fig. 3, there is ample variation in UV coloration among similarly coloured individuals (e.g. among reddish-brown or among white birds), and this variation can partly be attributed to origin-related factors (i.e. genetics or pre-hatching maternal effects; see Table 1 and Fig. 2). The present study therefore provides fundamentally new results compared with a previous one on human-visible coloration (Roulin and Dijkstra, 2003). In this previous study, we examined whether human-visible coloration is heritable, whereas in the present study we assessed whether, independently of human-visible coloration, variation in UV reflectance is sensitive to origin-related factors (using a different set of individuals). Our results are therefore not a mere outcome of the fact that UV coloration and human-visible coloration are correlated (Fig. 3), since we controlled for this property.

Usually, behavioural ecologists assume that UV coloration acts as an honest signal of quality, because it is commonly considered as a structural trait that might be sensitive to the environment and body condition (Andersson, 1996). The fact that reflectance in the UV part of the spectrum was maximal when feathers had less concentrated pigments (Figs. 1 and 3) can be explained by two hypotheses. First, most of the variation in UV reflectance may be due to inter-individual variation in feather microstructure, the structure of white and reddish-brown feathers being clearly different to the human eye (personal observation). Second, melanin pigments absorb UV light (Kollias *et al.*, 1991), and since lighter coloured feathers have less concentrated melanin pigments, they would reflect more in the UV part of the spectrum. The first hypothesis is unlikely because following Andersson (1996) the small size of the structures producing UV coloration should make them easily perturbed by environmental factors. However, in the present study we did not detect any significant effect of the components 'nest of rearing' and 'rank in the within-brood age hierarchy' (Table 1), suggesting that UV coloration is not or is only weakly sensitive to environmental factors and to body condition. We therefore prefer the second hypothesis, which suggests that UV coloration is sensitive to origin-related factors because melanin pigments absorb UV light. It is indeed known that the expression of melanin-based traits is under strong genetic control (Majerus, 1998; Roulin, 2004a), potentially implying that related individuals reflect similarly in the UV part of the spectrum because they produce similar amounts of melanin pigments.

Because UV coloration is more sensitive to origin-related factors, this trait may signal some aspects of genetic quality in the same way as pigmented colours, since UV coloration and human-visible coloration are strongly correlated (Fig. 3). Previous studies have shown that in the barn owl human-visible coloration is associated with diet (Roulin, 2004b) and paternal care (Roulin *et al.*, 2001), suggesting that this trait is not neutral with respect to key life-history traits. Therefore, the signalling content of UV coloration may not be more 'special' than that offered by other wavebands. This may be the case if UV coloration and human-visible coloration have some genes in common, or if pigments differ in their three-dimensional structure [e.g. eumelanins and pheomelanins (Slominski *et al.*, 2004)], thus altering feather microstructures or the way they reflect UV light.

The barn owl is a nocturnal bird, and we wonder whether variation in both UV coloration and human-visible coloration has an adaptive function. Even though it has been suggested that the tawny owl (*Strix aluco*) does not possess UV-sensitive visual pigments (Bowmaker and Martin, 1978), it remains to be determined whether the barn owl has UV vision or not, and if this is the case whether owls assess UV coloration during daylight hours or at night. Although it is unclear whether barn owls can see in the UV part of the spectrum, reflectance in this range of waves may affect foraging efficiency (e.g. Viitala *et al.*, 1995; Church *et al.*, 1998) because small mammals such as rats, mice and gerbils (Jacobs *et al.*, 1991), and also subterranean mammals (Peichl *et al.*, 2005), have retained the ability to see UV light. Whatever the adaptive function of UV coloration in the barn owl, our results show that in at least one bird species variation in a UV trait is strongly heritable. This implies that in species with UV vision, melanin-based traits can signal aspects of genetic quality not only because they reflect in the human-visible range of coloration but also in the UV part of the spectrum.

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