Nestling colouration is adjusted to parent visual performance in altricial birds

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Abstract

Hitherto, most of the investigation on the perceptual efficacy of begging signals has dwelled on how patterns of nestling colouration adjust to predominant nest luminosity. However, visual sensitivity of birds varies across species, which raises the question of whether colouration of traits involved in begging displays is adjusted to parent visual capacities. Here, by comparing nestling colouration and visual sensitivity across 22 altricial bird species, we provide a first test of this hypothesis. Firstly, we assessed differences in performance of typical UV-tuned and violet-tuned bird eyes when looking at the nestling traits under the light regimes prevailing at their nests. Secondly, while controlling for common ancestry in a comparative approach, we explored variation in colouration of nestlings in relation to parent visual system. The colour discrimination model indicated a general higher performance of the ultraviolet over the violet eye at detecting gape and body skin traits in either open- or hole-nest light conditions. Gape colouration was associated with parental visual system as the nestlings of UVS species displayed more yellow and less pure ultraviolet mouths than the nestlings of VS species. Thus, our results agree with an adaptive parent–offspring communication scenario where the nestlings' colours tuned the perception capacities of their parents.

Introduction

Animal communication often depends upon perception of coloured visual signals. These signals may be directed at individuals of the same [e.g. signals of identity, status, age, sex or quality (Andersson, 1994)] or different species [e.g. bright colours displayed to predators (aposematic colourations) (Siddiqi et al., 2004) or function in species recognition (Endler et al., 2005)]. An obvious example of intra-specific signals based on colour occurs in parent–offspring communication in altricial birds where nestlings, while performing conspicuous calls and extravagant movements such as stretching of the neck and wing shivering, exhibit their coloured gapes to their parents (Mock & Parker, 1997). Gape colouration is assumed to provide parents with information on nestling level of satiation or health (e.g. Kilner, 1997; Saino et al.,

2000, 2003), or with a conspicuous target towards which parents direct their feeds (Heeb et al., 2003). Moreover, irrespective of gape colour, parental feeding decisions may also respond to the changes in body skin colouration (Jourdie et al., 2004; Bize et al., 2006), because it may also reflect the nestling health status (Jourdie et al., 2004; Soler et al., 2007).

Traditionally, the colours of structures associated with begging displays (e.g. gape and body skin colours) in altricial birds are viewed as an adaptation to increase their detectability to feeding parents (Kilner, 2006). Hitherto, most of the investigation on the efficacy of begging signals has dwelled on how patterns of nestling colouration adjust to prevalent light environments in the nests (Ficken, 1965; Kilner & Davies, 1998). Luminosity can drastically vary from low levels in cavity nests to high levels in open nests (Kilner, 1999; Hunt et al., 2003; Avilés et al., 2008). Indeed, it has been shown that gape colouration as seen by feeding parents contrasts strongly with the background of nests, and that gape designs enhance efficacy by contrasting strongly with body skin

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colouration in dark nest environments (Avilés *et al.*, 2008). Nestling detectability, however, is an insight of feeding parents and, thus, cannot be judged without considering the peculiarities of parent visual systems (Bennett & Thery, 2007).

Virtually, all bird species have four single-cone types in their retina (e.g. Bowmaker *et al.*, 1997). Evidence suggests that the spectral sensitivity of the different cone types is remarkably consistent across species, except for the variation in the short-wavelength sensitive (SWS1) ultraviolet/violet visual pigment λ_{max} (Hart & Vorobyev, 2005; Hart & Hunt, 2007). There are two main possible spectral locations for this class of cone visual pigments that renders two main types of ultraviolet colour vision in birds. Although both types are sensitive to ultraviolet light, ultraviolet sensitive birds (UVS hereafter) have a UV-biased SWS1 with a λ_{max} between 355 and 380 nm, whereas violet sensitive (VS hereafter) birds have it between 402 and 426 nm (Hart, 2002; Hart & Hunt, 2007). These differences between UVS and VS species render changes in the perception not only of ultraviolet and violet colours, but also of all nonspectral colours in which SWS1 were involved (Cuthill *et al.*, 2000). Nestling detectability, therefore, cannot be judged without taking into account the characteristics of the parent visual system, and selection favouring the evolution of particular nestling's colouration may depend on retinal characteristics of parents' eyes.

Evidence of an adjustment of coloured signals to the visual system of the intended receivers has recently been reported for plumage colouration in birds (Håstad *et al.*, 2005; Mullen & Pohland, 2008). The question of whether an adjustment in begging signals to parent visual capacities in their particular nest light environments exists, therefore, become more intriguing in the light of recent studies demonstrating variation in the visual sensitivity of birds (see above). In an adaptive parent–offspring communication scenario where nestlings coevolve with their parents, a relationship between colouration of nestling traits and visual characteristics of their parents should exist. Nestling detectability could be maximized if (i) certain nestling colours tuned the perception capacities of their intended receiver (i.e. parents); (ii) alternatively, parents may have evolved particular visual systems that maximized the detectability of nestlings in their nests; and finally (iii) both nestling colouration and visual capacities of parents could be the result of a co-adaptation process. The third scenario would more likely occur whether the levels of selection for nestling detectability and parent visual performance were similar. The first and the second scenarios, however, imply the higher level of selection for nestling detectability and parent visual performance, respectively.

Here, we provide a first test of the hypothesis that nestling colouration is adjusted to parental visual performance in altricial birds. In a first step, we adopted a visual model approach to assess differences in performance of

typical UVS and VS bird eyes when looking at the nestling traits of 22 altricial bird species. Our avian visual models integrate reflectance spectra of nestling traits, the reflectance of natural backgrounds, and light regimes prevailing at the nests with published information for photoreceptor sensitivities, photoreceptor noise, and the transmission properties of avian ocular media (Hart *et al.*, 2000; Hart, 2001a) to calculate differences in colouration as differences in an avian colour space (Vorobyev *et al.*, 1998). In a second step, we explored the variation in achromatic and chromatic components of nestling colouration in relation to parental visual systems by using a comparative approach. Because nestling conspicuousness should be particularly important in a parent–offspring communication context, we specifically focused on mouth and flange colour variation, which are traits typically considered in visual begging displays (see above). However, we also dealt with variation in body skin colouration (i.e. head and breast) as recent findings suggest that ultraviolet body skin colouration may serve in parent–offspring communication (Jourdie *et al.*, 2004; Bize *et al.*, 2006). As differences in detection of different nestling traits and species by UVS and VS eyes were significant, we predicted an across-species adjustment between the colouration of nestlings and the visual system of their parents.

Materials and methods

Study area

We measured nestling colouration, visual background at the nests and light environments in the surroundings of Guadix (37°18′N, 3°11′W), southern-east Spain, in March–June 2005–2007. The predominant habitat includes the cultivated areas with some remains of holm oak forest, grows of almond trees, and olive trees and other tree crops in irrigated areas surrounding villages. We collected data on nestling colouration on 520 nestlings of 22 species included in 14 families (Table S1). Hole-nesting species were mostly located within holm oak cork nest-boxes recently (2003–2005) installed. All sampled chicks were measured at a standard relative age during their ontogeny [i.e. when they were in the first third of its normal nestling development; with closed eye and no pin feathers (Avilés *et al.*, 2008)].

Spectral reflectance of nestlings

Reflectance spectra (300–700 nm) of nestlings were recorded using an Ocean Optics equipment [S2000 spectrometer connected to a deuterium-halogen light (D2-W, mini) by a coaxial reflectance probe (QR-400-7-UV-vis) and the OOIBase32^{TM} operating software (Ocean Optics, Inc., Dunedin, FL, USA)]. Reflectance was always measured with the probe mounted inside a matte black plastic tube to exclude biases by ambient

light. The probe was placed at a constant distance and reaching the nestling at 45. Measurements were relative and referred to a standard white (WS-2) and to the dark, which we calibrated before the measurement of each nestling. To standardize ambient light while data collection, all the measurements were taken within a portable hide with opaque wall set in the surrounding of the nests. To avoid nest abandonment, we always left at least one chick with the parents in the nest while collecting reflectance spectra. Nestlings were returned to their nest before 15 min from removal, and subsequent visits to these nests confirmed that our manipulation was non-invasive. We characterized the nestling colour patterns by measuring colour of gape and body skin as evidence suggests that these two types of traits may play a role in parent–offspring communication (Avilés *et al.*, 2008). Mouth colour was measured by gently keeping the gape open and introducing the probe to the centre of the upper mouthpart. Flanges were measured by maintaining the nestlings with the mouth almost closed, and placing the probe on the angle of the mouth-flanges, thus, avoiding confusion with mouth colouration. Head and breast are the most prominent parts of the body skin exhibited by nestlings during their begging displays. Therefore, skin colouration of the head (close to the ear) and the breast was measured, while trying to avoid growing feathers. All colour measurements were repeated three times per nestling trait. This technique provided highly repeatable measures of nestling colour for the three first PC scores of a PCA summarizing 96.72% of whole variation in nestling colouration for the four nestling traits (mouth: $R = 0.68$–0.78, $F_{196,391} = 7.60$–11.97, $P < 0.00001$; flange: $R = 0.69$–0.81, $F_{196,391} = 7.69$–13.90, $P < 0.00001$; breast: $R = 0.56$–0.67, $F_{196,391} = 4.77$–7.04, $P < 0.0001$; and head: $R = 0.59$–0.76, $F_{196,391} = 5.23$–10.61, $P < 0.00001$). Therefore, mean values per nestling were calculated and used in the analyses. Average reflectance spectra by gape and skin of the considered species in which model calculations were based are displayed in fig. A1 of Avilés *et al.* (2008).

Spectral reflectance of nest background and irradiance spectra

The nests of the 22 studied species can be classified in four different types according to the main material constituting the line of their nests (Table S1; Avilés *et al.*, 2008): (i) ground type species: those that build no nest at all and their nestlings only can contrast with the substrate (e.g. owls, falcons and coraciiforms); (ii) straw type species: those that build a nest cup mainly constituted by dry grass [e.g. Turdidae or magpies (*Pica pica*)]; (iii) branch type species: the nest line is mainly composed of thin shrub or tree branches and no additional material is provided to line the nest (e.g. pigeons); and (iv) wool type species: those that line the nest with wool or feathers [e.g. Corvids (except magpies) shrikes, swallows or tits].

When nest size made it possible, the entire nest was collected and saved in a plastic bag. For species having big nests, however, only a representative fraction of the nest line was collected and preserved in plastic bags. Entire nests or parts of the nest line were always collected from active nests once nestlings had fledged. When arriving to the laboratory we measured nest line colouration with an Ocean Optics spectroradiometer using the above equipment and specifications for nestlings. All measurements were taken in dark. For every collected nest, the material of the nest line was disaggregated and representative materials laid flat on a black table for measurements. We obtained representative reflectance spectra of nest background in these four different types of nests by sampling a whole of 29 nests of 18 species. Ten readings were taken at every nest. This technique provided repeatable measures of nest colour for the three first PC scores of a PCA summarizing 98.62% of whole variation in nest colour (PC1: $R = 0.54$, $F_{28,268} = 12.78$, $P < 0.0001$; PC2: $R = 0.44$, $F_{28,268} = 29,61$, $P < 0.0001$; and PC3: $R = 0.64$, $F_{28,268} = 18.57$, $P < 0.0001$). Therefore, mean values per nest type were calculated based on mean values of species within the same group. Average reflectance spectra of nest background in the four types of nests in which model calculations were based are displayed in Fig. A2 in Avilés *et al.* (2008).

Ambient light measurements were collected during the morning (09.00–11.00 AM), when parental provisioning to the nests is maximal. Briefly, we used a cosine-corrected fibre-optic probe (P400-1-UV-VIS; Ocean Optics) with a 180° angle of acceptance and a measurement surface of 6 mm in diameter (CC-3-UV; Ocean Optics). The spectrometer was calibrated with light source of known colour temperature (LS-1-CAL; Ocean Optics). We measured the ambient light at open areas (10 readings) and in the entrance of nest-boxes (10 readings) with the measurement surface oriented to the skyward or roof, respectively, and the probe held perpendicular to the ground. We transformed irradiance readings into photon units as described by Endler (1990) and calculated mean values across open and hole nests to obtain average irradiance spectrum in these two nest environments. This is justified by the high repeatability of the PC1 scores of a PCA summarizing 96.34% of whole variation in nest colour irradiance at these two nest environments ($R = 0.98$, $F_{1,23} = 272.30$, $P < 0.0001$). Average irradiance spectra in open and hole nests in which model calculations were based are displayed in fig. A3 in Avilés *et al.* (2008).

Parental visual system

Information on vision type only exits for a few species (seven of 22 species) and most of the families (11 of 14 families) among the sampled in this study (Table S1). The VS type is the ancestral state in birds although the

UVS state has evolved independently at least four times (Ödeen & Håstad, 2003). However, evidence coincides that most of Passeridae are of the UVS type (Bowmaker *et al.*, 1997; Hart *et al.*, 1998, 2000) with the exception of members of the groups Corvidae and Tyrannidae (Ödeen & Håstad, 2003). Furthermore, no splits in the type of vision have so far been reported within a bird family (Ödeen & Håstad, 2003; Hart & Hunt, 2007) which suggests that vision type has a strong phylogenetic inertia in birds (Cuthill *et al.*, 2000). Therefore, we used cone sensitivities of a typical UVS bird for all Passeridae with the exception of the members of the family corvidae that were modelled as a VS species. The remaining sampled species were treated as VS birds (Table S1).

Avian colour space modelling

As a measure of colour distance between the different body parts of chick and the nest background, we used the discriminability model of Vorobyev & Osorio (1998) as developed for the tetrachromatic visual system of birds in its long form (Vorobyev *et al.*, 1998). The model has been demonstrated to describe precisely visual discrimination in birds (Vorobyev & Osorio, 1998; Goldsmith & Butler, 2005), and, recently, it has been successfully incorporated in comparative studies of bird colouration (e.g. Siddiqi *et al.*, 2004; Håstad *et al.*, 2005; Doucet *et al.*, 2007; Gómez & Théry, 2007; Avilés *et al.*, 2008). The model establishes a chromatic distance ΔS which describes the colour contrasts between two coloured patches as:

$$
\begin{aligned}
(\Delta S)^2 = [&(e_1 e_2)^2 (\Delta f_4 - \Delta f_3)^2 + (e_1 e_3)^2 (\Delta f_4 - \Delta f_2)^2 \\
&+ (e_1 e_4)^2 (\Delta f_2 - \Delta f_3)^2 + (e_2 e_3)^2 (\Delta f_4 - \Delta f_1)^2 \\
&+ (e_2 e_4)^2 (\Delta f_3 - \Delta f_1)^2 + (e_3 e_4)^2 (\Delta f_2 - \Delta f_1)^2] / \\
&[(e_1 e_2 e_3)^2 + (e_1 e_2 e_4)^2 + (e_1 e_3 e_4)^2 + (e_2 e_3 e_4)^2]
\end{aligned}
\tag{1}
$$

where Δf_i, is the log ratio of the quantum catches for cone i, for chick trait A and B and e_i is the signaling noise for each cone class i.

$$
\Delta f_i = \log \frac{\int_{300}^{700} R_A(\lambda) I(\lambda) S(\lambda) d\lambda}{\int_{300}^{700} R_B(\lambda) I(\lambda) S(\lambda) d\lambda},
\tag{2}
$$

where $R_A(\lambda)$ represents the reflectance of the patch A, $R_B(\lambda)$ is the reflectance of the patch B, $I(\lambda)$ is the spectral irradiance of the illuminant, and $S(\lambda)$ is the spectral sensitivity of the receptor i. From the eqn 1, ΔS is expressed in jnd (just noticeable differences), where 1.0 jnd is the threshold value for discrimination of two colours. Thus, $\Delta S < 1.0$ indicate colours that are indistinguishable, whereas $\Delta S > 1.0$ indicate the magnitude of discrimination above threshold (Osorio & Vorobyev, 1996; Siddiqi *et al.*, 2004; Eaton, 2005; Avilés, 2008). Spectral sensitivities have not been measured in most of

the sampled species (see Supporting Information), but following recently published literature, we used spectral sensitivity data from the blue tit *Cyanistes caeruleus* and the peafowl *Pavo cristatus* as representative of the UVS and the VS system respectively (e.g. Håstad *et al.*, 2005; Gómez & Théry, 2007; Avilés *et al.*, 2008).

Discriminability of stimuli depends on the relative numbers of the different cone types in the avian retina that may vary quite a lot between different species (Hart, 2001b). Unfortunately, information on cone ratios for the sampled species only exists for the blackbird *Turdus merula* (Hart, 2001b) which precludes using species-specific data in the model. However, the ratios between the different cone types for the 22 species reported in Hart (2001b) do not significantly differ between UVS and VS species (one-way ANOVAs; UVS/VS single: $F_{1,20} = 0.24$, $P = 0.62$; SWS single: $F_{1,20} = 0.04$, $P = 0.83$; MWS single: $F_{1,20} = 1.92$, $P = 0.18$; LWS single: $F_{1,20} = 1.78$, $P = 0.20$); which suggests that differences in discriminability between average UVS and VS eyes, if exited, would not be due to differences in cone type proportions between UVS and VS species. Therefore, following recently published works (Håstad *et al.*, 2005; Gómez & Théry, 2007; Avilés *et al.*, 2008), for the noise calculations we used cone proportions of 1, 1.92, 2.68 and 2.7 for UVS (Hart *et al.*, 2000) and, 1, 1.9, 2.2 and 2.1 for VS (Hart, 2002) and assumed that the signaling noise for each cone was independent of light intensity.

$$
e_i = \omega / \sqrt{\eta_i},
\tag{3}
$$

where ω is the Weber fraction (taken as 0.05) and η_i is the relative density of the cone class i on the retina.

Because we were interested in studying the role of differences in visual perception on the conspicuousness of nestling traits, calculations were repeated for every sampled species and nestling trait by using both spectral sensitivity data and cone proportions of a typical UVS and VS bird.

Colour variables

The model by Vorobyev–Osorio defines the colour discrimination based on the integration across the entire range of visual wavelengths and, therefore, does not provide information on the relative contributions of specific wavelengths causing perceptual differences. Beyond perception of nestlings in their nests, we also aimed to study across species variation in nestling colouration in relation to parent visual systems. Previous works have shown that ultraviolet (Hunt *et al.*, 2003; Jourdie *et al.*, 2004) and yellow vs. red (Heeb *et al.*, 2003) colourations of nestling traits may enhance chick detection by parents. In addition, the well-known absence of blue–green skin colours from altricial chicks (e.g. Baicich & Harrison, 1997) was confirmed by spectrophotometric measurements (Avilés *et al.*, 2008). Therefore, reflectance data collected on nestlings were summarized by

calculating seven colour variables focusing on the ultra-violet (300–400 nm), yellow (550–625 nm) and red (625–700 nm) wavelengths. First, we summed reflectance in the whole spectrum (300–700 nm) to calculate an index of total brightness (e.g. Andersson *et al.*, 1998). However, brightness is difficult to compare among species that differ in colour patterns because different wavelengths may contribute to its whole value in different species. Therefore, to explore the importance of different wavelength intervals differentially contributing to total brightness in different species, we also calculated UV, yellow and red intensities as the means of reflectance values in 5-nm intervals from 300 to 400 nm, from 550 to 625 nm and from 625 to 700 nm, respectively. In addition, we calculated UV, yellow and red chroma as the ratio between the summed reflectance values at every 5-nm intervals within the corresponding region and the summed reflectance values at every 5-nm intervals within the whole spectrum (300–700 nm) (Andersson *et al.*, 1998; Bize *et al.*, 2006).

Nesting site and sibling competition

Irradiance measurements collected in open- and hole-nests have shown that hole-nests are less illuminated than open-nests (Avilés *et al.*, 2008), which has favoured the evolution of coloured traits involved in visual communication adjusted to the predominant light conditions in the nests (Avilés *et al.*, 2006, 2008). Therefore, a spurious correlation between nestling colouration and parental visual systems may arise from a nonrandom distribution of species differing in parental visual systems between open- and hole-nests. To avoid this potential source of biases, species were classified either as hole nester or as open nester based on information provided by Harrison (1975) (Table S1).

In a previous study, we have found that species with larger clutch sizes show larger general achromatic contrasts with the nest (Avilés *et al.*, 2008), that can be interpreted as nestling colouration being adjusted to the levels of sibling competition, as estimated by brood size, within nests (e.g. Kilner & Davies, 1998). Therefore, a spurious relationship between nestling colouration and parent visual system may arise if species with variable levels of sibling competition (as estimated by clutch size) were not evenly distributed between UVS and VS species. Therefore, to control for this possibility, we used mean clutch size for each species as reported in Cramp (1998) as an index of sibling competition.

Statistical analyses

Distribution of chromatic contrasts between nestling traits and the nest background did not depart from normality (Kolmogorov–Smirnov tests, $P > 0.2$) and, therefore, we used paired t-tests for dependent samples to explore the influence of bird visual systems (UVS vs.

VS) on the conspicuousness of the different nestling colour patterns of hole- and open-nester species.

Analyses considering a set of colour variables should consider that colour variables are typically interrelated (Endler, 1990; Cuthill *et al.*, 1999). Mean values per species for the seven colour descriptors at each body region (i.e. flange, mouth, head and breast) were therefore entered into four principal component analyses (PCA) to yield colour scores per species that were then used in the subsequent analyses (Table S1). The two first principal components explained 79%, 77%, 73% and 79% of across-species variation in colouration at the flange, mouth, head and breast, respectively (Table 1). The contribution of every colour variable in each axe of the four PCA is reported in Table 1. The logic behind the use of scores from PCA on describing among species variation in nestling colouration can be summarized in the following example. The second principal component (PC2) for the flanges explained 33% of across-species variation in colour (Table 1). Red intensity and red chroma loaded negatively (eigen values = −0.79 and −0.87, respectively), whereas UV chroma loaded positively (eigen value = 0.75). Therefore, species with a high positive PC2 colour score for the flanges displayed an overall more saturated ultraviolet, and showed a less red colouration than individuals with negative PC2 colour scores.

All colour variables for the flange, mouth and head and the brightness for the breast approximately fitted a normal distribution (Kolmogorov–Smirnov tests, $P > 0.2$), while UV intensity and brightness for the breast were log transformed before the analyses. We tested for the relationships of gape colouration with parental visual system with General Linear Models (GLM) with variables defining gape colouration (i.e. PC1 and PC2 colour scores for flanges and mouth) as dependent variables and parental visual system, nesting habit and log-transformed clutch size as independent variables. Finally, to adjust for the potentially confounding effect of body size, we entered untransformed body mass (Kolmogorov–Smirnov test,

Table 1 Factor loadings of axes from principal component analyses performed on colour variables at each body region.

	Flanges		Mouth		Breast		Head	
	PC1	PC2	PC1	PC2	PC1	PC2	PC1	PC2
UV intensity	**0.88**	0.02	**0.89**	0.29	0.47	**0.67**	0.20	**0.94**
UV chroma	−0.08	**0.75**	0.43	**−0.49**	**0.88**	−0.26	−0.17	**0.64**
Yellow intensity	**0.80**	−0.29	−0.34	**0.80**	−0.25	0.62	**−0.94**	−0.13
Yellow chroma	**0.75**	−0.53	−0.41	**0.88**	**−0.71**	0.58	**−0.81**	−0.37
Red intensity	−0.48	**−0.79**	**−0.92**	−0.22	**−0.79**	−0.38	**0.89**	−0.36
Red chroma	−0.44	**−0.87**	**−0.90**	−0.05	**−0.88**	−0.30	**0.86**	−0.45
Brightness	**0.89**	−0.10	**0.69**	0.49	−0.10	**0.78**	0.31	**0.68**
% Variance	46	33	48	29	43	30	47	32

Percentage of variance explained by each axis is also shown.
Loadings contributing more are displayed in bold.

$P > 0.2$) in the GLM together with the traits of interest. A second GLM was run to study the relationship between body skin colouration (i.e. PC1 and PC2 colour scores for the head and the breast) and parental visual system while controlling for nesting site, clutch size and body mass. Model selection was performed by removing (P-thresholds set at 0.05), one by one, the effects that were the furthest from statistical significance.

Phylogenetic analyses

Taxonomic groups such as species cannot be considered statistically independent observations due to the confounding effects of common ancestry (Felsenstein, 1985). Thus, we reassessed the association between nestling colour traits and visual system using Felsenstein's (1985) independent contrasts method as implemented in the computer program PDAP (version 6.0, module PDTREE) by Garland et al. (1999) and Garland & Ives (2000). Our phylogenetic hypothesis was based on the molecular phylogeny of Sibley & Ahlquist (1990), completed with recently published information (Sheldon & Winkler, 1993; Blondel et al., 1996; Cibois & Pasquet, 1999) (Fig. S1). This tapestry tree reconstructs branching and estimates branch lengths above the family level. At lower taxonomic level, and when the phylogenetic distance had not been previously established, we adopted Sibley & Ahlquist (1990) convection and set all branch lengths among genera within a family to 3.4 $\Delta T50H$ units, and among species within genera to 1.1 $\Delta T50H$ units (Bennett & Owens, 2002). We checked whether the phylogenetic contrasts of the colour variables were adequately standardized by plotting absolute values of standardized contrasts vs. their standard deviations (square roots of sums of corrected branch lengths) (e.g. Garland et al., 1991; Garland, 1992; Pagel, 1992). In no case did we find a significant correlation ($P > 0.1$), therefore, the resulting contrasts for each variable were used to perform GLM through the origin.

We adopted a second phylogenetic approach to deal with the fact that visual system is not a continuous variable and, following Garland et al. (1993) we used phylogenetic analysis of variance by computer simulations. Briefly, this statistical technique proposes the use of empirically scaled computer simulations of character evolving along known phylogenetic trees to obtain empirical F-distributions for hypothesis testing (Garland et al., 1993). Based on our composite phylogeny (see above), we performed 1.000 simulations with the program PDSIMUL by simulating a gradual and Brownian motion between two given traits (see details in Garland et al., 1993). After defining the two groups of species regarding visual system (i.e. UVS vs. VS), the software PDANOVA calculates the within- and between-group sums of squares, the mean squares and the corresponding F-ratio, for each of these simulations as in a conventional ANOVA. If the F-ratio obtained on the raw data exceeds the upper 95th percentile of the empirical null distribution of F-ratios, we would conclude that differences in the trait of interest between visual systems would be significant after controlling for phylogenetic inertia (Garland et al., 1993).

Results

Performance of UVS and VS eyes

Gaping traits (i.e. flanges and mouth) as well as body skin (i.e. breast and head) were significantly more conspicuous when they were perceived by an UVS eye than by a VS eye in hole-nester species (paired t-tests, $t > 5.99$, $P < 0.00004$ for the four nestling traits). The colour discrimination model indicated that all the sampled hole-nester species possessed at least one nestling trait for which differences in estimated performance between the visual systems exceeded the threshold value ΔS of 1.0 jnd [13 of 14 (85.7%) species for the flanges, and the head, and 100% of species for the mouth and the breast; Fig. 1a,c,e,g]. Noticeable differences in estimated performance arose from a general higher performance of the ultraviolet eye over the violet eye at detecting nestling traits within holes (i.e. points below the lower dashed line; Fig. 1a,c,e,g). Only flanges of *Coracias garrulus* were better perceived with the violet eye (Fig. 1a).

Gape and body skin of nestlings of open nester species, except for the head of *Columba palumbus* (Fig. 1h), were also more conspicuous when viewed by an UVS eye than by a VS eye (paired t-tests, $t > 5.81$, $P < 0.0006$ for the four nestling traits) (Fig. 1). Differences in conspicuousness of nestling traits between the UVS and the VS eyes were in all cases larger than the threshold value for discrimination set at 1.0 jnd (Fig. 1b,d,f,h).

Nestling colouration in relation to parental visual system

Gape colouration was significantly associated with parental visual system among the sampled species once we controlled for the significant effect of nesting site (Table 2). Specifically, nestlings of UVS species have more brilliant, more intensely ultraviolet and more yellow coloured flanges (i.e. higher PC1 scores for flanges, Table 1) than nestlings of VS species (Fig. 2a,b). In addition, the nestlings of UVS species displayed more yellow and less pure ultraviolet mouths than the nestlings of VS species (i.e. higher PC2 scores for mouths, Table 1) (Fig. 2c,d). Analyses performed on phylogenetic independent contrasts, and phylogenetically controlled ANOVAS with PC2 scores for mouths as dependent variable, confirmed the found pattern for the mouth (Table 2; phylogenetically controlled ANOVA: PC2 scores for mouth, $P = 0.023$). The relationship between PC1 scores for the flanges and parental visual system, however, was not robust to statistical control (Table 2;
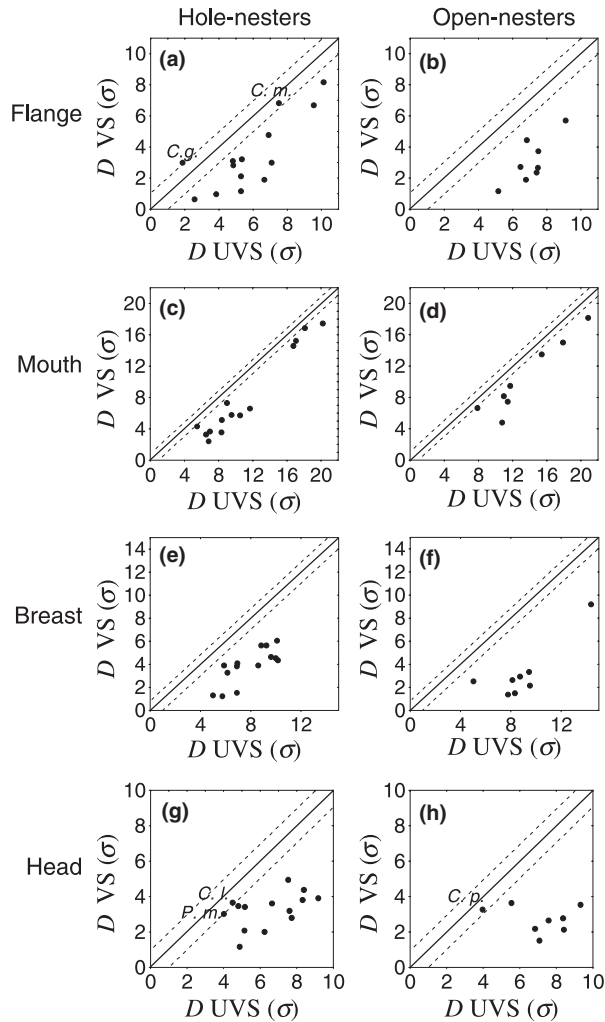
Fig. 1 Differences in nestling colour detectability against the nest when viewed by an UVS or a VS bird. Hole-nesters [a (flange), c (mouth), e (breast) and g (head)], open-nesters [b (flange), d (mouth), f (breast) and h (head)]. Solid line indicates equal chromatic contrasts between nestling traits and the nest background for both vision systems. Points below the solid line correspond to traits that are more conspicuous to an UV than to a violet sensitive system, whereas points above the solid line are traits that are more conspicuous to a violet than to an UV sensitive system. The two dashed lines indicate the threshold values for discrimination ($\Delta S = 1.0$ jnd) between the ultraviolet and the violet sensitive visual systems.

phylogenetically controlled ANOVA: PC1 scores for flanges, $P = 0.11$).

Body skin colouration (head and breast) of nestlings, however, did not differ with parental visual systems when the effects of body mass, nesting site and clutch size were considered (Table 3). This pattern remained unaltered when phylogenetic relationships were considered (Table 3; phylogenetically controlled ANOVAS: $P > 0.3$ in all cases).

Discussion

Performance of UVS and VS eyes

The colour discrimination model estimated a general higher performance of the UVS eye over the VS eye at detecting gape and body skin traits in either open- or hole-nest light conditions. Provided that UVS and VS cones have the same level of noise in open- and hole-nest light conditions, UV vision is beneficial for discriminating nestling colour signals. Previous studies have already shown a better performance of the UVS over the VS eye at discriminating colour signals as bird plumage (Vorobyev *et al.*, 1998), or fruit colours under bright light regimes (Schaefer *et al.*, 2007).

We have not found evidence that the advantage in estimated performance of the ultraviolet over the violet sensitive visual system was associated with a particular nesting environment (hole- vs. open-nests), and so our results do not support the scenario in which parent vision evolved in altricial birds to favour nestling discrimination. Previous attempts have also failed to establish a connection between ecological attributes of birds such as habitat type and foraging method and the spectral sensitivities of the different cone types across avian species (Hart & Vorobyev, 2005). Earlier spectrophotometric analyses of visual pigments revealed a wider range of avian taxa possessing a violet sensitive visual system (Hart, 2001a). Only some species belonging to the orders Psittaciformes and the Passeriformes have a clear-cut UV-biased vision (Hart, 2001a). These findings together with the fact that two palaeognathus species also possessed the violet system (Wright & Bowmaker, 1998) have lead largely to assume that the character UVS/VS has a strong phylogenetic inertia in birds. Recent findings, however, have challenged this assumption. Ödeen & Håstad (2003) have sequenced a part of the gene coding for the ultraviolet or violet absorbing opsin in the retina of several bird species and found that UVS vision is present inter-scattered with VS vision in at least nine families of four different avian orders. Thus, the UVS character has independently been acquired in each of these groups, which would suggest that the distribution of the UVS/VS character within the avian phylogeny may have an adaptive basis. It must be highlighted that our visual model approach exclusively allowed us to compare the performance of retinal designs varying in the spectral locations of the pigments that appear in the short-wavelength sensitive class of visual cones. Variation in other attributes of avian retina, such as the proportion of the different cone type, their disposition, quantity of yellow–orange carotenoids pigments, etc., may, however, modulate eye spectral sensitivities in response to specific microhabitat conditions (Bowmaker & Martin, 1978; Hart, 2001a). For instance, aerial insectivorous as the barn swallow or the sand martin *Riparia riparia* show a clear predominance of cones in their retinas as well as very few orange and yellow carotenoids

Table 2 Results of general linear models, including variables defining gape colour (PC1 and PC2 for flanges and mouth) as dependent variables, and nesting site, parental visual system, body mass and clutch size as independent variables.

Variables in the model	F	d.f.	P-value	PC1 (flange) β	(SE)	t	P-value	PC2 (flange) β	(SE)	t	P-value	PC1 (mouth) β	(SE)	t	P-value	PC2 (mouth) β	(SE)	t	P-value
Raw data																			
Excluded terms																			
Body mass	0.55	4,14	0.69																
Clutch size	1.62	4,15	0.22																
Included terms																			
Intercept	0.62	4,16	0.65			0.70	0.48			0.05	0.95			1.24	0.22			0.05	0.96
Nesting site	9.47	4,16	0.0003	−0.55	0.14	4.05	0.0006	0.08	0.22	0.36	0.72	0.30	0.16	3.96	0.0008	−0.25	0.16	4.28	0.0004
Parental visual system	8.06	4,16	0.0009	−0.58	0.14	3.89	0.0009	0.12	0.23	0.53	0.60	−0.63	0.16	1.89	0.07	−0.68	0.16	1.56	0.13
Contrasts																			
Excluded terms																			
Body mass	0.32	4,14	0.86																
Clutch size	1.11	4,15	0.38																
Included terms																			
Nesting site	2.71	4,16	0.0006	0.64	0.16	3.79	0.001	−0.13	0.22	0.61	0.54	0.65	0.17	3.89	0.0009	0.32	0.20	1.66	0.11
Parental visual system	8.56	4,16	0.06	0.31	0.17	1.82	0.08	−0.08	0.22	0.35	0.73	−0.16	0.16	0.93	0.36	0.48	0.20	2.53	0.01

Analyses were performed on raw data (i.e. species as independent data points) and on phylogenetically independent contrasts. In the last case, the regression line was forced through the origin and degrees of freedom were corrected by subtracting the number of polytomies in the phylogenetic tree.

Model selection was carried out by removing, one by one, the effects that were the furthest from statistical significance.
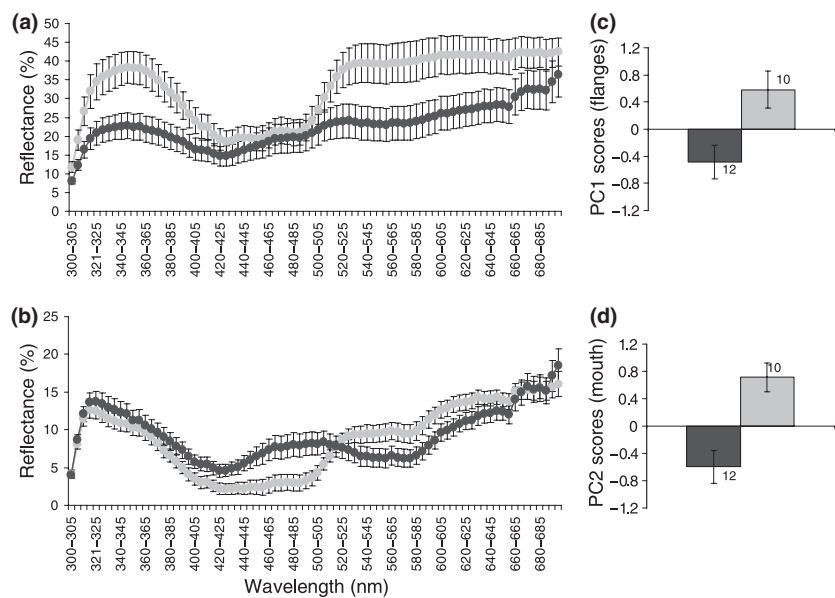

Fig. 2 Average (± standard error) nestling gape colour [a (% of reflectance for flange), b (PC1 for flange), c (% of reflectance for mouth), d (PC2 for mouth)] in relation to parental visual system [VS species (black dots and bars) and UVS species (grey dots and bars)]. PC scores came from two PCAs combining seven colour descriptors at flanges and mouths respectively (see Materials and methods). The corresponding factor loadings are displayed in Table 1. Numbers of sampled species are on bars.

oil droplets probably as an adaptation to capture small, fast moving insect (Hart, 2001a). Therefore, although we have not found that the advantage in performance of the ultraviolet vs. the violet eye was associated with a particular nesting environment, anatomical studies analysing retina designs in species with a variable range of nesting environment would be necessary to discard a possible adaptive role of avian vision through enhanced nestling discriminability.

If UVS bird vision appears to perform better than VS bird vision when discriminating nestling in the nest in relation to gaping structures, why do not all birds evolve UVS vision? Several nonmutually exclusive explanations are possible. It could be that the optimal vision for locating nestlings within the nests, or distinguishing between nestlings with variable body colouration differed from that required for escaping from predators, searching mates and/or searching for food. Secondly, it is possible that even with a VS visual system birds may reach a good level of discrimination of their nestlings in the nests. In our sample, chromatic contrasts of nestling traits against the nest were largely over the discrimination threshold value

Table 3 Results of general linear models, including variables defining skin colour (PC1 and PC2 for heads and breast) as dependent variables, and nesting site, parental visual system, body mass and clutch size as independent variables.

Excluded terms	F	d.f.	P-value
Raw data			
Nesting site	0.51	4,14	0.73
Clutch size	0.89	4,15	0.49
Body mass	1.77	4,16	0.18
Parental visual system	1.51	4,17	0.24
Intercept	0.01	4,17	0.99
Contrasts			
Parental visual system	0.13	4,14	0.96
Body mass	0.41	4,15	0.80
Nesting site	0.43	4,16	0.78
Clutch size	1.26	4,17	0.32

Analyses were performed on raw data (i.e. species as independent data points) and on phylogenetically independent contrasts. In the last case, the regression line was forced through the origin and degrees of freedom were corrected by subtracting the number of polytomies in the phylogenetic tree.
Model selection was carried out by removing, one by one, the effects that were the furthest from statistical significance.

ΔS of 1.0 jnd when the calculation was not only based on an UVS visual system (mean $\Delta S = 8.29$, standard deviation = 3.63, range = 1.88–20.84), but also when based on the parameters of a VS visual system ($\Delta S = 4.70$, standard deviation = 3.80, range = 0.64–18.17). Finally, perhaps the adjustment of nestling colouration to parent visual system was a more parsimonious evolutionary trajectory than the evolution of parent visual system. Indeed, phylogenetics constraints on gape colouration seem to be weak as closely related species display variable gape colourations (Kilner & Davies, 1998), while the visual system has a strong phylogenetic inertia in birds (Cuthill *et al.*, 2000).

It must be highlighted that our discriminability model describes whether a colour distance is big enough to be detected or not. However, it is not obvious that the model predicts detectability beyond the threshold. Our model rests on the assumption that the signalling noise for each cone was independent of light intensity (see above), however, the parents' reaction to nestling colours may saturate at twice detection threshold and not discriminate between even larger differences. Therefore, behavioural experiments should be performed or referred to that show when parent reaction saturates to qualify the better performance of the UVS eye over the VS eye at detecting nesting traits. Finally, although our results were robust to the variation among UVS and VS species in reported cone proportion (see Materials and methods), spectral sensitivity data for most of the considered species were not available in the literature, and therefore we parameterized the model with blue tit and peafowl data as representative of typical ultraviolet and violet sensitive birds, respectively. Thus, before

sensitivity data for all these species are available we cannot preclude that model parameterization was not adequate enough.

Nestling colouration in relation to parental visual system

We have found that chromatic components of gape but not body skin design were associated with parent visual system among the sampled species. More concretely, the nestlings of UVS species showed generally more yellow and less pure ultraviolet mouths than the nestlings of VS species once the possible confounding effect of nesting site and phylogenetic inertia was considered. Flanges also tended to be more ultraviolet and yellow among the nestlings of UVS species than among the nestlings of VS species once we control for nesting site, although this result was not robust after considering the effect of common ancestry ($P = 0.08$).

Early comparative studies showed that mouth colouration of nestling passerines ranges from yellow pale to depth red (Ficken, 1965). More recently, Hunt *et al.* (2003) have reported that both mouths and the surrounding flanges of eight passerines showed a striking peak of reflectance in the ultraviolet. Also, the nestlings of nonpasserine altricial birds have gape structures in which ultraviolet and yellow–red shades are predominant (Avilés *et al.*, 2008). Several sources of evidence provide support for a role of ultraviolet and yellow gape colourations in nestling detectability. Indeed, Jourdie *et al.* (2004) have shown that the mouth and the body skin of nestlings of the European starling (*Sturnus vulgaris*) substantially reflect in the ultraviolet wavelength [see also Soler *et al.*, 2007 for the spotless starling (*Sturnus unicolor*)], and that chicks in which this reflectance was artificially reduced gained less mass than controls (see also, Ayala *et al.*, 2007). Also, the finding that the nestlings of the great tits (*Parus major*) with artificially painted yellow flanges and mouths were preferentially fed by their parents over red-painted siblings under poor illuminated conditions suggests a detectability role for yellowness of gape structures (Heeb *et al.*, 2003). The relative advantage of the UV vision at detecting chromatic contrasts is assumed to be the consequence of a lower level of overlap between the violet- and the blue-sensitive cone types (Schaefer *et al.*, 2007), which leads to an increase in the number of discriminable colour shades (Vorobyev, 2003) in both the ultraviolet (300–400 nm) and the human visible part of the colour spectra (400–700 nm) (Eaton, 2005). The high discrimination capacity of UVS eyes may explain why the nestlings of UVS species displayed more yellow and less pure ultraviolet mouths than nestlings of VS species. In addition, physiological constraints or costs associated with the production of the yellow and ultraviolet shades of gape structures may differ and, consequently, may provide parents with different kind of information (e.g.

nestlings detectability, nestlings condition, etc.) that would explain the higher importance of yellow chroma at the expenses of the ultraviolet signal for the nestlings of UVS species.

In a previous study, we have found that the nestling colour designs are adjusted to the ecological conditions (i.e. nest site) where the begging displays occur to enhance signal efficacy (Avilés *et al.*, 2008). Based on recent evidence that avian visual capacities varied across species, here we have hypothesized that in a scenario of parent–offspring visual communication, efficacy of coloured begging signals may also arise through an adjustment of nestling colouration to the visual system of the parents. This hypothesis predicts changes in nestling colouration related to the visual system of the species. We have provided a functional basis for this hypothesis as we have shown that a typical UVS bird visual system performs consistently better at detecting nestlings in the nests than a typical VS bird over a wide range of luminal conditions. In addition, we have found that the colouration of gaping structures implicated in begging displays varied with parent visual system (i.e. UVS vs. VS) across the studied species. Although more data would be desirable to preclude that bird vision evolved to favour nestling discrimination our findings globally agree with the hypothesis that the nestlings have been selected to increase their detectability for feeding parents through tuning of their gape colouration to their parent visual performance.

Acknowledgments

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Supporting information

Additional supporting information may be found in the online version of this article:

Figure S1 Phylogenetic relationships among species considered based on analyses of DNA-DNA hybridization (Sibley & Ahlquist, 1990). The scale for branch length is given in the bottom left.

Table S1 Raw data in which analyses were based. See main text for sources of data.

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