

Dark Nests and Conspicuousness in Color Patterns of Nestlings of Altricial Birds

Jesús M. Avilés,^{1,2,*} Tomás Pérez-Contreras,^{1,†} Carlos Navarro,^{1,‡} and Juan J. Soler^{1,§}

1. Departamento de Ecología Funcional y Evolutiva, Estación Experimental de Zonas Áridas (Consejo Superior de Investigaciones Científicas), General Segura 1, E-04001 Almería, Spain;

2. Departamento de Biología Animal y Ecología, Universidad de Granada, E-18071 Granada, Spain

Submitted February 26, 2007; Accepted October 31, 2007;
Electronically published January 15, 2008

Online enhancements: appendix table, figures.

ABSTRACT: Nests of altricial birds exhibit variable spectral properties that may affect the efficacy (conspicuousness) of the colored begging traits that a nestling displays to its parents. Here we explored whether selection for efficient perception has favored the evolution of nestling color designs that maximizes nestling detectability in variable light environments. Visual models were used to estimate how parents perceive the coloration of mouths, flanges, heads, and breasts of nestlings within their nest in 21 species of European birds. We show that the largest chromatic and achromatic contrasts against the nest background appeared for nestling mouths and flanges, respectively. Nestlings of open-nesting species showed a larger general achromatic contrast with the nest than did nestlings of hole-nesting species. However, nestlings of hole nesters showed a more evident achromatic contrast between flanges and other traits than did nestlings of open nesters. In addition, species with larger clutch sizes showed larger general achromatic contrasts with the nest. Gaping traits of open-nesting species contrasting with the nest background were better perceived under rich light regimes than under poor ones. These findings are consistent with a scenario in which selection for nestling detectability in dark environments has favored the evolution of particular achromatic components of gape coloration but also nestling traits that enhance signal efficacy by maximizing color contrasts within a nestling.

Keywords: altricial birds, nestling coloration, dark nest, detectability, begging, gape color.

Avian nestlings commonly beg to obtain food from their parents. Begging comprises vocal and visual displays, and the details of this behavior, as well as the physical properties of nests in which these displays are performed, are highly variable between species. Among the visual components of begging, gape coloration has received increased interest (e.g., Kilner and Davies 1998; Kilner 1999, 2006; Saino et al. 2000, 2003; Heeb et al. 2003; Hunt et al. 2003; Ayala et al. 2007). Beyond the coloration of traits involved in gaping behavior (i.e., mouths and flanges), recent findings have demonstrated that chromatic characteristics of the skin at other body regions of nestlings may also function as visual begging signals. Indeed, Jourdie et al. (2004) have shown that the skin of the mouth and body of nestlings of the hole-nesting European starling (*Sturnus vulgaris*) is a substantial reflector 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 did controls. Also, Bize et al. (2006) have recently reported that body skin reflectance for the hole-nesting Alpine swift (*Apus melba*; Apodiforme) showed a peak in the ultraviolet wavelength that influenced parental feeding decisions. However, no attempt has been made to assess nestling color design in terms of signal efficacy theory. Efficacy of any visual signal (i.e., conspicuousness) is influenced by the color of the signal itself, the environment in which the signal is perceived, the perceptual abilities of the intended receiver, and the receiver's physiology (Endler 1990; Guilford and Dawkins 1991; Vorobyev et al. 1998; Théry 2006). Thus, a more thorough understanding of the evolution of nestling colorations will require nestling conspicuousness assessments from the perspective of the adult birds.

Among the factors influencing signal efficacy, light available for reflection plays a major role (Endler 1990; Endler and Théry 1996; Gómez and Théry 2004; Théry 2006). Nest light environment often varies between species, with light levels inside cavity nests being considerably lower

* Corresponding author; e-mail: javiles@eeza.csic.es.

† E-mail: tomapc@eeza.csic.es.

‡ E-mail: cnavarro@eeza.csic.es.

§ E-mail: jsoler@eeza.csic.es.

than levels in open nests (Kilner 1999; Hunt et al. 2003). Thus, nest luminosity may act as a strong selective factor that influences the evolution of nestling color designs used in parent-offspring communication in altricial birds (Ficken 1965; Kilner and Davies 1998; Heeb et al. 2003). Previous studies have focused on reporting variation in the coloration of gaping structures in relation to the type of nest on the basis of human-based methods for the assessment of coloration (Kilner and Davies 1998). Also, the finding that nestlings of great tits (*Parus major*) with artificially painted yellow gapes were preferentially fed by their parents over red-painted siblings under poorly illuminated conditions suggests a role of nest luminosity in detectability of colored gape structures (Heeb et al. 2003). These studies, however, have neglected the role of receptor-perceiver capacities in the efficacy of begging signals.

Here, in a comparative study on altricial birds, we tested whether the coloration of different nestling traits varied between species in relation to nest light environment. We used a visual model approach to assess differences in coloration from the perspective of a bird. Our visual models integrate reflectance spectra of nestling traits (mouths, flanges, heads, and breasts), the reflectance of natural backgrounds, and light regimes with published information about photoreceptor sensitivities, photoreceptor noise, and the transmission properties of avian ocular media (Hart et al. 2000; Hart 2001) to calculate differences in coloration as differences in an avian color space (Vorobyev et al. 1998). In a first step, we tested two main predictions of the nestling detectability hypothesis, which suggests that selection has favored the evolution of nestling traits that enhance signal efficiency by adopting conspicuous colorations. We predicted that traits implicated in the visual display of begging of species nesting in dark environments contrasted more with the nest background than did those of open-nesting species. In addition, because in a scenario of sibling competition for parental feeding it is likely that parents preferentially feed nestlings that are more conspicuous, a positive relationship can be predicted at the interspecific level between contrasts of nestling traits with the nest background and degree of sibling competition (i.e., clutch size).

Nestling conspicuousness can also arise through the contrast between the different traits within an individual (Marchetti 1993; Kilner and Davies 1998). Higher within-nestling contrast should facilitate parent detection at shorter viewing distances within a nest (Endler and Théry 1996), and thus, selection for conspicuousness may favor the evolution of traits that enhance signal efficacy by maximizing color contrasts between different traits within an individual nestling. We thus predicted a higher degree of within-nestling skin contrasts for species nesting in dark environments than for open-nesting species.

Finally, we have analyzed how natural light conditions in the nest may affect the conspicuousness of different nestling color designs to parents. Using a paired design, we assessed the perception of visible nestling coloration for every species under contrasting nest light environments (open nests vs. hole nests). Because nestling color designs should maximize their conspicuousness within their specific environmental light conditions, we predicted that hole-nesting and open-nesting species were better perceived under poor and rich light conditions, respectively.

Methods

The field study was carried out in the surroundings of Guadix (37°18'N, 3°11'W), southeast Spain, in March–June 2005–2007. Vegetation is sparse in the area and includes cultivated cereals, some remains of holm oak forests, groves of almond trees and olive trees, and other tree crops in irrigated areas surrounding villages. We collected data on nestling coloration of 486 nestlings of 21 species included in 13 families (see table A1 in the online appendix of the *American Naturalist*). Hole-nesting species were located mostly within nest boxes installed recently (2003–2005). All nestlings were measured at a standard relative age during their ontogeny (i.e., when they were in the first third of their normal nestling development, with closed eyes and no pin feathers).

Spectral Reflectance of Nestlings

Spectral reflectance (300–700 nm) of nestlings was recorded using an Ocean Optics (Dunedin, FL) S2000 spectrometer, connected to a deuterium-halogen light (D2-W, mini) by a coaxial reflectance probe (QR-400–7-UV-vis), and the OOIBase32 operating software. Reflectance was measured with the probe placed at a consistent distance, reaching the nestling at 45°. Measurements were relative and referred to standard white (WS-2) and dark, which we calibrated before the measurement of each nestling. All measurements were taken within a portable shelter with an opaque wall placed in the surrounding of the nests. To avoid nest abandonment, we left at least one chick in the nest while measuring reflectance. Nestlings were returned to their nest after 15 min, and subsequent visits to these nests confirmed that our manipulation was noninvasive. Mouth color was measured by gently keeping the gape open and introducing the probe to the center of the upper mouthpart. Flanges were measured by keeping the nestlings' mouths almost closed and placing the probe on the angle of the mouth flanges, thus avoiding confusion with mouth coloration. Finally, skin coloration was measured at the head, close to the ear, and at the breast, where we tried to avoid growing feathers. Measurements were re-

peated three times per nestling trait, and mean values per nestling were calculated and used in the analyses (fig. A1 in the online edition of the *American Naturalist*).

Spectral Reflectance of Nest Background and Irradiance Spectra

Materials used for nest lining are highly variable between pairs of the same species (J. M. Avilés, personal observation). For instance, species that use feathers for lining their nests may carry white, gray, or black feathers, depending on local abundance of white hens, pigeons, or corvids, respectively. In spite of this considerably intra-specific variation, the 21 studied species could be classified into four different types according to the main material constituting the lining of their nests (table A1): (i) ground-type species: those that build no nest at all and whose nestlings can contrast only with the substrate (e.g., owls, falcons, and coraciiforms); (ii) straw-type species: those that build a nest cup mainly composed of dry grass (e.g., Turdidae or magpies *Pica pica*); (iii) branch-type species: those whose nest lining is composed mainly of thin shrub or tree branches, when 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).

Nest lining material was collected from active nests after nestlings had fledged. In the laboratory, we measured nest lining coloration at dark with an Ocean Optics spectroradiometer using the above specifications for nestlings. Nest lining material was disaggregated and 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 total of 29 nests of 18 species. Ten readings were taken at every nest, and mean values per nest type were calculated on the basis of mean values per species (table A1; fig. A2 in the online edition of the *American Naturalist*).

Ambient light measurements were collected during the morning (9:00–11:00 a.m.), when parental provisioning to the nests was maximal. Briefly, we used a cosine-corrected fiber-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 a light source of known color temperature (LS-1-CAL; Ocean Optics). We measured the ambient light at open areas (10 readings) and a few centimeters beyond the entrance of nest boxes (10 readings), with the measurement surface oriented to the sky or to the 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 the

average irradiance spectrum in these two nest environments (fig. A3 in the online edition of the *American Naturalist*).

Parental Visual System

Virtually all birds have four single cone types in their retina, although there are two main types of color vision in birds (Cuthill et al. 2000). Both types are sensitive to ultraviolet light, but they differ profoundly in the wavelength of peak absorbance (λ_{\max}) of the opsin in the ultraviolet/violet (SWS1) cone. Ultraviolet-sensitive (UVS) birds have a UV-biased SWS1 with a λ_{\max} between 355 and 380 nm, while violet-sensitive (VS) birds have λ_{\max} between 402 and 426 nm (Hart 2002; Hart and Hunt 2007). In addition, the λ_{\max} of the second short-wavelength opsin is significantly shifted toward shorter wavelengths in UVS birds and toward longer wavelengths in VS species (Hart 2001). These differences between UVS and VS species render changes in the perception not only of ultraviolet and violet colors but also of all nonspectral colors in which SWS1 are involved. Information on species-specific vision type is available for seven species among those sampled (table A1). However, all previous studies concur that most Passeridae are of the UVS type (Bowermaker et al. 1997; Hart et al. 1998, 2000), with the exception of members of the groups Corvidae and Tyrannidae (Ödeen and Håstad 2003); accordingly, all Passeridae, with the exception of the Corvidae, were modeled as UVS type, and the remaining sampled species were treated as VS birds (table A1).

Avian Color Space Modeling

We used the discriminability model of Vorobyev and Osorio (1998), as developed for the tetrachromatic visual system of birds, in its long form (Vorobyev et al. 1998). This model provides a meaningful way of addressing the evolution of bird coloration traits from the perspective of a bird while accounting for visual pigment absorbance, oil droplet transmittance, and ocular media transmittance (Hart et al. 2000; Hart 2001). This approach has recently been successfully incorporated in comparative studies of bird coloration (e.g., Siddiqi et al. 2004; Håstad et al. 2005; Doucet et al. 2007; Gómez and Théry 2007). The model establishes a color distance, ΔS , which describes the color contrasts between two colored patches as

$$\Delta S^2 = [(e_1 e_2)^2 (\Delta f_4 - \Delta f_3)^2 + (e_1 e_3)^2 (\Delta f_4 - \Delta f_2)^2 + (e_1 e_4)^2 (\Delta f_2 - \Delta f_3)^2 + (e_2 e_3)^2 (\Delta f_4 - \Delta f_1)^2 + (e_2 e_4)^2 (\Delta f_3 - \Delta f_1)^2 + (e_3 e_4)^2 (\Delta f_2 - \Delta f_1)^2] / [(e_1 e_2 e_3)^2 + (e_1 e_2 e_4)^2 + (e_1 e_3 e_4)^2 + (e_2 e_3 e_4)^2], \quad (1)$$

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

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

where $R_A(\lambda)$ represents the reflectance of patch A , $R_B(\lambda)$ is the reflectance of patch B , $I(\lambda)$ is the spectral irradiance of the illuminant, and $S(\lambda)$ is the spectral sensitivity of the receptor i . Results of calculations using equation (1) provide the chromatic distance (ΔS) separating the perceptual value of two spectra in receptor space. The units for ΔS are just noticeable differences (JNDs); values greater than 1 JND have been suggested to indicate that the two spectra can be distinguished, while values below 1 JND would correspond to indistinguishable spectra (Osorio and Vorobyev 1996). Spectral sensitivities have not been mea-

sured in most of the sampled species (table A1), 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 VS systems, respectively (e.g., Håstad et al. 2005; Gómez and Théry 2007). Further, following Håstad et al. (2005) 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 we assumed that the signaling noise for each cone was independent of light intensity:

$$e_i = \frac{\omega}{\sqrt{\eta_i}}, \quad (3)$$

where ω is the Weber fraction and η_i is the relative density of the cone class i on the retina.

It is well known that birds can use achromatic (brightness) contrasts in discriminatory tasks (reviewed in Kelber et al. 2003). In birds, double cones are assumed to be responsible for achromatic visual detection (e.g., Osorio et al. 1999a, 1999b). Therefore, we calculated receptor signals for double cones using the formula above and the spectral sensitivities for double cones in blue tit (Hart et al. 2000) and peafowl (Hart 2002). To illustrate the influ-

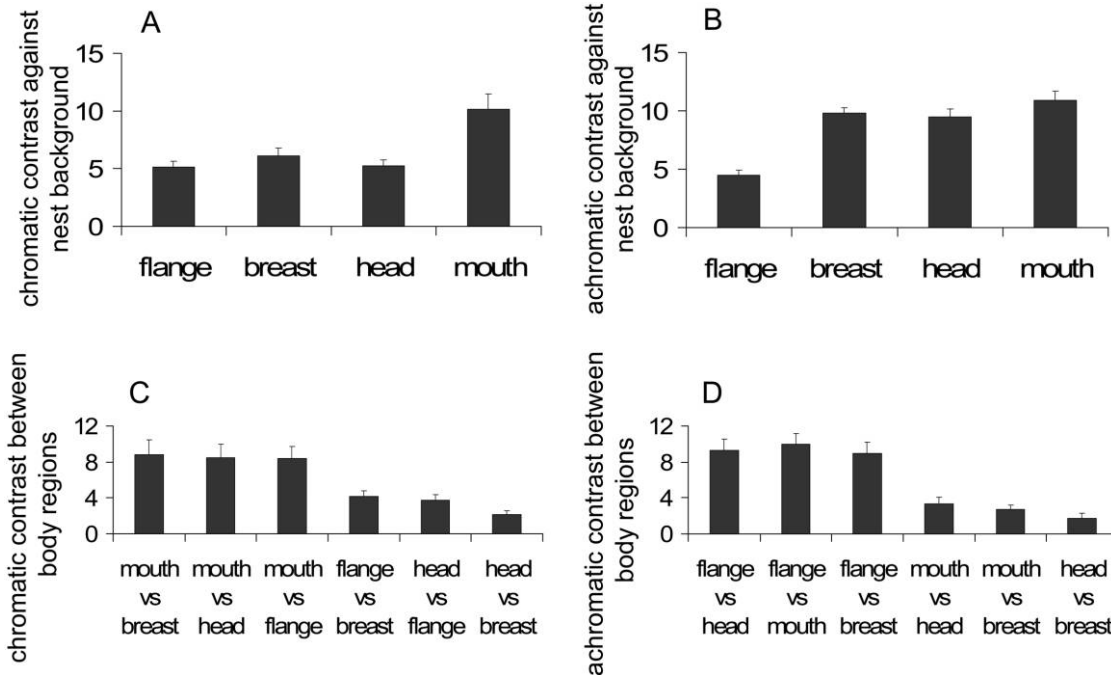


Figure 1: Mean values of chromatic (A) and achromatic (B) contrasts against the nest background and chromatic (C) and achromatic contrasts (D) between nestling body regions. Vertical bars are standard errors. Note that order of pairs of nestling traits in C and D changes to emphasize significant differences in table 2.

Table 1: Determinants of nestling contrasts against the nest background

Effect	All species				1 species/genus			
	<i>F</i>	<i>df</i>	<i>P</i>	<i>Z</i>	<i>F</i>	<i>df</i>	<i>P</i>	<i>Z</i>
Chromatic contrast:								
Excluded terms:								
Nesting site × body part	.61	3, 57	.61		.58	3, 51	.63	
Clutch size	.17	1, 60	.68		2.60	1, 54	.11	
Nesting site	.69	1, 60	.41		.63	1, 54	.43	
Body mass	1.27	1, 60	.26		.64	1, 54	.43	
Included terms:								
Nestling period	59.76	1, 60	<.0001		42.24	1, 54	<.0001	
Body part	16.49	3, 60	<.0001		18.36	3, 54	<.0001	
Species			.26	.62			.15	1.02
Achromatic contrast:								
Excluded terms:								
Nesting site × body part	1.48	3, 57	.23		2.51	3, 48	.07	
Nestling period	.14	1, 60	.70		.02	1, 51	.87	
Body mass	.97	1, 60	.33		.53	1, 51	.47	
Included terms:								
Nesting site	11.12	1, 60	.001		10.73	1, 51	.002	
Body part	25.18	3, 60	<.0001		22.70	3, 51	<.0001	
Clutch size	9.09	1, 60	.003		5.16	1, 51	.02	
Species			.13	1.12			.11	1.22

Note: Model selection was carried out by removing, one by one, the effects that were the furthest from statistical significance, starting with the highest-order interactions and down to the main effects. Results of general linear mixed models include chromatic contrasts and achromatic contrasts as dependent variables and nesting site and nestling body part as independent fixed factors. In the models, body mass, clutch size, and duration of the nestling period were entered as covariables, and species identity was included as a random factor. Analyses were performed on all species and also using a single randomly selected species per genus.

ence of nest luminosity on conspicuousness of nestling color patterns, we repeated calculations for every sampled species by using irradiance spectra of both a typical open nest and a typical hole nest.

Nesting Site and Sibling Competition

Each species was classified either as a hole nester (a score of 0) or an open nester (a score of 1) on the basis of information provided by Harrison (1975; table A1). Irradiance measurements collected with a spectrometer in open nests and hole nests in Great Britain (Hunt et al. 2003) and in our study population (fig. A3) provide support for the underlying assumption that hole nests are less illuminated than open nests. Following Kilner and Davies (1998), we used mean clutch size for each species, as reported by Cramp (1998), as an index of sibling competition.

Confounding Variables

Prolonged parental care at the nests and body size may confound the predicted relationships between coloration of nestlings and nesting habits and/or clutch size. Cavity-

nesting birds have longer nestling periods and larger clutch sizes than do open-nesting birds (Martin and Li 1992). In addition, nestling traits of larger species could be more easily detected in a parent-offspring communication scenario, and nestling body mass may trade with clutch size or be constrained in cavity nests (Bennett and Owens 2002). Therefore, we used the length of the nestling period in days and body mass in grams, as reported by Cramp (1998), as surrogate measures of the duration of parental care at the nest and body size in our comparative framework, respectively (Avilés et al. 2006; table A1).

Statistical Methods

After being log transformed, chromatic and achromatic contrasts of nestlings with the nest background and between different nestling body regions were fitted to a normal distribution (Kolmogorov-Smirnov tests, $P > .05$). We tested for the relationships of nestling conspicuousness in nesting sites with generalized linear mixed models. Variables defining chromatic and achromatic contrasts between nestling traits and the nest background and between different body parts were included as dependent variables, while nest type, log-transformed clutch size,

Table 2: Determinants of nestling contrasts between different body parts

Effect	All species				1 species/genus			
	F	df	P	Z	F	df	P	Z
Chromatic contrast:								
Excluded terms:								
Nesting site × body part	1.72	5, 95	.18		1.19	5, 85	.32	
Clutch size	.00	1, 100	.94		.11	1, 85	.74	
Nesting site	.20	1, 100	.65		.04	1, 85	.85	
Body mass	.19	1, 100	.66		.34	1, 85	.56	
Included terms:								
Nesting period	20.02	1, 100	<.0001		18.70	1, 85	<.0001	
Body part	10.42	5, 100	<.0001		10.02	5, 85	<.0001	
Species			.04	1.71			.05	1.61
Achromatic contrast:								
Excluded terms:								
Clutch size	1.98	1, 95	.16		.87	1, 80	.35	
Body mass	1.18	1, 95	.27		.54	1, 80	.46	
Nesting period	1.42	1, 95	.23		1.65	1, 80	.20	
Included terms:								
Nesting site × body part	3.26	1, 95	.009		3.64	5, 80	.005	
Nesting site	.37	1, 95	.54		.10	1, 80	.75	
Body part	17.99	5, 95	<.0001		17.41	5, 80	.0001	
Species			.009	2.37			.01	2.10

Note: Model selection was carried out by removing, one by one, the effects that were the furthest from statistical significance, starting with the highest-order interactions and down to the main effects. Results of general linear mixed models include chromatic contrasts and achromatic contrasts as dependent variables and nesting site and nestling body regions involved in the contrast estimations as independent fixed factors. In the models, body mass, clutch size, and duration of the nestling period were entered as covariables, and species identity was included as random factor. Analyses were performed on all species and also using a single randomly selected species per genus.

log-transformed body mass, and length of the nestling period were the independent variables. Species identity was included in the analyses as a random factor, to account for the nonindependence of measures of different traits within the same species. Finally, we used paired *t*-tests for dependent variables to explore the influence of different light environments on the conspicuousness of the different nestling color patterns.

Observations of taxonomic groups, such as species, cannot be considered statistically independent because of the confounding effects of common ancestry. Trying to partially control for phylogenetic effects, we reassessed the association between nestling color conspicuousness and nesting habits by using only one randomly selected species per genus (e.g., Harvey and Pagel 1991; Doucet et al. 2007).

Results

Variation in Skin Conspicuousness across Species and Body Regions

Chromatic contrasts of different body regions of nestlings against the nest background varied significantly among the sampled species (fig. 1A; table 1). Mouths were manifestly more conspicuous than heads, flanges, and breasts (fig.

1A; post hoc Scheffe tests, $P < .0001$ in all cases). Achromatic contrasts of different body regions of nestlings against the nest background also varied (fig. 1B; table 1). Indeed, flanges were remarkably less contrasted with the nest background than were heads, breasts, and mouths (post hoc Scheffe tests, $P < .00001$ in all cases).

Variation in Within-Nestling Skin Contrasts

Chromatic conspicuousness varied between pairs of nestling traits, depending on the traits involved in the estimations (table 2). Chromatic contrasts between the mouth and the rest of the body parts trended to be higher than those estimated from pairs of nestling traits that did not include the mouth (fig. 1C; Scheffe tests, $P < .006$ in all cases). Achromatic contrasts between body parts also varied, depending on the pairs of traits used for the estimations (table 2), and they were larger when flanges were included (fig. 1D; Scheffe tests, $P < .003$ in all cases).

Nesting Habits, Sibling Competition, and Nestling Skin Contrasts with Nest Background

Chromatic nestling conspicuousness against the nest background was independent of nesting habits and clutch size

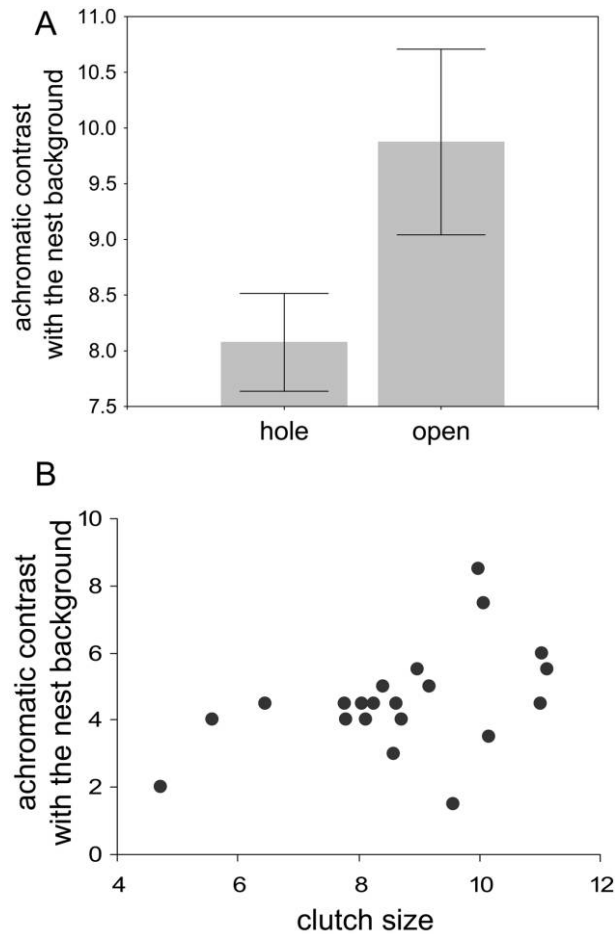


Figure 2: Mean values of achromatic contrasts between nestlings and nest background in relation to nesting site (A) and clutch size (B). Vertical bars are standard errors.

(table 1). Achromatic contrasts, however, were significantly associated with clutch size and nesting site (table 1). Nestlings of open-nesting species showed larger achromatic contrasts with the nest background than did nestlings of hole-nesting species (fig. 2A). In addition, nestlings of species with larger clutch sizes exhibited larger general achromatic contrasts with the nest background than those exhibited by species with a lower clutch size (fig. 2B). These patterns were qualitatively confirmed when only one species per genus was considered (table 1).

Nesting Habits, Sibling Competition, and Within-Nestling Skin Contrasts

Chromatic differences between pairs of nestling traits were not related to nesting habits or clutch size (table 2). Achromatic contrasts within the different nestling traits, how-

ever, varied in relation to nesting site in interaction with body part. That was the case irrespective of using information from all species or only one species per genus (table 2). Nestlings of hole-nesting species showed more evident achromatic contrasts between flanges and other body regions than did nestlings of open nesters (fig. 3). Clutch size was unrelated to achromatic contrasts between different body regions of nestlings (table 2).

Nest Luminosity and Nestling Detectability

Nongaping traits (i.e., heads and breasts) showed higher chromatic contrasts with the nest background when viewed under high-light conditions both in hole-nesting species (paired *t*-tests, heads: $t = 4.46$, $df = 13$, $P = .0006$; breasts: $t = 5.89$, $df = 13$, $P < .0001$) and in open-nesting species (paired *t*-tests, heads: $t = 2.0425$, $df = 6$, $P = .07$; breasts: $t = 3.79$, $df = 6$, $P = .008$; fig. 4A, 4B). Nest luminosity did not affect conspicuousness of achromatic contrasts between the head and the nest or between the breast and the nest in hole-nesting species (paired *t*-tests, head: $t = 0.32$, $df = 13$, $P = .74$; breast: $t = 1.71$, $df = 13$, $P = .11$; fig. 4C) or in open-nesting species (paired *t*-tests, head: $t = 0.49$, $df = 6$, $P = .64$; breast: $t = 0.33$, $df = 6$, $P = .75$; fig. 4D).

Perception of gaping structures (i.e., flange and mouth), however, was affected by nest luminosity in open-nesting but not in hole-nesting species (fig. 4). Flanges showed higher chromatic contrasts with the background when viewed under high-light conditions in open nesters (paired *t*-tests, $t = 2.12$, $df = 6$, $P = .07$) but not in hole nesters (paired *t*-tests, $t = 1.51$, $df = 13$, $P = .15$; fig. 4A, 4B). Mouth achromatic contrasts with the nest background were more conspicuous under high-light regimes in open nesters (paired *t*-test, $t = 2.51$, $df = 6$, $P = .04$) but not in hole nesters (paired *t*-test, $t = 1.16$, $df = 13$, $P = .26$; fig. 4C, 4D).

Within-nestling skin chromatic contrasts were equally affected by luminosity in hole-nesting and open-nesting species (fig. 5). The chromatic contrasts between the mouth and the flanges and between the mouth and the breast, but not those between other body parts of nestlings, were more conspicuous under low-light conditions (paired *t*-tests, mouth vs. flanges in hole nesters: $t = 2.97$, $df = 13$, $P = .01$; mouth vs. flange in open nesters: $t = 2.63$, $df = 6$, $P = .04$; mouth vs. breast in hole nesters: $t = 2.14$, $df = 13$, $P = .05$; mouth vs. breast in open nesters: $t = 2.64$, $df = 6$, $P = .04$; fig. 5A, 5B). Within-nestling achromatic contrasts, however, were differently affected by luminosity in hole-nesting and open-nesting species (fig. 5C, 5D). Contrasts between flanges and the mouth and between flanges and the head were always more conspicuous when viewed under high luminosity in hole nesters

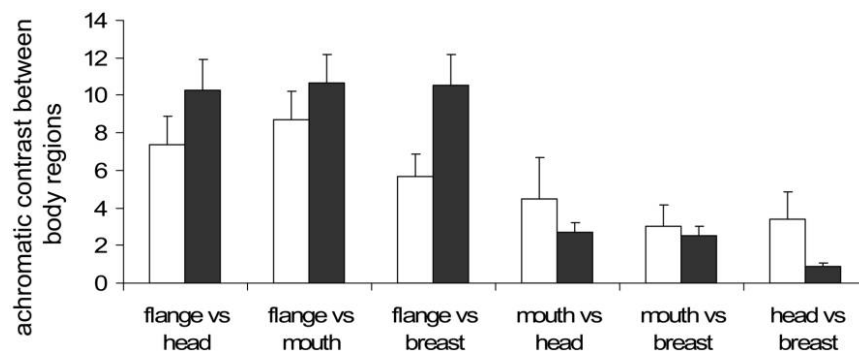


Figure 3: Mean values of achromatic contrasts between nestling body regions estimated for open-nesting (*open bars*) and hole-nesting (*filled bars*) species. Vertical bars are standard errors.

(paired *t*-test, flanges vs. mouth: $t = 3.63$, $df = 13$, $P = .003$; flanges vs. heads: $t = 3.18$, $df = 13$, $P = .007$; fig. 5C). The importance of the achromatic brightness of flanges was diminished among the open nesters, and only when it contrasted with the mouth was it more perceptible under high-light conditions (paired *t*-tests, $t = 4.86$, $df = 6$, $P = .002$; fig. 5D). On the other hand, the achromatic contrasts between the mouths and the breasts of open-nesting species were also more conspicuous when perceived under high-light regimes in the open nesters (paired *t*-tests, $t = 4.14$, $df = 6$, $P = .006$; fig. 5D).

Discussion

Variation in Nestling Conspicuousness across Species and Body Regions

We have found that structures implicated in gaping behavior as well as the body skin of nestlings of a large number of altricial birds strongly contrasted in coloration with the nest background. The largest within-nestling skin conspicuousness was found when gaping structures (i.e., flanges and mouths) were contrasted against nestling body skin (i.e., head and breast; fig. 1). Within-nestling skin conspicuousness, however, arose in two ways: (i) because the chromatic contrast of the mouth with all the other nestling traits was large or (ii) because the achromatic contrast of the flanges with the other traits was large (fig. 1). The importance of flange coloration determining nestling conspicuousness, however, dwells in its role as a contrasting element when visualizing it together with the mouth and the body skin, because flanges were the less contrasted nestling trait with the nest background. Finally, we have found only a weak level of covariation in chromatic and achromatic contrasts with the nest background between structures implicated in gaping (i.e., flanges and mouth) and the other body regions (i.e., head and breast;

species effect; table 1), which suggests that selection for conspicuousness of begging displays may differently affect traits implicated in gaping and those at other body parts.

Nesting Habits, Sibling Competition, and Nestling Color Design

We have found that achromatic but not chromatic components of nestling design are associated with certain types of nesting sites among the sampled species. More precisely, hole-nesting species showed generally smaller achromatic contrasts of their traits with the nest background than did open-nesting species (fig. 2A). However, flanges of nestlings of hole-nesting species were brighter (fig. A1) and showed higher achromatic contrasts with the mouth, head, and breast than did those of open-nesting species (fig. 3). Finally, species with larger clutch sizes displayed general higher achromatic contrasts between their body structures and the nest background (fig. 2B). Previous studies have demonstrated that under natural light conditions, the strongest stimulus for avian discriminatory tasks appears in the achromatic dimension (i.e., differences in achromatic brightness; Vorobyev and Osorio 1998). Our results therefore support this scenario and previous findings suggesting that nest light properties may have influenced the evolution of designs of traits that are used in visual detection within the nests.

An early suggestion by Ficken (1965) that brightly colored gapes enhance nestling detectability previously received only partial support. Kilner and Davies (1998), in a comparative study on 31 European species, found that the coloration of the mouth and flanges was not related to light intensity in the nests. They found that color contrasts between flanges and mouths were larger for species nesting in darker nests (Kilner and Davies 1998). These analyses, however, calculated color parameters from video images, which do not account for ultraviolet information

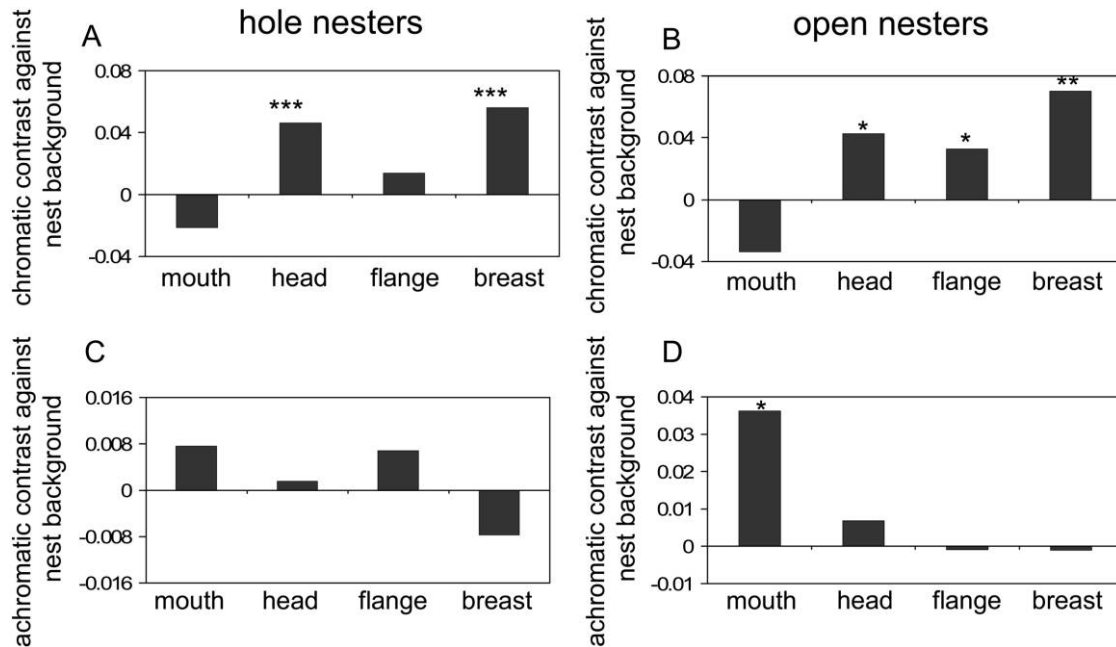


Figure 4: Differences in perception under low- and high-light conditions of chromatic (A) and achromatic contrasts (C) against the nest background for hole-nesting species and chromatic (B) and achromatic contrasts (D) against the nest background for open-nesting species. Differences were calculated deducting the value of a contrast in high-light conditions from the value in low-light conditions. Therefore, positive differences indicate that a particular trait is better perceived under high-light conditions, whereas negative differences indicate that it is better perceived under low-light conditions. Significant paired comparisons are marked. *One asterisk* = $P < .05$; *two asterisks* = $P < .01$; *three asterisks* = $P < .001$

that birds can detect (e.g., Cuthill et al. 2000). Recently, Hunt et al. (2003) have reported brighter flanges among hole-nesting than among open-nesting species. However, they did not evaluate their findings from the perspective of an adult bird looking at its offspring (Hunt et al. 2003), and they sampled a reduced number of species. Our results, based on a visual model approach that considers how parents perceive coloration of their nestlings within their nests, support Ficken's (1965) hypothesis and reveal a main role of flange design in determining nestling conspicuousness under low-light conditions.

It has been suggested that particular chromatic components may enhance the conspicuousness of colored traits within hole nests (Heeb et al. 2003; Hunt et al. 2003; Avilés et al. 2006). Here, we have found that the largest chromatic contrasts appeared when comparing nestling mouths to nest backgrounds and other body parts of nestlings (fig. 1). Gape structures (particularly flanges) of nestlings, as well as most nest material, are somehow richer in reflectance at the yellow wavelengths (figs. A1, A2), explaining, at least partially, that flanges were the nestling trait with the smallest chromatic contrasts with the nest background. Therefore, nestling chromatic conspicuousness can arise throughout the chromatic contrasts between the mouth and the remaining nestling traits. Chromatic conspicu-

ousness of nestlings, however, did not vary with nesting site. Thus, mouth coloration may have been selected to provide highly detectable cues, irrespective of the nest type.

There is growing evidence supporting a role of body skin coloration in parental feeding decisions (Jourdie et al. 2004; Bize et al. 2006; Soler et al. 2007). One possibility that may explain the importance of coloration of non-gaping traits in parental feeding decisions is that parents, rather than detecting coloration of each trait, evaluate gape coloration in relation to the background of body skin. Indeed, we have found that the largest achromatic and chromatic contrasts of gaping traits against nest background and against the rest of the body of nestlings had similar values (fig. 1). Further, the possible role of color pattern of nestling skin as the background that highlights gaping structures may be more important in species that nest in cavities because their nestlings showed higher achromatic contrasts between structures implicated in gaping and the rest of the body of nestlings (fig. 3). These results provide further support for the hypothesis that body skin coloration may have evolved to have a detectability function in nestlings, which is especially important for hole-nesting altricial birds.

Following the approach of Kilner and Davies (1998), we have considered average clutch size for each species as

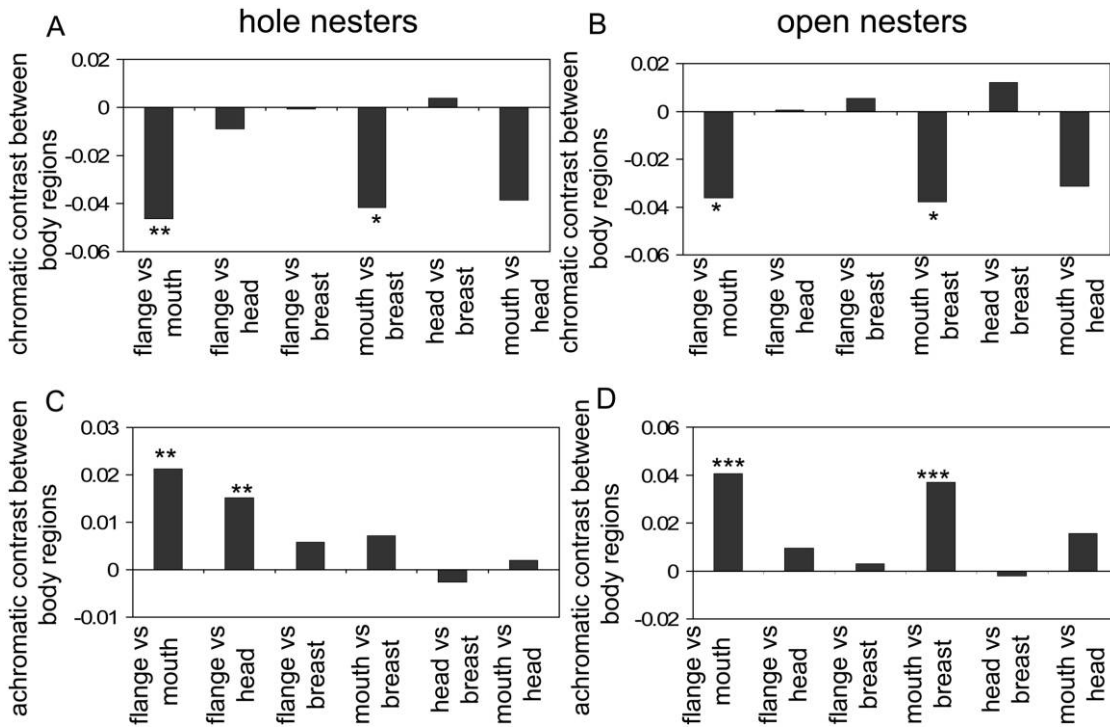


Figure 5: Differences in perception under low- and high-light conditions of chromatic (A) and achromatic (C) contrasts between nestling body regions for hole-nesting species and chromatic (B) and achromatic contrasts (D) between nestling body regions for open-nesting species. Differences were calculated deducting the value of contrast in high-light conditions from the value in low-light conditions. Therefore, positive differences indicate that a particular trait is better perceived under high-light conditions, whereas negative differences indicate that it is better perceived under low-light conditions. Significant paired comparisons are marked. *One asterisk* = $P < .05$; *two asterisks* = $P < .01$; *three asterisks* = $P < .001$.

an index of degree of competition in the nest to explore the relationship between nestling coloration and sibling competition. Kilner and Davies (1998) did not find a significant relationship between clutch size and gape coloration. In a second comparative attempt, Kilner (1999) found that mouth coloration of nestlings reared in lighter open nests was related to the degree of extrapair copulation. Here, we have found that nestlings of species with larger clutch sizes showed larger general achromatic contrasts between their bodies and the nest (fig. 3B). This result may arise if species with larger clutch size had less brilliant nests, which would result in larger achromatic contrasts with nestlings. However, the achromatic and chromatic components of nest coloration were unrelated to clutch size among the sampled species (Pearson correlations between clutch size and scores extracted from a principal components analysis (PCA) summarizing 98.03% of variation in nest reflectance, PC1: $r = 0.05$, $P = .81$; PC2: $r = -0.007$, $P = .97$; PC3: $r = 0.22$, $P = .37$; $N = 18$ species). Therefore, we interpret this as the result of selection pressures affecting parental feeding

decisions, which are probably higher in species with larger brood size.

Nest Luminosity and Nestling Detectability

In general, more intense light regimes favored a higher conspicuousness against the nest of those nestling traits that are not implicated in gaping, irrespective of the nesting habits (fig. 4). The design of the mouth and flanges of the open nesters but not of the hole nesters, however, was better perceived under high-light regimes (fig. 4). Gaping structures of hole-nesting species were highly reflective (fig. 1A), and contrasts between mouth and flanges were of a higher value than were those of open nesters (fig. 3), while coloration of nest material did not differ between open-nesting and hole-nesting species (one-way ANOVA on PC scores extracted from a PCA summarizing reflectance of nests, PC1: $F = 0.31$, $df = 1, 16$, $P = .58$; PC2: $F = 0.52$, $df = 1, 16$, $P = .47$; PC3: $F = 0.0005$, $df = 1, 16$, $P = .98$; $N = 18$ species). These results are in accordance with the hypothetical importance of environ-

mental light conditions driving the evolution of coloration of nestling gapes. Conspicuousness of gape design of hole nesters, however, was not significantly affected by nest luminosity. Perhaps differences in coloration between gape and nests are so evident in hole nesters that they would be easily perceivable even under low luminosity.

When considering contrasts between mouth and flanges, the effect of luminosity at the nests did not differ for hole-nesting and open-nesting species. Chromatic contrasts were better perceived under low-light conditions, and achromatic contrasts were better perceived under high-light conditions, irrespective of the nesting habit (fig. 5). These results challenge our expectations of nest luminosity being an important factor driving the evolution of nestling coloration. However, the effect of luminosity on values of achromatic contrasts for gaping structures (i.e., flanges vs. mouth) of open nesters was almost twice that on the value of hole-nesting species (repeated-measures ANOVA with luminosity as a within-factor interaction term and nesting site as a between-factor interaction term, $F = 5.07$, $df = 1, 130$, $P < .02$). Consequently, because the achromatic components of nestling coloration differ between hole-nesting and open-nesting species, our results are in accordance with the hypothesis that light conditions during nestling development are a prime factor affecting the evolution of nestling coloration.

Interpretation of trait perception by parents should rely on the proportion of signals in units greater than 1 JND (e.g., Osorio and Vorobyev 1996; Schaefer et al. 2007). Despite the detected statistical significance of differences in contrasts between different irradiances, they are far below the theoretical threshold discrimination value of 1 (figs. 4, 5), which might suggest that those differences are not perceived by parents. Theoretically fixed threshold values for discrimination, however, should depend on selective advantage associated with such ability. In particular, selection for discriminating between two spectra in a context of a parent-offspring communication scenario is expected to be particularly strong because parent fitness depends greatly on an efficient chick provisioning. Consequently, although detected differences concerning perception of nestling traits under different light regimes would fit predictions from the nestling detectability hypothesis, this result should be carefully considered until a discrimination threshold for two spectra can be experimentally established in a context of parent-offspring communication.

Conclusions

In conclusion, relying on a wide range of birds, we have found comparative support for an association between achromatic components of nestling design and nesting

habits and degree of sibling competition. In addition, we have found that gaping designs of open-nesting species are better perceived under high-light regimes. These findings globally agree with the nestling detectability hypothesis, suggesting that selection has favored the evolution of nestling color designs that enhance signal efficacy.

Acknowledgments

We are indebted to J. D. Ibáñez, D. Martín-Gálvez, M. Martín-Vivaldi, and J. M. Peralta for field assistance. We thank two anonymous reviewers for constructive comments on a previous draft. We thank S. M. Doucet and N. S. Hart for advice during the revision and C. Soler, who kindly checked the English. During manuscript preparation, J.M.A. was partially funded by a I3P contract from the European Community and a Ramon y Cajal fellowship. C.N. and T.P.-C. were supported by a predoctoral fellowship by the Ministerio de Ciencia y Tecnología (MCyT) and by a I3P contract from the European Community, respectively. The work was also funded by the Spanish MCyT (CGL2004-01777/BOS, MEC-FEDER) and the Junta de Andalucía (RNM 340). The authorization for carrying out the experimental work on animals in the field was granted by the Dirección General de Gestión del Medio Natural of the Consejería de Medio Ambiente of Junta de Andalucía.

Literature Cited

- Avilés, J. M., J. J. Soler, and T. Pérez-Contreras. 2006. Dark nests and egg colour in birds: a possible functional role of ultraviolet reflectance in egg detectability. *Proceedings of the Royal Society B: Biological Sciences* 273:2821–2829.
- Ayala, R. M., N. Saino, A. P. Møller, and C. Anselmi. 2007. Mouth coloration of nestlings covaries with offspring quality and influences parental feeding behaviour. *Behavioural Ecology* 18:526–534.
- Bennett, P. M., and I. P. F. Owens. 2002. *Evolutionary ecology of birds: life histories, mating systems, and extinction*. Oxford University Press, Oxford.
- Bize, P., R. Paillet, B. Moureau, and P. Heeb. 2006. A UV signal of offspring condition mediates context-dependent parental favouritism. *Proceedings of the Royal Society B: Biological Sciences* 273:2063–2068.
- Bowmaker, J. K., and G. R. Martin. 1978. Visual pigments and color vision in a nocturnal bird, *Strix aluco* (tawny owl). *Vision Research* 18:1125–1130.
- Bowmaker, J. K., L. A. Heath, S. E. Wilkie, and D. M. Hunt. 1997. Visual pigments and oil droplets from six classes of photoreceptor in the retinas of birds. *Vision Research* 37:2183–2194.
- Cramp, S. 1998. *The complete birds of the western Palearctic*. Oxford University Press, Oxford.
- Cuthill, I. C., J. C. Partridge, A. T. D. Bennett, S. C. Church, N. S. Hart, and S. Hunt. 2000. Ultraviolet vision in birds. *Advances in the Study of Behaviour* 29:159–214.
- Doucet, S. M., D. J. Mennill, and G. E. Hill. 2007. The evolution of

- signal design in manakin plumage ornaments. *American Naturalist* 169(suppl.):S62–S80.
- Endler, J. A. 1990. On the measurement and classification of colour in studies of animal colour patterns. *Biological Journal of the Linnean Society* 41:315–352.
- Endler, J. A., and M. Théry. 1996. Interacting effects of lek placement, display behavior, ambient light, and color patterns in three Neotropical forest-dwelling birds. *American Naturalist* 148:421–452.
- Ficken, M. S. 1965. Mouth color of nestling passerines and its use in taxonomy. *Wilson Bulletin* 77:71–75.
- Gómez, D., and M. Théry. 2004. Influence of ambient light on the evolution of colour signals: comparative analysis of Neotropical rainforest bird community. *Ecology Letters* 7:279–284.
- . 2007. Simultaneous crypsis and conspicuousness in color patterns: comparative analysis of a Neotropical rainforest bird community. *American Naturalist* 169(suppl.):S42–S61.
- Guilford, T., and M. S. Dawkins. 1991. Receiver psychology and the evolution of animal signals. *Animal Behaviour* 42:1–14.
- Harrison, C. 1975. *A field guide to the nests, eggs, and nestlings of European birds with North Africa and the middle east*. Collins, London.
- Hart, N. S. 2001. The visual ecology of avian photoreceptors. *Progress in Retinal and Eye Research* 20:675–703.
- . 2002. Vision in the peafowl (*Aves: Pavo cristatus*). *Journal of Experimental Biology* 205:3925–3935.
- Hart, N. S., and D. M. Hunt. 2007. Avian visual pigments: characteristics, spectral tuning, and evolution. *American Naturalist* 169(suppl.):S7–S26.
- Hart, N. S., J. C. Partridge, and I. C. Cuthill. 1998. Visual pigments, oil droplets and cone photoreceptor distribution in the European starling (*Sturnus vulgaris*). *Journal of Experimental Biology* 201:1433–1446.
- Hart, N. S., J. C. Partridge, I. C. Cuthill, and A. T. D. Bennett. 2000. Visual pigments, oil droplets, ocular media and cone photoreceptor distribution in two species of passerine bird: the blue tit (*Parus caeruleus* L.) and the blackbird (*Turdus merula* L.). *Journal of Comparative Physiology A* 186:375–387.
- Harvey, P. H., and M. D. Pagel. 1991. *The comparative method in evolutionary biology*. Oxford University Press, Oxford.
- Håstad, O., J. Victorsson, and A. Ödeen. 2005. Differences in color vision make passerines less conspicuous in the eyes of their predators. *Proceedings of the National Academy of Sciences of the USA* 102:6391–6394.
- Heeb, P., T. Schwander, and S. Faoro. 2003. Nestling detectability affects parental feeding preferences in a cavity-nesting bird. *Animal Behaviour* 66:637–642.
- Hunt, S., R. M. Kilner, N. E. Langmore, and A. T. D. Bennett. 2003. Conspicuous, ultraviolet-rich mouth colours in begging chicks. *Proceedings of the Royal Society B: Biological Sciences* 270:S25–S28.
- Jourdie, V., B. Moureau, A. T. D. Bennett, and P. Heeb. 2004. Ultraviolet reflectance by the skin of nestlings. *Nature* 431:262.
- Kelber, A., M. Vorobyev, and D. Osorio. 2003. Animal colour vision: behavioural tests and physiological concepts. *Biological Reviews* 78:81–118.
- Kilner, R. M. 1999. Family conflicts and the evolution of nestling mouth colour. *Behaviour* 136:779–804.
- . 2006. Function and evolution of color in young birds. Pages 201–232 in G. E. Hill and K. J. McGraw, eds. *Bird coloration: function and evolution*. Vol. 2. Harvard University Press, Cambridge, MA.
- Kilner, R. M., and N. B. Davies. 1998. Nestling mouth colour: ecological correlates of a begging signal. *Animal Behaviour* 56:705–712.
- Marchetti, K. 1993. Dark habitats and bright birds illustrate the role of the environment in species divergence. *Nature* 362:149–152.
- Martin, T. E., and P. J. Li. 1992. Life-history traits of open-nesting vs. cavity-nesting birds. *Ecology* 73:579–592.
- Ödeen, A., and O. Håstad. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. *Molecular Biology and Evolution* 20:855–861.
- Osorio, D., and M. Vorobyev. 1996. Colour vision as an adaptation to frugivory in primates. *Proceedings of the Royal Society B: Biological Sciences* 263:593–599.
- Osorio, D., M. Vorobyev, and C. D. Jones. 1999a. Colour vision of domestic chicks. *Journal of Experimental Biology* 202:2951–2959.
- Osorio, D., A. Miklosi, and Z. Gonda. 1999b. Visual ecology and perception of coloration patterns by domestic chicks. *Evolutionary Ecology* 13:673–689.
- Saino, N., P. Ninni, S. Calza, R. Martinelli, F. de Bernardi, and A. P. Møller. 2000. Better red than dead: carotenoids-based mouth coloration reveals infection in barn swallow nestlings. *Proceedings of the Royal Society B: Biological Sciences* 267:57–61.
- Saino, N., R. Ambrosini, R. Martinelli, P. Ninni, and A. P. Møller. 2003. Gape coloration reliably reflects immunocompetence of barn swallow (*Hirundo rustica*) nestlings. *Behavioral Ecology* 14:16–22.
- Schaefer, M. H., V. Schaefer, and M. Vorobyev. 2007. Are fruit colors adapted to consumer vision and birds equally efficient in detecting colorful signals? *American Naturalist* 169(suppl.):S159–S169.
- Siddiqi, A., T. W. Cronin, E. R. Loew, M. Vorobyev, and K. Summers. 2004. Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *Journal of Experimental Biology* 207:2471–2485.
- Soler, J. J., J. M. Avilés, J. J. Cuervo, and T. Pérez-Contreras. 2007. Is the relationship between colour and immune response mediated by nutritional condition in spotless starling nestlings? *Animal Behaviour* 74:1139–1145.
- Théry, M. 2006. Effects of light environment on color communication. Pages 148–176 in G. E. Hill and K. J. McGraw, eds. *Bird coloration*. Vol. 1. Mechanisms and measurements. Harvard University Press, Cambridge, MA.
- Vorobyev, M., and D. Osorio. 1998. Receptor noise as a determinant of colour thresholds. *Proceedings of the Royal Society B: Biological Sciences* 265:351–358.
- Vorobyev, M., D. Osorio, A. T. D. Bennett, N. J. Marshall, and I. C. Cuthill. 1998. Tetrachromacy, oil droplets and bird plumage colours. *Journal of Comparative Physiology A* 183:621–633.

Associate Editor: Justin Marshall
 Editor: Michael C. Whitlock