

Conspicuous, ultraviolet-rich mouth colours in begging chicks

Sarah Hunt^{1*}, Rebecca M. Kilner²,
Naomi E. Langmore³ and Andrew T. D. Bennett¹

¹*School of Biological Sciences, University of Bristol, Bristol BS8 1UG, UK*

²*Department of Zoology, University of Cambridge, Cambridge CB2 3EJ, UK*

³*School of Botany and Zoology, Australian National University, Canberra ACT 0200, Australia*

**Author for correspondence (sarah.hunt@bristol.ac.uk).*

Recd 31.01.03; Accptd 19.02.03; Online 11.04.03

There is as yet no clear consensus on the function of vivid mouth colours in begging chicks. A major obstacle to our understanding has been that no studies have measured gape colours independently of human colour perception. Here, we present the first study, to our knowledge, to use UV–VIS spectrometry to quantify the gape colour, background nest colour and nest light environment of eight European passerines. Both mouths and the surrounding flanges show striking and previously unreported peaks of reflectance in the ultraviolet, coupled with high long-wavelength reflectance responsible for the human-visible appearance of the gape. High ultraviolet reflectance is likely to have an important effect on the conspicuousness of nestling mouths, since contrast with the nest background is maximal in the ultraviolet. Furthermore, the dual-peak nature of the spectra suggests that gapes are avian non-spectral colours analogous to human purple.

Keywords: begging; mouth colour; conspicuous; ultraviolet

1. INTRODUCTION

Mouth colours among nestling passerines range from vivid yellows to deep reds, yet what role, if any, the coloration plays in begging and why it varies from species to species remains unclear. Two main hypotheses have been proposed. The first is that coloured gapes provide conspicuous targets towards which parents direct food (Pycraft 1907), perhaps improving the accuracy or speed of food delivery in the darkened light environment of the nest. The second hypothesis, which is not mutually exclusive, is that gape colours are reliable signals of the need or condition of the chicks (Kilner 1997; Saino *et al.* 2000, 2003).

While recent evidence suggests that the long-wavelength (LW) ‘redness’ of the mouth may be the key to its signalling role (e.g. Götmark & Ahlstrom 1997; Kilner 1997; Saino *et al.* 2000), no studies have measured colour using methods that are independent of human colour perception. Previous studies have ranked gape colours using human observers (e.g. Saino *et al.* 2000) or calculated colour parameters from photographs or video images (e.g. Kilner 1997; Kilner & Davies 1998; Saino *et al.* 2003). Such anthropocentric measurements are inappropriate

where birds are the intended receivers of the signal (Bennett *et al.* 1994; Cuthill *et al.* 2000), chiefly because birds are sensitive to ultraviolet (UV) A wavelengths (*ca.* 320–400 nm) to which humans are blind, and have a fourth class of single-cone photoreceptors, probably giving birds an extra dimension to their colour vision compared with humans (Bennett *et al.* 1994; Cuthill *et al.* 2000). Thus, for no species have we had objective information on the colour of the gape.

In the present study we measured the mouth and flange colours of eight species of European passerine using UV–VIS reflectance spectrophotometry (300–700 nm). We chose species with a range of gape colours (figure 1*a*) and various nesting habits. We also measured the reflectance of the nest background against which gapes are viewed and calculated the contrast between the mouth and flange and the nest, as well as recording the spectral distribution of light at each nest. We ask how gapes appear to the parent bird, compare mouth colour with skin colour to address the question of whether gape colours might be non-functional and discuss the potential implications of these data for the hypothesized role(s) of gape colour in begging.

2. MATERIAL AND METHODS

We temporarily removed chicks from nests at 3–5 days old, under licence from English Nature (licence 20000698) and transported them to a field laboratory where gape colour measurements were performed. At least one chick was left in the parental nest at all times. All chicks underwent controlled begging trials based on those of Kilner & Davies (1998), to standardize the temperature and hunger of the chicks. On arrival at the field laboratory, chicks were fed to satiation with Nectarblend rearing mix (Haith’s Seeds, Cleethorpes, UK). We recorded reflectance spectra after 90 min without food, by which time the nestlings would beg if prompted by whistling and tapping the nest (see Kilner & Davies 1998). After measurement of the gape colour, the nestlings were again fed to satiation before returning them to the nest.

Reflectance spectra (300–700 nm) were collected using an S2000 spectrometer, PX-2 xenon strobe lamp and 2.5 mm diameter coaxial reflectance probe (Ocean Optics, Inc., Dunedin, FL, USA). Gapes were gently held open while the probe, small enough to be inserted inside the mouth, was placed perpendicularly to a tangent to the surface. The strobe illuminated areas *ca.* 1.5 mm in diameter. The reflectance was calculated relative to a 99% white Spectralon reference tablet and sampled between every four to eight scans.

We took 10 mouth and eight flange spectra from each chick. In each case we also measured the reflectance of the nest itself and the spectral irradiance (=light environment) at the nest. Nest reflectance was measured as described in the previous paragraph. To obtain the light environment data, we replaced the reflectance probe with a 600 µm fibre optic terminating in a cosine corrector (Ocean Optics, Inc.), held vertically above the nest. We took eight nest reflectance spectra and eight irradiance spectra at each nest.

3. RESULTS AND DISCUSSION

The mouth and flange of every species we measured show not only the high LW reflectance predicted by their human-visible coloration (figure 1*a*), but also a previously unreported peak of reflectance in the UV (figure 1*b*). The spectra from the flange are particularly striking; flanges tend to be highly reflective across much of the avian spectrum (except 400–500 nm; see below); they are, therefore, considerably brighter than the mouth itself and, owing to the steep slopes in the reflectance curves (figure 1*b*), are probably highly saturated hues. In a preliminary analysis, the ‘dark’ nesters (figure 1(i–iv); for definition see Kilner 1999) had significantly brighter flanges than the ‘light’ nesting species (figure 1(v–viii); comparison of total reflectance 300–700 nm: $t_{1,6} = 4.24$, $p = 0.005$), supporting the idea that a bright, well defined edge to the mouth is

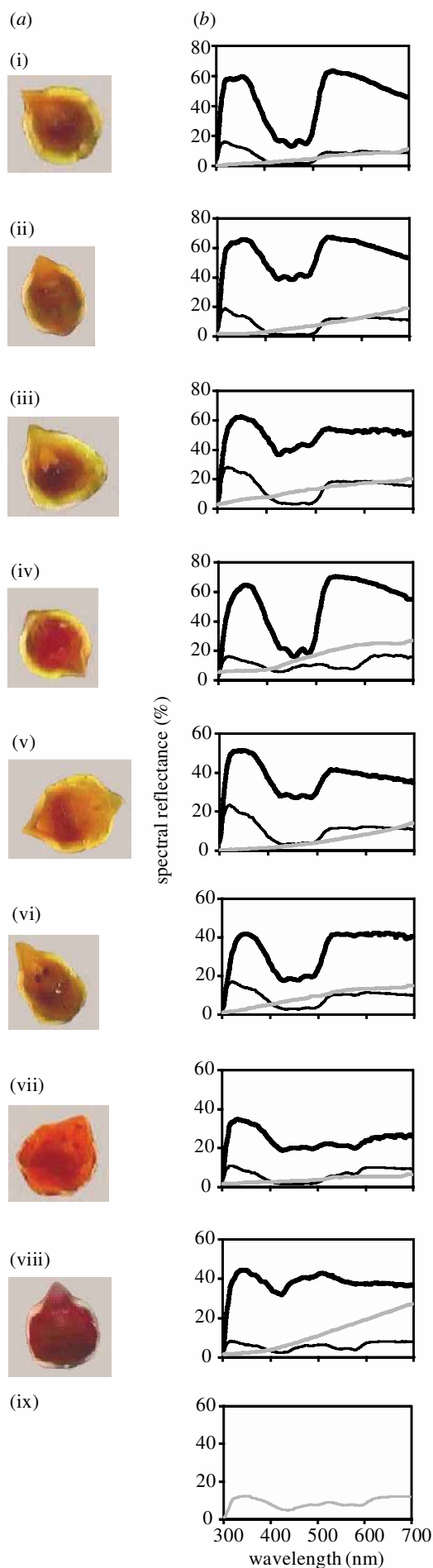


Figure 1. Gape colour, nest colour and typical skin colour of nestling passerines. (a) Photographs illustrating human appearance; (b(i–viii)) spectral reflectance (300–700 nm) of the mouth (thin black lines), flange (thick black lines) and nest background (thick grey lines), (ix) reflectance of unfeathered blackbird skin (thin grey line). (a,b) (i) Blue tit (*Parus caeruleus*), (ii) pied flycatcher (*Ficedula hypoleuca*), (iii) barn swallow (*Hirundo rustica*), (iv) house sparrow (*Passer domesticus*), (v) blackbird (*Turdus merula*), (vi) reed warbler (*Acrocephalus scirpaceus*), (vii) dunnock (*Prunella modularis*), (viii) blackcap (*Sylvia atricapilla*). Gape reflectance curves are the mean of individual means of 10 mouth and eight flange measurements from each chick; nest spectra are the mean of individual means of eight measurements from each nest ((i–vii) $n_{\text{chicks}} = 10$, $n_{\text{nests}} = 5$; (viii) $n_{\text{chicks}} = 4$, $n_{\text{nests}} = 2$); the skin spectrum is the mean of individual means of four spectra sampled from the pink back of each blackbird chick ($n_{\text{chicks}} = 10$).

particularly advantageous in dark nest habitats (Pycraft 1907; Ficken 1965; Kilner & Davies 1998).

Gape reflectance in the UV region is much greater relative to LW reflection than that recorded from most red and yellow plumages to date (Burkhardt 1989; Andersson *et al.* 2002), and may be structural in origin (Prum *et al.* 1999). We suggest that high UV reflectance greatly increases the conspicuousness of the gape against the nest background. In each species, nest reflectance increases gradually towards LWs (figure 1b). The resulting large contrast in reflectance between the mouth/flange and nest (figure 2) means that gapes are inherently conspicuous against the background, but particularly so in the UV region, where nest reflectance is very low. These data are therefore consistent with the hypothesis that gape colours are designed to provide highly detectable targets for parent birds (see also Heeb *et al.* 2003).

The hue that humans perceive is correlated with the human-visible wavelength at which reflection increases most rapidly (Endler 1990). Birds, however, are likely to perceive these gape colours very differently. The striking dual-peaked spectra imply that nestling gape coloration is dominated by avian non-spectral colours (Burkhardt 1989). Non-spectral colours, which do not appear in the rainbow, are produced by stimulation of non-spectrally adjacent cones. ‘Purple’ is the only such colour for humans, produced when our ‘red’ and ‘blue’ cones are highly stimulated but the ‘green’ cone, most sensitive to intermediate wavelengths, is not. However, with four single-cone types, tetrachromatic birds may have as many as five non-spectral colours (Burkhardt 1989; Cuthill *et al.* 2000). Why birds should exploit such colours remains to be explored, but they may be particularly conspicuous against common natural backgrounds including foliage and bark.

Although highly contrasting, there are potential gape colours (e.g. bright whites) that are probably even more conspicuous than those recorded here. This suggests that there is an additional explanation for the particular coloration we observe. Yellow flanges (figure 1b(i–vi)) and yellow–orange mouths (figure 1b(i–iii,v–vii)), exhibit little reflection between 400 and 500 nm, providing further evidence that yellow–orange coloration is based at least partly on carotenoids (Saino *et al.* 2000), known to absorb

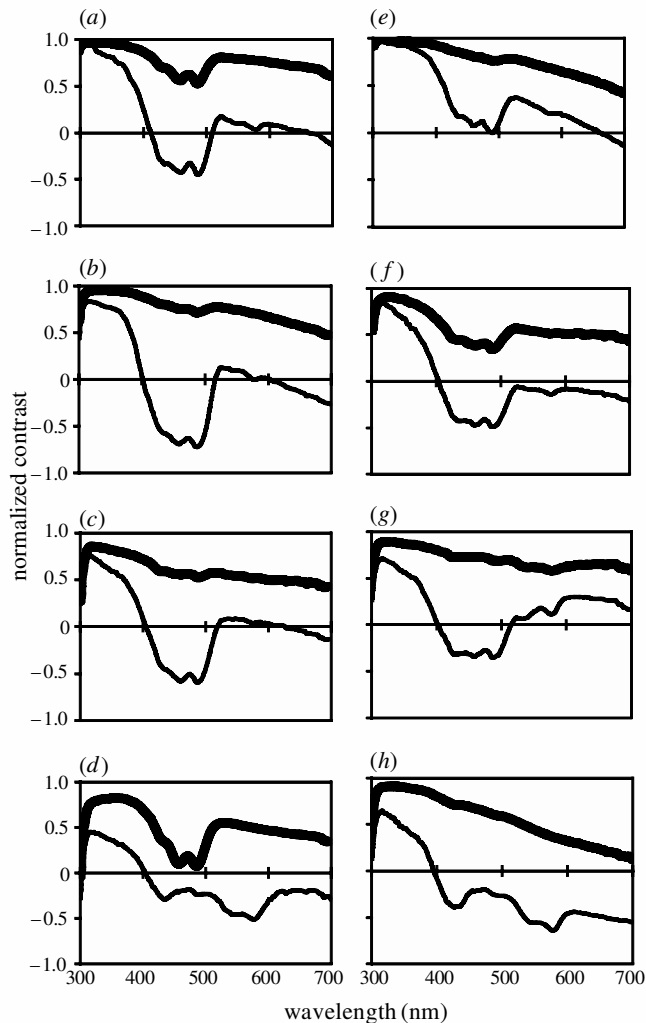


Figure 2. Normalized contrast (300–700 nm) between the spectral reflectance of the nest background and the mouth ($(R_{\text{mouth}} - R_{\text{nest}})/(R_{\text{mouth}} + R_{\text{nest}})$ (thin curves) and the flange ($(R_{\text{flange}} - R_{\text{nest}})/(R_{\text{flange}} + R_{\text{nest}})$ (thick curves). (a) Blue tit, (b) pied flycatcher, (c) barn swallow, (d) house sparrow, (e) blackbird, (f) reed warbler, (g) dunnoek, (h) blackcap.

strongly in this region of the spectrum (Burkhardt 1989). As in carotenoid-based sexual ornaments, dietary limitations (Hill *et al.* 2002) and/or a trade-off between using carotenoids for coloration and immune functions (Olson & Owens 1998), potentially allows the resulting coloration to serve as a reliable signal of need or condition (e.g. Saino *et al.* 2000).

Unlike yellow mouths, red mouths show three broad peaks in reflectance (figure 1*b(iv,viii)*), with no obvious absorption of middle wavelengths, presumably the result of blood (e.g. haemoglobin) rather than carotenoid pigments. Interestingly, red mouths have a very similar shaped reflectance to typical nestling skin (figure 1*b(ix)*). The phenomenon of high LW reflectance associated with high UV reflectance is therefore not unique to gape coloration, and red mouth coloration (but not yellow) is potentially a by-product of a highly vascularized surface. Nevertheless, red mouth coloration probably has a functional role in increasing the conspicuousness of begging chicks, as described above. Furthermore, there is already good evidence that red mouth coloration signals need in canaries (Kilner 1997) and other seed-regurgitating

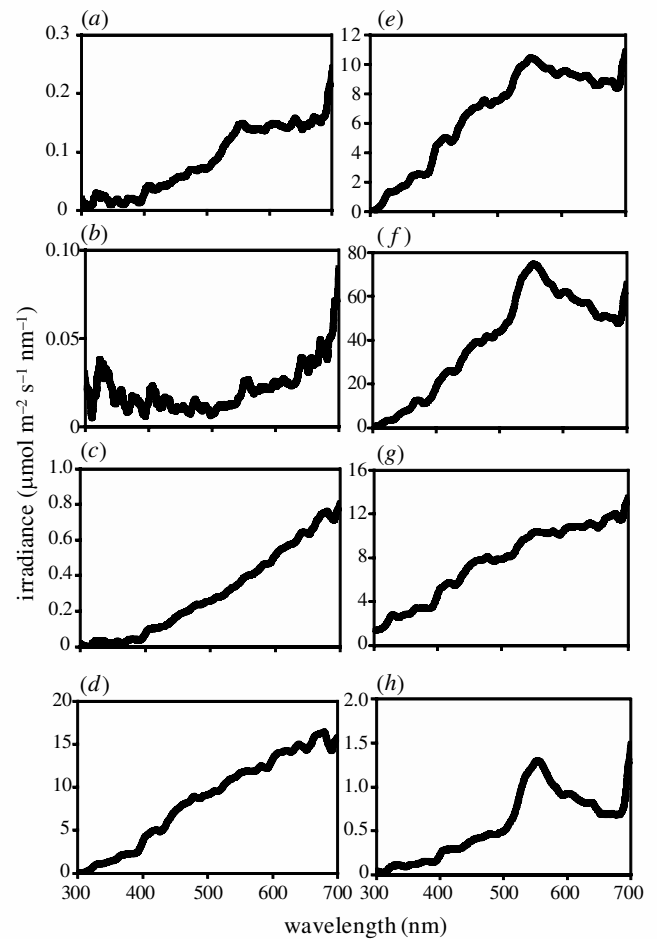


Figure 3. Nest light environment (spectral irradiance, 300–700 nm). Curves are the mean of individual means of eight measurements at each nest ((a–g) $n_{\text{nests}} = 5$; (h) $n_{\text{nests}} = 2$). (a) Blue tit, (b) pied flycatcher, (c) barn swallow, (d) house sparrow, (e) blackbird, (f) reed warbler, (g) dunnoek, (h) blackcap.

finches, perhaps most crucially in the contrast it creates with the surrounding flange (Kilner & Davies 1998; Kilner 1999). A similarity with skin coloration therefore does not rule out a signalling role.

How gape colours are perceived may depend on the light environment at the nest (for an example of how light environments can affect visual plumage displays see Endler & Théry (1996)). Nest light environments vary dramatically among the species presented here (figure 3). Not surprisingly, light levels inside cavity nests (figure 3*a,b,d*) tend to be low, but further investigation will be needed to determine whether these are such that vision is photopic (cone based), mesopic (intermediate) or scotopic (rod based) and, if photopic, the likely contribution of each cone type. While low levels of UV light may seem to preclude the perception of UV gape reflectance, the reverse may be true since low levels of short-wavelength illumination may serve, via adaptation, to heighten sensitivity to UV (Vorobyev *et al.* 1998).

The begging behaviour of young chicks has long been a focus of empiricists and theoreticians investigating parent–offspring conflict (Godfray 1991; Wright & Leonard 2002), yet the role of mouth colour in begging remains poorly understood. Our data are consistent with earlier work suggesting that yellow–orange gape colours are based

on carotenoid pigments and therefore have the potential to provide reliable information on the condition of the chicks (e.g. Saino *et al.* 2000, 2003). However, the nature of these colours also suggests that the role of selection for conspicuousness in shaping gape colour has been underestimated. Furthermore, where sufficient illumination occurs, a major component of the conspicuousness of gapes is likely to be the striking peak of reflectance in the UV, not the LW reflection visible to humans and underlying the reds, oranges and yellows that have attracted attention in the past.

Acknowledgements

The authors thank the Cambridge University Botanic Gardens, C. Hinde, J. Wright and A. Kazem, S. Griffiths, N. Davies and M. de L. Brooke for generously providing nests and nestlings, and R. Douglas for assistance calibrating the spectrophotometer. S.H. was supported by BBSRC grant no. 7/S12981 held by A.T.D.B. and R.M.K. R.M.K. was supported by a Royal Society Dorothy Hodgkin fellowship and University Research Fellowship and N.E.L. by an ARC postdoctoral fellowship.

Andersson, S., Pryke, S. R., Örnborg, J., Lawes, M. J. & Andersson, M. 2002 Multiple receivers, multiple ornaments, and a trade-off between agonistic and epigamic signaling in a widowbird. *Am. Nat.* **160**, 683–691.

Bennett, A. T. D., Cuthill, I. C. & Norris, K. J. 1994 Sexual selection and the mismeasure of color. *Am. Nat.* **144**, 848–860.

Burkhardt, D. 1989 UV vision: a bird's eye view of feathers. *J. Comp. Physiol. A* **164**, 787–796.

Cuthill, I. C., Partridge, J. C., Bennett, A. T. D., Church, S. C., Hart, N. S. & Hunt, S. 2000 Ultraviolet vision in birds. *Adv. Stud. Behav.* **29**, 159–214.

Endler, J. A. 1990 On the measurement and classification of colour in studies of animal colour patterns. *Biol. J. Linn. Soc.* **41**, 315–352.

Endler, J. A. & Théry, M. 1996 Interacting effects of lek placement, display behavior, ambient light, and color patterns in three neotropical forest-dwelling birds. *Am. Nat.* **148**, 421–452.

Ficken, M. S. 1965 Mouth color of nestling passerines and its use in taxonomy. *Wilson Bull.* **77**, 71–75.

Godfray, H. C. J. 1991 Signalling of need by offspring to their parents. *Nature* **352**, 328–330.

Götmark, F. & Ahlstrom, M. 1997 Parental preference for red mouth of chicks in a songbird. *Proc. R. Soc. Lond. B* **264**, 959–962. (DOI 10.1098/rspb.1997.0132.)

Heeb, P., Schwander, T. & Faoro, S. 2003 Nestling detectability affects parental feeding preferences in a cavity nesting bird. *Anim. Behav.* (In the press.)

Hill, G. E., Inouye, C. Y. & Montgomerie, R. 2002 Dietary carotenoids predict plumage coloration in wild house finches. *Proc. R. Soc. Lond. B* **269**, 1119–1124. (DOI 10.1098/rspb.2002.1980.)

Kilner, R. 1997 Mouth colour is a reliable signal of need in begging canary nestlings. *Proc. R. Soc. Lond. B* **264**, 963–968. (DOI 10.1098/rspb.1997.0133.)

Kilner, R. & Davies, N. B. 1998 Nestling mouth colour: ecological correlates of a begging signal. *Anim. Behav.* **56**, 705–712.

Kilner, R. M. 1999 Family conflicts and the evolution of nestling mouth colour. *Behaviour* **136**, 779–804.

Olson, V. A. & Owens, I. P. F. 1998 Costly sexual signals: are carotenoids rare, risky or required? *Trends Ecol. Evol.* **13**, 510–514.

Prum, R. O., Torres, R., Kovach, C., Williamson, S. & Goodman, S. M. 1999 Coherent light scattering by nanostructured collagen arrays in the caruncles of the Malagasy Asities (Eurylaimidae: Aves). *J. Exp. Biol.* **202**, 3507–3522.

Pycraft, W. P. 1907 Nestling birds, and some of the problems they present II. *Br. Birds* **1**, 129–132.

Saino, N., Calza, S., Martinelli, R., De Bernardi, F., Ninni, P. & Møller, A. P. 2000 Better red than dead: carotenoid-based mouth coloration reveals infection in barn swallow nestlings. *Proc. R. Soc. Lond. B* **267**, 57–61. (DOI 10.1098/rspb.2000.0966.)

Saino, N., Ambrosini, R., Martinelli, R., Ninni, P. & Møller, A. P. 2003 Gape coloration reliably reflects immunocompetence of barn swallow (*Hirundo rustica*) nestlings. *Behav. Ecol.* **14**, 16–22.

Vorobyev, M., Osorio, D., Bennett, A. T. D., Marshall, N. J. & Cuthill, I. C. 1998 Tetrachromacy, oil droplets and bird plumage colours. *J. Comp. Physiol. A* **183**, 621–633.

Wright, J. & Leonard, M. L. (eds) 2002 *The evolution of begging*. Dordrecht, The Netherlands: Kluwer.