

Spectral reflectance and directional properties of structural coloration in bird plumage

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Summary

Bird plumage is coloured both by pigments and by spectrally selective interference in the light reflected from feather barbs. These barbs are composites of high- and low-refractive-index materials, and light is reflected at refractive index boundaries. The spatial structure determines the wavelengths where constructive interference occurs and, hence, the spectral tuning. The spectral tuning of interference colours often varies with angles of illumination and reflection, which produces iridescence. Iridescence and other optical effects mean that interference coloration looks different from pigmentation and is visually striking. To study the optical and visual properties of structural plumage colours, we

recorded the reflectance spectra of feathers and in particular their directional properties. A fixed spot on a feather was viewed from a fixed position, whilst the feather orientation and the angle of illumination were varied. We recognise two main types of coloration, 'directional' and 'diffuse'. Within these types, there is considerable variation, and five examples illustrate some features of structural plumage colours and suggest how their optical and visual properties can be measured and described.

Key words: feather, colour, iridescence, interference colour, bird.

Introduction

Colour varies across pigmented surfaces in a fairly straightforward way. The pigment produces a spectrally selective reflection, which is diffusing and unpolarised. To this is added to a directional specular reflection of the illuminant, which is often polarised. Moving the light source or rotating the object causes predictable colour changes (see Figs 1, 2), where the spectral location of the reflectance peak (λ_{max}) is fixed. For humans, uniformly pigmented surfaces vary in brightness and saturation, but not in hue. The position on the surface of the specular highlight is predictable from optical geometry, and its angular distribution depends on optical texture, making surfaces glossy or matte.

Structural colours, not produced by pigments, are quite widespread in animals (Land, 1972; Fox, 1976; Prum et al., 1998, 1999; Parker, 2000; Vukusic et al., 1999, 2002; Land and Nilsson, 2001). They arise in three ways: (i) scattering by high-refractive-index particles whose size is close to or below that of visible wavelengths and that are separated by distances greater than the wavelength of light; (ii) colours produced by reflection from finely ridged surfaces, which act as diffraction gratings; and (iii) interference colours from structures made of composites of high- and low-refractive-index media. If the refractive index boundaries are separated by less than a wavelength of light, rays reflected from successive layers interfere constructively when in phase to give a spectrally tuned reflection. With flat equally spaced layers and light

incident normal to the surface, constructive interference occurs when the refractive index boundaries are a quarter of a wavelength apart (Land, 1972; Land and Nilsson, 2001).

Structural coloration in bird plumage is common and is especially important in producing blues, greens and iridescence. Structural coloration can be recognised in several ways; for instance, the colours of reflected and transmitted light differ. Feather barbs work as interference reflectors because they contain keratin (refractive index 1.56), melanin (refractive index approximately 2.0) and air pockets (refractive index 1.0; Land, 1972). Previously, it was thought that laminar interference reflectors produce iridescent coloration and that diffusing structural colours are due to incoherent scattering (Fox, 1976; Finger, 1995). However, Rayleigh scattering does not account for the observed spectral tuning of reflected light, which should give reflectance spectra dominated by short wavelengths. To account for this discrepancy, Finger (1995) proposed that a combination of scattering and selective absorption by pigments can account for feather reflectance. There is no doubt that colours are caused by a combination of pigmentation and structural coloration, e.g. the greens of many parrots (Fox, 1976). However, Prum et al. (1998, 1999) suggested that scattering is less important than previously thought. They found that diffuse bluish colours in two parrots, a cotinga and an estrildid finch, were produced by coherent reflection (i.e. wavelength-selective interference with

refractive index boundaries less than 1 wavelength apart) from a foam-like structure in which spatial variation is the same in all directions.

Iridescence is ‘glittering or flashing with colours which change according to the position from which they are viewed’ (Oxford English Dictionary, second edition, 1989). Colour in this sense means ‘hue’ (for humans; Wyszecki and Stiles, 1982) and, for our purposes, iridescent coloration is characterised by variation in the spectral location of reflectance maxima, λ_{\max} , with viewing geometry. Other features that often distinguishes structural coloration from pigmentation are that saturated colours are reflected directionally and that the brightest colours are not desaturated specular highlights.

We set out to ‘unweave the rainbow’ of structural plumage coloration with some misgivings. This study does not directly add to knowledge of the physical mechanisms, and surely their brilliance alone says much about the colours’ biological role. Iridescence attracts humans and presumably birds, where it is often most prominent on adult males. However, carotenoid and melanin pigmentation in the plumage appears to provide information about qualities such as health and social rank (Olson and Owens, 1998; Senar and Camerino, 1998; Badyaev and Hill, 2000; Badyaev et al., 2001), and it would be interesting to know whether the same applies to structural, and especially to iridescent, colours. The iridescent colours of starlings (Cuthill et al., 1999) and bluethroat (*Luscinia svecica*), blue-tit (*Parus caeruleus*) and blue grosbeak (*Guiraca caerulea*) ‘blues’ are implicated in mate-choice (Andersson and Amundsen, 1997; Hunt et al., 1999; Keyser and Hill, 2000), but little is known about the possible costs of structural colours or how they might reflect physical condition.

To understand how plumage colours vary and whether birds can detect this variation, it is useful to measure reflectance spectra (Vorobyev et al., 1998). Spectra of pigment colours can be recorded with a fixed viewing geometry; typically one that minimises the contribution of specularly (see Figs 1A, 2), but even so, a single spectrum does not capture surface lustre. With iridescent plumage, no single geometry can give a useful (i.e. non-black) reflectance spectrum for all feathers (Cuthill et al., 1999), and a fixed geometry will not show how the colours change according to view (see Fig. 3). The problem is that theoretically very many measurements are needed to describe structural coloration completely. The colours produced by diffraction on the surface of a compact disc indicate the potential complexity of the problem. Here, we aim to complement work on the structural bases of plumage colours (Land, 1972; Finger,

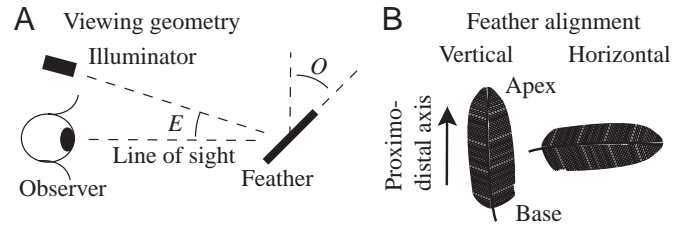


Fig. 1. Viewing geometry. (A) Reflectance spectra were recorded from a 1 mm diameter spot on the feather surface, with the vane perpendicular to the line of sight. This spot was on the horizontal axis of rotation of the specimen holder, which lay perpendicular to the line of sight. The orientation of the feather surface and the position of the light source are specified relative to the line of sight. Surface orientation, O , is the rotation of the surface relative to the perpendicular to the line of sight and is measured clockwise in this figure (i.e. at $O=90^\circ$, the surface faced upwards). The light source moved in azimuth and elevation, but we refer mainly to effects of varying elevation, with the angle E being given by clockwise rotation from the line of sight (i.e. at $E=90^\circ$, the light source was directly above the specimen). (B) Feathers were mounted in two alignments. At $O=0^\circ$, when vertically mounted, the apex was vertically above the base; when horizontally mounted, the vane was horizontal.

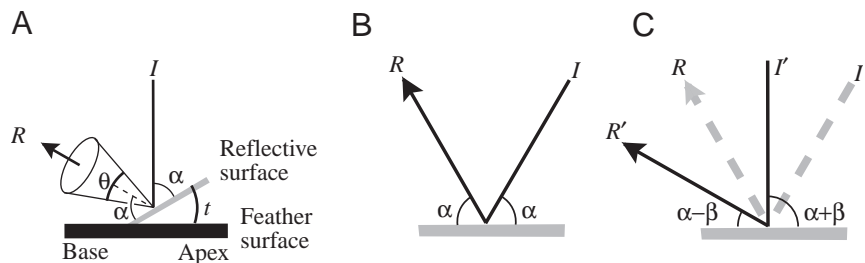


Fig. 2. Reflectance geometry. (A) Directionality. A directionally iridescent feather can be understood as an imperfect spectrally tuned mirror. Light from a point source, I , incident at angle α , is reflected in a diffuse beam centred on axis R at $180^\circ - \alpha$. The width of this (approximately circular) beam at 50% of maximum intensity is θ . The structurally reflective surface is not always in the same plane as the feather vane, and its tilt, t , out of this plane can be calculated from the angles I and R with respect to the feather surface. Tilt was predominantly away from the proximo-distal axis. For $t > 0^\circ$, light from directly above the feather is directed towards its base, and for $t < 0^\circ$ towards the apex. Unlike the iridescent reflection, the direction of non-spectrally selective specular reflection was consistent with the reflective surface being in (or close to) the plane of the feather vane. Spectral tuning of laminar interference reflectors varies with angle of incidence, α (see Fig. 7 in Land, 1972). (B) The spectral location of the reflectance peak, λ_{\max} , varied across the reflected beam. For a fixed observer (see Fig. 1A), λ_{\max} was independent of surface orientation, O , and a linear function of the angle, E , separating I from the line of sight. i.e. $\lambda_{\max} = a - bE$, where a is λ_{\max} at $E=0^\circ$, and b is a constant. (C) We can see why λ_{\max} might be independent of O because, on the axis of reflection, the angles of incidence (I') and reflectance (R') are equal, here being α . If O varies and E is fixed, then the angle of incidence and reflectance shift from α by equal and opposite amounts, $\pm\beta$. Consequently, spectral shifts in λ_{\max} for the incident and reflected light are approximately equal and opposite, compared with the value of λ_{\max} , where angles of incidence and reflectance are equal and can be expected to cancel each other out.

1995; Prum et al., 1998, 1999; Andersson, 1999) by looking in more detail at their spectral reflectance and visual qualities. We also outline a simple way of measuring the structural coloration of feathers.

Materials and methods

We measured the reflectance of a fixed spot on a feather from a fixed viewpoint whilst varying the feather's orientation and the position of the illumination (Fig. 1). A feather or feather fragment was mounted on a 25 mm×25 mm square of glass and held flat by a piece of acetate in which there was a 7 mm aperture. The glass and acetate were painted matte black. The mount was then secured behind an aperture in the faceplate of a specimen holder, which located the feather's surface on the holder's axis of rotation. The feather was visible over a solid angle of 150°. The specimen was then centred in a 160 mm radius Cardan arm perimeter, which held a 6 mm (i.e. 2.1°) quartz light-guide. The light-guide was aligned towards the specimen and lit by a 400 W Xenon arc. For our purposes, the light-guide tip is a point source. The light-guide moved in both azimuth and elevation, but viewing and illumination beams could not be co-axial, and the lowest possible elevation of the light source (at 0° azimuth) was 5° (Fig. 1A).

We also used a simple integrating sphere to give (approximately) uniform diffuse illumination. The mounting of the feather was the same as with the point source, but the feather was centred in a 260 mm diameter sphere, which was lined with a reflective coating of expanded polystyrene. This was lit by an 8 V quartz–halogen lamp 25 mm from the specimen, but separated from it by a baffle to block direct illumination, and on the axis of rotation of the specimen holder.

Reflectance measurements

A 1 mm diameter spot on the sample was focused by a quartz lens onto a 0.1 mm light-guide. This connected to a spectroradiometer (S2000, Ocean Optics) which recorded from 300 to 800 nm. In the integrating sphere, low ultraviolet intensity meant that measurements were unreliable below approximately 400 nm. Reflectance was measured relative to a standard of freshly pressed (medical-grade) barium sulphate, which was a near-perfect diffusing surface (i.e. intensity was independent of surface orientation). When compared with the diffusing standard, it should be noted that specular

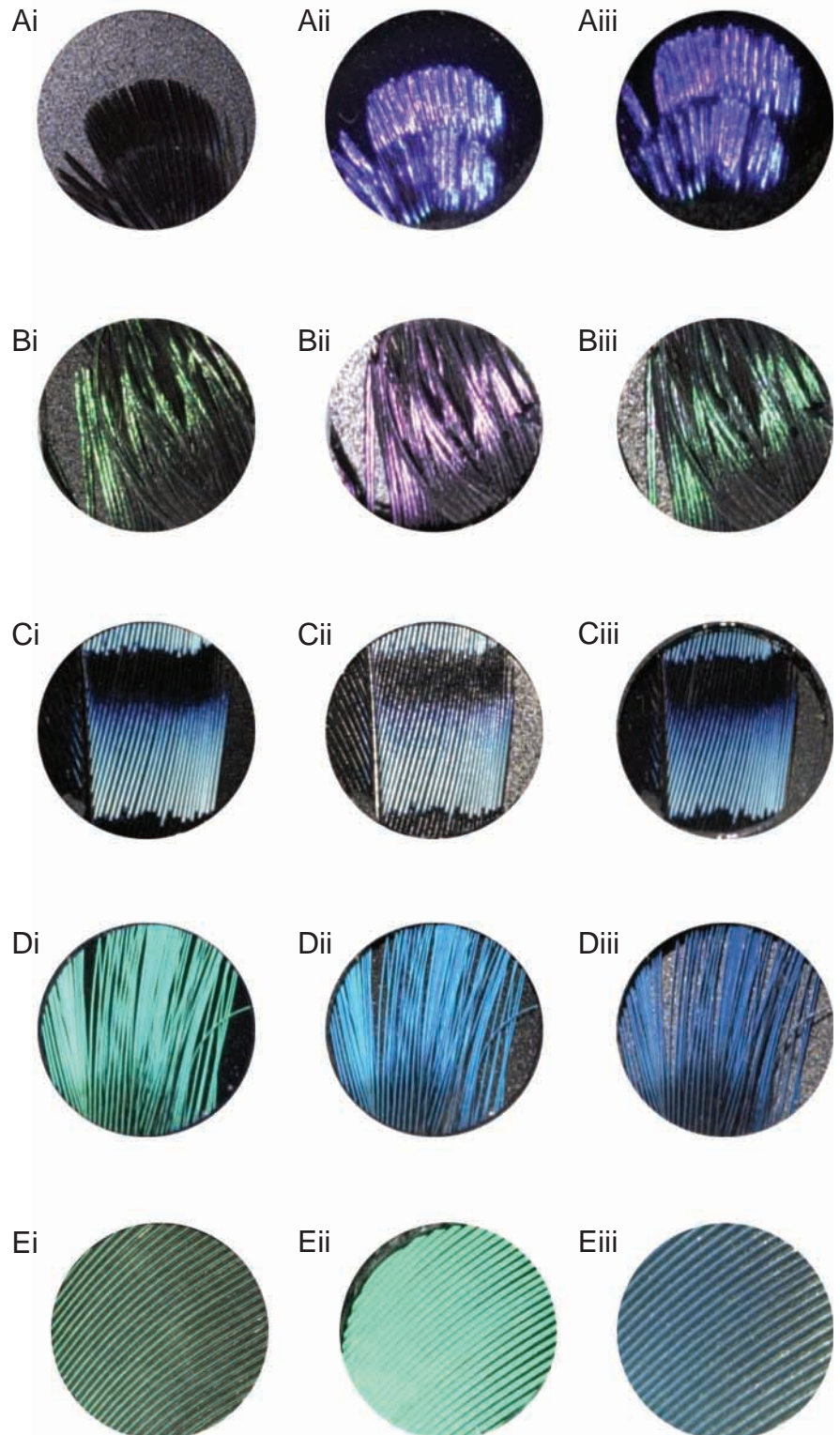


Fig. 3. Photographs of feathers indicating how colours alter with varying surface orientation (O) and illumination elevation (E). The feathers are aligned vertically (Fig. 1); see Materials and methods for details. (A) Magnificent hummingbird cap. (i) $O=0^\circ$, $E=5^\circ$; the feather is black; (ii) $O=45^\circ$, $E=5^\circ$; (iii) $O=0^\circ$, $E=-75^\circ$. (B) Feral pigeon. (i) $O=0^\circ$, $E=5^\circ$; (ii) $O=30^\circ$, $E=80^\circ$; (iii) $O=45^\circ$, $E=100^\circ$. (C) European jay. (i) $O=0^\circ$, $E=5^\circ$; the feather shows a specular highlight; (ii) $O=5^\circ$, $E=5^\circ$; (iii) $O=45^\circ$, $E=70^\circ$. (D) Common kingfisher. (i) $O=30^\circ$, $E=5^\circ$; (ii) $O=30^\circ$, $E=45^\circ$; (iii) $O=30^\circ$, $E=90^\circ$. (E) Indian roller. (i) $O=0^\circ$, $E=5^\circ$; (ii) $O=45^\circ$, $E=5^\circ$; (iii) $O=45^\circ$, $E=90^\circ$.

surfaces can give reflectance values exceeding 1.0 (e.g. Fig. 4A).

Viewing geometry

For a fixed observer viewing a fixed point on a surface illuminated by a point source of fixed intensity, there are five independent variables that might affect the surface colour (i.e. reflectance spectrum). The light source can vary in azimuth and in elevation, and the object can rotate about three axes. Dealing systematically with all these variables presents a formidable problem, and we did not vary all five degrees of freedom (Fig. 1A). Both the elevation (E) and azimuth of the light source could be varied, but the specimen could be rotated only about the horizontal axis perpendicular to the line of sight (i.e. pitch). The angle of rotation is called surface orientation (O ; Fig. 1A). Also, the feather was placed in two alignments in the holder, which we call vertical and horizontal, according to the direction of its main axis when perpendicular to the line of sight (Fig. 1B). In practice, we do not deal with effects of varying illumination azimuth since this seemed to be redundant

once the effective tilt of the reflective surface had been taken into account (Fig. 2A; see below).

Photography

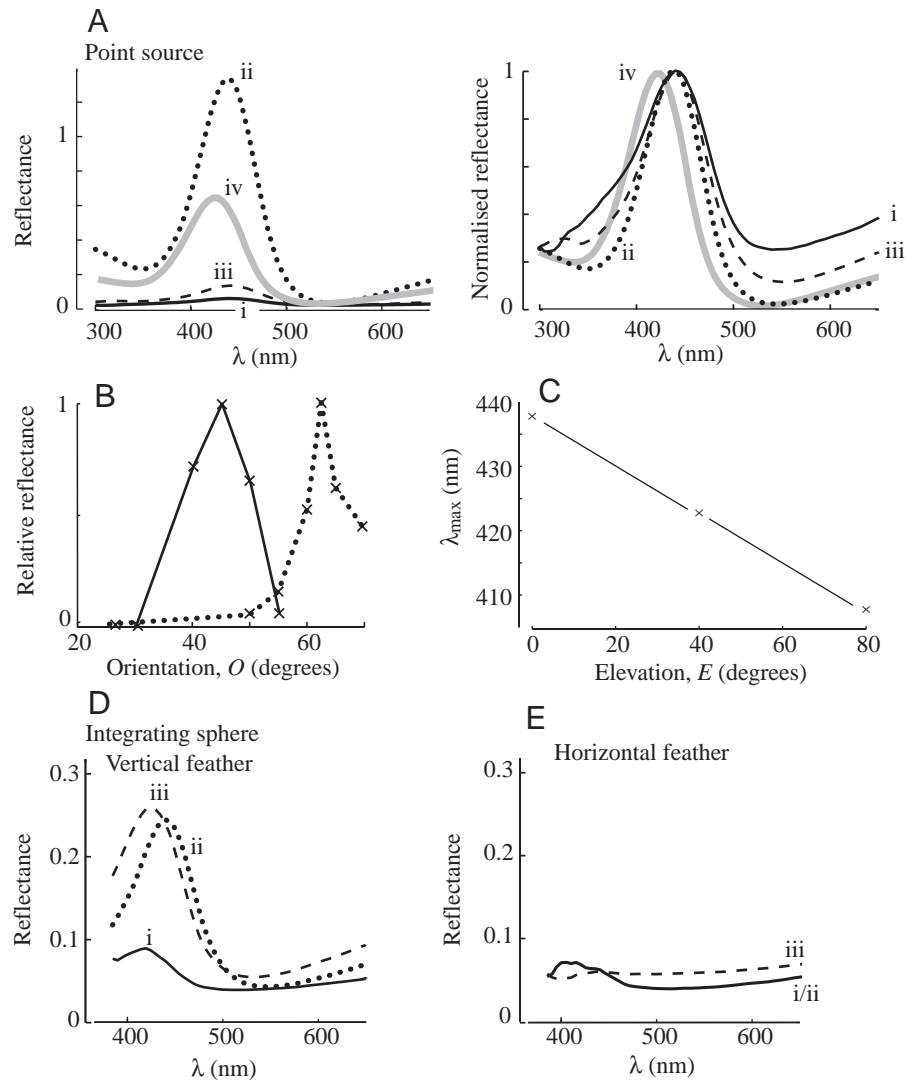
The five feathers described in some detail (see Figs 4–8) were photographed (see Fig. 3) with the same equipment used for recording spectra (Fig. 1A) except that the viewing lens was replaced with a digital camera (Canon D1; Nikkor 55 mm Macro lens, aperture set to f-16). Pictures were modified digitally so that the specimen filled a circular frame, even with oblique surface orientations.

Samples

Feathers were from freshly dead or live birds. Those from live birds had been obtained (under licence) for other purposes; dead birds had been killed by cats, on roads, etc. Often, more than one colour was measured from a given species.

We obtained reflectance spectra from structurally coloured feathers of 15 bird species: magnificent frigatebird *Fregata magnificens*; mallard *Anas platyrhynchos*; common pheasant

Fig. 4. Reflectance spectra of the magnificent hummingbird crown. This had directional coloration, with a single main reflectance peak and a reflective mechanism tilted relative to the plane of the feather vane. All data, except in E, are from a vertically aligned feather (see Fig. 1B). (A) Reflectance under localised illumination for four viewing geometries: (i) $E=5^\circ$; $O=30^\circ$; (ii) $E=5^\circ$; $O=45^\circ$; (iii) $E=5^\circ$; $O=55^\circ$; (iv) $E=40^\circ$; $O=70^\circ$. The left panel gives reflectance relative to diffuse white standard, and the right panel gives reflectance curves normalised to the maximum. The spectral location of the reflectance peak (λ_{\max}) is dependent on the value of E but independent of O . (B) Relative reflectance maxima versus O for $E=5^\circ$ (solid line) and $E=40^\circ$ (dotted line). These data imply that the reflective structure was tilted at approximately 40° to the plane of the feather vane (see Fig. 2A) and that light was diffused into a cone approximately 40° across. (C) λ_{\max} versus illumination elevation, for $O=50^\circ$. (D) Reflectance of the vertically oriented feather under diffuse lighting for three orientations: (i) $O=0^\circ$; (ii) $O=30^\circ$; (iii) $O=60^\circ$. The reflectance peak was broader than under a point source, and reflectance was greatest when the feather was viewed obliquely. (E) Reflectance of the horizontally oriented feather under diffuse lighting for three orientations, as in D. The feather remained dark over all orientations. O , surface orientation; E , illumination elevation.



Phasianus colchicus; common peafowl *Pavo cristata*; rock dove *Columba livia* (feral pigeon); magnificent hummingbird *Eugenes fulgens*; black-chinned hummingbird *Archilochus alexandri*; common kingfisher *Alcedo atthis*; Indian roller *Coracias benghalensis*; blue-tit *Parus caeruleus*; common magpie *Pica pica*; European jay *Garrulus glandarius*; rook, *Corvus frugilegus*; carrion crow *Corvus corone*; and common starling *Sturnus vulgaris*. Not all are mentioned specifically in the text.

Results

Given a fixed viewpoint, rotating either the surface being viewed or the light source (Figs 1A, 2) causes colour changes. With pigmented surfaces, these changes depend mainly on the location of specular highlights, but with structural colours the variation is less predictable and can produce striking visual effects. This paper outlines a method for describing these colours and identifies some ways in which colour varies in different types of structurally coloured feathers. First, we deal with some general properties of these feathers; we then examine five examples in more detail.

Spectra were recorded from a fixed viewpoint, with variable elevation of the light source, E , surface orientation, O , and the alignment of the feather in the holder – which was either horizontal or vertical (Fig. 1).

Summarising feather reflectance

Plumage reflectance spectra can be treated as having three components: (i) caused by pigmentation; (ii) caused by spectrally unselective specular reflection of the illumination, or ‘ordinary specularity’; (iii) caused by structural coloration, especially interference reflection. Feathers often combine all three components (Fox, 1976), but those illustrated (see Figs 3–8) probably lacked appreciable pigment colour. Two had substantial ordinary specularity (see Figs 6A, 7A) and all had structural coloration.

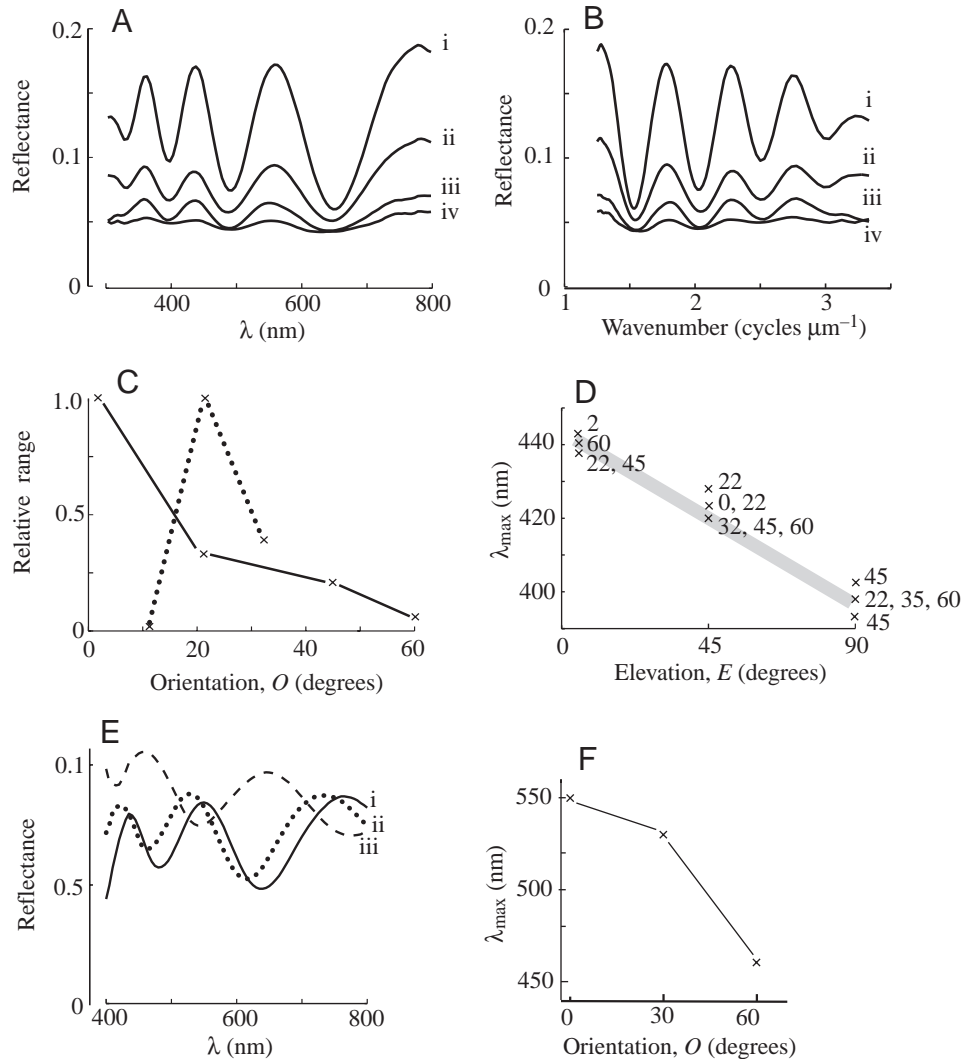


Fig. 5. Reflectance spectra of the feral pigeon nape. This had directional coloration, with multiply peaked reflectance. The bird was in poor condition, which may explain the generally low reflectance. (A) Reflectance *versus* wavelength at $E=5^\circ$. (i) $O=0^\circ$; (ii) $O=22^\circ$; (iii) $O=45^\circ$; (iv) $O=60^\circ$. The feather was aligned horizontally. (B) As in A plot, with reflectance plotted *versus* frequency (as wavenumber). The period is $0.5 \text{ cycles } \mu\text{m}^{-1}$. (C) Reflectance range *versus* O from the peak near 440 nm to the trough near 500 nm for the spectra in A (solid line) and for illumination at an elevation of 45° with a vertically oriented feather (dotted line). (D) The spectral location of the reflectance peak (λ_{max}) *versus* E for the peak below 450 nm . Values of O (in degrees) are given on the plot. Data are from both horizontally and vertically aligned feathers. (E) Reflectance spectra under diffuse lighting for three orientations of a vertically oriented feather: (i) $O=0^\circ$; (ii) $O=30^\circ$; (iii) $O=60^\circ$. Curves for orientations of -30° and -60° were virtually the same as for $+30^\circ$ and $+60^\circ$. The peaks were more widely separated than with a point source. As expected, the modulation depth of the reflectance spectrum was smaller than under a point source. (F) λ_{max} *versus* O under diffuse lighting for the reflectance peak between 450 and 550 nm . λ_{max} for -30° and -60° are the same as for $+30^\circ$ and $+60^\circ$. The variation in λ_{max} is discussed in the text. O , surface orientation; E , illumination elevation.

Reflectance spectra of structural colours differ from pigment spectra, especially the carotenoids and melanin pigments used by most birds (Fox, 1976). Structural spectra can be narrower (in waveband) (e.g. Fig. 4A) and have multiple spectral peaks (e.g. Fig. 5A). Also, very few plumage pigments preferentially reflect short-wavelength or green light (Fox, 1976). For

convenience, we recognise two main types of structural coloration: ‘directional’ and ‘diffuse’. Directional coloration is illustrated by hummingbird and pigeon feathers (see Figs 4, 5). These feathers took the colour of the feather pigment (often black) over a wide range of viewing angles. Their reflectance spectra had a roughly sinusoidal form, one or more peaks within the avian visible spectrum (300–700 nm). Rejection at spectral minima was very good; for example, falling to approximately 1 % of peak reflectance on the magnificent hummingbird crown (see Fig. 4A). Spectra with a single main reflectance peak were seen on hummingbirds and mallard speculum. Pigeon nape feathers (see Fig. 5A) had multiple reflectance peaks of roughly equal amplitude, as did magnificent frigatebird, common pheasant and common starling feathers.

Whilst laminar structures produce directional coloration (see Fig. 4 in Land, 1972; Land and Nilsson, 2001), diffuse coloration may be attributable to a more foam-like structure in the feather barb (Prum et al., 1998, 1999). This type of structure should produce relatively broadly tuned spectra, which are not iridescent; the blue of a European jay (see Figs 3, 6) is a good example. Other feathers that we classify as having diffuse coloration come from the European kingfisher and Indian roller (see Figs 3, 7, 8). They also have relatively broad reflectance spectra but are, nonetheless, iridescent and have other intriguing qualities.

Directionality

Both ordinary specularity and structural coloration can be directional. We look first at how intensity varies with viewing geometry (Fig. 2A) and then at spectral variation (Fig. 2B,C).

Structurally coloured feathers (in our sample) diffuse light into an approximately circular cone, which can be defined by its angular subtense, θ , at 50 % of maximum intensity (Fig. 2A). With a perfectly diffusing – Lambertian – surface, luminance is independent of orientation, i.e. $\theta=180^\circ$. We measured values of θ ranging from approximately 40° for the hummingbird crown (see Fig. 4) to 180° for the jay (see Fig. 6).

In addition to the angle over which light is diffused, the direction in which it is reflected is important. The directionality of a planar mirror is given by simple optical geometry (Fig. 2A), but even without structural coloration a feather could be complicated. This is because a feather is not a continuous flat structure, but a lattice in which surfaces need not be parallel to the overall plane of the vane. In practice, however, when ordinary (spectrally unselective) specular reflection was visible (e.g. Figs 3C, 6, 7), its direction indicated that the reflective surface was in (or close to) the plane of the vane itself.

In contrast, the reflective ‘surface’ producing structural coloration appeared, in some cases, to be tilted relative to the vane (Fig. 2A). This tilt was most obvious with directional coloration (see Fig. 4B) and was away from the main proximo-distal axis, not the lateral axis (as if, for a vertical feather, Fig. 1B, the structural reflectors resemble the louvres

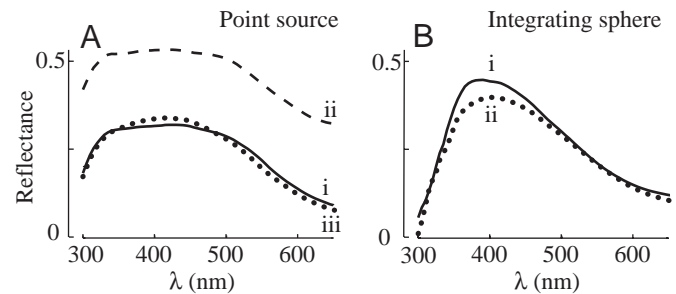


Fig. 6. Reflectance spectra of a European jay wing covert, which had diffuse coloration with a specular highlight. (A) Reflectance under localised illumination for three viewing geometries: (i) $E=5^\circ$; $O=0^\circ$; (ii) $E=5^\circ$; $O=5^\circ$; (iii) $E=90^\circ$; $O=45^\circ$. Curve ii is elevated across the spectrum, consistent with a specular highlight. Curves i and iii are alike, implying that the structural colour (rather than the highlight) was insensitive to viewing geometry. (B) Reflectance under diffuse illumination for two orientations: (i) $O=0^\circ$; (ii) $O=60^\circ$. At $O=30^\circ$, reflectance resembled that at $O=0^\circ$. These reflectance curves had narrower peaks than for localised illumination, probably because they were recorded from different locations on the blue coloration band (this feather grades from white through black and is most saturated at an intermediate location). Otherwise the reflectance was unaffected by the difference in lighting. O , surface orientation; E , illumination elevation.

of a Venetian blind). This means that light is directed towards the feather’s base or apex. Positive values of tilt, t , imply that the reflector is tilted so that light from above a near-horizontal feather is directed towards its base (Fig. 2A) and negative values imply reflection towards the apex.

Tilt of the structural reflector was 0° for feathers from the pigeon, magnificent frigatebird, common magpie and carrion crow. Non-zero values of t ranged from -20° for a pheasant neck feather to more than 40° for the magnificent hummingbird crown (see Fig. 4B). Across the peacock’s eyespot, t varies so that, as the tail rotates, colours ‘switch on and off’ separately, adding to the spectacle.

Variation in the reflectance maximum

The spectral location of maximum reflectance, λ_{\max} , varied with viewing geometry in nearly all the structural colours we examined. This is expected for laminar interference coloration, because the angle of incidence affects the effective spacing of the layers (see Fig. 7 in Land, 1972). However, feathers differ from ideal interference mirrors, not least because they are not optically flat (i.e. $\theta \gg 0^\circ$; Fig. 2A). We found that, given a fixed viewpoint, λ_{\max} was independent of orientation O and was linearly dependent on the angular separation of the viewer and illumination elevation, E . That is, $\lambda_{\max}=a-bE$, where a is λ_{\max} at $E=0^\circ$ (i.e. illumination and line-of-sight co-axial). In our sample, the constant b was between 0 and $1.2 \text{ nm degree}^{-1}$. It was interesting that the largest shifts in λ_{\max} were from diffuse coloration, such as kingfisher and Indian roller feathers (Figs 7, 8), rather than from directionally coloured feathers.

The finding that λ_{\max} was independent of O was unexpected

because theoretical treatments (e.g. Land, 1972) do not deal with diffuse interference reflectors. However, from optical geometry (Fig. 2B,C), one can see that, as the light source moves relative to the feather, $\lambda_{\max}(R)$, the reflectance peak on the axis of reflection, is given by:

$$\lambda_{\max}(R) = a - 2b(90 - \alpha),$$

where α is the angle of incidence. The effect of angle of incidence on $\lambda_{\max}(R)$ is twice the value of b given above; i.e. up to $2.5 \text{ nm degree}^{-1}$. This value is smaller than theory predicts for laminar reflectors (shift $>5 \text{ nm degree}^{-1}$; see Fig. 6 in Land, 1972).

We now illustrate some properties of structural plumage coloration with five selected examples (Fig. 3), the first two classified as directional and the other three as diffuse.

Magnificent hummingbird crown

The crown of the magnificent hummingbird (Fig. 4) is a good example of directional coloration, but we should start by noting that, when the structural colour was not visible, the feather was almost perfectly black, with a pigment reflectance of 0.025. Also, the feather was ‘matte’, lacking a spectrally unselective specular reflection (Fig. 3A). With a low light elevation, $E=5^\circ$, and the feather turned to maximise this specular reflection, the spectrally unselective reflectance added approximately 0.01. By comparison, an ordinary ‘black’ pigmented feather from a male European blackbird (*Turdus merula*) produced a specular reflection of 0.04 (in addition to a reflectance of 0.04 for the pigment colour).

This black ‘background’ gave a strong visual contrast for the structural colour, which was relatively directional; light from a point source was diffused over a cone 40° across (Fig. 2A, 4B). Also, the feather was black when illumination was (nearly) co-axial with the line of sight (Fig. 3A). For a normal glossy pigmented surface, this viewing geometry should give a relatively bright colour. That this did not apply to the hummingbird feather was consistent with the reflective structure being tilted relative to the plane of the vane. This tilt, t , was approximately 42° , which meant that light from above a near-horizontal crown feather would be reflected towards its base (i.e. forward over the bird’s head). Reflectance spectra had a single peak in the visible range, $\lambda_{\max}=440 \text{ nm}$, at $E=5^\circ$, with a half-width of approximately 70 nm . There were secondary maxima outside the visible range, one probably at twice the wavelength of the primary peak. The reflectance minimum was 0.025, indicating virtually perfect rejection. As the light source

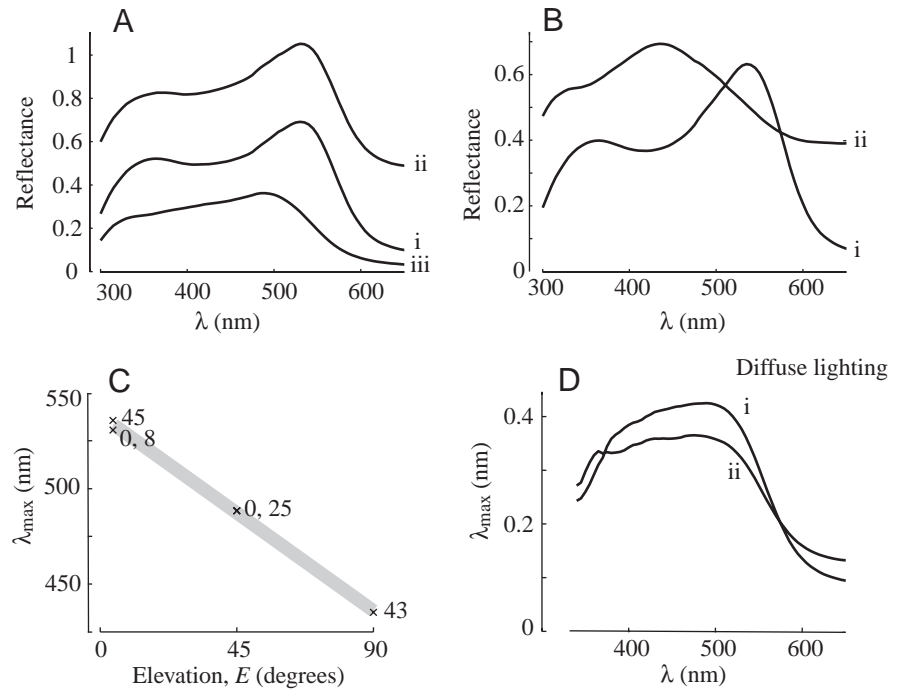


Fig. 7. Reflectance spectra of the kingfisher crown. Data are for a vertically aligned feather, but the horizontal alignment spectra are the same. This feather had diffuse coloration, with a spectrally non-selective specular reflectance. Variation in reflectance across the spectrum was greatest with the surface perpendicular to the line of sight. (A) Spectra for illumination near co-axial with the line of sight, $E=5^\circ$: (i) $O=0^\circ$; (ii) $O=8^\circ$; (iii) $O=45^\circ$. (B) Spectra for oblique orientation, $O=45^\circ$: (i) $E=5^\circ$; (ii) $E=90^\circ$. Spectrum i is the same as spectrum i in A. (C) The spectral location of the reflectance peak (λ_{\max}) versus E . Values of O are given in degrees. (D) Reflectance under diffuse illumination. (i) $O=0^\circ$; (ii) $O=60^\circ$. At $O=30^\circ$, the spectrum was intermediate between the two illustrated. O , surface orientation; E , illumination elevation.

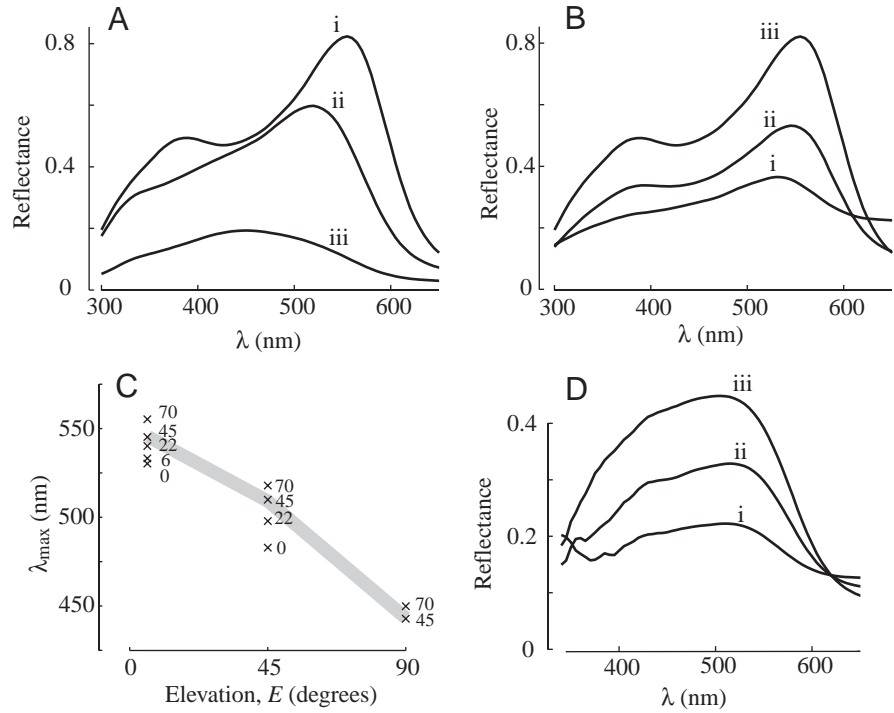
moved, λ_{\max} varied according to the formula: $\lambda_{\max}=442-0.40E$ (Fig. 4C).

Under diffuse illumination, in the integrating sphere, the hummingbird feather had low reflectance (maximum approximately 0.1) when perpendicular to the line of sight and at all orientations when aligned horizontally (Figs 1B, 4D). By comparison, the vertically aligned feather was brightly coloured when viewed obliquely. Also, λ_{\max} was dependent upon orientation. Thus, even under diffuse illumination, viewing geometry affects the colourfulness of this feather; in nature, the ‘brightest’ colours would appear when the bird was level with and facing a viewer. This directionality under diffuse light is intriguing and reminiscent of, but less marked than, that produced by the butterfly *Ancyluris meliboeus* (Vukusic et al., 2002), in which both diffraction and multilayer reflection are involved.

Feral pigeon nape

As with the magnificent hummingbird, the coloration of pigeon neck feathers (Fig. 5) is directional and probably produced by a laminar structure. When structural coloration was not visible, reflectance was 0.05 and spectrally flat (Fig. 5A), indicating that the pigeon feather’s pigmentation

Fig. 8. Reflectance spectra of the turquoise patch on an Indian roller tail. This had diffuse coloration, which looked most ‘colourful’ when viewed obliquely with the light behind the observer. Data are for a feather aligned vertically (see Fig. 1B), but rotating the feather to a horizontal alignment had no effect on reflectance. (A) Reflectance with $O=70^\circ$: (i) $E=5^\circ$; (ii) $E=45^\circ$; (iii) $E=70^\circ$. (B) Reflectance with $E=5^\circ$: (i) $O=0^\circ$; (ii) $O=45^\circ$; (iii) $O=70^\circ$. Spectrum iii is the same as spectrum I in A. (C) The spectral location of the reflectance peak (λ_{\max}) versus E . Values of O (in degrees) are given beside the cross to which they refer. There is a consistent shift to longer wavelengths with increasingly oblique viewing angles. (D) Reflectance under diffuse lighting: (i) $O=0^\circ$; (ii) $O=30^\circ$; (iii) $O=60^\circ$. O , surface orientation; E , illumination elevation.



was paler than the hummingbird's. Spectrally non-selective specular reflection was low, but difficult to measure.

Although directional, the pigeon's feather diffused light over a larger angle ($\theta=70^\circ$) than did the hummingbird crown (Figs 2A, 5C). The reflective surface was not tilted relative to the feather surface ($t=0^\circ$), unlike the hummingbird feather. A notable characteristic was that reflectance spectra had multiple maxima of approximately equal amplitude. These peaks were separated by a fixed frequency, forming a harmonic series (Fig. 5B). For instance, with roughly co-axial ($E=5^\circ$) illumination and viewing angles, maxima were at 310, 365, 441, 559 and 781 nm. The separation of these peaks was close to a wave-number of $1/2000\text{ nm}^{-1}$ (i.e. $1.5 \times 10^{14}\text{ Hz}$). As the light source moved, λ_{\max} varied (Fig. 5D), with the 'violet' peak shifting according to the formula: $\lambda_{\max}=438-0.48E$.

Under diffuse illumination (Fig. 5E,F), unlike the hummingbird, the pigeon's reflectance spectra were alike for vertical and horizontal feather alignments and were symmetrical about the plane perpendicular to the line of sight. This symmetry is consistent with the structural reflector being parallel with the feather surface. λ_{\max} varied markedly with orientation (O), shifting by approximately -2 nm degree^{-1} as the surface rotated away from the plane perpendicular to the line of sight (Figs 1A, 5F). Given that, under point illumination, λ_{\max} was independent of orientation, this effect might be seem surprising. The reason is that the feather is a directional reflector so that, as orientation varies, so does the effective elevation of the light source and, hence, λ_{\max} (Fig. 2B). Consequently, a static viewer sees the pigeon's iridescent coloration change during displays, at least when the bird is under diffuse lighting.

European jay wing covert

European jay wing covert feathers (Fig. 6) are striped, with white shading through bright blue bands into black (Fig. 3C). This structural coloration diffused reflected light more-or-less like pigmentation (Fig. 6A). Also, the feather had a spectrally flat specular highlight characteristic of a glossy surface, which increased reflectance by approximately 0.25 (Fig. 3C). Again, as with pigmentation, λ_{\max} was unaffected by viewing geometry; the reflectance maximum was approximately 260 nm wide at 50 % of maximum intensity (this value varied with position on the band). Under diffuse lighting (Fig. 6B), reflectance spectra resembled those seen under a point source.

The jay's blue coloration resembled the non-directional colours described by Prum et al. (1998, 1999). We now look at two further examples of diffusing coloration, but these are more complex, being iridescent and having other directional properties.

Common kingfisher crown

With a fixed light position, the kingfisher's crown feather resembled the jay's feathers in having a diffuse, spectrally tuned reflectance and a spectrally unselective specularity (Fig. 7A,B). Also, the reflectance spectrum was broad, but in this case one or two comparatively narrow peaks rose above the plateau. However, the location of the spectral peak was not fixed, varying according to the formula: $\lambda_{\max}=535-1.22E$ (Figs 3D, 7C).

In addition to the variation in λ_{\max} , the form of the kingfisher feather reflectance spectrum altered with viewing geometry in that, with illumination near the line of sight ($E=5^\circ$), reflectance varied more strongly across the spectrum than with illumination perpendicular to the line of sight ($E=90^\circ$;

Fig. 7B). As a result, the kingfisher's colour tends to be most saturated when the bird is lit from behind the viewer. There was no effect of feather alignment (Fig. 1B) on reflectance spectra, suggesting that the reflecting structure is in the plane of the feather vane (i.e. $t=0^\circ$).

Under diffuse lighting (Fig. 7D), the reflectance spectra were broader than with a point source and λ_{\max} was insensitive to orientation and to feather alignment. This is perhaps to be expected for diffuse coloration and can be contrasted with the pigeon's nape, where λ_{\max} varied with orientation (Fig. 5E,F).

Indian roller tail

The feathers of the Indian roller's tail are dark blue with a greenish-blue patch. The two colours share similar optical properties, and we describe the greenish-blue (Fig. 3E). As with the kingfisher crown, the reflectance spectrum had a broad plateau with one or two comparatively narrow peaks (Fig. 8A,B). The location of the peak reflectance was given by the formula: $\lambda_{\max}=555-1.22E$ (Fig. 8C). The directional properties of Indian roller tail coloration superficially resembled those of the kingfisher crown, but the way in which colour varied with viewing geometry was different. For example, there was little spectrally unselective specular highlight. Instead, both intensity and the ratio of maximum to minimum reflectance (and hence 'saturation') varied with viewing angle such that, given a fixed light source, both brightness and saturation increased with surface orientation (O ; Figs 1A, 3E, 8B). Also, given a fixed orientation, reflectance fell with increasing angular separation of the viewer and the light source (E ; Figs 3E, 8A).

These directional properties mean that the Indian roller's tail looks brightest and the colour most saturated when it is viewed obliquely and lit from behind the observer (Fig. 3E). As it turns towards the observer, the feather darkens and becomes greyer, which gives the impression of translucence. These directional properties cannot adequately be summarised by the scheme outlined in Fig. 2A but, as with the kingfisher, there was no effect of feather alignment (Fig. 1B) on reflectance spectra, again suggesting that the reflecting structure was parallel to the plane of the feather vane (i.e. $t=0^\circ$).

Under diffuse lighting (Fig. 8D), the Indian roller tail resembled the kingfisher crown in that spectra were broader than under the point source and λ_{\max} was insensitive to orientation and to feather alignment (Fig. 1). Both the maximum reflectance and variation in reflectance across the spectrum increased with surface orientation, which was consistent with observations under a point source.

Discussion

Feathers often combine pigmentation and structural colour, especially to make green (Fox, 1976), but the five feathers illustrated mainly had structural coloration. The blue on the jay's wing covert resembled a glossy pigmented surface (Fig. 6), while the remaining four feathers were iridescent in

that λ_{\max} varied with viewing geometry (see Introduction). Three of the examples lacked a significant spectrally unselective specular highlight, which meant that the brightest colours were not desaturated. Directionality and the high saturation of the brightest colours underlie the arresting visual qualities of iridescent coloration.

Feathers as interference reflectors

Laminar interference reflectors can give a range of spectral reflectance curves depending upon the relative thickness, refractive index difference and number of layers (see Fig. 4 in Land, 1972). Land's models can be used to generate spectra that resemble those we recorded from directionally coloured feathers (Figs 4, 5). Interference reflectors with multiple (more than five) equally spaced layers can produce both single- and multiple-peaked spectra (Figs 4A, 5A,B; see Fig. 4c in Land, 1972; Land and Nilsson, 2001). Variation in the spacing of layers whitens the reflectance spectrum, which means that spectra with good rejection at reflectance minima – and hence saturated colours – probably require equally spaced layers. By comparison with multilayered reflectors, a reflector with relatively few layers should produce wider peaks with lower reflectance and, hence, relatively dull colours (Land, 1972). The iridescent glosses on corvid feathers – including European magpie, rook and carrion crow plumage – had spectra of this kind.

Of the examples of diffuse coloration illustrated, the jay wing covert (Fig. 6) most resembles the type described by Prum et al. (1998, 1999) in which the spectral reflectance is independent of viewing geometry. The kingfisher and Indian roller's coloration (Figs 7, 8) was diffuse but also iridescent. These feathers might combine features of laminar and foam-like structures.

How colours vary with viewing geometry

Iridescence and other directional properties are distinctive qualities of structural coloration. Some features of plumage colours that affect their visual appearance are as follows.

(i) Pigment reflectance was often very low, i.e. black. For example, with the feather perpendicular to the line of sight ($O=0^\circ$) and a low light elevation, $E=5^\circ$, the reflectance of the hummingbird crown feather at 500 nm was 0.025, whereas for a typical black bird, the male European blackbird (*Turdus merula*), reflectance was 0.04.

(ii) Coloration sometimes, but not always, lacked an ordinary specular highlight, i.e. the feather surfaces were matte. A matte black background means that the structural colour produces a high-contrast signal when the feather 'catches the light' (Fig. 3A).

(iii) Iridescence is expected for interference colours because their spectral tuning is dependent on the effective spacing of the structural layers, and this varies with the angle of incidence (Land, 1972). However, models of flat mirrors do not predict how λ_{\max} varies across a diffuse beam from a surface such as a feather. We found that, under a point light source, λ_{\max} was independent of viewing angle O and linearly

related to the angle between the light source and the line-of-sight E (Figs 1A, 2B, 4C, 5D, 7C, 8C). These relationships can be understood if it is assumed that spectral tuning in a diffuse beam depends upon the mean of the angles of incident and (diffusely) reflected light paths through the feather barb (Fig. 2C).

The fact that when a surface is lit by a point source (e.g. the sun) λ_{\max} is independent of viewing angle might seem surprising because feathers can change in colour (hue) as a bird moves. The reason is that although λ_{\max} is independent of surface orientation under a point source, for directional coloration under diffuse light, the effective location of the light source (e.g. the part of the sky best reflected by the feather) varies with orientation (Figs 4D, 5E,F). With diffuse coloration, λ_{\max} is indeed fixed unless the viewer moves relative to the light source (Figs 7, 8).

Another reason that the effects of viewing geometry on λ_{\max} can lead to very different types of (visually perceived) colour change is that the way colour varies depends upon the spectral reflectance function. Single-peaked spectra (Fig. 4) resemble spectral lights, and colour changes are 'along' the spectrum. However, multiply peaked spectra (Fig. 5) can give 'non-spectral' colours such as purples or achromatic colours (Finger and Burkhardt, 1994). This is why, for human viewers, the colours of a pigeon nape shift from green to purple through grey (Fig. 3B). Birds have four spectral types of (single) cone photoreceptors (Hart, 2001), and the 'non-spectral' colours and the colour changes that they might see when viewing multiply peaked plumage spectra may well not appear elsewhere in nature.

(iv) The reflective structure producing coloration may be tilted relative to the plane of the feather blade (Fig. 2A). This means that no single viewing geometry can be used to maximise spectral signals from iridescent feathers (Cuthill et al., 1999). Where present, this tilt was away from the feather's main (proximo-distal) axis (Fig. 1B). The tilt affects when the structural colour is visible and, presumably, its use in displays. By comparison, ordinary (spectrally unselective) specularly always appeared to originate from a surface that was roughly coplanar with the feather blade (Figs 6A, 7A).

The directional properties of the diffuse coloration of kingfisher and Indian roller feathers are less easy to understand than those of directional coloration, but they too affect their visual appearance. For example, the Indian roller tail look most brilliant (brightest and most saturated) when viewed obliquely and lit from behind the observer (Fig. 8).

Iridescent colours as signals

There is evidence that carotenoid-based pigmentation, giving red, orange and yellow colours (sometimes with a secondary ultraviolet peak), influences mate choice by birds. Also, the ability to obtain or use carotenoids may be correlated with other less visually obvious measures of a bird's health or 'quality' (Olson and Owens, 1998; Badyaev et al., 2001). Are iridescent colours simply a cheap way of attracting attention,

or might they also convey information? The basic materials, keratin and melanin, are common to all plumage, but it is possible that the formation of a regular composite structure, which is necessary for a well-tuned and bright reflectance spectrum, is energetically demanding. For example, the multiple harmonically spaced spectral peaks seen on the pigeon's nape feather (Fig. 5) are characteristic of a structure formed of many layers (see Fig. 4 in Land, 1972). The modulation of reflectance across the spectrum is very sensitive to any variation in the separation of these layers; unequal layering would produce greyish rather than spectrally tuned iridescence. Also, the directionality may depend on local and long-range order in the structure of the feather.

Alternatively, it might be that iridescence is a by-product of feather growth, perhaps produced by a robust process resembling crystallisation. Even so, colour could be informative if iridescent coloration is sensitive to damage. Answering these questions requires electron microscopy of feather barb structure and comparisons of iridescent coloration within a single species.

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