

ORIGINAL PAPER

M. Vorobyev · D. Osorio · A. T. D. Bennett
N. J. Marshall · I. C. Cuthill

Tetrachromacy, oil droplets and bird plumage colours

Accepted: 3 July 1998

Abstract There is a growing body of data on avian eyes, including measurements of visual pigment and oil droplet spectral absorption, and of receptor densities and their distributions across the retina. These data are sufficient to predict psychophysical colour discrimination thresholds for light-adapted eyes, and hence provide a basis for relating eye design to visual needs. We examine the advantages of coloured oil droplets, UV vision and tetrachromacy for discriminating a diverse set of avian plumage spectra under natural illumination. Discriminability is enhanced both by tetrachromacy and coloured oil droplets. Oil droplets may also improve colour constancy. Comparison of the performance of a pigeon's eye, where the shortest wavelength receptor peak is at 410 nm, with that of the passerine *Leiothrix*, where the ultraviolet-sensitive peak is at 365 nm, generally shows a small advantage to the latter, but this advantage depends critically on the noise level in the sensitivity mechanism and on the set of spectra being viewed.

Key words Bird · Colour · Vision · UV · Plumage

M. Vorobyev¹
Sechenov Institute of Evolutionary Physiology and Biochemistry,
Russian Academy of Science, Pr. Thorez 44, 194223,
St. Petersburg, Russia

D. Osorio (✉)
School of Biological Sciences, University of Sussex,
Brighton BN1 9QG, UK
e-mail: d.osorio@sussex.ac.uk; Fax: +44-1273-678433

A.T.D. Bennett · I.C. Cuthill
School of Biological Sciences, University of Bristol,
Woodland Rd, Bristol BS8 1UG, UK

N.J. Marshall
Vision, Touch and Hearing Research Centre,
Department of Physiology and Pharmacology,
University of Queensland, St Lucia,
Queensland 4072, Australia

Present address:

¹Institut für Neurobiologie, Freie Universität Berlin,
Königin-Luise-Strasse 28–30, D-14195 Berlin, Germany

Abbreviations *LWS* long-wave sensitive · *MWS* medium-wave-sensitive · *SWS* short-wave-sensitive · *UVS* ultraviolet-sensitive

Introduction

Bird eyes have a number of features which suggest they are well adapted for colour vision. There are four types of cone photopigment with peak sensitivities ranging from 365 nm to 565 nm (Fig. 1), and each cone contains a coloured oil droplet which sharpens spectral tuning (Bowmaker 1980). Given the colourfulness of their plumage to humans, and the evolutionary importance of their visual displays, it is interesting to ask how oil droplets, UV sensitivity and tetrachromacy affect birds' colour vision, and how their perception of plumage coloration might differ from our own (Burkhardt 1989; Bennett et al. 1994).

To provide a framework for understanding the avian view of plumage spectra, we use a model which assumes that photoreceptor noise sets visual thresholds. Performance is predicted most accurately for small differences (i.e. close to threshold). Thus a key notion is that colour is used for precise judgement of object quality; for example, a fruit's ripeness, or health of a potential mate.

Teleost fish evolved four cone opsins (Hisatomi et al. 1994) and most (possibly all) birds have retained them. Spectral sensitivities of cones, and oil droplet absorption spectra, are known for at least 11 species from 8 orders (Fig. 1; Bowmaker et al. 1997; Hart et al. 1998)¹. The four pigments reside in four types of single cone, and

¹In an owl (Strigiformes) *Strix aluco* and a penguin (Sphenisciformes) *Spheniscus humboldti* three types of cone pigment were found, with four in the remaining eight species from the orders: Procellariiformes (*Puffinus puffinus*), Anseriformes (*Anas platyrhynchos*), Psittaciformes (*Melopsittacus undulatus*), Galliformes (*Gallus gallus*, *Coturnix japonica*), Columbiformes (*Columba livia*) and Passeriformes (*Leiothrix lutea*, *Taenopygia guttata*). The starling (*Sturnus vulgaris*), a passerine, also has four cone pigments (Hart et al. 1998).

one also in a double cone. The peaks of the long-wavelength-sensitive (LWS) and medium-wavelength-sensitive (MWS) pigments differ little between species, that of the short-wave-sensitive (SWS) pigment varies over a range of about 25 nm, while the shortest wavelength (UVS) pigment is most variable. In some species (e.g. passerines *Leiothrix lutea* and *Sturnus vulgaris*; and budgerigar *Melopsittacus undulatus*) the UVS peak is at about 365 nm, while in others (e.g. pigeon, *Columba livia*) it is at 410 nm (Bowmaker et al. 1997; Hart et al. 1998). There is evidence from electroretinography of pigeon for a fifth receptor with a peak below 400 nm (Hzn et al. 1994); however this observation is not substantiated by microspectrophotometry or behavioural evidence (see also Vorobyev and Osorio 1998).

Cone inner segments of most classes of vertebrate contain an oil droplet, and these are coloured in lungfish, reptiles and birds (Walls 1942; Robinson 1994). Amongst suggested roles for oil droplets have been: colour vision, prevention of short-wave photodamage and reduction of chromatic aberration (Walls 1942; Bowmaker 1980; Govardovskii 1983; Partridge 1989). In avian single cones, each visual pigment is associated with one type of oil droplet which acts as a cut-off filter, absorbing wavelengths below a critical value, and transmitting longer wavelengths (Maier and Bowmaker 1993; Bowmaker et al. 1997). Oil droplets in the LWS cones and MWS cones, called 'red' and 'yellow', respectively, cut off close to the sensitivity maxima of their photopigments, narrowing spectral tuning and reducing absolute sensitivity by ca. 50% (Fig. 1). By contrast, SWS cone and UVS cone oil droplets, called 'clear' and 'transparent', affect spectral tuning less. Double cones, which contain the LWS opsin, have a droplet of variable colour in their large member (Bowmaker et al. 1997).

The receptor noise model of visual thresholds

To understand performance of the avian eye in discrimination and recognition of plumage colours, we compare eyes modelled on those of the Pekin robin, *Leiothrix lutea* (henceforth called *Leiothrix*) and pigeon (Fig. 1), with modified versions where either one of the receptor types, or the oil droplets are removed. Relating eye design to visual ability is worthwhile only if behaviourally significant discrimination thresholds are set by the eye. Here, performance is predicted using a model of colour coding which attributes thresholds to receptor noise (Osorio and Vorobyev 1996; Brandt and Vorobyev 1997; Vorobyev and Osorio 1998). No assumptions are made about neural mechanisms such as opponency coding, save that the achromatic signal is disregarded. Predictions (Fig. 2) are accurate for *light-adapted* eyes of pigeon (yellow but not red retinal field; Remy and Emmerton 1989) and of *Leiothrix*, as well as for other animals including humans (Vorobyev and Osorio 1998).

A notable prediction of the model is the elevated spectral sensitivity in the near-UV, found in *Leiothrix*

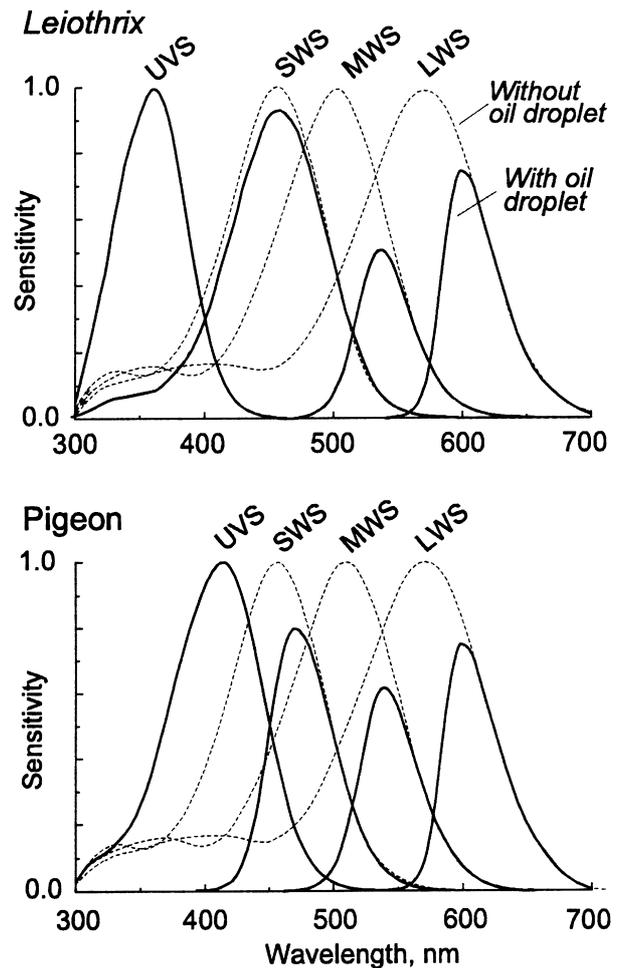


Fig. 1 Spectral sensitivities of single cones in Pekin robin (*Leiothrix lutea*) and pigeon (*Columba livia*) eyes based on optical models derived from microspectrophotometry of the cone photopigments, and of oil droplets. The data are from Bowmaker et al. (1997), and curves fitted to pigment peaks using Maximov's (1988) formula. Optical density of cones at λ_{\max} is assumed to be 0.4. Sensitivity maxima are around 565 nm (long-wavelength-sensitive; LWS), 505 nm (medium-wavelength-sensitive; MWS), 450 nm (short-wavelength-sensitive; SWS), and either around 410 nm (pigeon and chicken) or 365 nm (passerines and budgerigar; violet/UV-sensitive; UVS). 410 nm is close to the 420 nm peak of the human 'blue' cone pigment, but pigeons have greater sensitivity to UV light than humans owing to the high UV transmittance of their ocular media (Emmerton et al. 1980)

and for pigeon (Fig. 2). This is not due to especially high sensitivity of the UV mechanism (which in *Leiothrix* is the noisiest of the four), but rather the combination of UVS–SWS chromatic signals for short-wavelength monochromatic lights, and low adapting intensity in the UV part of the spectrum (c.f. Burkhardt and Maier 1989; Maier 1994). For pigeon the model predicts spectral sensitivity in the short-wave part of the spectrum well, and there is no evidence for a fifth, UV, receptor (c.f. Hzn et al. 1994). Deviations from the predictions, which occur in dim conditions, and in the pigeon red field, are probably attributable to inputs from an achromatic mechanism (Vorobyev and Osorio 1998).

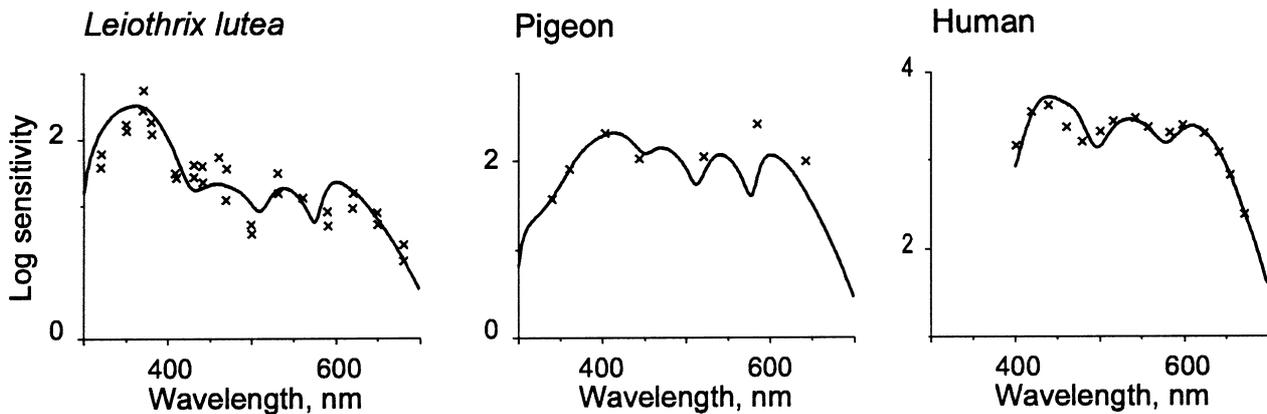


Fig. 2 Predictions of the model compared with measured spectral sensitivities for birds and human (modified from Vorobyev and Osorio 1998; sources King-Smith and Carden 1976; Remy and Emmerton 1989; Maier 1992). The accuracy of these predictions emphasises the importance of eye design (i.e. receptor spectral sensitivities and noise) as opposed to later neural processing in setting thresholds

This work is, in essence, a quantitative comparison of different eye designs, based on simulation of the responses of model eyes to real spectra. The remainder of the Introduction explains this approach.

Constraints on eye design 1: receptor noise limited discrimination

First, it is important to emphasise that the relative merits of different eye designs for colour vision depend critically upon the nature of the stimuli being viewed and the illumination conditions (Barlow 1982; van Hateren 1993; Osorio and Vorobyev 1996). For example, oil droplets narrow spectral tuning of avian cones compared to unfiltered visual pigment (especially for LWS and MWS cones), and they reduce quantal catch (Fig. 1). Sharpened spectral tuning is beneficial for colour vision if targets have similar sharply varying reflectance spectra; i.e. sampling and stimuli are matched (Barlow 1982). By comparison, where reflectance spectra vary smoothly with wavelength there is no additional 'spectral detail' to be encoded by receptors with oil droplets. At the other extreme, the reduction in spectral overlap of the cones due to oil droplets is potentially deleterious for discrimination of monochromatic lights, and may also increase metamerism (spectral aliasing), where lights of differing spectral composition give the same sets of cone excitations. Where it is set by quantal catch, receptor noise is intensity dependent (De Vries 1943), in which case any benefits from oil droplets are traded off against the increase in this noise. This predicts reduced filtering, as well as the rod-dominated retina of the nocturnal owl *Strix aluco* (Bowmaker and Martin 1978).

Similar costs and benefits apply to variations in the numbers of receptors, and to the positions of their

spectral peaks (e.g. Barlow 1982; van Hateren 1993; Osorio and Vorobyev 1996). Each additional cone type potentially increases the dimensionality of the receptor space, but reduces the numbers of other cones (given a fixed eye size), and hence the signal-to-noise ratio of each receptor mechanism. Consequently, the optimal number of receptor types for accurately encoding natural spectra depends upon the amount of 'detail', such as narrow peaks, they contain, and on signal-to-noise ratios in photoreceptors (van Hateren 1993).

Constraints on eye design 2: colour constancy

Noise in receptors or later neural processing is normally considered to limit reliability of a sensory mechanisms, and hence to dictate eye design (Laughlin 1987), but quite different constraints on eye design may arise from the need to extract reliable signals from complex natural scenes. Primates probably use colour vision mainly for object recognition (Mollon 1989). While the primary purpose of colour vision in birds awaits further study, here too a role for colour in judgement of object quality seems likely; for example, in mate choice (Finger and Burkhardt 1994; Bennett et al. 1996, 1997; Amundsen et al. 1997; Andersson and Amundsen 1997), or in recognition of food (Burkhardt 1982).

Seeing a given reflectance spectrum as a fixed 'colour' under variable illumination demands colour constancy. Although colour constancy is not a unitary process (Hurlbert 1998), a large part can be attributed to independent normalisation of receptor mechanisms (though not necessarily of the receptors themselves) to the mean background (Eq. 2; Wyszecki and Stiles 1982; Hurlbert 1998). This normalisation, known as a von Kries transformation, is in general done best by narrow-band receptors (Worthey and Brill 1986)², while a small spectral separation of receptors also favours colour

²For a monochromatic receptor sensitive to wavelength λ the response to given target, i , viewed on a background, b , is $R_i(\lambda)/R_b(\lambda)$, where $R_i(\lambda)$ and $R_b(\lambda)$ are the reflectances of the target and background at λ . This ratio is independent of the illuminant, giving perfect colour constancy. (see also Eqs. 1, 2; Worthey and Brill 1986).

constancy (Osorio 1997; Osorio et al. 1997). Filtering by oil droplets narrows spectral tuning, and we estimate its effects on colour constancy of plumage spectra under natural illuminants (Fig. 3).

Characterisation of natural spectra

Using the principles of coding theory we can estimate the performance of a given eye design for encoding a population of spectral stimuli (Barlow 1982; van Hateren 1993). Outside colour vision, the notion that eyes are adapted to optimise information encoded is a very useful basis for understanding eye design and neural processing. For the spatio-temporal domain statistical models of natural images permit generalisation about the properties of natural images (Laughlin 1987; van Hateren 1992; Ruderman 1994). Such theoretical models require that the distribution of stimuli in receptor space is Gaussian (or otherwise known). Animal colours are, however, caused by a small number of distinct physical mechanisms, and have quite distinct types of spectra (Fox and Vevers 1960; Lythgoe 1979; Burkhardt and

Finger 1991; Finger et al. 1992). For example, green leaves and some green feathers have a reflectance peak at 555 nm; carotenoid reflectances resemble step functions; melanin reflectance increases more smoothly with wavelength, while structural colours may be relatively narrow band or have multiple peaks. Taken together, the distinct mechanisms give a population of stimuli that does not appear to satisfy the assumptions of general coding theoretical approaches used when modelling stimulus populations, for example random phase and Gaussian statistics (Barlow 1982; van Hateren 1993). While we have not proven that plumage spectra give a population of stimuli with non-Gaussian statistics there are reasons to doubt that this is so (Vorobyev et al., unpublished observations), so that it is prudent to avoid use of statistical models of natural spectra. Instead, we do not model the stimulus population, but simulate retinal responses to 424 real plumage spectra (Figs. 4, 5).

An alternative to our approach is to characterise sample spectra by principal component analysis (Maloney 1986; Endler 1990; Endler and Thery 1996; Bennett et al. 1997), but this is of limited value for understanding eye design. For example, in the 400- to 700-nm spectral window used by humans, Maloney (1986) found that two components account for ca. 99% of the variance in the spectra of natural surfaces measured by Krinov (1953). This result might be taken to imply that a dichromat could encode virtually all the information in the dataset. In practice, however, this analysis does not directly predict the number of photoreceptor types required to encode Krinov's spectra, because their principal components cannot be derived by linear combination of receptor sensitivities (Vorobyev et al., unpublished observations). Principal components are, of course, valid for describing populations of spectra (Bennett et al. 1997; Cuthill et al. 1998).

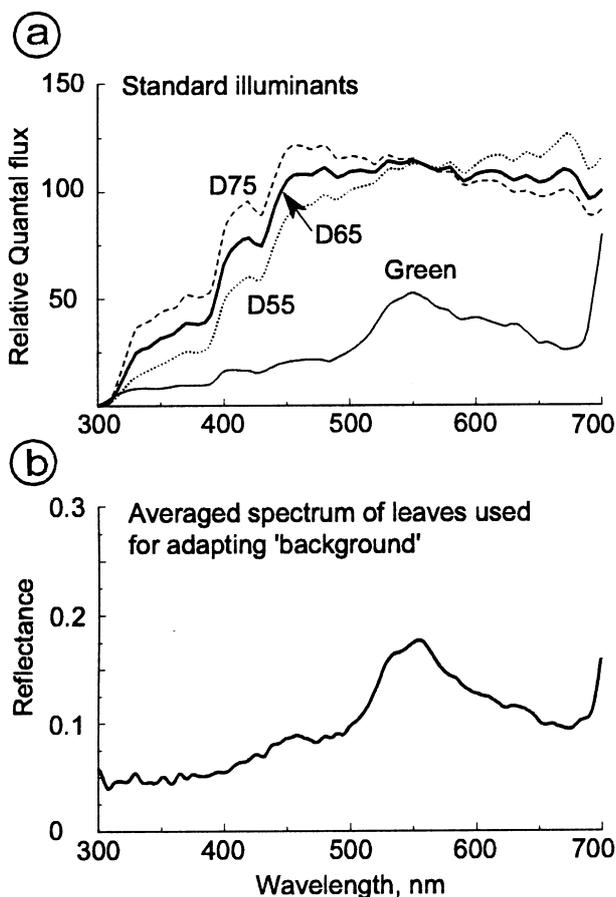


Fig. 3 **a** Illuminants. Three are standard sources D65 (standard daylight), D55 (sunlight), D75 ('North' light), and one the green light of forest shade (Endler 1993). **b** Spectrum of leaf green adapting background used for colour constancy calculations (Fig. 6). The spectrum is the mean from a large dataset of leaf spectra

Materials and methods

Spectroradiometry

Reflectance spectra of the major plumage regions of 65 species or colour morphs of bird were obtained from fresh material or good quality museum specimens, giving 424 distinct spectra (Appendix 1). Measurements were made, as described elsewhere (Bennett et al. 1997; Fig. 3), by a Zeiss MCS 230 diode-array photometer, an Oriel Instaspec IV CCD spectrophotometer, or an Ocean Optics S1000 spectrophotometer. The spectral range was from 300 nm or 330 nm to at least 700 nm.

Illumination spectra used in the models (Fig. 3a) were standard illuminants (Wyszecki and Stiles 1982), namely D55 (sunlight), D65 (standard daylight) or D75 (skylight), and also a 'forest shade' spectrum (Endler 1993) from warm temperate forest (Yakushima Island, Japan) measured with a spectroradiometer (Ocean Optics S1000 calibrated by an NPL Clarke/Berry standard lamp, No JS1).

The model

To predict discrimination we assume that colour is coded by unspecified opponent mechanisms, while the achromatic signal is

disregarded. Colour discrimination is assumed to be limited by photoreceptor noise. Using this assumption we can, for a number of animals, accurately predict photopic spectral sensitivity – that is discriminability of minimally saturated colours from achromatic background (Vorobyev and Osorio 1998; see Fig. 2). Here we describe discriminability of plumage colours, which are quite saturated, and also assume a chromatic background – green leaves, and changing illumination (Figs. 3, 6; Table 3). To extend the model we make two additional assumptions. First, that receptors independently adapt to the background following von Kries' coefficient law, and second that the Weber-Fechner law is valid for receptor signals (this permits prediction of suprathreshold differences between saturated colours). The von Kries' law gives a mechanism for colour constancy by independent adaptation of receptor mechanisms (i.e. cone signals; Wyszecki and Stiles 1982; Worthey and Brill 1986). For humans, both assumptions hold for a broad range of illumination conditions (Wyszecki and Stiles 1982).

Mathematical formulation of the model is given elsewhere (Osorio and Vorobyev 1996; Vorobyev and Osorio 1998), but the following formulae suffice to predict the discriminability of any two of spectra for any eye, provided only that receptor spectral sensitivities and noise can be estimated. Colour is defined as a point in a perceptual space whose co-ordinate axes represent quantum catches of receptors (Poirson and Wandell 1990). Discriminability of any two colours is described by the "distance" between them, ΔS . Where the separation of a given pair of points in this space is below a certain threshold distance, ΔS^t , the colours are indistinguishable. The value of ΔS^t depends on the threshold criterion, and on viewing conditions.

For an eye with n spectral classes of photoreceptor viewing a surface with a reflectance spectrum, $S(\lambda)$, receptor quantum catches are given by:

$$Q_i = \int_{\lambda} R_i(\lambda) S(\lambda) I(\lambda) d\lambda, \quad (1)$$

where λ denotes wavelength, $i = 1, 2, \dots, n$; Q_i is the quantum catch of receptor i , $R_i(\lambda)$ spectral sensitivity of receptor i , $I(\lambda)$ the spectrum of light entering the eye, and integration is over the visible spectrum. To take account of receptor adaptation, receptor quantum catches, Q_i , are normalised to the background to give a value $q_i = k_i Q_i$. The coefficients k_i describe the von Kries transformation, and they are chosen so that the quantum catches for adapting background (Fig. 3) is constant, i.e.

$$k_i = 1 / \int_{\lambda} R_i(\lambda) S^b(\lambda) I(\lambda) d\lambda, \quad (2)$$

where $S^b(\lambda)$ is the reflectance spectrum of the background.

Let f_i be the signal of receptor mechanism i , and Δf_i be the differences of the signals in receptor mechanisms between the stimuli. According to Weber's law relative rather than absolute values of the quantum catches are coded, thus:

$$\Delta f_i = \Delta q_i / q_i, \quad (3)$$

where Δq_i denotes the difference in the quantum catch between the stimuli. Integration of Eq. 3 gives the Fechner law, i.e., the signal of receptor channel is proportional to the logarithm of the quantum catch:

$$f_i = \log(q_i). \quad (4)$$

Note that since for the background $q_i = 1$, the difference in the signals of receptor channels close to background is simply given by the difference of receptor quantum catches, i.e. $\Delta f_i \approx \Delta q_i$.

Receptor noise is described by the signal-to-noise ratio, or by its inverse, the Weber fraction, ω_i . Weber fractions may either be constant (typically at high intensities), or inversely proportional to the square root of the quantum flux (typically at low intensities; De Vries 1943; Wyszecki and Stiles 1982).

It may be noted that the signal in each colour opponent mechanism, x_k , is given by:

$$x_k = \sum_{i=1}^{i=n} C_{ki} f_i, \quad (5)$$

where C_{ki} describes the input weighting of the receptor mechanism i to the opponent mechanism k . Opponent signals vanish for the stimuli which differ from achromatic stimulus only in intensity. We assume that (owing to receptor adaptation) the background is effectively achromatic, and hence the sum, $\sum_{i=1}^{i=n} C_{ki} = 0$. Because the accuracy of opponent mechanisms is limited by receptor noise (Vorobyev and Osorio 1998), the accuracy of colour discrimination is independent of the opponent coding and the expressions for colour distance do not contain the parameters C_{ki} .

The following equations then relate colour distance to receptor noise (Vorobyev and Osorio 1998). For dichromatic vision:

$$(\Delta S)^2 = \frac{(\Delta f_1 - \Delta f_2)^2}{\omega_1^2 + \omega_2^2}, \quad (6)$$

for trichromatic vision:

$$(\Delta S)^2 = \frac{\omega_1^2 (\Delta f_3 - \Delta f_2)^2 + \omega_2^2 (\Delta f_3 - \Delta f_1)^2 + \omega_3^2 (\Delta f_1 - \Delta f_2)^2}{(\omega_1 \omega_2)^2 + (\omega_1 \omega_3)^2 + (\omega_2 \omega_3)^2}, \quad (7)$$

and for tetrachromatic vision:

$$\begin{aligned} (\Delta S)^2 = & (\omega_1 \omega_2)^2 (\Delta f_4 - \Delta f_3)^2 + (\omega_1 \omega_3)^2 (\Delta f_4 - \Delta f_2)^2 \\ & + (\omega_1 \omega_4)^2 (\Delta f_3 - \Delta f_2)^2 + (\omega_2 \omega_3)^2 (\Delta f_4 - \Delta f_1)^2 \\ & + (\omega_2 \omega_4)^2 (\Delta f_3 - \Delta f_1)^2 \\ & + (\omega_3 \omega_4)^2 (\Delta f_2 - \Delta f_1)^2 / ((\omega_1 \omega_2 \omega_3)^2 \\ & + (\omega_1 \omega_2 \omega_4)^2 + (\omega_1 \omega_3 \omega_4)^2 + (\omega_2 \omega_3 \omega_4)^2), \end{aligned} \quad (8)$$

Cone spectral sensitivities and receptor noise

Implementation of the model requires physiological data on spectral sensitivities and noise in receptors – or more accurately in receptor mechanisms (Wyszecki and Stiles 1982). Here, opsin spectral sensitivities are described by fitting a standard nomogram (Maximov 1988) to the peak sensitivities measured by microspectrophotometry in *Leiothrix* and pigeon (Bowmaker et al. 1997). Oil droplet functions are modelled as hyperbolic tangents fitted to the midpoint and slope of the measured absorption of oil droplets (Maier and Bowmaker 1993; Bowmaker et al. 1997). Spectral absorption by the ocular media, which is significant below about 400 nm (Emmerton et al. 1980; Maier 1994), is taken into account.

Estimation of noise in receptor mechanisms is less easy. However, the following accurately predicts avian psychophysical thresholds (Fig. 2; Vorobyev and Osorio 1998). It is assumed that the proportion of incident photons transduced at the opsin sensitivity maximum is independent of spectral class, as are noise characteristics of the cones. Relative quantum efficiencies are then given by multiplying the rhodopsin function, normalised to unity at its sensitivity peak, by the absorption of the ocular media and (where appropriate) the corresponding oil droplet.

If quantum fluctuations determine receptor noise, this noise is given by the square root of the number of absorbed quanta across the integration area of the receptor mechanism (e.g. ganglion cell receptive field). Let Q_i be the quantum catch of the receptor cell i , and η_i the number of receptor cells of type i within the receptive field. Noise-to-signal ratio in the colour channel i (ω_i) is then given by:

$$\omega_i = 1 / \sqrt{q_i \eta_i}. \quad (9)$$

If receptor noise is independent of number of absorbed quanta, so that the Weber fraction is independent of intensity, then:

$$\omega_i = v_i / \sqrt{\eta_i}, \quad (10)$$

where v_i is the noise-to-signal ratio of a single cone.

In practice, the intensity at which the contrast threshold ceases to be intensity dependent is difficult to establish, and in any case depends upon viewing conditions (Rovamo et al. 1994, 1995;

García-Pérez and Peli 1997). For this reason we model eyes both with intensity-dependent (Eq. 9) and with fixed (Eq. 10) contrast thresholds.

Differences between mechanisms depend upon relative numbers of the four single cone types. We use the following ratios: in *Leiothrix* UV, S, M, L at 1:2:2:4 (Maier and Bowmaker 1993), while in pigeon yellow field UV, S, M, L at 1:1:1:2 (Bowmaker et al. 1997). These values are approximate, but given experimental error, they predict spectral sensitivities accurately (Fig. 2). It should be noted that the effects of errors in these estimates will be limited because signal-to-noise ratio varies with the square root of cone density. To estimate the absolute value of the Weber fractions we use the data for *Leiothrix lutea* (Maier 1992). According to this estimate (see Appendix B) the Weber fraction in the LWS mechanism is 0.1 (cf. ca. 0.02 for human red cone; Wyszecki and Stiles 1982). Double cones are assumed not to be used for colour (Maier and Bowmaker 1993), if they are included predictions are not accurate. The broad spectral tuning and greater absolute sensitivity of double cones (Fig. 1) suggest they are more important for luminance than for colour vision.

Measures of performance I: discriminable colours

In the absence of a general statistical model of plumage spectra (see Introduction) a convenient measure of performance is the probability that any two spectra chosen at random from the population (i.e. our dataset) are *not* discriminable (Tables 1, 2; Osorio and Vorobyev 1996). This statistic was calculated by estimating the discriminability of all possible pairs of plumage spectra. Accuracy of visual performance depends on viewing conditions, and is likely to differ between species; also, what is “discriminable” depends on the definition of threshold. Thus, the spectra which are discriminable in an experiment are not necessarily discriminated in natural conditions (or vice versa). We consider thresholds corresponding to 1, 2 and 3 just noticeable steps (jnds) as inferred from the spectral sensitivity of *Leiothrix* (Maier 1992). This takes account of the effects of variability of thresholds, and also predicts the relative magnitudes of supra-threshold differences.

Measures of performance II: colour constancy (Fig. 6; Table 3)

We evaluate shifts in chromatic signals of plumage spectra viewed under a range of illumination spectra (Fig. 3a), for eyes with and without oil droplets. Constancy is assumed to be based on normalisation of receptor mechanisms to a mean background (Worthy and Brill 1986; Foster and Nascimento 1994), which is either achromatic, or has the spectrum of foliage (Fig. 3b; the mean from a dataset of over 300 leaf spectra). Each shift, given in jnds, is the difference between the response to the stimulus viewed under a standard daylight source (D65) and one of the three other illuminants.

Results

The spectra

Bird species which are brightly coloured to the human eye, predominantly Australasian parrots and passerines (Appendix A), were chosen to provide a diverse set of spectra. Spectra were from as many plumage regions as possible on each specimen, replicates being discarded after collection. In all, 424 distinct spectra from 61 species or sexual morphs were measured (Fig. 4). A selection of spectra are illustrated (Fig. 5). The different types of spectra can be attributed to the different phys-

ico-chemical mechanisms that generate them (Fox and Vevers 1960; Finger and Burkhardt 1994; Finger et al. 1992). These include pigments such as carotenoids and melanin in the zebra finch (Ploceidae, *Taenopygia guttata*) and the ‘ptilins’ (Dyck 1987) from fruit pigeons (Columbidae, *Ptilinopus* spp.), and physical mechanisms such as multilayer interference which may give iridescent colours of starlings and Mie effects that give short wavelength spectra (Finger 1995).

Performance of the avian eye

We model discrimination of plumage colours by eyes containing the normal complement of receptors, and compare them to hypothetical avian eyes lacking either one receptor type or oil droplets. Failures of colour constancy are estimated for a range of natural illuminants; otherwise the illuminant is D65 (Table 2; Fig. 3). Comparisons are as follows:

1. *Leiothrix* type eye (where the UVS receptor peak is at 365 nm) versus pigeon type (where the UVS peak is at 410 nm; Fig. 1).
2. Eyes with oil droplets versus eyes without oil droplets.
3. Tetrachromat eyes versus the four possible trichromat colour-deficient eyes.

Eyes where photon noise sets thresholds, so that performance is intensity dependent (e.g. in dim illumination), and those where receptor noise is independent of intensity (e.g. in bright illumination) are modelled separately.

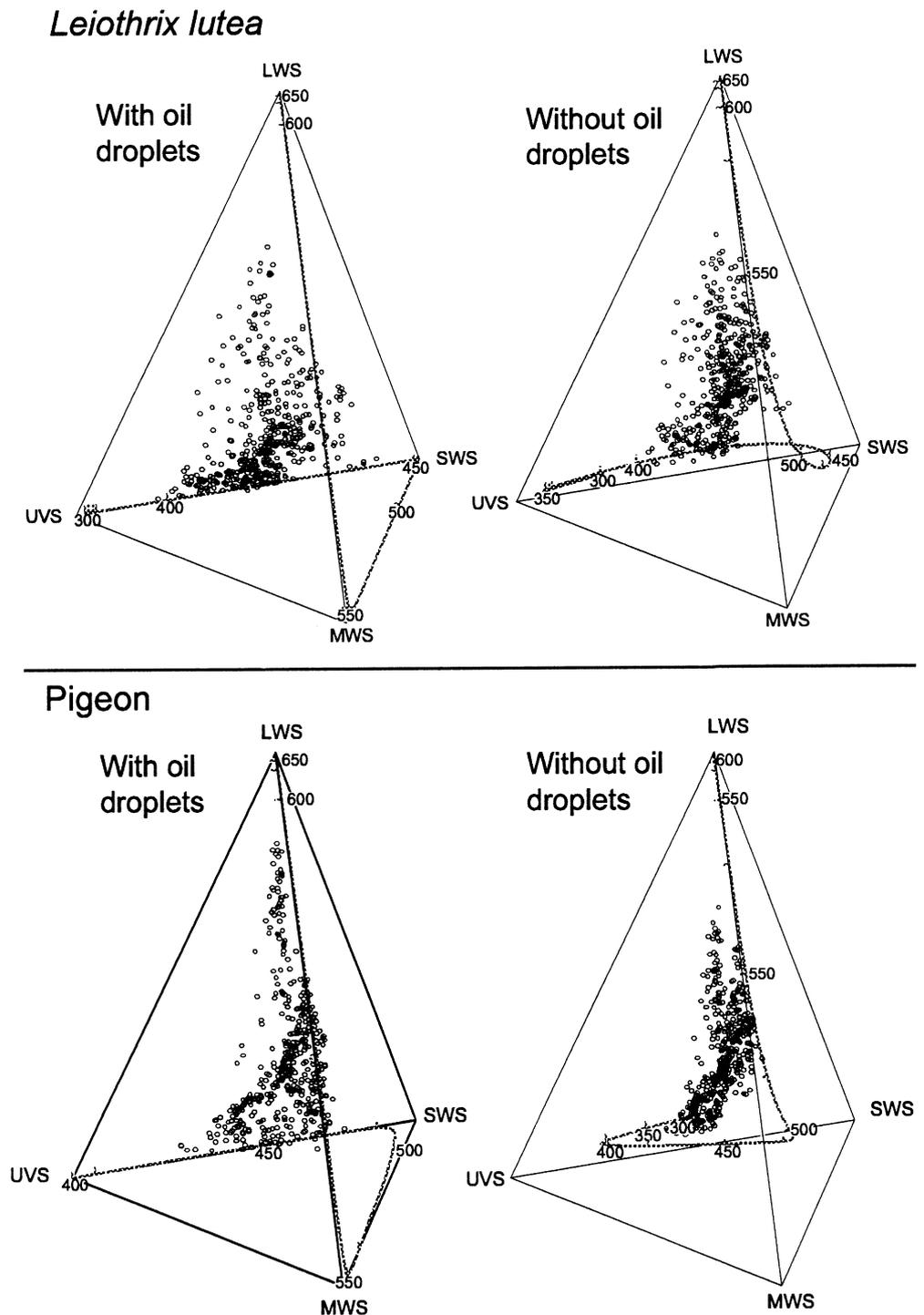
365-nm versus 410-nm UVS receptors

In *Leiothrix lutea*, like other passerines and budgerigar, the UVS receptor peak is at about 365 nm (estimates range from 355 nm to 380 nm), while pigeon and chicken UVS peaks are at 410 and 420 nm, respectively (Bowmaker et al. 1997). Comparing these two types of eye gives an indication of the utility of vision below 400 nm, where illumination intensity falls rapidly with wavelength (Fig. 3a). The low intensity of sub-400-nm light is deleterious for photon-noise-limited mechanisms. However the disadvantage in quantum catch for the *Leiothrix* eye UVS receptor is partly offset by the greater filtering by the oil droplet on the pigeon’s SWS receptor (Fig. 1). For our dataset of plumage spectra the model *Leiothrix* eye slightly outperforms the pigeon both when receptor noise is not intensity dependent and when photon noise sets thresholds.

The role of oil droplets

Oil droplets reduce the spectral overlap of the cones (Fig. 1), which means that monochromatic lights nor-

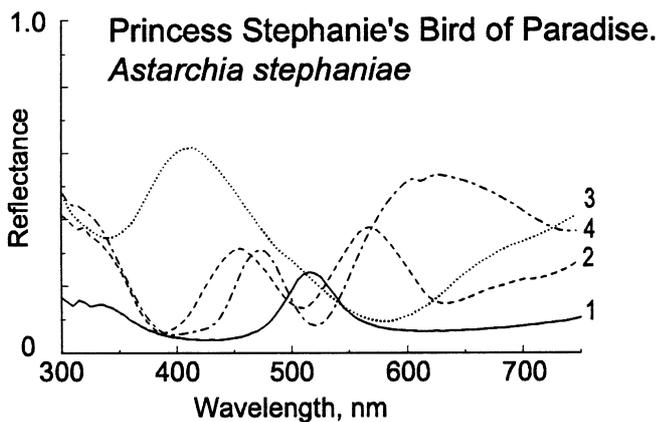
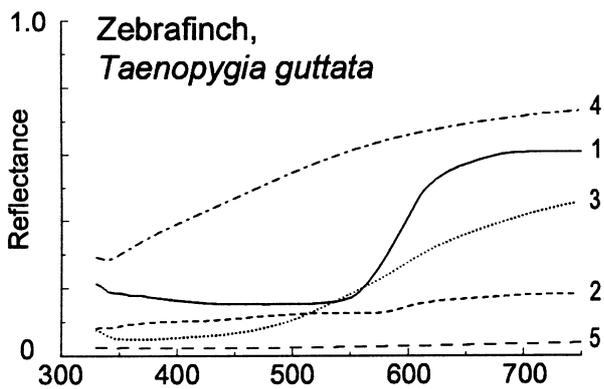
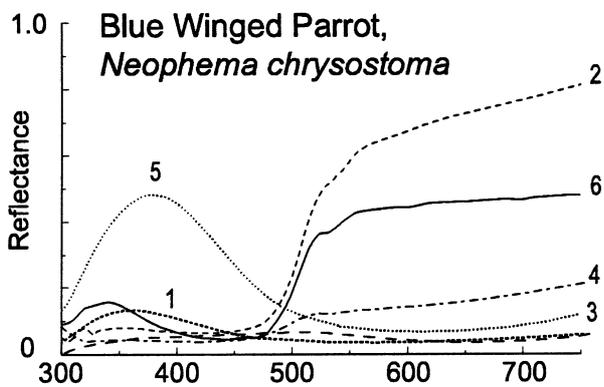
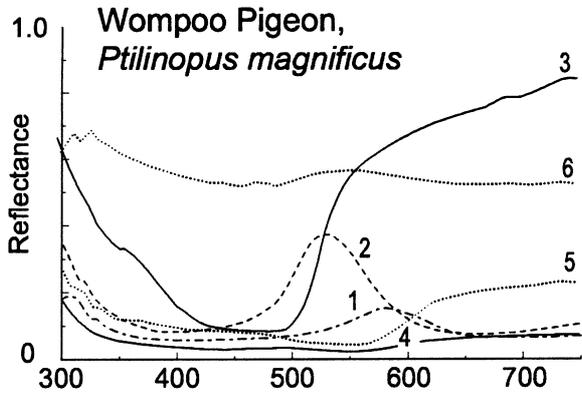
Fig. 4 Loci of plumage spectra on 3-D chromatic hypersurfaces in avian receptor spaces, for eyes with and without oil droplets. The edges of the tetrahedron represent the boundary of the receptor space. The monochromatic locus is shown by the line labelled at 50-nm intervals. Loci of plumage spectra are noticeably more dispersed in the eyes with oil droplets than in those without. An explanation of this type of chromaticity diagram is given by Goldsmith (1990)



mally excite no more than two receptors. This is why the monochromatic locus is closer to the edge of the 3-D chromatic hypersurface (or chromatic space) in the 4-D receptor space (Goldsmith 1990) for filtered than for unfiltered receptors (Fig. 4). More generally, filtering increases the number of physically realisable spectra that can be discriminated (Govardovskii and Vorobyev 1989). Plumage spectra are a (tiny) subset of all possible

spectra, and are not uniformly distributed in avian chromatic space (Fig. 4). Nonetheless, oil droplets do increase their dispersion, and for our dataset the discriminability of the plumage spectra is more than doubled where the Weber fraction is fixed. Predictably, the advantage of oil droplets is greater where thresholds are low and independent of photon noise, conditions likely to hold in bright illumination.

Plumage Spectra



Human vs. avian separations

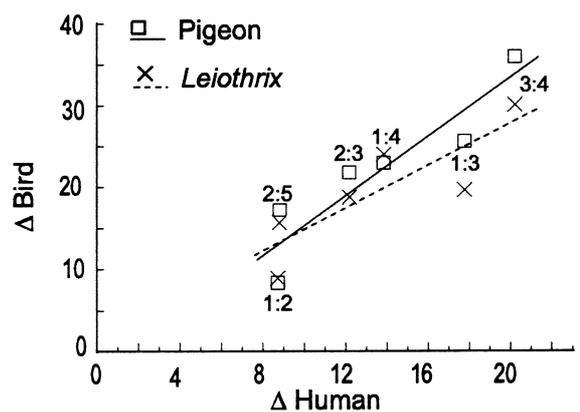
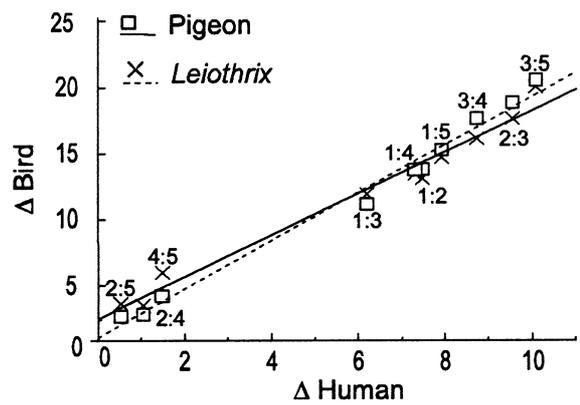
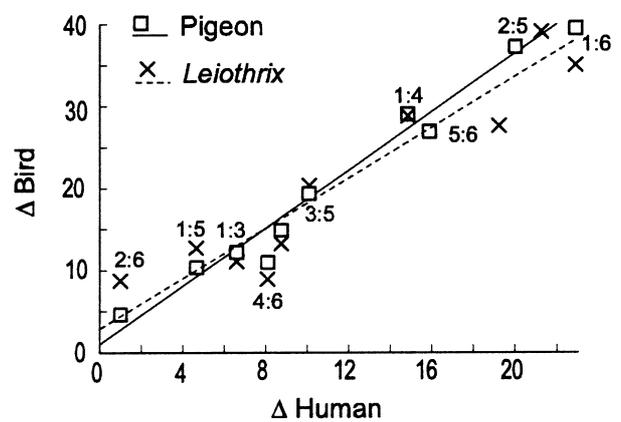
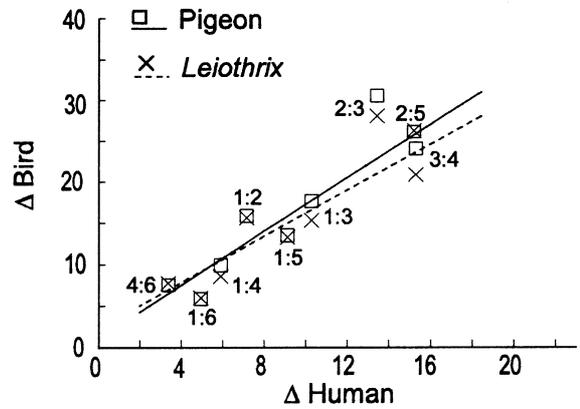




Fig. 5 *Left*: examples of plumage spectra plotted from 330 nm to 700 nm from the Wompoo pigeon (*Ptilinopus magnificus*), blue-winged parrot (*Neophema chrysostoma*), zebra finch (*Taenopygia guttata*), and Princess Stephanie's bird of paradise (*Astartichia stephanaie*). *Right*: plot of the separations of pairs of spectra in human receptor space compared to *Leiothrix* and pigeon. This is a measure of how well the human eye might predict the colourfulness of the bird's pattern to the bird's own eye. A high correlation indicates that pairs of colours on the plumage spectra that look distinct to humans might also look distinct to the avian eye and vice versa. Numbers indicate pairs of spectra shown in the left hand panel compared. All possible spectral pairs were used for the calculation, but not all are plotted

proving their signal-to-noise ratios. Thus a trichromat eye can in principle outperform a tetrachromat (van Hateren 1993; Osorio and Vorobyev 1996). In practice, loss of a receptor invariably reduces the discriminability of plumage spectra. Reduction in the discriminability of the spectra is greatest for loss of the LWS receptor; i.e., it is the most useful of the four. The pigeon's 410-nm UVS receptor is always the second most important, but *Leiothrix*'s 365-nm UVS receptor is less useful than its SWS receptor where photon noise sets thresholds. This is partly due to the shortage of photons below 400 nm, and helps explain the variation in tuning of avian UVS photopigments.

Tetrachromacy versus trichromacy

Comparison of the performance of hypothetical 'colour deficient' avian trichromats with normal tetrachromat eyes gives an indication of the usefulness of different regions of the spectrum for plumage discrimination, and of the utility of tetrachromacy. We assume that when a receptor class is lost, the 'free' cones are shared pro rata between the remaining three mechanisms, thereby im-

Comparisons with human colour vision

It is interesting to compare human and bird's eye views of an individual's plumage (Bennett et al. 1994). A measure of the 'colourfulness' of a pattern, and of the contrast of colours within it, is the separation in receptor space (in jnds) of all possible pairs of spectra (Fig. 4). Discriminability of spectra can be estimated

Table 1 The utility of oil droplets, and comparison of pigeon and *Leiothrix* eyes viewing plumage spectra under D65 illumination. The table gives an estimate of the probability that any two spectra from the population will *not* be discriminable; thus, the higher the number, the worse the performance. The advantage of oil droplets

is lower for photon-noise-limited performance than with a fixed Weber fraction. Values are normalised to the performance of the pigeon at 1 jnd. The pigeon confuses each spectrum with 1.1% of the other spectra in the dataset where the Weber fraction is fixed, and with 2.5% where it is photon noise limited

Rel. threshold	Pigeon		<i>Leiothrix</i>	
	Oil filters	No filters	Oil filters	No filters
Fixed Weber fraction				
1 jnd	1.0	2.4	0.6	1.4
2 jnds	3.4	8.0	2.6	5.8
3 inds	6.8	15	5.8	12.6
Photon noise limited				
1 jnd	1.0	1.4	0.8	1.4
2 jnds	3.3	4.5	2.8	4.9
3 jnds	6.6	8.5	5.9	9.8

Table 2 The utility of tetrachromacy. As for Table 1 we give the probability that any two spectra will not be discriminable by the four possible trichromatic eyes, relative to that for the tetrachromatic eye with oil droplets operating under the same conditions (Table 1). Thus, the larger the value tabulated, the worse the hy-

pothetical eye, and the larger the cost of losing that receptor type. Oil droplets are assumed to be present. Without oil droplets, the tetrachromat still outperforms any trichromat, although the advantage of tetrachromacy is generally smaller

Threshold	Pigeon				<i>Leiothrix</i>			
	No UVS	No SWS	No MWS	No LWS	No UVS	No SWS	No MWS	No LWS
Fixed Weber fraction								
1 jnd	3.4	1.8	2.0	3.6	4.3	3.0	3.3	5.0
2 jnds	2.5	1.6	1.8	3.1	2.8	2.4	2.6	3.7
3 jnds	2.1	1.4	1.7	2.7	2.2	2.0	2.2	3.2
Photon noise limited								
1 jnd	2.9	1.6	1.8	3.1	3.3	3.4	3.1	4.5
2 jnds	2.3	1.4	1.6	2.6	2.5	2.7	2.6	3.6
3 jnds	2.1	1.3	1.5	2.2	2.1	2.3	2.0	2.9

for a human, just as for birds (Osorio and Vorobyev 1996). As an example, estimates are compared for human and the two types of avian eye, for four species (Fig. 5). With the relatively ‘dull’ zebra finch, separations of plumage spectra are highly correlated for bird and human eyes, so that our judgement of overall ‘colourfulness’ in zebra finches, and of the relative distinctness of the different plumage regions *might* map quite well into avian perception. By comparison, correlations between avian and human receptor signals are less good for the bird of paradise, the parrot and the fruit pigeon. Differences probably arise where spectra vary in the UV, or are complex with multiple-reflectance peaks.

Colour constancy

Illumination spectra vary between the different phases of daylight, and between open habitats and green forest lights (Endler 1993). Colour constancy is the ability of vision to compensate for these variations. Where judgement of plumage properties is important, as in intraspecific communication, failures of colour constancy that exceed discrimination thresholds may limit the reliability of colour vision (Osorio 1997; Osorio et al. 1997). Birds compete for display sites in specific illumination (Endler and Thery 1996), and this could reflect the need to control or optimise signal quality.

We estimate, for each plumage spectrum, the shift of chromatic signals in jnds for illumination changes from a standard daylight (D65) to one of three other conditions (see Materials and methods). The size of shifts varies considerably for different plumage spectra; the largest are for spectra that differ most strongly from the background, namely bright colours (Fig. 6). Shifts are largest between standard daylight and illumination

Fig. 6 a Failures of colour constancy assuming receptor mechanisms are independently and completely adapted to the background, see also Table 3. The background is leaf green (Fig. 3b; results are similar for an achromatic background). Histograms plot the shift in jnds for all spectra moved from a D65 illumination to one of the other two illuminants (Fig. 3a). Shifts are largest for leaf shade illumination (Endler 1993). Differences between the shifts for pigeon and *Leiothrix* type eyes are small as are those between achromatic and leaf green backgrounds. The leaf spectrum used is the average from a large dataset of samples. Shifts for shifting from D65 to D75 were also estimated, these are similar to but slightly smaller than those for D55 (Table 3). **b** Examples of spectra that show small and large colour shifts. The shift in jnds for the spectra moved from D65 to the forest shade for pigeon and *Leiothrix*, respectively are given in brackets. Although the overall distribution of shifts for the two types of eye are roughly equal, substantial differences in predicted constancy occur for some spectra. *Upper panel*: spectra giving small color shifts. 1. *Neophema chrysostoma* (0.35, 0.04); 2. *N. chrysostoma* (0.06, 0.14); 3. *Astarchia stephaniae* (0.32, 0.23); 4. *Ptilinopus magnificus* (0.17, 0.3). *Lower panel*: spectra giving large color shifts. 1. *A. stephaniae* (0.37, 0.77); 2. *A. stephaniae* (0.77, 0.76); 3. *P. magnificus* (1.25, 0.97); 4. *N. chrysostoma* (1.11, 1.11)

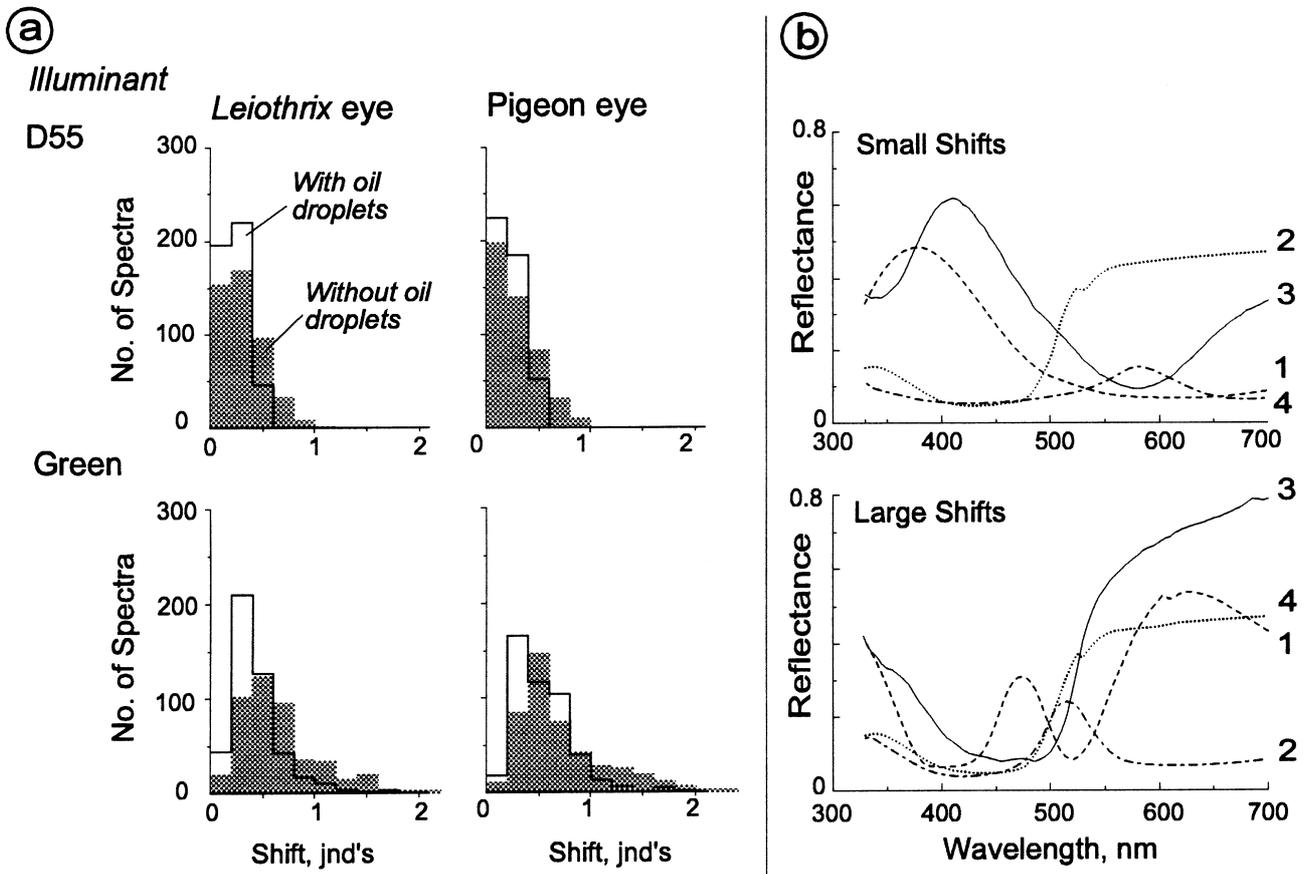


Table 3 The size of colour constancy failures, given as shifts in jnds from D65 illumination (standard daylight) for stimuli viewed by an eye adapted to an background of leaves. Shifts are largest when the D65 light is replaced by forest shade. Loss of oil droplets increases failures of colour constancy by about 50% for pigeon and 60% for *Leiothrix*. Estimates of shifts on an achromatic background give very similar results. See also Fig. 6

<i>P</i>	Quartiles		
	0.25	0.5	0.75
<i>Pigeon</i>			
D55			
Oil droplets	0.08	0.15	0.27
No oil droplets	0.11	0.26	0.42
D75			
Oil droplets	0.06	0.10	0.19
No oil droplets	0.09	0.18	0.32
Forest shade			
Oil droplets	0.18	0.36	0.63
No oil droplets	0.23	0.51	0.8
<i>Leiothrix</i>			
D55			
Oil droplets	0.10	0.18	0.29
No oil droplets	0.14	0.32	0.46
D75			
Oil droplets	0.07	0.13	0.20
No oil droplets	0.11	0.24	0.35
Forest shade			
Oil droplets	0.18	0.31	0.55
No oil droplets	0.27	0.46	0.77

resembling the green light of 'forest shade' (Endler 1993), an illuminant that, although ecologically important, is not generally used in colour science. Theoretical considerations predict better constancy where oil droplets narrow spectral tuning than for receptors without filters (Worthey and Brill 1986; Osorio et al. 1997), and this is indeed the case for all conditions modelled. Were the receptors to lose their oil droplets the chromatic shift under variable illumination would increase by about 50% for pigeon and about 60% for *Leiothrix* (Table 3).

Discussion

Information on avian eye design is accruing quite rapidly at present (Bowmaker et al. 1997), and this can be used to give a bird's eye view of colour (Burkhardt 1989; Burkhardt and Finger 1991; Bennett et al. 1994). Going from eyes to perception may seem futile, or at least foolhardy, but the approach here is a sound basis for quantitative work on eye design. The key assumptions are that the task requires fine judgements, and that discrimination thresholds are set by (or at least match) receptor noise levels. A compelling argument in favour of these assumptions is that if performance at threshold were not essential, or if receptor noise did not set (or match) thresholds, then – to economise of resources – the eye would simply be smaller, or the number of cones serving colour vision fewer.

This model can be applied to understanding the role of colour in avian biology, either with regard to understanding eye design or plumage coloration. For predicting absolute thresholds the main difficulty is in

estimating the Weber fractions for the cone mechanisms. Here Maier's (1992) work on *Leiothrix* is used (Appendix B), and it is probably reasonable to assume that physiologically most avian species of single cone are similar. Differences in visual performance are then due to directly measurable physiological parameters such as eye size, receptor numbers and cone tuning. Verification of the model's predictions with a test using a behaviour of interest would of course be worthwhile, and is comparatively simple.

The design of bird eyes is much like that of some reptiles (Walls 1942; Hisatomi et al. 1994), and their primary evolutionary function remains a mystery. Nonetheless, for our dataset, a bird with normal colour vision can discriminate more plumage colours than a colour-deficient individual, lacking either oil droplets or one the four cone pigments (Tables 1, 2); oil droplets also benefit colour constancy (Table 3, Fig. 6). In reality, an individual bird never needs to discriminate all the 424 spectra in our dataset, which emphasises showy groups such as parrots, birds of paradise, and Australian *Malurus* wrens. Duller birds would give different results, with less advantage to tetrachromacy and oil droplets. The dataset does, however, give an indication of the range of spectra which bird eyes must encode, and we can be fairly sure that for some species the avian eye design is indeed beneficial compared with simpler alternatives.

Acknowledgements We thank Glen Ingram at The Queensland Museum, Fran Hausmann at University of Queensland and staff at the Currumbin Sanctuary for providing material. M.V. was supported by a DFG (Me 365/20-1) grant to R. Menzel, who we thank for support. This work was carried out in compliance with the laws of the United Kingdom and Australia.

Appendix A: species list

A total of 424 spectra were measured from the following 61 species and morphs (M: male; F: female). Where multiple spectra from a given bird were essentially identical, only one of the set were retained. The criterion used for treating spectra as the same was that quantal absorption (Eq. 1) did not differ by more than 5% in any receptor for both pigeon and *Leiothrix*.

Columbiformes

Ptilinopus regina (rose-crowned pigeon); *P. magnificus* (wompoo pigeon).

Psittaciformes

Cacatuidae: *Cacatua roseicapilla* (galah)

Psittacidae: *Eclectus roratus* (eclectus parrot, M and F); *Geoffroyus geoffroyi* (red-cheeked parrot, M)

Loridae: *Lorius lory* (lory); *L. hypoinchorous*; *Trichoglossus haematodus* (rainbow lorikeet; red-collared and Eastern forms); *T. chlorolepidotus* (scaly breasted lorikeet, M and F); *Psittuteles versicolor* (varied lorikeet, M); *Glossopsitta pusilla* (little lorikeet); *G. concinna* (musk lorikeet; M)

Opopsittidae: *Psittaculirostris diophthalma* (double-eyed fig parrot, M)

Polytelidae: *Alisterus scapularis* (king parrot, M and F); *Aprosmictus erythropterus* (red-winged parrot, M and F); *P. swainsonii* (superb parrot, M); *Polytelis alexandre* (princess parrot, M); *P. anthopeplus* (regent parrot); *Nymphicus hollandicus* (cockatiel).

Platyercidae: *Melopsittacus undulatus* (budgerigar); *Purpuricephalus spurius* (red-capped parrot); *Platyercus adscitus* (pale-headed rosella, M); *P. icterotis* (western Rosella, M); *P. eximius* (eastern rosella, M); *P. elegans* (crimson rosella); *Barnardius barnardi* (ring-necked parrot, M); *Psephotus pulcherimus* (paradise parrot, M and F); *P. dissimilis* (hooded parrot, M and F); *Northiella haematogaster* (blue bonnet, M and F); *Neophema petrophila* (rock parrot, M); *N. splendida* (scarlet-chested parrot, M); *N. pulchella* (turquoise parrot; M and F); *N. chrysostoma* (blue-winged parrot); *N. bourkii* (Bourke's parrot; M).

Coraciiformes: Alcenidae

Halcyon sancta (sacred kingfisher, M); *Alcedo atthis* (kingfisher).

Passeriformes

Maluridae (males): *Malurus leucopterus* (blue and white wren); *M. assimilis* (purple-backed wren); *M. lamberti* (variegated wren); *M. splendens* (spp. *splendens* and *melantotus*, splendid wren); *Malurus melanocephalus* (red-backed wren).

Paradisidae (males): *Paradisaea apoda*; *P. rudolphi* (blue bird of paradise); *Craspedophora claudia*; *Ciciniurus reginus* (M); *Astrarchia stephaniae* (Princess Stephanie's bird of paradise); *Epiurachus meyeri*; *Ailuroedus crassirostris* (green catbird, sex unknown).

Other passerines: *Parus caeruleus* (blue tit); *P. major* (great tit); *Taenopygia gutata* (zebra finch); *Carduelis chloris* (greenfinch); *Sturnus vulgaris* (starling, M and F); *Cardinalis cardinalis* (northern cardinal).

Appendix B: an estimate of the avian Weber fraction

Estimates of avian Weber fractions are based on behavioural data for *Leiothrix lutea* (Maier 1992). The value of the LWS Weber fraction was adjusted so that the theoretically predicted threshold

spectral-sensitivity curve matches the data. Since the ratio of Weber fractions is defined by the ratios of the cone numbers, for which (approximates) are obtained from anatomical data (Eq. 10; Bowmaker et al. 1997), the shape of the theoretical curve is then fixed. Variation of the value of LWS Weber fraction simply shifts the curve on the log-sensitivity axis (ordinate).

The spectral sensitivity is the inverse of threshold intensity, $I^t(\lambda)$, i.e. of the minimum intensity of monochromatic light of wavelength, λ , detectable over an adapting background. The difference in the quantum catch between background and the stimulus is given by:

$$\Delta q_i = k_i R_i(\lambda) I^t(\lambda). \quad (\text{A1})$$

Variables are as for Eq. 1. At threshold, the distance between the stimuli, ΔS , is by definition, equal to 1. Substitution of Eq. A1 into Eqs. 6, 7 and 8 with $\Delta S = 1$ gives the expressions for threshold spectral sensitivity as a function of wavelength. Note that in the vicinity of the background the difference in the signals of receptor channels is given by the difference of receptor quantum catches, i.e. $\Delta f_i = \Delta q_i$.

The values of the scaling factors, k_i , were obtained from the reflectance spectrum of background and illumination spectra (see Eq. 2) as reported by Maier (1992). We assume the background was a perfect diffuser with the reflectance spectrum, $S(\lambda)$ (Maier 1992; Fig. 1). In this case the following equation (Wyszecki and Stiles 1982) relates the spectral radiance of the reflected light, $I^R(\lambda)$ with the quantum flux of illumination, $I(\lambda)$:

$$I^R(\lambda) = (I(\lambda)S(\lambda))/\pi. \quad (\text{A2})$$

Illumination was provided by daylight tubes (Osram 5000 Daylight de Lux) which gave the irradiance of 0.1 W m^{-2} at the start position ($70 \text{ mm} \times 80 \text{ mm}$ entrance of the chamber). We assume that background wall ($270 \text{ mm} \times 210 \text{ mm}$) was homogeneously illuminated and no light lost. This gives a background irradiance of:

$$0.1(70 \times 80)/(270 \times 210) \text{ W m}^{-2} = 0.01 \text{ W m}^{-2}.$$

The spectrum in the energy units, $E(\lambda)$ is converted to the quantum units by the following equation (Wyszecki and Stiles 1982):

$$I(\lambda) = E(\lambda)\lambda/(hc10^4) \text{ photons cm}^{-2} \text{ s}^{-1} \text{ nm}^{-1} \quad (\text{A3})$$

References

- Amundsen T, Forsgren E, Hansen LTT (1997) On the function of female ornaments: male bluethroats prefer colourful females. *Proc R Soc Lond Ser B* 264: 1579–1586
- Andersson S, Amundsen T (1997) Ultraviolet colour vision and ornamentation in bluethroats. *Proc R Soc Lond Ser B* 264: 1587–1591
- Barlow HB (1982) What causes trichromacy? A theoretical analysis using comb filtered spectra. *Vision Res* 22: 635–643
- Bennett ATD, Cuthill IC, Norris KN (1994) Sexual selection and the mismeasure of color. *Am Nat* 144: 848–860
- Bennett ATD, Cuthill IC, Partridge JC, Maier EJ (1996) Ultraviolet vision and mate choice in zebra finches. *Nature (Lond)* 380: 433–435
- Bennett ATD, Cuthill IC, Partridge JC, Lunau K (1997) Ultraviolet plumage colors predict mate preferences in starlings. *Proc Natl Acad Sci USA* 96: 8618–8621
- Bowmaker JK (1980) Colour vision in birds and the role of oil droplets. *Trends Neurosci* 3: 196–199
- Bowmaker JK, Martin GR (1978) Visual pigments and colour vision in a nocturnal bird, *Strix aluco* (tawny owl). *Vision Res* 18: 1125–1130
- Bowmaker JK, Heath LA, Wilkie SE, Hunt DM (1997) Visual pigments and oil droplets from six classes of photoreceptor in the retina of birds. *Vision Res* 37: 2183–2194
- Brandt R, Vorobyev M (1997) Metric analysis of threshold spectral sensitivity in the honeybee. *Vision Res* 37: 425–439

- Burkhardt D (1982) Birds, berries and UV. *Naturwissenschaften* 69: 153–157
- Burkhardt D (1989) UV vision: a bird's eye view of feathers. *J Comp Physiol A* 164: 787–796
- Burkhardt D, Finger E (1991) Black, white and UV: how birds see birds. *Naturwissenschaften* 78: 279–280
- Burkhardt D, Maier E (1989) The spectral sensitivity of a passerine bird is highest in the UV. *Naturwissenschaften* 76: 82–83
- Cuthill IC, Bennett ATD, Partridge JC, Maier EH (1998) Ultraviolet reflectance and the objective assessment of avian sexual dichromatism. *Am Nat* (in press)
- De Vries H (1943) The quantum character of light and its bearing upon the threshold of vision, the differential sensitivity, and visual acuity of the eye. *Physika* 10: 553–564
- Dyck J (1987) Structure and light reflection of green feathers of fruit doves (*Ptilinopus* spp.) and an imperial pigeon (*Ducula concinna*). *Biologiske Skrifter* 30: 1–43
- Emmerton J, Schwemer J, Muth J, Schlecht P (1980) Spectral transmission of the ocular media of the pigeon (*Columbia livia*). *Invest Ophthalmol Vis Sci* 19: 1382–1387
- Endler JA (1990) On the measurement and classification of color in studies of animal color patterns. *Biol J Linn Soc* 41: 315–352
- Endler JA (1993) The color of light in forests and its implications. *Ecol Monogr* 63: 1–27
- Endler JA, Thery M (1996) Interacting effects of lek placement, display behavior, ambient light, and color patterns in 3 neotropical forest-dwelling birds. *Am Nat* 148: 421–452
- Finger E (1995) Visible and UV coloration in birds: Mie scattering as the basis of color in many bird feathers. *Naturwissenschaften* 82: 570–573
- Finger E, Burkhardt D (1994) Biological aspects of bird coloration and avian color-vision including ultraviolet range. *Vision Res* 34: 1509–1514
- Finger E, Burkhardt D, Dyck J (1992) Avian plumage colors. Origin of UV reflection in a black parrot. *Naturwissenschaften* 79: 187–188
- Foster DH, Nascimento SM (1994) Relational colour constancy from invariant cone-excitation ratios. *Proc R Soc Lond Ser B* 257: 115–121
- Fox HM, Vevers G (1960) *The nature of animal colours*. Sidgwick and Jackson, London
- García-Pérez MA, Peli E (1997) Transition from DeVries-Rose to Weber's law: reply to Rovamo, Mustonen and Näsänen. *Vision Res* 37: 2573–2576
- Goldsmith TH (1990) Optimization, constraint, and history in the evolution of eyes. *Q Rev Biol* 65: 281–322
- Govardovskii VI (1983) The role of oil droplets in color vision. *Vision Res* 23: 1739–1740
- Govardovskii VI, Vorobyev M (1989) The role of coloured oil droplets in colour vision (in Russian). *Sensornye Systemy (Sensory Systems)* 3: 150–159
- Hart N, Partridge, JC, Cuthill IC (1998) Spectral absorptance and the retinal distribution of the visual pigments and oil droplets of the starling. *J Exp Biol* 201: 1433–1446
- Hateren JH van (1992) A theory of maximizing sensory information. *Biol Cybern* 68: 23–29
- Hateren JH van (1993) Spatial, temporal and spectral pre-processing for colour vision. *Proc R Soc Lond Ser B* 251: 61–68
- Hisatomi O, Kayada S, Aoki Y, Iwasa T, Tokunaga F (1994) Phylogenetic relationships among vertebrate visual pigments. *Vision Res* 34: 3097–3102
- Hurlbert AC (1998) Computational models of colour constancy. In: Walsh V, Kulikowski J (eds) *Perceptual constancies*. Cambridge University Press (in press)
- Hzn JJV, Coemans MAJM, Nuboer JFW (1994) The photopic sensitivity of the yellow field of the pigeons retina to ultraviolet-light. *Vision Res* 34: 1419–1425
- King-Smith PE, Carden D (1976) Luminance and opponent-color contributions to visual detection and adaptation and to temporal and spatial integration. *J Opt Soc Am* 66: 709–717
- Krinov EL (1953) Spectral reflectance properties of natural formations. *Nat Res Council Can Technol Trans* TT-439
- Laughlin SB (1987) Form and function in retinal processing. *Trends Neurosci* 10: 478–483
- Lythgoe JN (1979) *The ecology of vision*, Clarendon, Oxford
- Maier EJ (1992) Spectral sensitivities including the ultraviolet of the passeriform bird *Leiothrix lutea*. *J Comp Physiol A* 170: 709–714
- Maier EJ (1994) Ultraviolet vision in a passeriform bird: from receptor spectral sensitivity to overall spectral sensitivity in *Leiothrix lutea*. *Vision Res* 34: 1415–1418
- Maier EJ, Bowmaker JK (1993) Colour vision in the passeriform bird, *Leiothrix lutea*: correlation of visual pigment absorbance and oil droplet transmission with spectral sensitivity. *J Comp Physiol A* 172: 295–301
- Maloney LT (1986) Evaluation of linear models of surface spectral reflectance with small numbers of parameters. *J Opt Soc Am A* 3: 1673–1683
- Maximov VV (1988) An approximation of visual absorption spectra (in Russian). *Sensornye Systemy (Sensory Systems)* 2: 3–8
- Mollon JD (1989) “tho' she kneel'd in that place where they grew”. The uses and origins of primate colour vision. *J Exp Biol* 146: 21–38
- Osorio D (1997) A functional view of cone pigments and colour vision. In: CM Dickinson, IJ Murray, D Carden (eds) *John Dalton's colour vision legacy*. Taylor and Francis, London, pp 483–489
- Osorio D, Vorobyev M (1996) Colour vision as an adaptation to frugivory in primates. *Proc R Soc Lond Ser B* 263: 593–599
- Osorio D, Marshall NJ, Cronin TW (1997) Stomatopod photoreceptor tuning as an adaptation to colour constancy underwater. *Vision Res* 37: 3299–3309
- Partridge JC (1989) The visual ecology of avian cone oil droplets. *J Comp Physiol A* 165: 415–426
- Poirson AB, Wandell BA (1990) The ellipsoidal representation of spectral sensitivity. *Vision Res* 30: 647–652
- Remy M, Emmerton J (1989) Behavioral spectral sensitivities of different retinal areas in pigeons. *Behav Neurosci* 103: 170–177
- Robinson SR (1994) Early vertebrate colour vision. *Nature (Lond)* 367: 121
- Rovamo J, Mustonen J, Näsänen R (1994) Modeling contrast sensitivity as a function of retinal illuminance and grating area. *Vision Res* 34: 1301–1314
- Rovamo J, Mustonen J, Näsänen R (1995) Neural modulation transfer-function of the human visual-system at various eccentricities. *Vision Res* 35: 767–774
- Ruderman DL (1994) The statistics of natural images. *Netw Comput Neural Syst* 5: 517–548
- Vorobyev M, Osorio D (1998) Receptor noise as a determinant of colour thresholds. *Proc R Soc Lond Ser B* 265: 315–358
- Walls GL (1942) *The vertebrate eye and its adaptive radiation*. Bloomford Hills, Michigan
- Worthey JA, Brill MH (1986) Heuristic analysis of von Kries color constancy. *J Opt Soc Am A* 3: 1708–1712
- Wyszecki G, Stiles WS (1982) *Color science, concepts and methods, quantitative data and formulae*, 2nd edn. John Wiley, New York