A review of the evolution of animal colour vision and visual communication signals

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A B S T R A C T

The visual displays of animals and plants are often colourful, and colour vision allows animals to respond to these signals as they forage for food, choose mates and so-forth. This article discusses the evolutionary relationship between photoreceptor spectral sensitivities of four groups of land animals—birds, butterflies, primates and hymenopteran insects (bees and wasps)—, the colour signals that are relevant to them, and how understanding is informed by models of spectral coding and colour vision. Although the spectral sensitivities of photoreceptors are known to vary adaptively under natural selection there is little evidence that those of hymenopterans, birds and primates are specifically adapted to the reflectance spectra of food plants or animal visual signals. On the other hand, the colours of fruit, flowers and feathers may have evolved to be more discriminable for the colour vision of their natural receivers than for other groups of animals. Butterflies are unusual in that they have enjoyed a major radiation in receptor numbers and spectral sensitivities. The reasons for the radiation and diversity of butterfly colour vision remain unknown, but may include their need to find food plants and to select mates.

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1. Introduction

1.1. Evolutionary diversity of photoreceptor spectral sensitivities and their relation to natural stimuli

Allen's remarkable book 'The colour sense' (Allen, 1879) asks how animal colour vision evolved and sets human colour vision in an evolutionary context. Allen proposed that initially colour vision was used to locate the edible parts of plants, such as young leaves, flowers and fruit, whose pigmentation differed from mature leaves. Once colour vision had appeared plants and animals could use colourful signals for communication. Allen favoured Darwin's (1871) theory of sexual selection, and he explains how sensory preferences that were associated with feeding could lead to the evolution of elaborate courtship displays (Endler & Basolo, 1998). Unfortunately the evidence was limited; Allen argued that animals such as butterflies that feed on fruit and flowers have superior colour vision and more colourful displays than carnivores such as dragonflies. (In fact dragonflies use colour for communication and probably have good colour vision; Andrés, Sánchez-Guillén, & Cordero Rivera, 2002; Yang & Osorio, 1996.) Similarly, primates eat fruit and they have better colour vision than other mammals, and are relatively colourful (Sumner & Mollon, 2003). Wallace did not accept that sexual selection was distinct from natural

selection (Cronin, 1991), and wrote a sceptical review of 'The colour sense' in Nature (Wallace, 1879). Discussing the prevalence of colour deficiency in humans, Wallace comments: 'It seems probable, therefore, that the prevalence of colour-blindness is really an indication of the colour sense in man having been a comparatively recent development, instead of being, as Mr. Allen thinks, a disease of civilisation.' We now have a good understanding of the genetic basis of colour deficiencies (Nathans, 1999), and it is plausible that both views have some validity.

Recent years have seen a return of interest in the evolutionary relationship between animal senses and communication signals (Bradbury & Vehrencamp, 1998; Cronin, 1991; Endler & Basolo, 1998; Horth, 2007); for example in questions about the information content of signals, and the role of courtship displays in species formation (Dijkstra, Seehausen, & Groothuis, 2008; Gray & Mackinnon, 2006; Kronforst et al., 2006; Seddon, Merrill, & Tobias, 2008; Terai et al., 2006). The evolution of a sensory system will be influenced by many factors, but it is helpful to compare two contrasting scenarios. One is that communication signals evolve in response to a fixed sensory system (Endler & Basolo, 1998), the other is that senses and signals co-evolve as a specialised communication system.

Specialised systems are familiar in pheromonal and acoustic communication, and in bioluminescent signalling (Lall, Seliger, Biggley, & Lloyd, 1980; Matsui, Seidou, Horiuchi, Uchiyama, & Kito, 1988), but otherwise seem to be unusual in vision. A possible example is the relationship between primate trichromacy and fruit colours (Mollon, 1989; Regan et al., 2001; Surridge, Osorio, &

Mundy, 2003). It may be that trichromacy initially evolved to allow primates to find fruit that were adapted to be seen by birds, and subsequently fruit dispersed by primates acquired different colours from bird-dispersed fruit (e.g. orange rather than red; Fisher & Chapman, 1993; Gautier-Hion et al., 1985; see also Fig. 4). It should however be noted that there is no evidence for consistent differences in the colours of fruit that are consumed by routinely trichromatic primates and predominantly dichromatic species, or that primates that eat ripe fruit are more consistently trichromatic than those that do not (see below and Lucas et al., 2003).

Recent years have seen substantial advances in knowledge of spectral sensitivities of visual photoreceptors and their evolutionary history, and of the spectral reflectance of objects, such as fruit, feathers and flowers (Figs. 1–3). We now discuss these findings in the light of the questions about the relationship between senses and signals that were raised over a century ago by Allen, Darwin and others.

1.2. Spectral coding of natural images

To learn about the evolutionary function of a sensory system—that is the relevant signals and the information that is coded about them—one can model its responses to natural stimuli, and then compare the performance to that of possible alternatives. Performance is defined in terms of coding efficiency or some comparable criterion that takes account of metabolic and other costs (e.g. number of ATP molecules per bit of information; Barlow, 1961; Niven & Laughlin, 2008). For colour vision this approach is relatively straightforward; it is easy to measure reflectance and illumination spectra, there is a good deal of information on the spectral sensitivities of animal photoreceptors. As well as comparing naturally occurring eyes one can predict the effects of evolutionary change by modeling hypothetical eyes with varying complements of visual pigments.

A basic question concerns the number of receptor types and their spectral tuning (Barlow, 1982). Young (1802) recognized that the retina makes both spectral and spatial measurements of the image, and he proposed that trichromacy (i.e. having three spectral receptors) is a compromise between these incompatible functions. However, reflectance spectra tend to vary smoothly with wavelength, so that—in contrast to spatial resolution—there may be[1] little fine spectral detail to be recovered by increasing the number of receptors. For instance, Maloney (1986) found that three principal components (PC's) account for over 98% of the variance in reflectance in natural spectra over the human visible spectrum. Given that a communication channel needs to have a workable signal to noise ratio to be useful van Hateren (1993) asked how noise (e.g. from photon catch) would affect spectral coding. He took Fourier transforms of natural spectra to give an average spectral power spectrum, and compared the signal as a function of spectral frequency to the estimated receptor noise. This model predicts that either trichromacy or dichromacy maximizes the spectral information coded by noisy photoreceptors. van Hateren (1993) also found that when photon noise is significant the spectral bandwidth of rhodopsin (c. 100 nm) is near optimal, so that narrowing the tuning curve would not increase spectral information encoded by the eye. This conclusion is clearly relevant to understanding the extent to which receptor spectral sensitivities are narrowed by coloured filters such as oil droplets in the eyes of birds and other animals (see below and Vorobyev, 2003).

The models outlined above are concerned mainly with the number of spectral receptors rather than their specific location. As well

as varying smoothly, the spectra of natural pigments such as chlorophyll, carotenoids and melanin have relatively fixed forms (Osorio & Bossomaier, 1992). For example, chlorophyll gives leaves a peak reflectance near to 555 nm, while carotenoids have step-like spectra (Fig. 2). These characteristics mean that information about reflectance is not uniformly distributed across the spectrum. In particular long wavelengths are generally more variable than short wavelengths, especially for plant and animal pigments; this is likely to have significant consequences for the ideal spectral location of receptors (Osorio & Vorobyev, 2005).

To investigate the spectral location as well as the number of receptors Vorobyev (1997a) put forward a model that uses accuracy of reconstruction of reflectance spectra from photoreceptor quantum catches as the performance criterion. This predicts that for realistic levels of receptor noise the complement of receptors present in (standard) trichromatic primates is optimal for reconstructing flower and fruit spectra in the human visible range (400–700 nm). Decreasing the number of cone spectral types from three to two significantly decreases the accuracy of reconstruction, while increasing the number of cones to four would not improve accuracy. Similarly, tetrachromatic vision of birds is optimal for reconstructing the reflectance spectra within the bird visible range (300–700 nm): decreasing the number of cones from four to three significantly decreases the accuracy of reconstruction, while increasing the number of cones from four to five has practically no benefit.

In a recent study Lewis and Zhaoping (2006) asked how the spectral location of photoreceptors affects the mutual information between reflectance spectra and receptor outputs. They used three sets of data: (i) representative spectra of natural scenes; (ii) spectra from hyperspectral images, and (iii) spectra of fruit consumed by primates in Uganda. The model took account of the effects of natural illumination spectra on photon noise, but found a negligible effect of varying the illuminant on mutual information. Lewis and Zhaoping found that for a dichromatic eye (lacking M cones) the normal spectral sensitivities of primate L and S cones are close to optimal, both for fruit and for natural image spectra. Also, given fixed L and S receptors the location the M cone is also close to optimal (Fig. 1). The advantage of a relatively long wavelength M cone is due to the long wavelength weighting of spectral information. Red-shifting the L cone would however benefit colour vision for trichromatic eyes. In this context it is interesting that birds and butterflies have receptors with sensitivity maxima at or above 600 nm (Section 2; Osorio & Vorobyev, 2005).

At this point a note of caution is in order. Models of sensory coding—self-evidently—do not replicate visual perception. In particular they normally assume that optimal use of made of information coded by the photoreceptors or neural receptive fields that are the subject of the study. It is therefore interesting that a psychophysical study (Nascimento, Foster, & Amano, 2005) found that for natural images as many as eight principal components may be needed to fully represent spectral data in natural images. The reasons for the discrepancy between this empirical result and models are not clear, but may be connected with the nature of the images, the effects of small errors of reconstruction on visual appearance, or perhaps inadequacies in PCA as a method for representing the data (Nascimento et al., 2005).

A further consideration is that the need to recover reflectance under variable illumination (i.e. colour constancy) may have consequences for both the number and the tuning of spectral receptors. Variable illumination increases the number of degrees of freedom in the signal (Maloney & Wandell, 1986), and may favour sharply tuned receptors (Finlayson, Drew, & Funt, 1994; Worthey & Brill, 1986). The effects depend upon the mechanism of colour constancy, but if it is the case that spatial ratios of cone excitations are important (Nascimento & Foster, 1997), then

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[1] Maloney's (1986) PCA analysis was based on reflectance data from Krinov (1947) that were averaged from multiple measurements and so may have underestimated the variation.
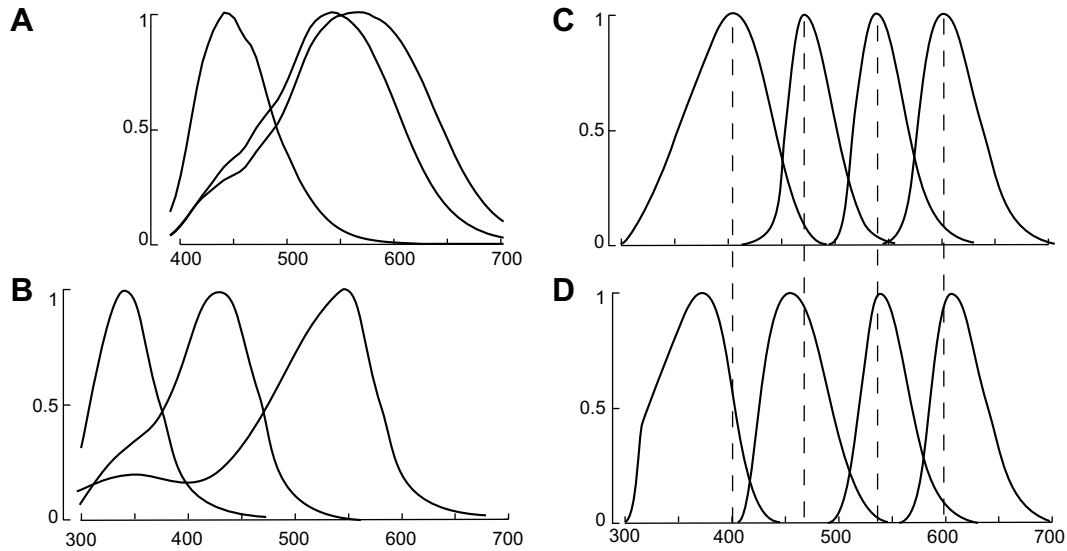
Fig. 1. Normalized photoreceptor spectral sensitivities of: (A) Human; (B) Honeybee; (C) Pigeon; (D) Starling.
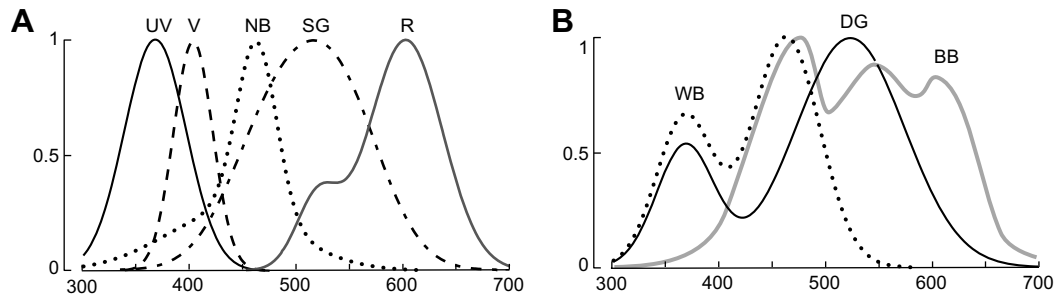

Fig. 2. Spectral sensitivities of the eight types of photoreceptor found in the swallow tail butterfly *Papilio xuthus* (Koshitaka et al., 2008). (A) Narrow band receptors; (B) Broad band receptors. Receptors are named as follows: UV; V, Violet; NB, Narrow blue; SG, Single green; R, red; WB, Wide blue; DG, Double green; BB, Broad band. These receptors are found in three different types of ommatidium. When foraging for nectar these butterflies can discriminate wavelengths differences of 1 nm. A model of *P. xuthus's* spectral sensitivity suggests that when they are tetrachromatic with inputs from the UV, blue (narrow-band and wide-band), green (double-peaked) and red classes. Butterflies have a much greater diversity of spectral receptor types than other groups of land animals.
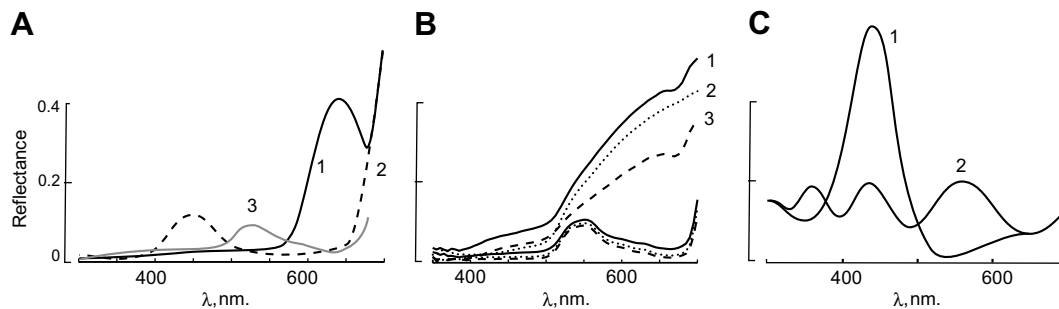

Fig. 3. Spectral reflectances of different types of natural object: (A) Flowers and a leaf: 1. *Zinnia peruviana*, 2. *Salvia guaranitica*; 3. *Salvia* leaf; (B) Fruit consumed by tamarin monkeys (upper curves) and leaves (lower curves) of Neotropical trees of the genus *Abuta*: 1. *A. imene*; 2. *A. fluminum*; 3. *A. rufescens*; (C) Iridescent bird feathers. 1: Magnificent hummingbird crown; 2: Feral pigeon neck. Spectra in (A) are from N. Hempel di Ibarra, and in (B) from A. Smith.

information about the illuminant itself may not be necessary for this recovery task.

Although questions remain, it seems that, contrary to Young's (1802) intuition, primate trichromacy is 'about right' for spectral coding. This leaves open the question of why animals have such diverse spectral photoreceptors (Figs. 1 and 2). Usually receptors are more uniformly distributed across the spectrum than in primates, and coloured filters often narrow sensitivity curves. The reduction

of the overlap between receptor spectral sensitivities can be expected to increase the number of colours that a visual system can discriminate (Vorobyev, 1997b, 2003, 2004; Vorobyev & Menzel, 1999). Thus the fact that primates have overlapping spectral sensitivities may indicate that their colour vision is evolutionary adapted to tasks different from those of other animals (Vorobyev, 2004). We now look in more detail at the evolutionary radiation of photoreceptor spectral sensitivities in land animals.

1.3. Spectral tuning and the adaptive radiation of visual photopigments and photoreceptor spectral sensitivities

The spectral sensitivity of rhodopsin pigments depends upon the energy level of π-electron orbitals in the chromophore, which is controlled by a small number of amino acids in the opsin. For instance, in the short wavelength (SWS1)[2] pigments of birds, the substitution of cysteine with serine at amino acid 90 shifts their peak absorbance (λ_{max}) from about 370 to 405 nm (Carvalho, Cowing, Wilkie, Bowmaker, & Hunt, 2007; Wilkie et al., 2000). Similarly, the shift between primate MWS (λ_{max} 530 nm) and LWS (λ_{max} 560 nm) pigment sensitivities is due to the substitution of non-polar with hydroxyl residues at three sites (Chan, Lee, & Sakmar, 1992; Neitz, Neitz, & Jacobs, 1991).

The simple relationship between genotype and the spectral phenotype of photopigments allows us to infer spectral sensitivity directly from DNA sequence. More importantly, the fact that a single amino acid substitution can shift spectral sensitivity facilitates adaptive change. It is known that relevant substitutions have occurred on multiple occasions in the evolutionary history of birds and primates, which is convincing evidence that changes are adaptive (they are under positive selection; Carvalho et al., 2007; Surridge et al., 2003). This conclusion is supported by the convergent evolution of butterfly and primate opsins, which use comparable amino acid substitutions to control pigment sensitivities in the 530–560 nm range (Briscoe, 2001; Frentiu et al., 2007a). The implication that the spectral tuning in terrestrial animals is adaptive complements ample evidence that fish photopigments vary according to the light spectrum in the water (Bowmaker, 1999).

Adaptive variation of rhodopsin pigments is however constrained. The spectral absorption function of rhodopsins is a characteristic of the chromophore, while the opsin controls only one degree of freedom, which is identified with λ_{max} (Dartnall, 1953; Govardovskii, Fyhrquist, Reuter, Kuzmin, & Donner, 2000). Also, empirical data suggest that there is a long wavelength limit λ_{max} for visual pigments that use retinal or 3-hydroxyretinal as a chromophore (Seki & Vogt, 1998). Vertebrates reach 565 nm, while a butterfly, Apodemia mormo has a 600 nm pigment (Frentiu et al., 2007a). The reason for this limit is not known. The best known hypothesis is that long wavelength pigments suffer because the rate of spontaneous isomerization (or thermal dark noise) increases with λ_{max} (Ala-Laurila, Donner, & Koskelainen, 2004; Ala-Laurila, Pahlberg, Koskelainen, & Donner, 2004; Rieke & Baylor, 2000). However this seems unlikely to account for the limit. For example, vertebrate cone pigments have far higher dark noise than any insect visual pigment (review Osorio & Nilsson, 2004), but work well at daylight intensities and (aside from Apodemia) not are noticeably blue shifted.

Coloured filters made of photostable pigments can circumvent the long wavelength limit on photopigments, but at the cost of reduced sensitivity (van Hateren, 1993; Vorobyev, 2003). Vertebrates, including reptiles and birds, use coloured oil droplets in the cone inner-segment, while butterflies and other insects have pigment cells in their compound eye. These filters probably benefit colour vision, by narrowing spectral tuning and giving receptors with λ_{max} up to 640 nm (Lewis & Zhaoping, 2006; Martin & Osorio, 2008; Osorio & Vorobyev, 2005; Partridge, 1989; Vorobyev, 1997b, 2004). Coloured filters also allow animals such as birds and butterflies to produce a range of receptor sensitivities with a single photopigment (Section 2).

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[2] The nomenclature for cone opsin genes follows Yokoyama (1994, 2000), who defined the four main classes: LWS/MWS, RH2, SWS2, and SWS1 (Osorio & Vorobyev, 2005).

2. Evolutionary diversity of photoreceptor spectral sensitivities in land animals

The extensive knowledge of photopigment genes and photoreceptor spectral sensitivities allow broad and detailed comparisons of colour vision across the animal kingdom (Briscoe & Chittka, 2001; Bowmaker, 1999; Kelber, Vorobyev, & Osorio, 2003). Spectral sensitivities can be measured by spectrophotometry and electrophysiology, or inferred from DNA sequences (Cavalho et al., 2007; Nathans, 1999; Neitz et al., 1991). Four well-known groups of terrestrial animal are primates, birds, bees and wasps (hymenopterans) and butterflies (Figs. 1 and 2). We now outline the diversity of receptor sensitivities in each of these groups and discuss their evolution in relation to the spectral signals that are relevant to them (Fig. 3).

2.1. Bees and wasps

Honeybees (Apis mellifera) have three spectral types of photoreceptors, with peaks at 340, 440 and 540 nm (Fig. 1). In view of the importance of colour vision to bees one might expect these receptor sensitivities to reflect their specific visual ecology; for example the types of flowers that they visit. However, the main groups of hymenopteran insects excluding ants (i.e. bees, wasps and sawflies) mostly have three types of photoreceptor, with spectral sensitivities similar the honeybee's (Briscoe & Chittka, 2001; Peitsch et al., 1992; Skorupski, Doering, & Chittka, 2007). The implication is that the three receptors were present in common ancestor of hymenopterans, and that they have not evolved in response to changes in lifestyle such as nectar feeding in bees. Exceptions to this general picture all enhance red sensitivity. The bee Osmia has a 572 nm wavelength receptor (Menzel, Steinmann, De Souza, & Backhaus, 1988), a wasp, Sphex cognatus has red filters in its eye (Stavenga, 2004), and sawflies (Tenthridinidae), have an additional red receptor (Peitsch et al., 1992). It may be relevant that sawfly larvae eat leaves, like caterpillars of Lepidoptera, so that females may use colour to find food plants for their eggs.

2.2. Birds

Birds have four types of single cone, which probably gives them tetrachromatic colour vision, and also double cones, which probably serve a 'luminance' system (Martin & Osorio, 2008; Osorio & Vorobyev, 2005). Each single cone contains one of the four main types of vertebrate cone photopigment (LWS/ MWS, RH2, SWS2 and SWS1; Hart & Hunt, 2007; Yokoyama, 2000) and has a coloured oil droplet in its inner segment. Double cones have the LWS pigment, but the oil droplet is different from the LWS single cones, which gives them a spectral sensitivity similar to the human L cone.

As with hymenopterans, there is little variation amongst avian visual pigments (Fig. 1). The peak sensitivities of the LWS, RH2 and SWS2 pigments are near to 565, 500, and 470 nm (Hart & Hunt, 2007; Martin & Osorio, 2008). As already mentioned, there are two types of SWS1 pigment, which have peaks around either 365 nm (UVS) or 405 nm (VS). The UVS variant has evolved at least five times from the (ancestral) VS form, including in parrots, most songbirds, gulls, rhea and a trogon (Carvalho et al., 2007; Ödeen & Håstad, 2003). There is no known relationship between the evolution of the UVS pigment and visual ecology. Penguins differ from the general avian pattern in that they have blue shifted pigments, and probably lack one of the SWS pigments (Bowmaker & Martin, 1985). More intriguingly, the bobolink (an oscine passerine; family Icteridae) lacks a blue single cones but it has two types of LWS single cones, with red and clear oil droplets, and expresses a blue opsin the accessory member of the double cone (Beason & Loew,

2008). This unexpected finding raises the possibility that birds are more diverse than work over the past three decades has implied (Hart & Hunt, 2007; Martin & Osorio, 2008).

Given the diversity of their visual ecology the uniformity of bird photopigment sensitivities is remarkable. It is hard to imagine how a seabird such as a shearwater, might use colour vision that (at the receptor level) is comparable to a peacock's (Hart, 2002, 2004). Oil droplets allow some variation for the three longer wavelength single cones (Fig. 1; Hart & Vorobyev, 2005; Partridge, 1989). For example, in a study of 25 species of bird (Hart & Vorobyev, 2005), LWS and MWS cone λ_{max} values range from 601 to 620 nm, and 534 to 547 nm, respectively. The spectral sensitivity of the UVS/VS cone affects the SWS cone oil droplet, so that birds with UVS cones (355–373 nm; $n = 11$) have SWS cones that range from 445 to 463 nm, while those with the VS cones (range 405–426 nm; $n = 9$) have SWS cones ranging from 472 to 480 nm, except for the Ostrich, which has a 405 nm VS receptor and a 459 nm SWS receptor.

Oil droplets probably mediate a tradeoff between absolute sensitivity and spectral tuning (Hart, Lisney, & Collin, 2006; Hart & Vorobyev, 2005; Martin & Osorio, 2008; van Hateren, 1993; Vorobyev, 2003). Their optical densities vary between species, across the visual field, and according to the light regime in which an individual is living (Hart et al., 2006). As might be expected, dim conditions seem to favour lower densities.

2.3. Primates

The evolution of primate cone pigments raises interesting general questions in evolutionary genetics, and is reviewed extensively elsewhere (Jacobs, 1996; Nathans, 1999; Surridge et al., 2003). Most mammals are dichromatic with L (long wavelength) and S (short wavelength) cone pigments, but Old-World monkeys (Catarrhini) and howler monkeys (*Alouatta* spp.) independently duplicated the single ancestral LWS/MWS gene, which is on the X-chromosome, to give separate LWS and MWS pigments. Pigment sensitivity maxima of howlers and all known Old-World species are at about 430 nm (SWS), 530 nm (MWS) and 560 nm (LWS). Other primates retain a single LWS/MWS gene, but in most New-World species (Platyrrhini) and several lemurs this gene is polymorphic so that heterozygotes (i.e. a proportion of females) are trichromats. The majority of individuals are dichromats, but depending on the number of alleles present in a population there are at least two types of dichromatic colour vision. That is the S cone is present with either an MWS of LWS type of cone.

The population genetic data make it clear that in primates with a single gene and polymorphic colour vision (i.e. lemurs and New-World monkeys) there is frequency dependent selection on the alleles (Surridge et al., 2003), with the fitness of a given allele being inversely related to its frequency. In our view, the likely explanation for this frequency dependence is that trichromacy is selectively favoured for all diurnal primates. The implication is that lineages with a single LWS/MWS gene are simply 'unlucky' not to have separate L and M cones (Osorio, Smith, Vorobyev, & Buchanan-Smith, 2004). However situations of this kind, where genetic polymorphism is maintained by heterozygote advantage (overdominance) are unusual (Osorio et al., 2004). The alternative possibility is that *phenotypic* polymorphism is favoured by frequency dependent selection—that is that individuals with rare types of colour vision have an advantage (Mollon, Bowmaker, & Jacobs, 1984). Consistent with this idea, there is evidence that dichromats are better than trichromats at finding cryptic insect prey (Melin, Fedigan, Hiramatsu, Sendall, & Kawamura, 2007); perhaps because colour vision 'distracts' animals from relevant cues to camouflage breaking (Morgan, Adam, & Mollon, 1992). Differences of this kind

within polymorphic populations could mean that individuals with a rare type of colour vision are at an advantage because they suffer reduced competition for food (Mollon et al., 1984; but see Melin, Fedigan, Hiramatsu, & Kawamura, 2008).

Further evidence for selection on receptor spectral sensitivities can be found in data on the occurrence of the different MW/LW alleles in polymorphic species. These show that there is selection against the shorter wavelength (535 nm) alleles in favour of 560 nm alleles or intermediate wavelength pigments (e.g. 545 nm; Osorio et al., 2004). Assuming that trichromacy favours the 535 nm/560 nm combination with equal allele frequencies, it is likely that the bias against the 535 nm allele arises in dichromats. This could be due either to the consequences for their dichromatic colour vision, which favours a wide separation of the two pigments (Lewis & Zhaoping, 2006; Osorio & Vorobyev, 1996), or in luminance vision (Osorio & Nilsson, 2004; Osorio & Vorobyev, 2005).

Because there is no evidence for any anatomical or molecular distinction between M/L cones in primates other than their photopigment an important problem for primates is in how information from these cones is segregated to allow chromatic opponent receptive fields in the visual system (e.g. primary visual cortex; Wachtler, Doi, Lee, & Sejnowski, 2007). The idea that trichromacy will follow naturally when the retina duplicates the M/L pigment, without concomitant genetic changes in neural development is supported by a recent study of mice that were genetically engineered to have the types of cone, and—at least sometimes—were trichromatic (Jacobs, Williams, Cahill, & Nathans, 2007). The evidence from mice and other considerations suggest that neural-wiring that gives red–green opponency is activity-dependent (Miller, 1994). This raises the question of whether the differences in activity between cone outputs are sufficient to allow chromatic coding. Matters are complicated because the magnitude of the achromatic signals is much greater than red–green chromatic signals (Ruderman, Cronin, & Chiao, 1998; Wachtler et al., 2007). Wachtler et al. (2007) simulated responses of primate retinas to natural images to show that for plausible mechanisms based on unsupervised learning a trichromatic retina containing 560 nm receptors and either 530 or 545 nm receptors could develop chromatic opponent neurons. This model predicted that correlations between receptor outputs would be such that an activity-dependent mechanism could not develop three separate opponent mechanisms as required for tetrachromacy. This could account for the apparent absence of tetrachromacy in women with three types of LW/MW pigment.

Except for genetically engineered mice (Jacobs et al., 2007), trichromatic primates may be unique in that the L and M cones are functionally alike. In particular the luminance mechanism combines multiple receptor types. This arrangement may well have consequences for the L and M cone sensitivities because luminance signals are degraded by chromatic noise, which increases with spectral separation of the cones (Osorio, Ruderman, & Cronin, 1998; Osorio & Vorobyev, 2005; Williams, Sekiguchi, & Brainard, 1993). It is not clear whether this problem compromises colour vision by limiting the spectral separation of the L and M cones. The large overlap of L and M sensitivities would seem to be bad for colour vision, but various studies suggest that the spectral tuning of the cones may indeed be well suited (or even optimized) to discrimination, detection or classification of the colours of fruit and leaves or other natural spectra (Lewis & Zhaoping, 2006; Mollon & Regan, 1999; Osorio & Vorobyev, 1996; Sumner & Mollon, 2000a, 2000b; Vorobyev, 1997a; see also Section 1.2), or even of skin colour (Changizi, Zhang, & Shimojo, 2006).

Regardless of the explanation for the specific spectral sensitivities of the L and M cones, the uniform trichromacy of Old-World primates and howler monkeys suggests, as with hymenopterans

and birds, that the selective influences are not tied to any particular diet or lifestyle.

2.4. Butterflies

For hymenopterans, birds and primates each group has its own distinctive set of visual photoreceptors, and there is little variation within the groups (Fig. 1; Briscoe & Chittka, 2001). Butterflies are strikingly different in having a remarkable radiation of photoreceptor spectral sensitivities (Briscoe, 2008; Stavenga & Arikawa, 2007). This radiation involves diversification in photopigment spectral sensitivities, duplication of long wavelength and of 'blue' photopigment genes (Frentiu, Bernard, Sison-Mangus, Van Zandt Brower, & Briscoe, 2007b; Frentiu et al., 2007a; Sison-Mangus, Briscoe, Zaccardi, Knuttel, & Kelber, 2008) and also intraocular filtering (Arikawa, Scholten, Kinoshita, & Stavenga, 1999; Stavenga & Arikawa, 2007). Butterflies evolved from moths, which have three spectral receptors each containing a specific visual pigment. Some butterflies have retained this ancestral arrangement (Briscoe, Bernard, Szeto, Nagy, & White, 2003), but most have more. The swallowtail butterfly *Papilio xuthus* has eight different spectral types of receptor and tetrachromatic colour vision (Fig. 2; Arikawa, 2003; Koshitaka, Kinoshita, Vorobyev, & Arikawa, 2008). Peirid butterflies ('Whites' and their allies) produce long wavelength (640 nm) receptors by means of red filters (Wakakuwa, Stavenga, Kurasawa, & Arikawa, 2004), and there are differences in UV sensitivity between closely related species and between sexes.

The reasons of the diversity of butterfly photoreceptor sensitivities are not known, but 'informed speculation' implicates recognition of food plants for egg laying and of butterfly wing colours (Kelber, 1999; Stavenga & Arikawa, 2007; Zaccardi, Kelber, Sison-Mangus, & Briscoe, 2006). Direct evidence for a co-evolutionary relationship between butterfly colour vision and wing colours is provided by sexual dimorphism in the violet receptors in the small-white butterfly *Pieris rapae crucivora* (Arikawa, Wakakuwa, Qiu, Kurasawa, & Stavenga, 2005). The male's violet receptors (λ_{max}: 416 nm) have a much narrower spectral sensitivity than the female's, which the authors propose probably evolved for discriminating of the different wing colours of male and female *P. rapae*, which differ in the short wavelength region of the spectrum. Interestingly, the males of the European subspecies of the small-white *P. rapae rapae* resemble those of females, and in this subspecies the wing reflectance spectra of the sexes are almost identical (Arikawa et al., 2005).

3. Animal colour vision and the colours of natural objects

Aside from butterflies the spectral sensitivities of visual photoreceptors in land animals are conservative within major taxonomic groups. The implication is that photoreceptor spectral sensitivities do not reflect specific lifestyle, and do not co-evolve with visual signals. This leaves open the question of how signals are adapted to their receivers. To address this question Chittka and Menzel (1992) used a model based on estimates of receptor excitations to argue that honeybee photoreceptors (Fig. 1) are optimally tuned to detect flowers against leaves and to discriminate amongst flower colours. Given that the bee's receptor sensitivities evolved before angiosperm flowers it is reasonable to assume that colours of insect pollinated flowers are generally selected to be optimally detectable or discriminable to bees and other pollinating insects (Chittka, 1997).

Chittka's work illustrates how modeling receptor responses might give insights into the evolution of colour vision. Spectra have been measured for a wide range of natural objects including fruit eaten by birds and primates, leaves, bird plumage (Figs. 4 and 5), and butterfly wings. It is relatively straightforward to estimate the relative quantal absorbance and hence photoreceptor

responses for animal eyes. One can then simulate the effects of altering spectral sensitivities or the number of receptor types on receptor excitations (Kelber et al., 2003; Lewis & Zhaoping, 2006; Regan et al., 2001).

3.1. Chromaticity and colour thresholds

Chittka and Menzel's (1992) work on bees and flowers uses a metric for discriminability given by separation of colour loci in a chromaticity diagram, which is based on receptor excitations (Backhaus & Menzel, 1987). This choice of model was based on experimental evidence that bees learn chromatic but not achromatic colour differences. Similar models, based chromatic differences are widely used in work on spectral coding (Regan et al., 2001; Vorobyev & Osorio, 1998), and we now look briefly at the reasons for this choice.

For humans, chromaticity (i.e. hue and saturation) refers to the aspects colour that distinguishes a stimulus from the most similar achromatic light. For non-human animals one can define chromaticity as the signal given by comparing receptor responses that are normalized to their joint mean. For example, with L and S receptors the *LS* chromatic signal is given by: $LS = (L - S)/(L + S)$, where L and S are the excitations of the two types of receptor. This formula is easily extended to higher dimensional colour vision. One can represent chromaticity in Cartesian plots whose axes are derived from receptor excitations (Figs. 4 and 5).

There is ample evidence that animals use chromatic and achromatic signals for different purposes (Osorio & Vorobyev, 2005), and that at least in bright light colour thresholds appear to be set by receptor noise in chromatic mechanisms (e.g. colour opponent neurons; Kelber et al., 2003; Vorobyev & Osorio, 1998). Models of colour thresholds leave open the question of how animals perceive the brilliant colours of visual displays; for example, the relationship between threshold and suprathreshold signals (Ham & Osorio, 2007; Stevens, 1957). It would also be interesting to know whether animals recognize colour categories, and how the requirements of colour categorization might be affected by the photoreceptors. For example, Mollon and Regan (1999) and Regan et al. (2001) proposed that primate L and M photoreceptors are tuned so that leaves give a fixed red–green chromatic signal, which may simplify the problem of separating leaves from fruit.

3.2. Chromaticities of natural objects

As we have explained signaling colours of animals and plants seems to evolve in response to more or less fixed spectral receptors. How then are these signals adapted to their natural receivers? Signals need to be detectable against their background, and/or recognizable—that is discriminable from related objects (Chittka & Menzel, 1992; Osorio & Vorobyev, 1996; Sumner & Mollon, 2000a, 2000b).

A straightforward way to approach this question is by examining the distribution of signaling colours in the perceptual spaces of different types of animal that are given by chromaticity diagrams derived from receptor signals (Figs. 4 and 5). For primates, bees and two types of bird we plot the spectra of European flowers (Chittka, Shmida, Troje, & Menzel, 1994), fruits eaten by birds (Schaefer, Schaefer, & Vorobyev, 2007), fruits eaten by primates (Osorio & Nilsson, 2004) and bird plumage (Vorobyev, Osorio, Bennett, Marshall, & Cuthill, 1998). Two points are readily apparent: firstly that the colours are not uniformly distributed across the receptor space, and secondly that there is a relationship between the distribution of colours and the vision of the natural receiver. For instance, flowers occupy a larger proportion of the space for bees than they do for primates, whereas the opposite applies to fruit that are consumed by primates. Interestingly, fruit eaten by
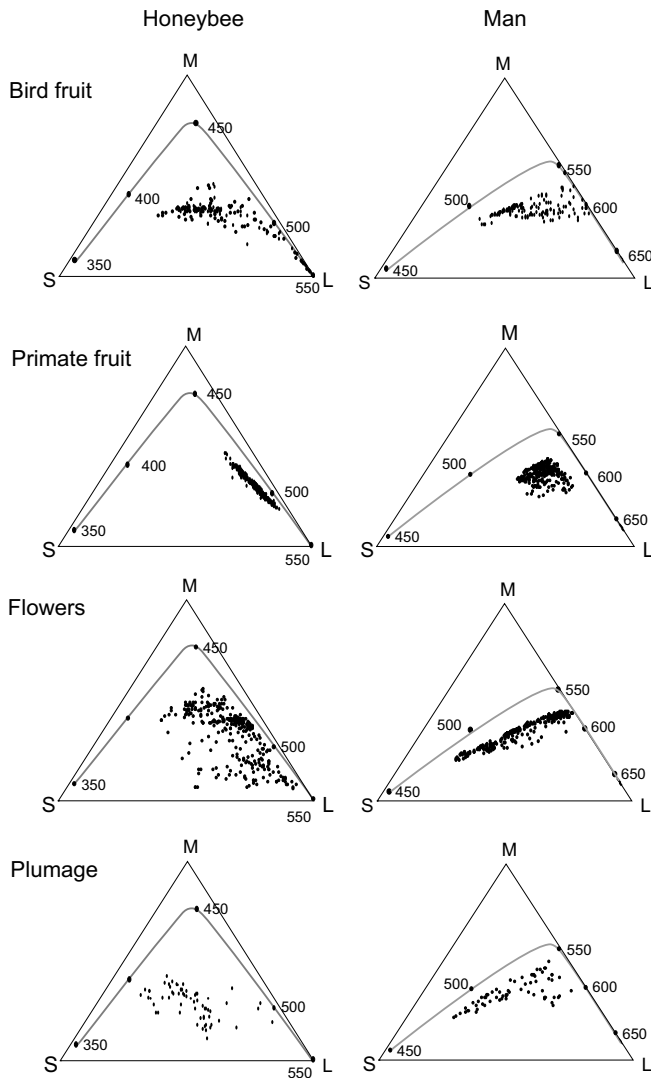
Fig. 4. Loci of four different classes of object plotted in chromaticity diagrams for trichromatic humans and honeybees. The vertices correspond to pure excitation of each of the three cone types and the lines gives the monochromatic loci with wavelength plotted at 50 nm intervals. Each dot plots the chromaticity of an individual spectrum. Bird fruits are species that are consumed by birds in South America (Schaefer et al., 2007); primate fruit are species that are consumed by primates in Kibale forest Uganda (Courtesy of P. Sumner), and Flowers are European species and therefore mainly pollinated by insects, plumage spectra are for a range of bird species (Vorobyev et al., 1998). It is readily apparent that the distribution of spectra is never uniform, and that the pattern varies according to the class of object and the type of eye. Fig. 5 plots loci of the same object for bird eyes. The plot is in Cartesian axes with: $X = \sqrt{1/2}\,(l - s)$; $Y = \sqrt{2/3}\,(m - 1/2\,(l - s))$, where l, m and s correspond to the excitations of the L, M and S photoreceptors relative to the illuminant.

birds clearly differ from fruit eaten by primates, and perhaps surprisingly they tend fall on a line in the avian receptor space. Starling and pigeon represent the two main types of avian eye, with a 365- and 410-nm SWS1 pigments here, respectively. In all cases the UV eye has a greater spread of colours, but the relatively poor quantum catch, and hence higher noise in the 365-nm receptor may offset the implied advantage (Schaefer et al., 2007; Vorobyev et al., 1998).

4. Conclusion

Understanding the ecology of colour vision inevitably starts with a consideration of how animal eyes are adapted to encode natural spectral signals. It is fairly straightforward to simulate
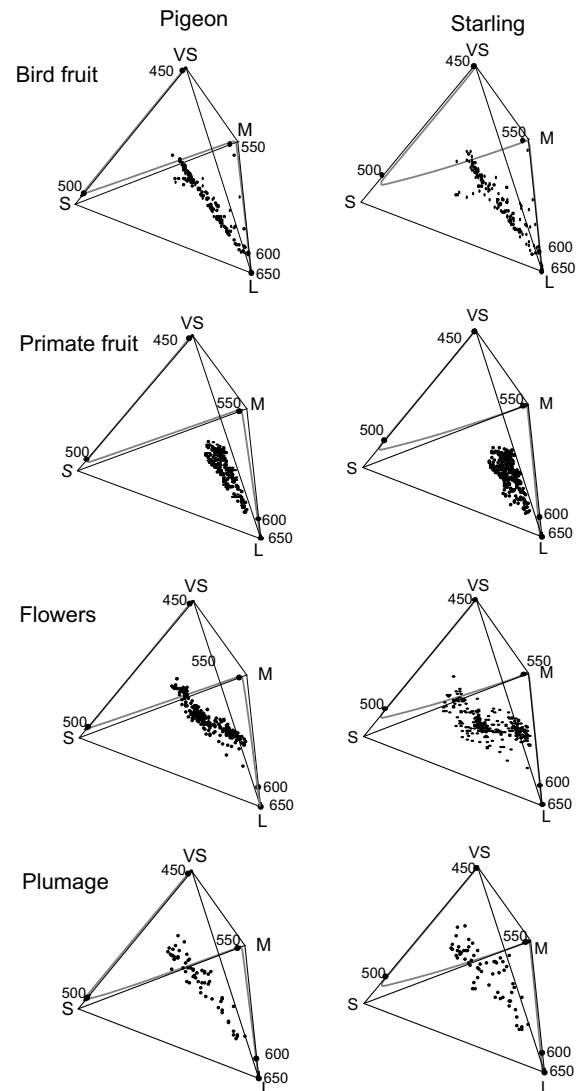
Fig. 5. Loci of four different classes of object plotted in chromaticity diagrams for tetrachromatic birds. Pigeons a VS receptor (λ_{max} 410 nm) and starlings have a UVS receptor (λ_{max} 370 nm). Further details are the same as for Fig. 4. The UV receptor enhances separation of the spectra at the expense of absolute sensitivity (Vorobyev et al., 1998). The plot is in Cartesian axes with axes as given by Kelber et al. (2003).

receptor responses to spectral stimuli (Figs. 4 and 5). We have shown how such simulations (projected onto a chromatic space) might inform understanding of the evolutionary relationship between vision and visual signals. This type of modeling complements work on the evolution and diversity of photoreceptor spectral sensitivities and spectral signals, where our understanding is unparalleled in sensory biology but new findings continue to emerge. Examples include findings on the diversity of avian and butterfly photoreceptors (Beason & Loew, 2008; Briscoe, 2008), the relationship between receptor sensitivities and communication signals in butterflies (Arikawa et al., 2005), and the detection of camouflaged prey by foraging primates (Melin et al., 2007).

It is self-evident that receptor responses ultimately set psychophysical thresholds, and the high metabolic cost of phototransduction cause strong selection for efficient use of receptor signals (Niven & Laughlin, 2008; Snyder, Laughlin, & Stavenga, 1977; van Hateren, 1993). One might therefore expect to find that the principle of coding efficiency should be applicable to spectral coding (Barlow, 1961, 1982). The obvious comparison is with achromatic vision where this principle has been successfully applied to spatial

and temporal sampling in the retina (Snyder, Bossomaier, & Hughes, 1986; Snyder et al., 1977), and to photoreceptor physiology (Niven & Laughlin, 2008), and to later neural processing (Simoncelli & Olshausen, 2001).

With the notable exception of butterflies comparative data on receptor sensitivities support the idea that colour vision is adapted for 'general-purpose' vision, rather than dealing with specific types of communication signal. Efficient coding of noisy data is almost certainly relevant (Lewis & Zhaoping, 2006; van Hateren, 1993; Vorobyev, 1997a), but it remains unclear whether coding efficiency of pictorial information can account for the receptor spectral sensitivities in birds, hymenopterans and primates.

The absence of an obvious explanation for receptor sensitivities has led to a range of accounts, which draw attention to the relationship between primary sensory coding and the subsequent neural processing and uses of sensory information. For example, coding spectral variation (Maloney, 1986; van Hateren, 1993; Lewis & Zhaoping, 2006) predicts different optima from recovery of reflectance spectra under variable illumination (i.e. colour constancy; Finlayson et al., 1994; Nascimento & Foster, 1997; Vorobyev, 1997a, 1997b; Worthey & Brill, 1986). It is also possible that suprathreshold tasks such as colour categorization are important. For instance, Mollon and Regan (1999) proposed that primate L and M cones are tuned to minimize the range of red-green signals given by leaf spectra, which could simplify the classification of leaves (see also Regan et al., 2001). Finally the requirements of spatial vision may well influence the evolution of receptor sensitivities (Osorio & Vorobyev, 2005; Williams et al., 1993; Young, 1802). While most work in this area focuses on primate trichromacy, we hope this article has shown the value of looking beyond our own idiosyncratic set of cones.

Acknowledgment

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