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Coevolution of coloration and colour vision?

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The evolutionary relationship between signals and animal senses has broad significance, with potential consequences for speciation, and for the efficacy and honesty of biological communication. Here we outline current understanding of the diversity of colour vision in two contrasting groups: the phylogenetically conservative birds, and the more variable butterflies. Evidence for coevolution of colour signals and vision exists in both groups, but is limited to observations of phenotypic differences between visual systems, which might be correlated with coloration. Here, to illustrate how one might interpret the evolutionary significance of such differences, we used colour vision modelling based on an avian eye to evaluate the effects of variation in three key characters: photoreceptor spectral sensitivity, oil droplet pigmentation and the proportions of different photoreceptor types. The models predict that physiologically realistic changes in any one character will have little effect, but complementary shifts in all three can substantially affect discriminability of three types of natural spectra. These observations about the adaptive landscape of colour vision may help to explain the general conservatism of photoreceptor spectral sensitivities in birds. This approach can be extended to other types of eye and spectra to inform future work on coevolution of coloration and colour vision.

This article is part of the themed issue 'Animal coloration: production, perception, function and application'.

1. Introduction

(a) Colour vision and evolutionary pressure

Like any sensory system, colour vision evolves in response to natural stimuli. Selection can influence colour vision in several ways, not least because the spectral sensitivity of visual photopigments depends primarily on the identity of a few amino acids in the opsin protein [1–3].[1] Spectral sensitivities of fish photoreceptors vary with the ambient illumination [5,7,8], and one might expect to find a similar dependence on reflectance spectra of objects such as food [9]. The latter could lead to coevolution of colour signals and colour vision within communication systems [10,11]. Coevolution is potentially important in speciation [12,13], and could also affect the efficacy and honesty of communication, especially when signallers and receivers have conflicting interests [14].

Therefore, it was surprising when in 1992, Peitsch *et al.* [15] found that an ecologically diverse selection of some 40 hymenopteran species (bees, wasps and sawflies) shared a similar set of three photoreceptor types, with sensitivity maxima (λ_{max}) at about 350 nm, 440 nm and 530 nm (four species had an additional long-wavelength receptor). Although the estimated λ_{max} values varied (partly due to experimental error), the conclusion that hymenopteran photoreceptor sensitivities are insensitive to specific visual ecology has stood [16,17]. Catarrhine primates [18] and birds [19,20] also have phylogenetically conserved spectral sensitivities, but the receptor sensitivities in each lineage

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are quite distinct from the others, which suggests that there are separate but stable 'optima' for colour vision. By comparison, some groups, including butterflies and teleosts, have had many changes in the numbers and spectral tuning of photoreceptors [4,21].

Physiological measurements and genetics provide a wealth of information about animal colour vision [5,22,23], particularly in two colourful groups—birds and butterflies—which appear to have different patterns of evolutionary diversification. Here we first outline the variety of bird and butterfly colour vision, highlighting evidence for coevolution. We then use the avian eye as a case study to show how modelling might aid interpretation of the effects of physiologically realistic changes to three principal characters: photoreceptor spectral sensitivity, intraocular filtering (i.e. cone oil droplets), and relative proportions of different receptor types across the retina.

(b) The diversity of colour vision in butterflies and birds

Originally Lepidoptera, like Hymenoptera [15–17], had three spectral types of visual photoreceptor [4,16], with λ_{max} close to 360 nm (UV),[2] 440 nm (B, blue) and 520 nm (G, green). The ancestral arrangement persists in many moths and butterflies, especially within Nymphalidae, but all papilionoid families (i.e. typical butterflies) have seen changes in the numbers and spectral tuning of receptors. These changes are due to duplication and diversification of opsin genes, regulation of gene expression, and the presence of photostable spectral filters [4], especially red filters, which produce receptors with sensitivity maxima beyond 570 nm (e.g. [24,25]). Papilionid and pierid butterflies seem to be most diverse, epitomized by fifteen spectral receptor types in the papilionid *Graphium sarpedon* [26]. Less extreme are *Papilio xuthus* with eight [24], the pierids *Pieris rapae* and *Colias erate* with eight [27] and nine respectively [28], and the nymphalid *Heliconius erato* with five receptor types [29]. Functional explanations for this diversity centre on foraging and mate choice. For instance, multiple long-wavelength receptors (λ_{max} 550–640 nm) could allow female butterflies to find food plants for oviposition [30,31]. Butterfly colour vision is also notable for sexual dimorphism: male *Heliconius erato*, for instance, have one UV photoreceptor type and females have two [29]; the dorsal eye of *Lycaena rubidus* has only UV and B receptors in males, but also long wavelength receptors in females [32]. In the Japanese *Pieris rapae crucivora*, the spectral sensitivities of violet photoreceptors are dimorphic [33], and it has been suggested—but not been confirmed—that this sexual dimorphism in vision mirrors a dimorphism in wing coloration of the species. Both dimorphic characters are absent from the European subspecies *P. r. rapae* [34], which hints at coevolution of vision and coloration.

Heliconius butterflies offer some of the best evidence for coevolution. *Heliconius* use wing coloration for mate recognition and as aposematic signals, so they risk confusing conspecifics with mimics. This problem might underlie the presence of two synapomorphies of the genus, namely the use of 3-hydroxykynurenine (3-OHK) as a 'yellow' wing pigment, and the duplication of the UV opsin gene to give two UV receptors with sensitivity maxima at about 365 and 390 nm [29,35]. Modelling suggests that the two UV receptors allow *Heliconius* species to classify 3-OHK wing pigmentation as colours distinct from the yellows used by non-*Heliconius* mimics better than tetrachromatic birds or trichromatic mimetic nymphalids can do [36].

By comparison with butterflies, bird colour vision seems to be conservative (e.g. [37]). Almost all species[3] express four types of cone opsin in five types of cone photoreceptor, each with a unique type of coloured oil droplet in the cone inner segment [42]. Sexual dimorphism is almost unknown (but see [11]). The photopigment spectral sensitivities vary little if at all, except for two forms of the shortest wavelength (SWS1) opsin, whose sensitivity maxima are either at about 365 nm (UV) or between 405 and 420 nm (V) [3]. The shift between the two forms has taken place at least 14 times in bird evolution [3]; it is attributed to protonation of the Schiff base linkage of the chromophore retinal to the opsin in the V form, and is often (but not always) caused by a single amino acid (Cys:Ser) substitution at amino acid residue 90. The functional significance of the UV–V difference is unclear, but *Malurus* wrens seem to have acquired UV sensitivity followed by one or more reversions to the V form, with the UV form being associated with short wavelength reflecting plumage colours [43,44].

Even if avian visual photopigments are rather invariant, the relative numbers of the different cone types in the retina and the composition and density of oil droplet pigmentation might co-evolve with colour signals [37]. The oil droplets are pigmented by carotenoids that act as long-pass filters, thereby narrowing and red-shifting the cones' spectral sensitivities at the expense of the total light absorption [6]. Each cone type has a specific oil droplet: transparent (T, no pigment) in the UV/V (SWS1 opsin) cone, clear (C) in the blue (SWS2 opsin) cone, yellow (Y) in the green (RH2 opsin) cone and red (R) in the red (LWS opsin) cone [42,45]. Avian double cones contain the LWS opsin and pale (P) oil droplets.

The oil droplets' carotenoid pigments seem to be evolutionarily conserved [45,46], but their concentrations vary, ranging from pale to intensely coloured (e.g. [47]). The reasons for this variation are unclear. In the chicken the pigment density depends on light intensity [48], and in various species deprivation of dietary carotenoids reduces oil droplet pigmentation [49,50]. Although their small size (ca. 2 µm diameter) and high refractive index make it difficult to measure or model the optical properties of oil droplets, natural variations in pigment density likely affect light absorption by the cone [6], and recent experiments find that in the quail *Coturnix japonica* dietary carotenoids can affect colour discrimination [51].

In some species, such as the scarlet tanager *Piranga olivacea*, and zebra finch *Taenopygia guttata*, the same pigments serve in oil droplets and plumage coloration, which can be sexually dimorphic [46,52,53]. It seems likely that the red astaxanthin pigment evolved first for vision [45] and was subsequently used for coloration [46]. Thus, the role of carotenoids in coloration and colour vision, along with their dependence on diet and health [54], might directly link receptor properties to visual signals, which could lead to evolutionarily significant scenarios, including assortative mating, and selectivity in mate choice. For instance, individuals with densely pigmented oil droplets might be especially good at discriminating plumage colours [55], but to our knowledge current evidence is restricted to observations of correlations between coloration and oil droplet pigmentation [52].

The proportions of the different types of cone could also affect colour vision [55]; these range from nearly equal (e.g. ratios of 1.5 : 1 : 1.5 : 2.1 for SWS1:SWS2:MWS:LWS in the short-tailed shearwater *Puffinus pacificus*) to highly skewed (e.g. 1 : 1.3 : 1.6 : 6.4 in the sacred kingfisher *Todiramphus sanctus*

and 1 : 9.6 : 16.8 : 14.3 in the black noddy *Anous minutus*) [19]. A difference in relative numbers of different cone types could underlie Bloch's [11] finding that the expression of SWS2 (blue) opsin mRNA is positively correlated with sexual dichromatism in female, but not male, New World warblers (Parulidae), suggesting that female SWS2 expression co-evolves with male coloration.

(c) The adaptive landscape of colour vision

In both butterflies and birds, evidence for coevolution of colour vision and coloration is inconclusive. A convincing case for reciprocal evolutionary interactions between signals and senses probably requires various types of evidence, but a relatively straightforward question concerns the effects of differences in eye design on the perception of colour signals.

Functional accounts of sensory systems are often based on models that compare their performance in encoding a specific ensemble of stimuli to a hypothetical optimum [56–58]. If they approach this optimum it may be that the receiver is adapted to the stimuli in question—or vice versa. The optimal system should be defined over a realistic phenotypic space, which, for colour vision, might concern the number of photoreceptor types, their spectral sensitivities and relative densities [59]. For instance, three spectral receptor types are sufficient to encode nearly all spectral information in natural images [59,60], but tetrachromatic vision could allow birds to discriminate avian plumage spectra better than trichromatic primates [61]. Models also imply that the spectral tuning of primate L, M and S cones is well suited to the discrimination of fruit spectra, and honeybee photoreceptors to European flower spectra [62,63]. Still, a match between sensory system and communication signals does not require coevolution, and it is likely that fruit or flower colours evolved largely in response to their dispersers' vision, rather than vice versa [20,62,64].

The idea that senses are optimized to a given class of signals is attractive [65], but because colour vision serves multiple behaviours, selection might produce a compromise, for example between the generality of background colours and some specific signals. Moreover, as we have mentioned, evidence for selection tends to be based on differences between visual systems, rather than claims for optimization for a particular task. It is therefore relevant to know whether observed differences between sexes or species are as expected if one type, but not the other, is under selection for a given task. Here we illustrate how a colour vision model can be used to investigate coevolution, and adaptation more generally. We use birds as case study because the range of their phenotypic variation is a subject of considerable interest (see above) and behavioural tests have validated models of avian colour vision [66–68], but the approach is general. Our aim is not to locate particular adaptive optima, but rather to explore the topography of the adaptive landscape of colour vision. This topography depends on the general shapes (or statistical characteristics) of reflectance spectra and photoreceptor spectral sensitivities [59,60], and is perhaps difficult to predict *a priori*.

To show how changes to three key characters—photopigment tuning, oil droplet density and relative abundance of the four types of single cone—might affect bird colour discrimination, we evaluate colour discriminability (in just noticeable differences, jnds) for three classes of spectra that capture characteristics of biological signalling colours (figure 1 and §2): namely, band-pass spectra (Gaussians)

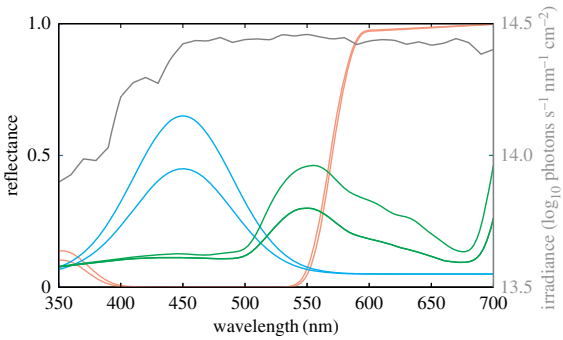

Figure 1. Spectra used for colour vision modelling. Colour contrast was calculated between two band-pass (blue), two long-pass (red) and two leaf (green) reflectance spectra (see §2a for details). We assume standard daylight illumination (D65, grey). For the zebra finch eye, the colour contrasts are 2.4, 2.0 and 3.6 jnds between these pairs of band-pass, long-pass and leaf spectra.

that resemble structural colours; long pass spectra resulting from carotenoid (astaxanthin) pigmentation, and spectra derived from leaves with varying levels of chlorophyll [69].

The first set of simulations use a receptor-noise limited (RNL) model [66] and vary photopigment tuning, oil droplet density, and relative abundance of the four single cone types separately, each over physiologically reasonable ranges (figure 2). Parameters are based on the zebra finch (*Taenopygia guttata*) eye, and we consider performance limited both by intrinsic (Weber) noise and by photon-shot noise (Rose–de Vries law).

The second set of simulations extend the first by using a hill-climbing optimization procedure [70] to compare optima for single physiological parameters to the best *combination* for the discrimination of each of the three types of spectra (figure 3). The procedure is 'blind' to the overall adaptive landscape [70], but indicates each parameter's potential to shift in a given direction. The algorithm optimizes colour discriminability over changes in physiological parameters. We start the hill-climbing runs with the parameters measured in zebra finches, and each step in the model either changes the visual pigment spectral sensitivity, oil droplet pigment density, or cone type abundance. First we run hill-climbing procedures separately for single parameters, where each step comprises a single change randomly assigned to one cone type. Then we test hill-climbing with changes randomly assigned to any of the three parameters (with equal probability) in one of the four single cone types. For each step, the new parameter configuration is retained if it increases colour discriminability. The procedure is stopped after a fixed number of steps that seems sufficient to allow the functions to converge on (local or global) maxima (figure 3).

2. Methods

(a) Stimuli

We model colour discrimination of three types of spectra, band-pass, long-pass and leaf spectra. Band-pass reflectance spectra were produced using a Gaussian function of different amplitude. Long-pass reflectance spectra were modelled from the normalized absorbance spectrum D of astaxanthin (from [45]) following [71]:

$$r(\lambda) = 10^{-aD(\lambda)}, \tag{2.1}$$

where r is reflectance and a is decadic optical density set to 10 and 11.5 for the two variants (figure 1). The reflectance spectra from

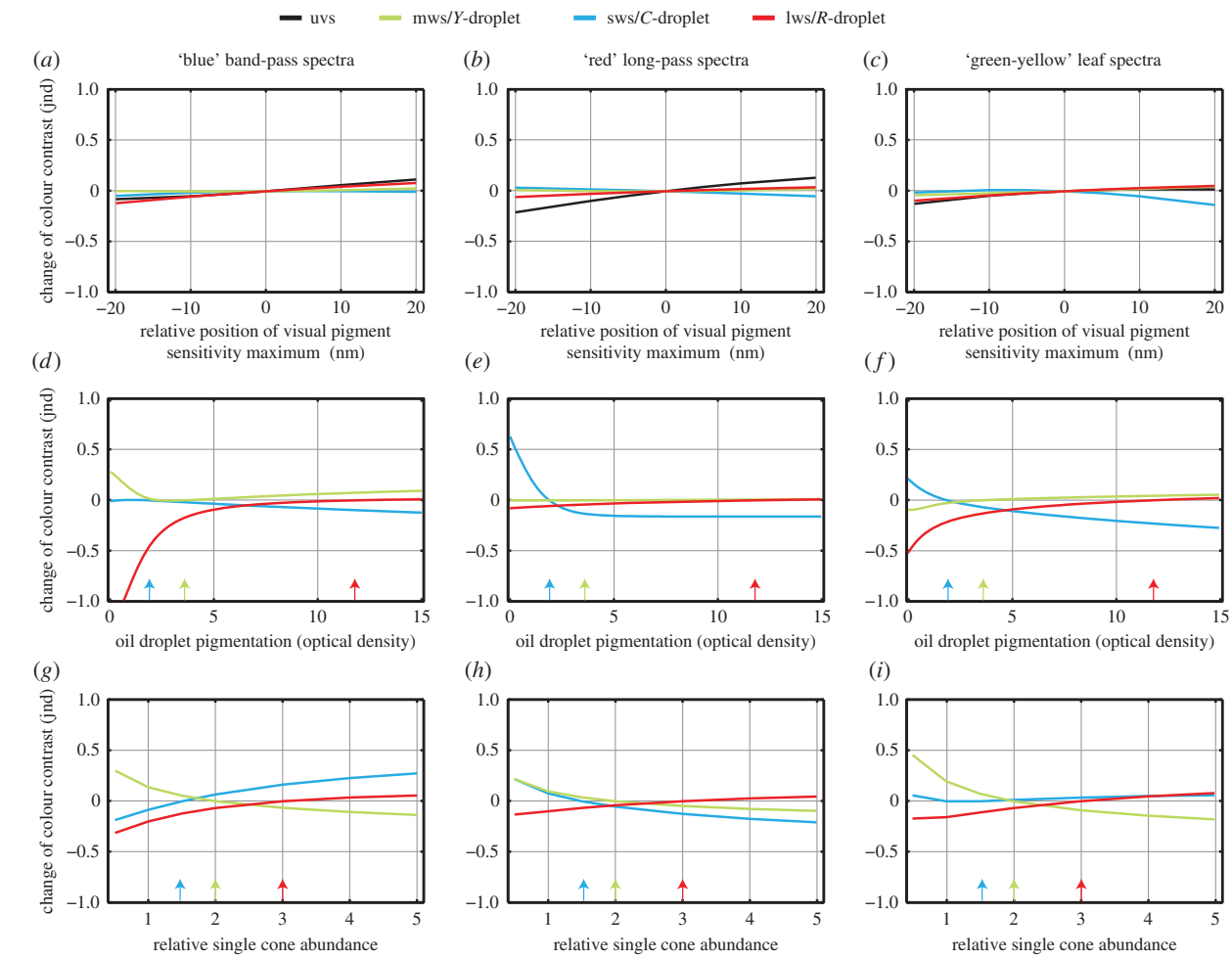

Figure 2. The change in colour contrast resulting from the manipulation of single parameters. The original parameters measured in zebra finch are set to zero for the relative position of visual pigment sensitivity (*a–c*), while for oil droplet pigmentation and receptor abundance, original states are denoted by arrows (*d–i*). Receptor abundance is given relative to the abundance of UVS cones. For example, the original ratio of zebra finch cones is 1:1.5:2:3 for UVS:SWS2:MWS:LWS as shown by the arrows in (*g–i*; UVS-ratio is fixed at 1 and not shown). Colour difference is measured in jnds, where 1 jnd corresponds to the visual threshold set by receptor noise at a certain choice criterion [66].

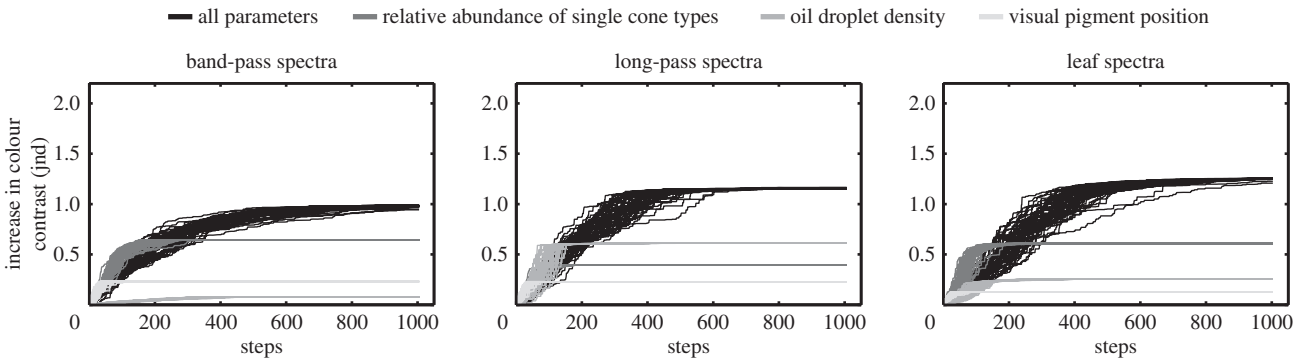

Figure 3. Optimal parameter positions for the discrimination of three types of colour spectra, estimated from a hill-climbing approach. For each spectral type, we repeated the hill-climbing procedure 50 times.

green and green-yellow leaves come from [69]. We assume standard daylight illumination [72] set to a maximum radiance of 4.57×10^{13} photons s^{-1} sr^{-1} cm^{-2} nm^{-1} at 550 nm.

(b) Colour vision model

We use the receptor noise-limited model of colour discrimination to estimate colour contrast in the eye of the zebra finch. We assume that single cones (UVS, SWS2, MWS, LWS) contribute to colour vision and for each cone type i we determine the quantum catch N as:

$$N_i(\lambda) = \Delta t\left(\frac{\pi}{4}\right)^2 R^2 d^2 K O(\lambda) P(\lambda)(1 - e^{-kA(\lambda)l})L(\lambda), \quad (2.2)$$

[55,73]. We set integration time Δt to 0.014 s (assuming a flicker fusion frequency of roughly 70 Hz) [74]. We set the acceptance angle R to 0.003 (which we assume is the acceptance angle in radians of one integrative unit for a chromatic spatial resolution of about

3 cycles deg^{-1}) multiplied by the abundance of the cone type relative to all cone types ($n_i/(n_{UVS}+n_{SWS2}+n_{MWS}+n_{LWS})$). Pupil diameter d is set to 2 mm and the quantum transduction efficiency K to 0.5 [73]. Ocular media transmittance O for zebra finch is taken from [75] and normalized to a maximum transmittance of 0.8. A is the normalized absorbance of the visual pigment given by the Govardovskii template [76] and λ_{max} data are from [77]. The absorption coefficient, k, is set to 0.035 μm^{-1} [78], and l is the length of the cone outer segment set to 10 µm. Stimulus radiance L is given by stimulus reflectance multiplied by the illuminant (see above).

We model the spectral transmittance of oil droplets, P, using equation (2.1), but set D to be the normalized absorbance spectrum of the C-droplet, Y-droplet, and R-droplet of the zebra finch SWS2, MWS, and LWS cones, obtained from droplets expanded in mineral oil (Matthew Toomey 2015, unpublished data). The optical densities, a, in zebra finch are estimated to be 1.9, 3.5, and 11.7 for the C-, Y-, and R-droplet, respectively (Matthew Toomey 2015, unpublished data).

The receptor specific contrast, between two stimuli with radiances $L1$ and $L2$ is

$$\Delta f_i = \ln\left(\frac{N_{i,L1}}{N_{i,L2}}\right), \tag{2.3}$$

and the chromatic contrast is:

$$\Delta S^2 = \frac{((e_1e_2)^2(\Delta f_4-\Delta f_3)^2+(e_1e_3)^2(\Delta f_4-\Delta f_2)^2+(e_1e_4)^2(\Delta f_3-\Delta f_2)^2+(e_2e_3)^2(\Delta f_4-\Delta f_1)^2+(e_2e_4)^2(\Delta f_3-\Delta f_1)^2+(e_3e_4)^2(\Delta f_2-\Delta f_1)^2)}{((e_1e_2e_3)^2+(e_1e_2e_4)^2+(e_1e_3e_4)^2+(e_2e_3e_4)^2)}, \tag{2.4}$$

where the subscripts denote cone type (1, 2, 3, 4 = UVS, SWS2, MWS, LWS).

We assume that noise, e, originates partly from intrinsic noise, so called Weber noise ω, and photon shot noise that relates to the square root of the quantum catch according to Poisson statistics:

$$e_i = \frac{\sqrt{\omega_i^2N_i^2+N_i}}{N_i}. \tag{2.5}$$

The intrinsic noise is given by:

$$\omega_i = \frac{v_i}{\sqrt{\eta_i}}, \tag{2.6}$$

where v is the noise of a single cone and η is the abundance of the cone type within the integrative unit.

When we model colour contrast for different cone abundance ratios, we fix the summed noise of the complete integrative unit to 0.4 (corresponding to a noise level of 0.1 in each cone type for a flat cone distribution).

(c) Step sizes in the hill-climbing procedure

Each step potentially introduces a change in the position of the visual pigment by ±5 nm (maximal range: UVS, 350–380 nm; SWS2, 407–447 nm; MWS, 485–525 nm; LWS, 546–586 nm), oil droplet pigmentation by ±0.1 in optical density (maximal range: C-type, 0–5 oil droplet pigment density; Y-type, 0–10 density; R-type, 0–15 density), or cone type abundance by ±0.1 (relative ratio to a fixed number of UVS cones, maximal range: 0.5–6).

3. Results and discussion

The results are surprising and useful. When manipulating single parameters of individual cones (figure 2), the shifts in the spectral sensitivity peak of the visual pigments have virtually no positive effects on colour discrimination (figure 2*a–c*). It should, however, be noted that oil droplets largely determine the short-wavelength cut-off of the cone spectral sensitivity. The benefits of varying oil droplet density (figure 2*d–f*) or receptor abundance (figure 2*g–i*) are larger, but never exceed 0.6 jnds. Even if these conclusions do not hold under all circumstances, any inference that a phenotypic change in an eye is attributable to selection to discriminate particular types of spectra (figure 1) needs to be treated with caution.

Table 1. Final values for optima in hill-climbing when all parameters are allowed to vary (average for 50 runs). Parameters with the potential to substantially enhance colour discrimination (as identified from figure 2) are shown in bold.

	UVS	SWS2	MWS	LWS
band-pass spectra				
visual pigment	379	446	523	586
oil droplet density	n.a.	0.1	**6.7**	14.7
cone abundance	1	**5**	**0.6**	5
long-pass spectra				
visual pigment	379	407	515	586
oil droplet density	n.a.	**0.1**	5.5	14.9
cone abundance	1	**1.6**	**0.6**	5
leaf spectra				
visual pigment	374	407	525	586
oil droplet density	n.a.	**0.1**	6.8	14.8
cone abundance	1	5	**0.6**	5

The hill-climbing procedures point to similar conclusions. For band-pass and leaf spectra, the largest increase in colour contrast is caused by change of cone type abundances (cf. [11]), while a depigmentation of the C-type (SWS2 cone) oil droplet dominates the increase in colour discrimination of long-pass carotenoid spectra (figure 3). There is some agreement on how the parameters should be configured for maximal discrimination of all spectra. For example, LWS cones should be placed at 586 nm, which coincides with the long-wavelength limit set for the modelling, R-droplets should contain high amounts of carotenoids, and LWS cones should be relatively abundant (table 1).[4]

Among the parameters with substantial effects, we find that relatively few MWS cones and unpigmented C-droplets increase colour contrast for all three types of spectra. In fact, MWS cones are usually more abundant than SWS1 and SWS2 cones, and C-droplets are pigmented, indicating that additional selective forces influence visual physiology, but it would be interesting to know of departures from these 'norms'.

Interestingly, for the discrimination of band-pass spectra, the hill-climbing procedure finds an optimal optical density of 6.7 for the Y-droplet (table 1), while the manipulation of single parameters in our first approach indicates a clear advantage of

a completely unpigmented Y-droplet (figure 2*d*). This disagreement results from using the measured optical density of 3.5 as a starting point in the hill-climbing procedures. Notably, any decrease in optical density impairs colour discrimination, except at very low optical density where the function changes direction (figure 2*d*). With the small step size for optical density employed in the hill-climbing procedure, this maximum is never reached. Instead, the system is locked in a suboptimal local maximum. Local maxima might then have far reaching consequences, not only for the interpretation of modelling results, but also for the evolution of visual systems; and for example explain the consistent differences between major taxa such as primates, hymenopterans and birds.

4. Conclusion

Evidence for coevolution of colour vision and colour signals is limited, but for both birds and butterflies there are species and sex differences in characters relevant to colour discrimination that seem at first to be consistent with coevolution [11,25,35,79,80]. In fact, modelling the effects of phenotypic differences suggests that at least for the spectra we use here (figure 1), most physiologically realistic changes have little consequence—that is the adaptive landscape is smooth and flat, with broad optima (figure 2). Nonetheless it may be worth looking for coordinated shifts in different characters, which can have much larger effects than independent shifts in single characters (figure 3). We suggest that this approach can be used to model other general scenarios, but also specific cases, in which differences between visual systems of sexes or species are, as suspected, to have co-evolved with differences in colour discrimination tasks.

Authors' contributions. O.L., A.K. and D.O. had the initial ideas for this review; O.L. performed the model calculations; O.L. and D.O. wrote the text with input of A.K. and M.J.H. All authors have given approval for the final version to be published. None of the authors have any relationship to the guest editors that impedes the independence of either side.

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Endnotes

[1]Colour discrimination is also affected by the chromophore, the presence of coloured filters within the eye and the relative proportions of different receptor types across the retina [4–6].

[2]The nomenclature used to designate the spectral photoreceptors and photopigments follows the terminology in source publications.

[3]Known exceptions are penguins that lack RH2 (green) opsin [38]; the bobolink that likely lacks the SWS2 (blue) gene [39], two passerines lacking a functional SWS1 (UV) gene [40], and possibly owls that may lack SWS1 opsin [41].

[4]The prediction for enhanced long-wavelength sensitivity is typical of the results of modelling of this kind, but it is likely that the benefit is offset by reduced absolute sensitivity and increases in receptor (dark) noise caused by red-shifting λ_{max} [79].

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