

Colour spaces in ecology and evolutionary biology

Julien P. Renoult^{1,*}, Almut Kelber² and H. Martin Schaefer³

¹*Institute of Arts Creations Theories & Aesthetics, CNRS-University Paris 1 Panthéon-Sorbonne, 47 r. des bergers, 75015, Paris, France*

²*Lund Vision Group, Department of Biology, Lund University, Helgonavägen 3, 22362, Lund, Sweden*

³*Department of Evolutionary Biology and Animal Ecology, Faculty of Biology, University of Freiburg, Hauptstrasse 1, 79104, Freiburg, Germany*

ABSTRACT

The recognition that animals sense the world in a different way than we do has unlocked important lines of research in ecology and evolutionary biology. In practice, the subjective study of natural stimuli has been permitted by perceptual spaces, which are graphical models of how stimuli are perceived by a given animal. Because colour vision is arguably the best-known sensory modality in most animals, a diversity of colour spaces are now available to visual ecologists, ranging from generalist and basic models allowing rough but robust predictions on colour perception, to species-specific, more complex models giving accurate but context-dependent predictions. Selecting among these models is most often influenced by historical contingencies that have associated models to specific questions and organisms; however, these associations are not always optimal. The aim of this review is to provide visual ecologists with a critical perspective on how models of colour space are built, how well they perform and where their main limitations are with regard to their most frequent uses in ecology and evolutionary biology. We propose a classification of models based on their complexity, defined as whether and how they model the mechanisms of chromatic adaptation and receptor opponency, the nonlinear association between the stimulus and its perception, and whether or not models have been fitted to experimental data. Then, we review the effect of modelling these mechanisms on predictions of colour detection and discrimination, colour conspicuousness, colour diversity and diversification, and for comparing the perception of colour traits between distinct perceivers. While a few rules emerge (e.g. opponent log–linear models should be preferred when analysing very distinct colours), in general model parameters still have poorly known effects. Colour spaces have nonetheless permitted significant advances in ecology and evolutionary biology, and more progress is expected if ecologists compare results between models and perform behavioural experiments more routinely. Such an approach would further contribute to a better understanding of colour vision and its links to the behavioural ecology of animals. While visual ecology is essentially a transfer of knowledge from visual sciences to evolutionary ecology, we hope that the discipline will benefit both fields more evenly in the future.

Key words: sensory ecology, visual communication, psychophysics, vision, signal, discrimination, conspicuousness, colour diversity, model selection.

CONTENTS

I. Introduction	2
II. Classification of colour spaces	3
(1) Spectral spaces	3
(2) Psychological colour spaces	4
(3) Psychophysical colour spaces	4
III. Colour detection and discrimination	6
(1) Which model to use?	6
(2) Variation in difference threshold	7

* Address for correspondence (Tel: 0033 615265240; E-mail: jurenoult@gmail.com).

IV. Colour conspicuousness	8
(1) Which model to use?	8
(a) Receptor opponency	8
(b) Nonlinearities	9
(2) The value of model predictions	9
V. Colour diversity	10
(1) The sensations of colour diversity	10
(a) Colourfulness	10
(b) Colour richness and distinctiveness	10
(2) Quantifying colour diversity	11
(a) Which space to use?	11
(b) Colourfulness	11
(c) Colour richness and distinctiveness	12
VI. Colour trait evolution and diversification	13
(1) Evolution and diversification in colour spaces	13
(2) Colour versus spectral spaces	13
VII. Signalling to multiple perceivers	13
VIII. Conclusions	14
IX. Acknowledgements	15
X. References	15
XI. Appendix	18
(1) Equations for modelling psychophysical colour spaces	18
(a) The four main steps of psychophysical models	18
(b) Basic models without chromatic adaptation, nonlinear transformation and opponent receptor processing	19
(c) Basic models with chromatic adaptation and nonlinear transformation, without opponent receptor processing	20
(d) Basic opponent model	20
(e) Scaled opponent models	21
(2) Chromatic adaptation and colour diversity	22
(3) Spectral spaces: proxy to colour spaces?	23

I. INTRODUCTION

In many terrestrial and aquatic animals, colour vision drives vital behaviours such as foraging, finding and choosing mates, socialising with congeners and avoiding predators. These behaviours have selected a diversified array of coloured traits in plants and animals that have evolved to be attractive, to go unnoticed or to facilitate recognition and memorisation (Guilford & Dawkins, 1991; Bradbury & Verhencamp, 1998; Stevens, 2013). Colour traits also contribute to sort species and colour morphs and thus to structure populations and communities (Menzel & Schmida, 1993; Schemske & Bradshaw, 1999; Binkenstein, Renoult & Schaefer, 2013). Due to their ubiquity, colour signals and colour vision have become central to many research programs in ecology and evolutionary biology, both referred to as visual ecology hereafter, which aim at elucidating the proximate mechanisms underlying the evolution of phenotypes and the structure of communities.

Colour traits can be studied in relation to colour vision using colour spaces, which are graphical representations intended to describe how visual stimuli appear to animals (Kuehni, 2003). In a colour space, the order of colour stimuli and the distance between them is expected to describe the internal representation of these stimuli resulting from colour

vision. Over the last decade, visual ecologists have added colour spaces to their toolkit to study colour traits through the eyes of animals (Bennett & Théry, 2007; Stevens, Stoddard & Higham, 2009). This new way of investigating colour traits has contributed to significant advances in the field of animal communication, pointing out putatively meaningful variations among coloured stimuli while dismissing irrelevant ones (e.g. Eaton, 2007).

A diversity of colour spaces is now available to visual ecologists. Generalist models are assumed to apply to a large array of animal species, in contrast to species-specific models. Some models are based on general assumptions on how animals process colour stimuli while others are more elaborate, accounting for fine physiological mechanisms to improve the fit between predictions and psychological, behavioural or physiological data (Kelber, Vorobyev & Osorio, 2003). Although selecting the appropriate model of colour space is an important step in visual ecology, with profound influence on results and their interpretation, it is not easy for visual ecologists not trained in psychophysics –the field of experimental psychology that attempts to link stimuli to perception. One goal of this review is to provide visual ecologists with guidelines to mindfully select and use colour spaces.

The choice of a model of colour space depends on four factors: the studied species, the knowledge of the

specific physiological mechanisms involved in colour vision, the biological question and the philosophy of modelling. The first factor determines whether colour vision can be modelled or not. A prerequisite of all models is to know the sensitivity of photoreceptors used to process colour stimuli. In some taxonomic groups, photoreceptor sensitivities have undergone radiations (crustaceans, fishes, butterflies; Osorio & Vorobyev, 2008), which prevents extrapolations across species (Renoult, Courtiol & Kjellberg, 2010). Knowing the specific physiology of colour vision determines whether a species-specific model can be used or not. Species-specific models exist for a very limited number of animal models such as humans and honeybees and in most instances generalist models are necessary.

Contrary to the first two factors, the importance of the biological question for selecting an appropriate colour space has been mostly overlooked in the literature. The different colour spaces routinely used by ecologists are not equally good at predicting the perception of colours. In the simplest spaces, distances between colour loci may correlate poorly with effectively perceived differences between colours. Such models should be avoided if quantitative assessments of colour differences are needed, as in the studies on sexual selection that evaluate the correlation between colour trait and male quality. However, these models can correctly represent the qualitative internal representation of colour stimuli. For example, they can predict that humans perceive pink as being more similar to red than to green. Such models could be used to characterise the evolutionary trajectories of colour traits.

Why is it not a good strategy to always choose the most elaborate model? Here the fourth factor, philosophy of modelling, is relevant. Psychophysicists and visual ecologists usually have different goals. Ultimately, psychophysicists aim at predicting the perception of colours in any visual condition as accurately as possible, ideally accounting for inter-individual variation in perception (Chittka & Brockmann, 2005). Tracing the history of colour spaces in human psychophysics shows an escalation towards ever-higher complexity of models (Fairchild, 2005). Such complexity is not always desirable in visual ecology where most researchers work with non-model animals. Here, modelling colour vision necessarily comes with uncertainties, which increase with the degree of refinement of the physiological mechanisms modelled. As pointed out by Stoddard & Prum (2008), ecologists expect colour spaces to illuminate the evolutionary ecology of a communication system adequately, not to be as accurate – and hence context specific – as possible. Thus, selecting a psychophysical model in visual ecology should follow the principle of parsimony, which states that the simpler of two otherwise equally adequate solutions should be preferred, e.g. the one resting on fewer assumptions. In visual ecology, model selection is currently left to the subjective appreciation of parsimony, which requires basic knowledge on the perceptual effects of the different physiological mechanisms included in alternative models.

This review is organised as follows. First, we briefly present the different types of colour spaces, emphasising those of interest for visual ecologists (Fig. 1). We assume that visual stimuli are characterised by their reflectance spectra obtained with a spectrophotometer (Andersson & Prager, 2006) or from standardised pictures (Stevens *et al.*, 2007). We limit our discussion to chromaticity diagrams, which are subspaces of colour spaces with constant luminance. The colour spaces discussed herein are therefore not suited for analysing traits that vary mostly from light to dark, and could not be used to study, e.g. evolution of greyness in the mantle of gulls or of albinism in cave fishes. Chromaticity diagrams are biologically meaningful on their own because most animals studied so far have separate neural pathways to process the achromatic (luminance) and chromatic (colour) components of visual stimuli (Kelber & Osorio, 2010). Although they are not colour spaces, we also include spectral spaces in this review because they can be insightful when studying the evolution of colour traits. The following sections review the suitability of colour spaces for addressing the most common issues in visual ecology: colour detection and discrimination, colour conspicuousness, colour trait diversity, evolution and diversification, and signalling to multiple perceivers. In each section, we discuss the benefits and limitations of the different models and metrics. We do not intend to provide recipes that should invariably be followed. Rather, the goal of this review is to help visual ecologists to select a method that best fits the question asked by understanding the significance of model parameters. It should nevertheless be kept in mind that very often the mechanisms of colour vision are poorly known and the effects of model parameters difficult to predict. As a rule-of-thumb, we recommend comparing results using different models whenever possible. Not only would such comparisons strengthen the robustness of conclusions, but they may also allow understanding of the mechanisms underlying colour vision in the studied organism.

II. CLASSIFICATION OF COLOUR SPACES

Graphical representations of colour stimuli can be ordered according to the mechanisms of colour vision that are accounted for. At one end, spectral spaces do not consider colour vision at all: they are objective descriptions of the physical variation among stimuli. At the other end, psychological colour spaces are built directly from psychological or behavioural data and map variation among colour stimuli as animals effectively experience them. In-between, psychophysical colour spaces are graphical displays of mathematical models describing physiological mechanisms and aim at reconstructing a psychological colour space based upon the spectral space.

(1) Spectral spaces

The most basic approach to study colour signals is to describe stimuli as they are emitted by the signaller. A colour stimulus

is characterised by a reflectance spectrum, which corresponds to a vector of several hundreds of values each indicating the amount of light reflected by a surface relative to a white standard for a given wavelength. A spectrum usually has a resolution of 1 nm. When recorded over the range 300–700 nm, i.e. the part of the electromagnetic spectrum visible to animals, the reflectance spectrum then contains 401 values. This results in a Euclidean space with 401 dimensions, and a colour stimulus is represented by one point in this space whose coordinates are given by the 401 values of its reflectance spectrum.

Reflectance spectra of natural surfaces are invariably characterised by a smooth shape indicative of strong correlation among the 401 values of reflected light (Cohen, 1964). The dimensionality of the spectral space can thus be reduced using classical mathematical methods of dimensionality reduction (Ramanath *et al.*, 2004). Principal component analysis (PCA) is the most widely used method in colour science (Tzeng & Berns, 2005). When applied to a data set of reflectance spectra, the first principal component typically explains approximately 70–80% of the variation among spectra and the first three components more than 95% (Maloney, 1986; Grill & Rush, 2000). Although most studies analyse these first three principal components only, depending on the biological system, relevant information can be extracted from other components (for a method to select the number of informative principal components, see Renoult, Courtiol & Schaefer, 2013a).

Independent component analysis (ICA) is another important method in colour technology (Hyvärinen & Oja, 2000). ICA performs equally well as PCA for reconstructing complete spectra from a few components (Ramanath *et al.*, 2004). Furthermore, ICA does not require a Gaussian structure of data, which is usually not met by reflectance data sets. ICA thus addresses one of the main limitations of PCA in visual ecology, i.e. that statistical tests of stimuli differences are invalid when using PC scores (Endler & Mielke, 2005). Despite these benefits, to our knowledge ICA has never been used with reflectance spectra in visual ecology (but for an application to study patterning in cuttlefishes, see Anderson *et al.*, 2003).

(2) Psychological colour spaces

In contrast to spectral spaces, colour spaces describe spectral variation while accounting for the capacities of the beholder to see colours. These capacities are determined by hard-wired characteristics of the visual system but also by plastic neural mechanisms (Wyszecki & Stiles, 1982). Colour vision can thus vary with time and past experiences with visual and other stimuli. Because a colour space is individual and time specific, it has been occasionally described as the ‘final frontier’ in visual neuroscience (Chittka & Brockmann, 2005).

This final frontier can be approached by psychological and behavioural experiments in which perceptual differences among stimuli are evaluated under defined viewing conditions. Perceptual differences are most often evaluated for small colour differences because it is much easier

to test whether or not an individual can discriminate between two colour stimuli (using food or mate reward for animals) than to quantify the magnitude of perceptual differences (Kelber *et al.*, 2003). Gustav Theodor Fechner (1801–1887), the father of psychophysics, postulated that colour discrimination thresholds, i.e. the smallest differences that could be perceived between two colours, could be considered perceptual units, and that threshold units add up to describe the magnitude of sensory perception. Based on this ‘Fechner assumption of additivity’, it is possible to use many pairs of just discriminable stimuli to reconstruct a complete psychological colour space (Kuehni, 2003).

In humans, the Munsell colour order system (Munsell Color Company, 1976) is one of the most popular psychological colour spaces. The Munsell system is a three-dimensional space in which colour stimuli are organised according to the three human perceptual attributes of colours: hue (the colour as it is colloquially termed; e.g. red, blue, green), chroma (the saturation, or colour purity, defined by the amount of grey in a colour patch) and brightness (how dark or light a colour patch is). Historically, the Munsell colour space was built following Fechner’s assumption of additivity: perceptually close stimuli were ordered and scaled by observers for each of the three perceptual attributes. Over 3 million visual evaluations allowed constructing a complete psychological space that is approximately uniform, meaning that equal distances between two points anywhere in the space are perceptually equally different (Wyszecki & Stiles, 1982).

Because of the huge number of psychological tests required to build a complete psychological space of colour vision like the Munsell system, there is currently no such space available for non-human animals. Yet behavioural experiments conducted in several model species to estimate discrimination thresholds (e.g. Backhaus, 1991; Brandt & Vorobyev, 1997), or to identify limits between colour categories (e.g. Osorio *et al.*, 2009) are attempts to understand specific aspects of the psychological colour space of animals.

(3) Psychophysical colour spaces

Psychophysical colour spaces are produced by mathematical models that predict the psychological experience of seeing a colour stimulus given its physical characteristics and the viewing conditions. The general principle for building a psychophysical model is to describe mathematically the physiological mechanisms underlying colour vision. The construction follows several steps, each corresponding to one physiological mechanism. Colour spaces used in visual ecology differ according to the number of steps included in the model (Fig. 1; formulae in Appendix 1).

The first step in building a psychophysical colour space is to calculate the number of photons emitted by the stimulus that are caught per unit time by a given type of photoreceptor (Equation A1.1). This allows building a photoreceptor excitation space, the dimensionality of which corresponds to the number of photoreceptor types used for colour vision and in which each coordinate axis indicates photon catches by one receptor type. This photoreceptor

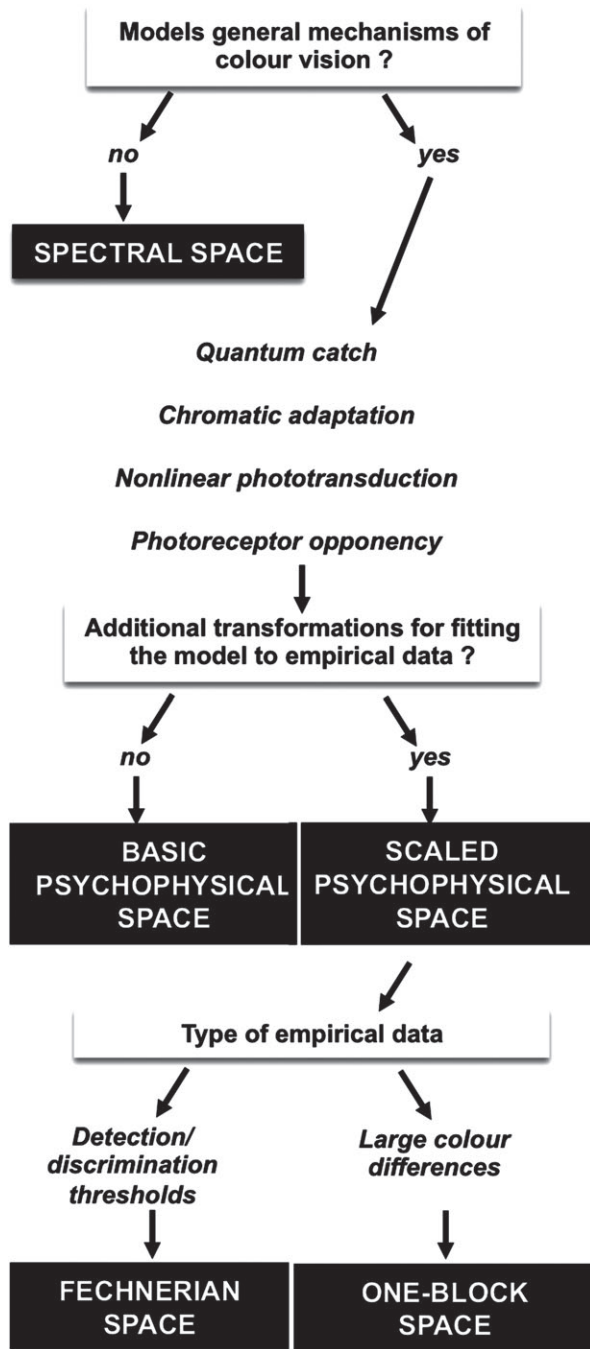


Fig. 1. Classification of colour spaces. Psychological spaces are not represented here because they are built very differently: they are purely representational models built from psychological experiments, not mathematical models as are spectral and psychophysical spaces.

excitation space encodes information both on chromatic and achromatic components of visual stimuli. Because animals usually process these two components separately (Kelber & Osorio, 2010), it is possible to isolate a subspace in which the sum of receptor photon catches is constant, meaning that stimuli are set to equal luminance (Wyszecki & Stiles, 1982). The resulting chromaticity diagram is thus one dimension

lower than that of the excitation space. The chromaticity diagram is a segment for dichromatic vision, an equilateral triangle for trichromatic vision (MacLeod & Boynton, 1979; for an application to honeybees, see Neumeyer, 1981), and a tetrahedron for tetrachromatic vision (Burckhardt, 1989; Goldsmith, 1990).

The second step in modelling a colour space incorporates a chromatic adaptation transformation. This accounts for the ability of visual systems to keep the appearance of colours approximately unchanged even if the illuminant changes (Walsh & Kulikowski, 1998). Chromatic adaptation is considered the most important visual phenomenon when modelling colour appearance in humans (Fairchild, 2005). Even though mechanisms of chromatic adaptation may occur in higher stages of the visual system (in bees, see Lotto & Wicklein, 2005; in fishes, see Ingle, 1985) and may include cognitive processes in humans (Foster, 2011), the gain control of individual photoreceptors is an important mechanism of chromatic adaptation that likely occurs in most animals (Neumeyer, 1998; Kelber & Osorio, 2010). The von Kries transformation (von Kries, 1904) is the main algorithm used in models relevant to visual ecologists (for a test of other algorithms in bees, see Faruq, McOwan & Chittka, 2013). The transformation normalises photon catches for the signal by photon catches for the whole visual scene (Equation A1.4). From a photoreceptor excitation space built from normalised photon catches, which is called a photoreceptor contrast space, a chromaticity diagram can be extracted as in the first step.

In the third step, normalised photon catches are non-linearly transformed. This is because the magnitude of the perception of a stimulus is nonlinearly related to the physical energy measurements of that stimulus (Fechner, 1860). Again, the mechanisms involved likely occur at various levels in the sensory systems. The most frequently used nonlinear transformation models the process of phototransduction by which photon catches are converted into neural signals at the photoreceptor level (Lipetz, 1971; Backhaus & Menzel, 1987). According to the Weber–Fechner law, the signal of the receptor channel is proportional to the logarithm of the photon catch (Equation A1.6; Fechner, 1860). Alternatives to the logarithmic transformation include power-law relationships (Stevens, 1961) and hyperbolic transformations (Equation A1.7; Backhaus, 1991).

The fourth step compares neural signals from different photoreceptors, a mechanism known as receptor opponency. Receptor opponency is an efficient way to reduce redundancy in information. According to information theory, two chromatic opponent mechanisms would be optimal to evaluate information arising from three photoreceptors (Buchsbaum & Gottschalk, 1983). This prediction has been confirmed in various animals with known trichromacy (for examples in primates, fishes and bees, see, respectively, De Valois *et al.*, 1958; Svaetichin, 1956; Backhaus, 1991). Several psychophysical models used in visual ecology account for receptor opponency. Models for trichromatic primates include specified opponent channels (one red–green and

one yellow–blue channel) that have been established by physiological and psychophysical data (Wyszecki & Stiles, 1982). Other models include unspecified opponent mechanisms, meaning that combinations of receptor responses do not necessarily represent the true neuronal connections (see Section IV.1*a*) Such models include the hexagon model of bee colour vision (Chittka, 1992; Equation A1.19), the colour-opponent coding (COC) model of bee colour vision (Backhaus, Menzel & Kreissl, 1987; Equation A1.21) and the receptor noise limited (RNL) model (Vorobyev & Osorio, 1998; Equations A1.23–A1.29).

This four-step procedure allows some variations (Table 1). One intermediate step can be missing. For example, the RNL model does (Vorobyev *et al.*, 1998) or does not (Vorobyev & Osorio, 1998) include a nonlinear (in this case logarithmic) transformation of photon catches. Steps can also be permuted. The CIE $L^*a^*b^*$ colour space 1976 for human colour vision uses the so-called ‘wrong von Kries transformation’ to model chromatic adaptation because normalisation is applied to nonlinearly transformed photon catches instead of raw photon catches as in the normal procedure (CIE Publication, 1986; Equation A1.34). Finally, steps can be added in order to model additional perceptual effects. The CIECAM02 colour appearance model, developed for humans, can account for different ‘background’ levels (proximal field, background and surround) and for spatial and temporal information (Fairchild, 2005).

The above-described steps correspond to general physiological mechanisms involved in colour vision. We use the term ‘basic psychophysical spaces’ for colour spaces made from these steps only (Fig. 1). Examples of such spaces are the Maxwell triangle, the bee hexagon or the Goldsmith tetrahedron. Other basic psychophysical spaces have been subsequently scaled to match specific physiological (e.g. RNL model), behavioural (e.g. COC model) or psychological data (e.g. CIE $L^*a^*b^*$ model). The RNL model, for example, further accounts for the noise in photoreceptors, which allows estimations of detection thresholds that match empirical data. We will call such colour spaces ‘scaled psychophysical spaces’ in the following. Scaled spaces can be further divided according to the primary goal of the model, which can be the estimation of large colour differences (‘one-block space’; e.g. CIE $L^*a^*b^*$), or of detection thresholds. The second type of models allows for reconstruction of large colour differences and thus of a complete space by relying on Fechner’s assumption of additivity; they are therefore called ‘Fechnerian spaces’ (e.g. RNL model; Fig. 1). As we will develop in the following sections, the choice among basic psychophysical, Fechnerian and one-block spaces depends in part on the type of ecological question that is asked.

III. COLOUR DETECTION AND DISCRIMINATION

The need to model colour detection and discrimination in visual ecology has been recognised in the fields of

camouflage and mimicry (Benitez-Vieyra *et al.*, 2007; Merilaita & Stevens, 2011; Stoddard, 2012). Although behavioural tests are most frequently used to test the efficiency of camouflage or mimicry, psychophysical models of colour space are useful to control or to test for the specific effects of patterning, chromatic and achromatic components of colour traits (e.g. Stobbe & Schaefer, 2008). Beyond camouflage and mimicry, animals need to detect relevant stimuli and to discriminate them from less-relevant ones in a variety of contexts. Discriminating among subtle variations in shades is important for frugivores to pick the most profitable fruits out of a crop (Schaefer, McGraw & Catoni, 2008), for pollinators to identify rewarding flowers (Shrestha *et al.*, 2013), for males to evaluate the fighting abilities of rivals (Hamilton, Whiting & Pryke, 2013) or for females to assess male quality (Cohen, 1984).

(1) Which model to use?

From a modelling perspective, detection and discrimination both are perceptual tasks determined by difference thresholds. As a rule of thumb, scaled spaces should be preferred over basic psychophysical spaces to study detection and discrimination. Indeed, psychophysical spaces perform best at or close to difference thresholds because these thresholds are the main empirical data used to build (Fechnerian spaces) or adjust the scale (e.g. in the one-block CIE $L^*a^*b^*$) of such spaces. By contrast, basic psychophysical spaces like chromaticity diagrams provide no information on discrimination abilities.

Yet a number of studies have proposed to use basic psychophysical spaces by importing data on colour discrimination into such spaces. Pike (2012) developed a method based on trilateration that rescales chromaticity diagrams in order to have distances matching those calculated with the RNL model. It is unclear to us, however, what benefits the method confers compared to using a graphical representation of the RNL model where coordinates have been derived analytically (see Equations A1.23–A1.29). In the bee hexagon, a body of behavioural experiments have allowed identifying how many hexagon units are equivalent to the detection threshold. In bumblebees (*Bombus terrestris*), for example, it is generally assumed that colour loci separated by less than 0.04 hexagon units cannot be perceived as distinct while those separated by more than 0.11 hexagon units are, whatever the type of conditioning procedure (in between, colours are distinguishable only after differential conditioning; Dyer, 2006). These values are, however, average discrimination thresholds that do not account for the fact that thresholds vary across the space and, for a given locus, across directions (Kelber *et al.*, 2003). By contrast, these variations are accounted for, at least in part, in scaled psychophysical spaces, in particular in Fechnerian spaces.

Another aspect is the importance of opponent mechanisms. Before the publication of the RNL model, other models had made the assumption that detection thresholds were determined mainly by receptor noise (e.g. Stiles, 1946).

Table 1. Characteristics of the models of colour space frequently used in visual ecology

	Classification	Illuminant	Chromatic adaptation	Phototransduction	Receptor opponency	Application	References
Maxwell triangle/Goldsmith tetrahedron	Basic	No	No	Linear	No	Generalist	Goldsmith (1990) and MacLeod & Boynton (1979)
MacLeod and Boynton chromaticity diagram	Basic	No	No	Linear	No	Human and possibly other trichromatic primates	MacLeod & Boynton (1979)
Regan chromaticity diagram	Basic	Yes	No	Linear	No	Di- and trichromatic primates	Regan <i>et al.</i> (1998, 2001)
Endler and Mielke tetrahedron	Basic	Yes	Yes	Logarithmic	No	Generalist [†]	Endler & Mielke (2005)
Bee colour hexagon	Basic	Yes	Yes	Hyperbolic	Yes	Generalist [†]	Chittka (1992)
Colour-opponent coding model	Scaled/ Fechnerian	Yes	Yes	Hyperbolic	Yes	Bees	Backhaus (1991)
Receptor noise limited model	Scaled/ Fechnerian	Yes	Yes	Linear/logarithmic	Yes	Generalist	Vorobyev <i>et al.</i> (2001) and Vorobyev & Osorio (1998)
CIE $L^*a^*b^*$	Scaled/ one-block	Yes	Yes	Cubic-root power law [‡]	Yes	Human and possibly other trichromatic primates	CIE Publication (1986)

For details, see Appendix 1.

[†]These models have been specifically developed for birds (Endler & Mielke, 2005) and honeybees (Chittka, 1992); however, they make general assumptions on colour vision that are likely generalisable to most tetrachromatic and trichromatic species, respectively.

[‡]The cubic-root transformation in CIE $L^*a^*b^*$ corrects for nonlinearities in the links between stimulus and perceptual intensity in general, not at the photoreceptor level only.

These early models were subsequently abandoned because they could not explain some empirical data. Vorobyev & Osorio (1998) demonstrated that these data could actually be explained by a RNL model accounting for opponency between photoreceptor signals. These authors thereby demonstrated the importance of modelling photoreceptor opponency for estimating very small colour differences.

(2) Variation in difference threshold

The large body of data on colour discrimination that has been used to build psychophysical models also documents the limitations of their predictive power. It is a general concern in psychophysics that models of colour spaces do not account for higher perceptual mechanisms including cognitive ones (Ham & Osorio, 2007). Regarding colour discrimination, this concern seems particularly critical (Avarguès-Weber & Giurfa, 2014). First, past experiences can have a strong influence on discrimination ability. Free-flying honeybees, for example, lower their detection threshold when trained with aversive conditioning (one stimulus is associated with sucrose solution and the other with bitter-tasting quinine) in comparison to regular training (sucrose *versus* water; Avarguès-Weber *et al.*, 2010). Second, imprecisions in memory coding and retrieving cause discrimination abilities to decrease strongly when coloured stimuli are

displayed successively instead of simultaneously. In humans, discrimination abilities had deteriorated already 60 ms after removing the alternative stimulus from the field of view of the observer (Uchikawa & Ikeda, 1981). In honeybees, poor visual acuity constrains foragers to fly very closely to visual stimuli in order to see the colour (e.g. less than 8 cm for a 2 cm wide flower; Giurfa *et al.*, 1996, 1997). This likely explains why Hempel, Giurfa & Vorobyev (2001) found a lowest discrimination threshold at 2.3 units in the RNL model when using targets 18 cm apart (thus likely perceived successively), while Dyer & Neumeyer (2005) found an eight times lower threshold at 0.3 units in a simultaneous discrimination test.

How should visual ecologists deal with such contrasting results? A first attitude could be to extrapolate these psychophysical data to the ecological context. For example, studies on pollinator constancy, the tendency of some pollinators to visit only one plant species during a given foraging bout, should work with the largest thresholds because these pollinators almost always use successive discrimination to identify flowers. Successive discrimination should also be considered in studies on mimicry, although here the conflicting interests between signallers and perceivers are expected to generate situations analogous to aversive conditioning, thus lowering the discrimination threshold of experienced individuals. By contrast, simultaneous discrimination is certainly at play in camouflage breaking. There is thus a

risk that previous studies on background matching that used thresholds corresponding to successive discrimination have over-confidently interpreted their results.

Researchers could also adopt a conservative attitude by which conclusions are not drawn from a binary categorisation of colour stimuli as ‘discriminated or not’. Indeed, it is now well appreciated that colour discrimination is better described with a sigmoidal probability curve: in a population of individuals performing the same discrimination task (both successive and simultaneous), there is always a fraction of individuals that fail, even if colour stimuli are quite dissimilar (in bees, see e.g. Dyer & Neumeyer, 2005). Reasonable interpretations of psychophysical discrimination models should thus better read like ‘this stimulus has a high/low probability of being detected (relative to known discrimination thresholds)’.

Caution with models of discrimination should be exercised also because it is largely unknown how robust these models are to variations in model parameters. For example the spectral sensitivities and the relative density of photoreceptor types typically used in the RNL model are average values that dismiss variations that occur between different eye regions in many organisms (Temple, 2011). Simulations in birds suggest that varying the relative density of receptor types has a limited effect on model predictions compared to other parameters such as photoreceptor noise (Lind & Kelber, 2009); but clearly more studies are needed to understand better the consequences of assuming homogeneous visual abilities within the eye.

Lastly, comparing perceptual distances or other chromatic descriptors between colour patches, individuals or species, can be more informative than interpreting a perceptual distance relative to an absolute threshold value. For example, Stoddard & Stevens (2011) calculated the overlap in colouration between the eggs of the common cuckoo (*Cuculus canorus*) and those of 11 host species within the Goldsmith tetrahedron. The authors showed a positive correlation between host rejection rate and colour overlap, which aptly illustrates the co-evolutionary arms race between the cuckoo and its hosts being mediated by visual matching. This example shows that the comparative approach allows the investigation of topics such as mimicry or camouflage even with basic psychophysical colour spaces.

IV. COLOUR CONSPICUOUSNESS

Colour conspicuousness is a very important aspect of the ecology and evolution of plants and animals. The colour conspicuousness of flowers and fruits determines attraction of pollinators and animal frugivores and thus the fitness of plants (Spaethe, Tautz & Chittka, 2001; Burns & Dalen, 2002; Schmidt, Schaefer & Winkler, 2004; Cazetta, Schaefer & Galetti, 2009; Katzenberger, Lunau & Junker, 2013). In sexual selection, male conspicuousness facilitates detection by females (e.g. Stuart-Fox & Moussalli, 2008). Conspicuous ornaments are then selected because they reduce search time

and thus predation risk for females (Schluter & Price, 1993), because they indicate male quality (e.g. through correlations between colouration and immune defences; McGraw, Nolan & Crino, 2011), or possibly because they have a greater aesthetic appeal independent of any natural selection (Prum, 2012). Conspicuous colours can also reduce predation risk for the bearer, by signalling unprofitability (Cortesi & Cheney, 2010) or owing to their startling effect (Stevens, Hardman & Stubbins, 2008).

(1) Which model to use?

(a) Receptor opponency

The conspicuousness of a colour is defined operationally as the distance in a colour space between the studied trait and the background loci. The choice of a colour space should thus be driven by the potential of the space reliably to predict the perception of large colour differences. In humans, it is possible to study the match between psychophysical colour spaces and a psychological space in order to appreciate whether a more complex model has a higher potential to predict large colour differences. Figure 2 represents the distribution of several colour stimuli in the Munsell psychological space (Fig. 2A) and in three psychophysical spaces. In the photoreceptor excitation space (Fig. 2B), stimuli of equal chroma form ellipses instead of the circles expected from the Munsell space. By contrast, in the perceptual opponent space, stimuli of equal chroma are arranged almost circularly (Fig. 2C). However, circularity is only moderately improved with the complex additional transformations that are required to convert the opponent space into the CIECAM space (Fig. 2D), one of the most elaborate models of human colour vision (Fairchild, 2005). Thus, it appears that in humans the opponent transformation is the most important step to match psychological data (Kuehni, 2003).

The importance of the opponent transformation for visual ecology depends on how general the improvement observed in Fig. 2C is. The compression pattern along the M/L axes reveals a strong correlation between these axes, which originates from the high overlap in spectral sensitivities of M and L photoreceptors in Old World primates. In most other animals spectral sensitivities are more uniformly distributed, however they almost always have a certain degree of overlap that is not necessarily similar between all pairs of receptors (Cronin *et al.*, 2014, p. 148). In general, chromaticity diagrams such as Maxwell triangles or the Goldsmith tetrahedron are thus expected to distort large colour distances heterogeneously throughout the colour space.

Chittka (1992) had already pointed out the decisive role of the opponent transformation for modelling colour vision in bees. Through a number of simulations, he demonstrated that a model could roughly fit empirical data if it includes two opponent mechanisms combining outputs from all three photoreceptors. He also showed that how photoreceptor outputs are combined has little importance. Although opponent mechanisms have been finely tuned to match

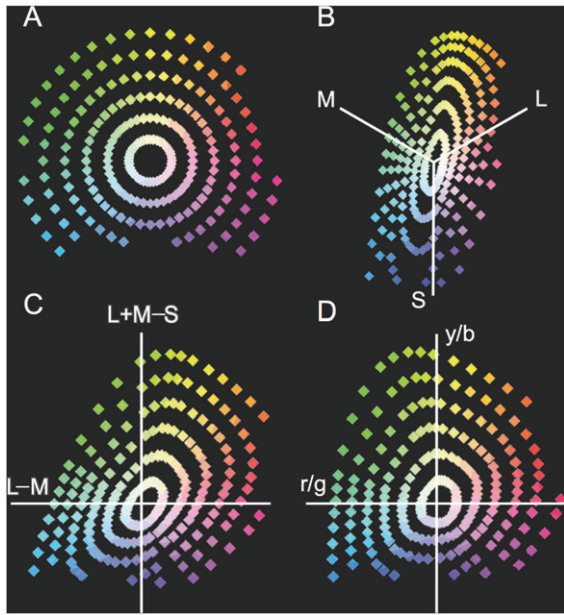


Fig. 2. Comparison of modelled and empirical colour spaces in the human. (A) Subspace of the Munsell colour system showing the location of colour chips at 2.5 hue intervals, for chroma ranging from 2 to 12, with fixed lightness (value = 8). Perceptual distances are similar between any contiguous pairs of colour chips, both in hue (defined by the rotation angle from the centre) and chroma (distance from the centre). (B) Three-dimensional excitation space of the three S, L and M photoreceptors after rotation perpendicular to the achromatic axis. Because colour chips all have the same lightness, the figure represents a chromaticity diagram. Photoreceptor sensitivity curves were obtained by applying the Smith & Pokorny (1975) transformation functions to Judd's 1951 matching functions. (C) Perceptual opponent space. The two axes give excitations along the $L - M$ and $L + M - S$ dimensions, which are expected to depict the yellow/blue and red/green opponent process of human colour vision. Comparing (C) and (A) reveals several mismatches; for example hue angles are not equally spaced around the hue circle and this elliptical distortion is more pronounced in the direction of yellow–green and violet–red. (D) Additional transformations with no biological bases were then added to (C) in the so-called CIECAM space. Illuminant, background and surround are assumed to be perfectly white. For details on CIECAM, see Fairchild (2005). Modified from www.handprint.com with author's agreement.

species-specific requirements, fine-tuning of photoreceptor combinations in opponencies only modestly improves the fit with empirical data compared to arbitrary combinations. As mentioned previously, Vorobyev & Osorio (1998) reached a similar conclusion for the RNL model. In sum, it appears that photoreceptor opponency is a critical step for building a modelled colour space that approximately predicts both small and large colour differences.

(b) Nonlinearities

Opponent functions addressed most of the compression issues in the photoreceptor excitation space of Fig. 2. The various

nonlinear response functions included in the CIECAM model ultimately circularised colours of similar chroma. In general, linear and nonlinear models (whatever the nonlinear transformation: logarithmic, hyperbolic or power law) make similar predictions on the link between stimulus and colour distances for small distances, but predictions increasingly diverge when larger distances are considered. Accounting for nonlinearities is therefore meaningful especially when analysing conspicuous colour traits.

Notably, the Weber–Fechner law can have important consequences on the co-evolutionary dynamics between signallers and perceivers. The law predicts that distances between stimuli should be larger as conspicuousness increases in order to match perceived differences. In sexual selection, for example, Ryan & Cummings (2013) highlighted that the Weber–Fechner law generates co-evolutionary dynamics similar to that predicted by the model of chase-away selection, in which females evolve even higher response thresholds as a resistance strategy balancing the costs of mating males with exaggerated traits. Another model of sexual selection, the Fisherian runaway (Lande, 1981), predicts that the ever-stronger genetic linkage between the heritable male trait and the corresponding heritable female preference that arises mechanically over generations can alone explain highly conspicuous ornaments and extravagant preferences. The extent to which the exponential evolution of the male trait is balanced by the relative decrease of perceived conspicuousness due the Weber–Fechner law remains to be investigated.

(2) The value of model predictions

Some authors have questioned the validity of estimates of conspicuousness by models of colour space (e.g. see Dyer, 2012). As highlighted previously, currently used spaces do not account for high-level perceptual mechanisms, such as colour categorisation that sets qualitative boundaries in a continuous colour space (Skorupski & Chittka, 2009; Bird *et al.*, 2014). Beyond humans, colour categorisation has been shown in birds and is likely to occur in bees (Jones, Osorio & Baddeley, 2001; Lynn, Cnaani & Papaj, 2005; Ham & Osorio, 2007; Kelber & Osorio, 2010). Another issue concerns the validity of the Fechner's assumption of additivity. This is not trifling because researchers who use the RNL model to describe differences between sexes and species with markedly different colours, a frequent situation, rely on this assumption. Investigations of the original Munsell system, a purely Fechnerian space, have shown that summing detection thresholds could provide reliable estimates of the true sensation of conspicuousness.

Independently of whether models can predict perceived colour differences, the value of model predictions also depends on how well they predict the behaviour of perceivers. In ecology and evolutionary biology, we are less interested in the perception than in the behavioural response of perceivers, because this determines selection and thus the evolution of stimuli. Several behavioural studies provide partial answers. Spaethe *et al.* (2001) for example analysed the correlation

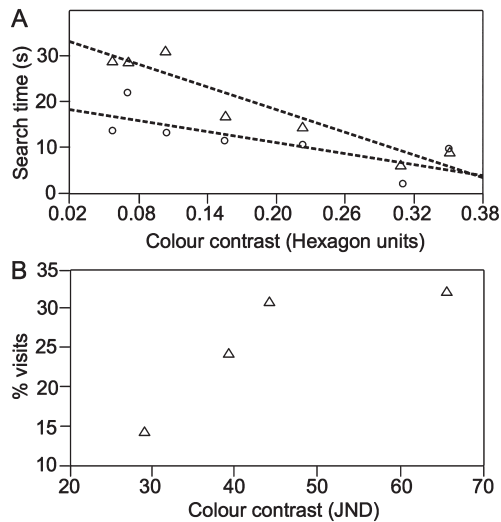


Fig. 3. Relation between colour contrast and perceiver behaviour. (A) Colour contrast of artificial flowers [28 (circles) and 15 (triangles) mm diameter] seen against a green background *versus* time needed for bumblebees to visit three flowers. From Spaethe *et al.* (2001). (B) Colour contrast of artificial fruits *versus* percentage of visits by birds in a Brazilian rainforest. One JND (for just noticeable difference) corresponds to one unit of detection threshold. From Cazetta *et al.* (2009).

between the colour contrast (measured in the bee hexagon model) of artificial flowers displayed on a green background and the time spent by bumblebees to visit three flowers of the same colour. The authors tested seven different colours and found that colour contrasts are linearly correlated with search time (Fig. 3A). In another study, Cazetta *et al.* (2009) worked out the relationship between the colour contrast of fruits and their attractiveness to birds. They used modelling clay of four different colours to build artificial fruits that were then attached to shrubs in the forest. After 4 days, the authors counted the number of pecked or removed fruits (indicating attractiveness). They found that attractiveness is correlated with the colour contrast between the fruit and its background (calculated with the log–linear version of the RNL model of bird colour vision; Fig. 3B).

These results stress two points. First, large colour contrasts as calculated with a psychophysical model can predict the behaviour of perceivers (see also Cortesi & Cheney, 2010). Second, colour contrasts do not predict behaviour equally well over the whole range of conspicuousness (see also Stuart, Dappen & Losin, 2012), because the behavioural response is not linearly correlated with the magnitude of the sensory input. Although these results stress that, overall, models of colour space can provide ecologically meaningful estimates of conspicuousness, only behavioural tests can identify response thresholds to large colour differences, and more generally allow a thorough understanding of the links between colour spaces and behaviours. Such studies do not require advanced psychophysical equipment and can be performed under field conditions.

V. COLOUR DIVERSITY

The characterisation of colour diversity is the primary step for investigating the ecological and evolutionary factors influencing the evolution of colouration. Spectral and colour spaces have allowed quantitative estimates of colour diversity and permit formal tests of deviations from null expectations about diversity (Gumbert, Kunze & Chittka, 1999; de Jager, Dreyer & Ellis, 2011; Binkenstein *et al.*, 2013; Stourmaras *et al.*, 2013; Muchhala, Johnsen & Smith, 2014). For example, McEwen & Vamosi (2010) used a principal component space to show that plant species flowering simultaneously tend to have more divergent floral colours than expected by chance. Correlating estimates of colour diversity with cognitive, physiological or ecological parameters can then be used to identify the proximate, ecological and evolutionary factors influencing this diversity (Chittka *et al.*, 1994; Stoddard & Prum, 2008; Dyer *et al.*, 2012; Binkenstein *et al.*, 2013; Maia, Rubenstein & Shawkey, 2013). In the preceding example, the high colour diversity of flowers possibly reflects a strategy that facilitates pollinator constancy and thus reduces inter-specific pollen transfer (McEwen & Vamosi, 2010).

The expression ‘colour diversity’ as currently used in visual ecology actually refers to two visual sensations that are involved in different evolutionary and ecological processes. The two sensations are best characterised in a colour space using different methods; thus a primary step when analysing colour diversity is to clearly identify the sensation that matters for the studied question.

(1) The sensations of colour diversity

(a) Colourfulness

Colour diversity may first refer to colourfulness, which is defined here as the overall colour contrast of a multi-coloured pattern. Colourfulness arises when colours are perceptually very different from one another and is essentially independent of the number of visually distinct colours. For humans, for example, a bicoloured blue and yellow bird is usually perceived as more colourful than a bird with 10 perceptually distinct but similar variations of either blue or yellow.

Colourfulness is mainly meaningful for the study of intra-individual colour diversity. It matters when hypothesizing that multi-coloured patterns have evolved to increase conspicuousness. Displaying multiple colours that maximise contrast allows maintaining high conspicuousness despite varying background colouration (Hebets & Papaj, 2005). For example, bowerbirds decorate their bowers with ornaments that increase contrast both to the background and their own colouration, possibly to increase mate stimulation (Endler *et al.*, 2005).

(b) Colour richness and distinctiveness

Colour richness refers to the number of colours that a perceiver potentially has to recognise and to memorise in a given context. It is mostly relevant for characterising

inter-individual and inter-specific colour diversity, in particular when colours signal specific or social identity, or quality of an individual. Colour richness is determined by the number of visually distinct colour stimuli. In addition, stimuli are more easily recognised and are stored longer in memory as their mutual contrasts increase (e.g. in bees: Niggebrügge *et al.*, 2009). The contrast between a given stimulus and other signalling stimuli is termed distinctiveness; it is different from conspicuousness, which is the contrast to the background. Thus, colour richness is jointly determined by the number of colours and by their distinctiveness.

In ecology, colour richness can inform about niche diversity. It is well suited for describing the diversity of flower colours in a meadow, for example, because pollinator constancy is facilitated when flowering plants are visually distinct from one another (de Jager *et al.*, 2011). In evolutionary biology, the diversity of colours within a clade is best characterised by colour richness because during speciation, the two derived species tend to evolve high distinctiveness, which promotes assortative mating and thus limits hybridisation (Hopkins & Rausher, 2012). An increase in colour richness over time can also indicate a co-evolutionary arms race between hosts and parasites (Spottiswoode & Stevens, 2012). Distinctiveness can help identify individuals or species that have experienced cultural or evolutionary innovations (Endler *et al.*, 2005) and can indicate the likelihood to mimic or to be mimicked (Papadopulos *et al.*, 2013). Distinctiveness is a property of aposematic signals, along with conspicuousness (Merilaita & Ruxton, 2007). Applied to a set of colour stimuli, colour richness can identify colour polymorphism as a discrete distribution of colour variants (Ajuria Ibarra & Reader, 2014). If the variants maximise distinctiveness or, in the case of camouflage, similarity to the local visual environment, colour richness can further inform on the role of the colour vision of congeners or predators in the maintenance of colour polymorphism (Stevens, Lown & Wood, 2014a).

(2) Quantifying colour diversity

(a) Which space to use?

Like conspicuousness, the sensations of colour diversity depend on colour distances within the space. Opponent and, if possible, nonlinear spaces should thus be preferred. For colour richness and distinctiveness, the space should further be able to identify discrimination thresholds, pointing towards Fechnerian colour spaces.

In addition to opponency and nonlinearities, modelling chromatic adaptation can have important effects on estimating colour diversity. There is numerous evidence from humans, birds (Maddocks, Church & Cuthill, 2001) and bees (Chittka *et al.*, 2014) that colour constancy is imperfect, and thus that the perception of colours changes when the illuminating spectrum changes. This imperfection is the physiological explanation to why the behaviour of displays or the colour signals themselves are frequently adapted to a specific lighting environment (Endler & Théry, 1996). In

honeybees (Dyer, 1999) and bumblebees (Dyer & Chittka, 2004), the shift in the perception of colouration is partly predicted by a von Kries-type model of chromatic adaptation. However, the range of the shift varies depending on the light levels (Brennan, 1987), and it is not similar everywhere throughout the colour space (Faruq *et al.*, 2013); two aspects that are not adequately taken into account by the von Kries transformation. In general it has remained mostly unknown in which conditions the von Kries transformation describes colour perception accurately and in which conditions it does not. Given that modelling chromatic adaptation may significantly influence the results when studying colour diversity (see Appendix 2), we recommend rigorous use of models with and without chromatic adaptation to check the consistency of conclusions.

(b) Colourfulness

Colourfulness is usually characterised by the mean or median distance between colour traits. Several authors have also estimated colourfulness from the area (or volume in three-dimensional spaces) of the convex hull, which is the smallest possible polygon (polyhedron) that encapsulates all colour traits in the studied space (e.g. Vorobyev, 2003; Stoddard & Prum, 2011; Hanley *et al.*, 2013; Stournaras *et al.*, 2013; Burd *et al.*, 2014). Because the area of the polygon strongly depends on extreme values, we recommend additionally to calculate the area of the 95% confidence ellipse, or to compare results based on area metrics and on pairwise distances (e.g. Langmore *et al.*, 2011).

Instead of analysing colours as a whole, it is common to analyse components of colours separately. Colour loci in chromaticity diagrams are often interpreted in terms of chroma and hue, with chroma defined by the Euclidean distance of the locus to the origin of the diagram (corresponding to the achromatic point) and hue by its angular position (Endler *et al.*, 2005; Stoddard & Prum, 2008, 2011). Hue disparity, the magnitude of the angle between two colour vectors, is a measure of contrast in hue independent of chroma (Stoddard & Prum, 2008). While these measures of hue and chroma can graphically reveal, at the photoreceptor level, the mechanism behind a shift in conspicuousness, we caution about interpreting them in terms of mechanisms of signal production, and of perceptual components of colours. In signallers there is not always a clear relationship between chroma and pigment concentration as it is sometimes stated. Most often, concentration covaries with a combination of chroma and hue, and in some circumstances it is linearly correlated with hue alone (Lancaster *et al.*, 1997; Andersson & Prager, 2006). From the perceiver side, there is no clear evidence that in animals other than humans, hue and chroma are qualitatively distinct components of colours (Kelber & Osorio, 2010). Even if they are, the way of modelling colour vision, in particular the mechanism of chromatic adaptation can dramatically change the relative contribution of chroma and hue in the distribution of colours within the space (Appendix 2).

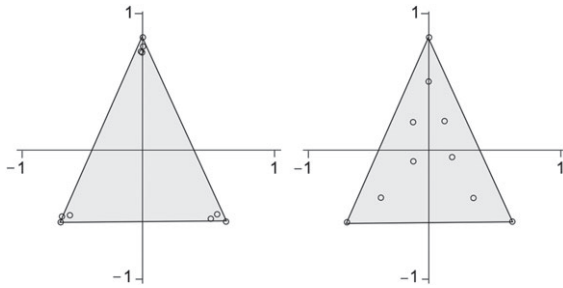


Fig. 4. Caveats of estimating colourfulness with dispersion measures. Triangles are theoretical chromaticity diagrams of a trichromatic perceiver in which 10 colour stimuli are mapped. The stimuli have similar mean distance and area of the convex hull between panels; yet they represent different levels of diversity in hue and chroma.

(c) Colour richness and distinctiveness

Colour richness is most simply described by the number of visually distinct colours. This can be estimated from a matrix of pairwise colour distances expressed in JND (just noticeable difference) units (e.g. Spottiswoode & Stevens, 2012) by counting the number of values above the discrimination threshold.

A more elaborate measure of colour richness further accounts for the magnitude of contrasts between colours. Measures of overall conspicuousness used for colourfulness are not always appropriate for estimating colour richness. For example, the 10 colour traits of Fig. 4 have similar mean distance and area of the convex hull between both panels. Yet the two distributions have different colour richness: the set of points in the right panel represents more diverse hues and chroma values than that displayed in the left panel. This type of diversity can be captured by analysing the homogeneity of point distribution across the space.

Variance or standard deviation of pairwise chromatic distances, hue angles and chroma have been used to describe homogeneity in colour distribution (Stoddard & Prum, 2008, 2011; Stournaras *et al.*, 2013). For example, the sum of average chroma and its standard deviation correlates significantly ($r=0.94$) with colour richness expressed by human observers rating natural images (Hasler & Suesstrunk, 2003). Another approach to analyse the homogeneity of distribution uses the kernel density estimation. This is a non-parametric method for estimating the probability density function (PDF) of a distribution that is widely used in spatial ecology, for example for estimating home range (Fieberg, 2007). The shape of the PDF can then be described with its statistical parameters. The variance of the PDF, for example, is an interesting measure of colour richness because it is influenced both by the area in the space occupied by colours, and by the homogeneity of colour distribution. The kurtosis is a better estimate of homogeneity independent of the area (Johansson, 2000). With a fixed bandwidth of the kernel, it is further possible to compare PDFs between data sets, for example to identify the regions in a colour space where two communities or taxa differ maximally (or minimally)

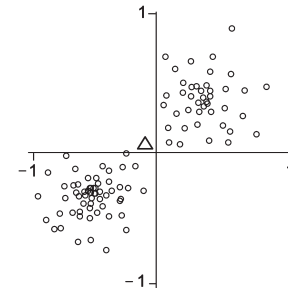


Fig. 5. Evaluating distinctiveness using mean or median distances. If considering circles within the upper right quadrant only (unimodal spatial distribution), the median distance between the triangle and circles would be significantly greater than the median of all other pair-wise distances. This result would not hold if considering all circles (bimodal spatial distribution). Thus, the triangle would qualify as a unique colour in the first analysis but not in the second.

in densities. Several algorithms allow computing kernel distributions in high-dimensional spaces (e.g. the package *np* in the R statistic program; Hayfield & Jeffrey, 2008).

Distinctiveness can be estimated directly as a measure of density at a given locus in the colour space using the PDF (Stournaras, Prum & Schaefer, 2015), or by counting the number of colour traits within a predefined area around a focal colour locus (Stournaras *et al.*, 2013). In their study on floral mimicry, Papadopulos *et al.* (2013) estimated colour distinctiveness in a bee hexagon space by comparing the median Euclidean distance between the putative mimic and models to the median of all other pairwise distances. This method provides reliable estimates of distinctiveness for unimodally distributed colour traits; however, it is flawed with multimodal distributions, i.e. the type of distribution that is most frequent in comparative studies of natural colours (see Fig. 5).

Finally, discriminant function and cluster analyses can be used to investigate how distinctive a group of individuals is compared to other individuals (Ajuria Ibarra & Reader, 2014; Feeney *et al.*, 2014). One should keep in mind, however, that statistically significant clusters may not be distinguished by a perceiver and thus can be visually irrelevant (Tastard *et al.*, 2008). In some cases, geographical data may also be necessary to interpret the value of colour clusters correctly. For example, let's assume two clusters in the colour space, which overlap partially, but which are both statistically and visually distinct (e.g. more than 95% of pairwise distances between the two clusters are above the discrimination threshold). If the distribution of intermediate phenotypes in the colour space is geographically autocorrelated, and if the colour distance between each intermediate phenotype and its closest geographic neighbour is below the discrimination threshold, then the colour variation would appear continuous to a perceiver (especially if the perceiver sees colour signals sequentially; for an example of a spatially explicit analysis of colour clustering, see Tastard *et al.*, 2008). In general, it is critical to interpret results from discrimination function and cluster analyses in the appropriate spatial context of both the signallers and the perceiver.

VI. COLOUR TRAIT EVOLUTION AND DIVERSIFICATION

(1) Evolution and diversification in colour spaces

The adaptation of signals to the visual system of perceivers is a major driver of colour evolution. This is also an important mechanism of colour diversification, not so much because of the evolution of visual systems, which is usually conservative (Osorio & Vorobyev, 2008), but mostly because of local and temporal variations in the viewing environment and in the community assembly of viewers (Endler *et al.*, 2001; Cummings, 2007; Fuller & Noa, 2010) or because of competition between sympatric pollinators (Muchhala *et al.*, 2014). If communication evolves primarily to stimulate sensory systems and thus to increase the efficiency of communication, e.g. by exploiting previously existing preferences, this is termed ‘sensory exploitation’ in evolutionary biology (Endler & Basolo, 1998).

Colour spaces, especially those suited for studying colour diversity, are particularly appropriate to explore the effects of sensory exploitation on the evolution and diversification of visual signals. These effects are diverse and depend on which aspects of communication have been selected. For example, signals may be selected to increase detectability and thus conspicuousness, or to facilitate recognition and memorisation and thus colour richness. Within a colour space, these effects can be evidenced by showing that distances between signal and background loci (Leal & Fleishman, 2004) or distinctiveness (Stournaras *et al.*, 2013), respectively, are larger than expected by chance. By reconstructing and plotting ancestral colours within the colour space and by analysing the direction of temporal shifts, it becomes possible to test hypotheses of convergent evolution (Burd *et al.*, 2014) or to identify whether derived colour traits are elaborations or innovations from ancestral traits (Endler *et al.*, 2005). In the current literature, colour spaces have therefore become a key tool for investigating evolution through sensory exploitation.

(2) Colour *versus* spectral spaces

Reflectance spectra are objective, physical descriptions of the colour of phenotypes. Very often, studies on plant and animal colouration are primarily interested in the genetic, histological or physical mechanisms of colour production. In such cases, spectral spaces should be preferred over colour spaces because variation among the emitted phenotypes more accurately depicts the diversity of producing mechanisms than variation in the perceived phenotypes does. Ultimately, colour spaces are unable to identify colour metamers, those stimuli that have markedly different spectral profiles but are perceptually similar for the studied perceiver (Wyszecki & Stiles, 1982). Although their actual importance for biological organisms remains to be evaluated, colour metamers are theoretically interesting examples of convergence in communication or of metabolic

optimisation of signal production without changes in the communication process.

The relevance of spectral spaces to predict or characterise the mechanisms underlying colour production depends on the nature of these mechanisms. When gradual and continuous changes in the producing mechanisms correlate linearly with spectral changes, the spectral space can be very useful (e.g. pH-determined variation from red to blue in flowers; Goto & Kondo, 1991). In other cases the spectral space poorly matches the genotypic and metabolic spaces, for instance when two metabolic pathways producing pigments with very distinct reflectance spectra differ by a single mutation (Rausher, 2008). Yet even in such cases, mapping colour variants in a spectral space can yield crucial information about the shape of the genotypic space and evolution throughout that space (Whibley *et al.*, 2006).

Because of its ability to describe phenotypic variation objectively, the spectral space represents a true morphospace and can thus be used for analysing the various processes generating phenotypic diversity (McGhee, 2007). For its part, the colour space can be thought of as spectral space filtered by a sensory system (but see Appendix 3). Comparing results between spectral and colour spaces could therefore be used for analysing the specific role of a sensory system in the evolution and diversification of phenotypes, i.e. to test hypotheses on sensory exploitation [alternatively, Burd *et al.* (2014), compared colour distribution in the colour space of the putative selective agent and in another colour space]. For example, stimuli that are organised in statistically significant clusters in the spectral space but not in a colour space describe a colour polymorphism that is not driven by the perception of the studied animal. Renoult *et al.* (2013*b*) extended this approach in their ‘stimulation landscape’, which combines a colour space with a spectral space. More precisely, the stimulation landscape is a spectral space to which one dimension is added, which indicates the perceptual distance of each stimulus described by the spectral space to a fixed, predefined stimulus (e.g. a background spectrum). In a stimulation landscape, conspicuousness is assumed to be a component of fitness. Fitness components are composite, fitness-correlated traits resulting from the direct interaction between phenotypic traits and one or multiple selective agents. Conspicuousness describes the interacting effect of a colour stimulus (the phenotypic trait) with the visual system of the perceiver. Under the hypothesis of sensory exploitation, the visual system is the agent of selection. The stimulation landscape thus describes the theoretical fitness surface expected under the hypothesis of sensory exploitation. Comparing gradients of selection and evolution in a stimulation landscape and in an empirical, typical fitness surface allow testing and quantifying evolution through sensory exploitation.

VII. SIGNALLING TO MULTIPLE PERCEIVERS

The colour space as a tool to model communication implies interactions between an emitter and a perceiver.

In the section on colour diversity, we have extended these binary interactions to multiple emitters, discussing how different colour signals could be compared within the colour space of single perceivers. Most if not all communication systems, however, are embedded into complex networks of interactions including multiple perceivers. This is most obvious in socio-sexual interactions where one emitter interact with several conspecifics. Modelling the specific colour vision of individuals would be especially important to understand how the various selection forces exerted within the social group combine to shape socio-sexual colour signals. While conflicts between mate evaluation and species recognition (Rosenthal & Ryan, 2011; Secondi & Théry, 2014) and between intrasexual and other social-sexual selection (Gerald *et al.*, 2010) has been well documented, it is still unknown how individual variation in colour vision contributes to these patterns.

In addition, most colour traits are also seen and selected by multiple perceivers belonging to distinct species. Flowers and fruits, for example, are frequently visited by dozens of mutualistic and antagonistic species (Bascombe & Jordano, 2007), which partly rely on colour vision for detection and choice (Junker *et al.*, 2013). Even in more specialised interactions, as in mate choice, communication is influenced by the perception of other species such as predators (Endler, 1980). Comparing the perception of colours between perceivers is thus a necessary step in order to reach an encompassing view of how visual communication systems evolve.

The main difficulty in comparative colour vision is the availability of data specific to the studied perceivers. In rare cases, such as in New World primates and some cichlid fishes (Hofmann *et al.*, 2010), discrete variation in visual phenotypes occurs within a population. In New World primates, males and homozygous females are dichromatic and heterozygous females are trichromatic (Jacobs, 2008). Colour vision phenotypes can here be identified by tracking focal mutations in the sequence of opsin genes (e.g. Vogel, Neitzn & Dominy, 2007; but see Hauser, van Hazel & Chang, 2014). Yet genetically based variation among individuals can also have a quantitative basis. For example, Endler *et al.* (2001) were able to select lines of guppies (*Poecilia reticulata*) for increased sensitivity to either blue or red stimuli and show significant heritability for sensitivity. In addition, spectral sensitivity may vary depending on diet and age (Flamarique, 2013). In order to account for both genetic and physiological variation in spectral sensitivities among individuals, behavioural tests can be performed. For example, Rick, Mehliis & Bakker (2011) used optomotor response thresholds to show that red colour expression in fathers of sticklebacks (*Gasterosteus aculeatus*) correlates with the red sensitivity of their daughters. Such non-invasive characterisations of spectral sensitivities are available only for a few groups of animals, however, and individual variation in colour vision could occur beyond the photoreceptor level. These limitations explain why there have been very few studies as yet investigating whether individual variation in sensitivities influences the evolution of colour signals.

In comparison, inter-specific variation in colour vision has been studied much more (Jacobs, 1993; Briscoe & Chittka, 2001; Kelber *et al.*, 2003; Osorio & Vorobyev, 2005). The variation concerns both spectral sensitivities and other factors influencing the perception of colours, in particular colour detection. In a series of pioneering studies on the community ecology of colour signalling, Théry and collaborators used models of colour discrimination to compare the detectability of crab-spiders to both prey (pollinating insects) and predators (birds). They showed that spider colouration provides camouflage to both types of perceivers, and that they select the region of flowers that minimises general detectability (Théry & Casas, 2002; Théry *et al.*, 2005; Defrize, Théry & Casas, 2010). Here, the community approach to colour signalling relies on a qualitative analysis of colour vision: using species-specific models of colour discrimination such as the RNL model, a binary assessment of detectability is made considering successively each community member (see also Siddiqi *et al.*, 2004; Crothers & Cummings, 2013). As we already discussed, however, there is a risk to interpreting results qualitatively from models of detectability because the conclusions depend strongly on the detection threshold *a priori* defined.

In many situations, a quantitative comparison of colour perception across species is needed. The difficulty is that perceptual distances are not directly comparable between colour spaces. For example, with the widely used formulae provided by Kelber *et al.* (2003) to model chromaticity diagrams for tetra- or trichromatic colour vision, the distance from the centre of the triangle to the apices is 0.82 while the distance from the centre of the tetrahedron to the vertices is 0.87. One possibility to render perceptual distances comparable between species is to standardise them (e.g. see Renoult *et al.*, 2013a). However, methods of standardisation are still mainly theoretical and should be tuned and validated using psychophysical experiments. In spite of the difficulty of designing behavioural tests to analyse large perceptual distances, we hope that the importance of inter-specific comparisons for the field of evolutionary ecology will foster psychophysical research in that direction.

VIII. CONCLUSIONS

(1) Interdisciplinary frameworks open avenues of research, but they necessarily come with a risk of misunderstanding the tools and concepts of either discipline. Colour spaces are very diverse, with simple and rough models that can apply to a large array of ecological conditions, and complex and accurate models that work in specific conditions only. Ultimately, visual ecologists should be able adequately to trade off between complexity and generalisation. The aim of this review is to provide visual ecologists with a critical perspective on how models of colour space are built, how well they perform and where their main limitations are regarding their most frequent uses in ecology and evolutionary biology.

(2) In general, photoreceptor excitation spaces provide good approximations of the qualitative internal organisation of colours. Such a qualitative modelling can be used to trace back evolutionary trajectories of colour signals, e.g. for detecting signal innovations. However, most applications in visual ecology require quantification of colour perception. Modelling photoreceptor opponency is a critical step for achieving a reasonably good prediction of both small (detection and discrimination thresholds) and large colour distances.

(3) Spectral spaces are currently treated by visual ecologists as out-dated compared to colour spaces, and as such they are now rarely used. However, the independence of the spectral space from any perceptual dimension could be a virtue to quantify the relative contribution of perception in the selection of colour signals through comparisons with colour spaces.

(4) The study of colour discrimination and detection is best achieved using opponent and Fechnerian models of colour space that estimate explicitly detection thresholds. The RNL model is the most widely used method for estimating such thresholds and performed well in a variety of tasks and organisms. It assumes that thresholds are set by noise in photoreceptors. However, detection thresholds can also be controlled by higher brain mechanisms, for example the motivational state. Because it is still speculative how such top-down controls are linked to the ecology of organisms (e.g. how starvation or sexual appetite lower detection and discrimination thresholds), visual ecologists should always consider the possibility that a modelled threshold does not predict the real abilities of animals. In general, more studies are needed on how detection thresholds estimated in controlled, laboratory conditions apply to natural environments.

(5) Opponent colour spaces in general correctly predict large colour differences. This seems to be true for Fechnerian spaces too, although they were originally designed to estimate detection thresholds only. Indeed, building an entire space by summing detection thresholds allows approximating the psychological space. Yet one should keep in mind that the psychological colour space is nonlinearly related to the behavioural response of the organism. Above a certain stimulation threshold an individual can respond similarly to two stimuli despite them being perceived differently. Establishing the link between perception and behaviour is crucial to understanding the evolutionary ecology of many communication systems. This can be achieved by visual ecologists using behavioural experiments.

(6) Colour diversity as currently investigated in ecology and evolutionary biology refers to two distinct sensations. Colourfulness is related to the overall contrast of a set of colours and is mostly relevant to describing the diversity of colours displayed by single individuals. High colourfulness increases detectability. Colour richness, when referring to the whole set of colours analysed, or distinctiveness when referring to a given colour or subset of colours, are sensed with stimuli used to signal identity or quality and are therefore mostly relevant for questions related to inter-individual or

inter-specific colour diversity. High distinctiveness facilitates recognition and memorisation.

(7) Modern ecology and evolutionary biology have emphasised the network nature of the interactions both within and between species. In order to decipher the role of visual communication as a determinant of these interactions, it is necessary to compare the perception of colours between species and individuals. Unfortunately, the study of individual variation in non-human animals is in its infancy and tools to compare colour vision quantitatively between species are mostly lacking. These are important avenues of research for psychophysicists.

(8) Overall, colour spaces have allowed important advances in ecology and evolution and will continue to do so. Noticeably, the observation that these relatively basic models of perception most often predict results that are ecologically sound stresses the primacy of low-level, hardwired perceptual mechanisms for animal colour vision. Ecologists must nevertheless keep in mind how poorly understood such mechanisms still are. For example, animals can activate only some of their photoreceptors to perform a given task (Koshitaka *et al.*, 2008). Many currently unknown aspects of colour vision can be understood better by means of behavioural studies. Comparing between models, varying model parameters and performing behavioural experiments under natural conditions would make ecological conclusions more robust and would highlight important aspects of colour vision. We thus hope that visual ecology becomes an interface between psychophysics and evolutionary ecology, advancing knowledge in both fields.

IX. ACKNOWLEDGEMENTS

We thank Tom Galewsky, Marie Charpentier and Charlotte Francesiaz for their comments on an earlier version of the manuscript. We are very grateful to three anonymous referees who provided helpful comments.

X. REFERENCES

- AJURIA IBARRA, H. & READER, T. (2014). Female-limited colour polymorphism in the crab spider *Synema globosum* (Araneae: Thomisidae). *Biological Journal of the Linnean Society* **113**, 368–383.
- ANDERSON, J., BADDELEY, R., OSORIO, D., SHASHAR, N., TYLER, C., RAMACHANDRAN, V., CROOK, A. & HANLON, R. (2003). Modular organization of adaptive colouration in flounder and cuttlefish revealed by independent component analysis. *Network: Computation in Neural Systems* **14**, 321–333.
- ANDERSSON, S. & PRAGER, M. (2006). Quantifying colors. In *Bird Coloration* (eds G. E. Hill and K. J. McGraw), pp 41–89. Harvard University Press, Cambridge.
- AVARGUÉS-WEBER, A., DE BRITO SANCHEZ, M. G., GIRUFA, M. & DYER, A. G. (2010). Aversive reinforcement improves visual discrimination learning in free-flying honeybees. *PLoS One* **5**, e15370.
- AVARGUÉS-WEBER, A. & GIURFA, M. (2014). Cognitive components of color vision in honey bees: how conditioning variables modulate color learning and discrimination. *Journal of Comparative Physiology A* **200**, 449–461.
- BACKHAUS, W. (1991). Color opponent coding in the visual system of the honeybee. *Vision Research* **31**, 1381–1397.
- BACKHAUS, W. & MENZEL, R. (1987). Color distance derived from a receptor model of color vision in the honeybee. *Biological Cybernetics* **55**, 321–331.

- BACKHAUS, W., MENZEL, R. & KREISSL, S. (1987). Multidimensional scaling of colour similarity in bees. *Biological Cybernetics* **56**, 293–304.
- BASCOMPTE, J. & JORDANO, P. (2007). Plant-animal mutualistic networks: the architecture of biodiversity. *Annual Review of Ecology, Evolution, and Systematics* **38**, 567–593.
- BENITEZ-VIEYRA, S., HEMPEL DE IBARRA, N., WERTLEN, A. M. & COCUCCI, A. A. (2007). How to look like a mallow: evidence of floral mimicry between Turneraceae and Malvaceae. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **274**, 2239–2248.
- BENNETT, A. T. D. & THÉRY, M. (2007). Avian color vision and coloration: multidisciplinary evolutionary biology. *American Naturalist* **169**, S1–S6.
- BINKENSTEIN, J., RENOULT, J. P. & SCHAEFER, H. M. (2013). Increasing land-use intensity decreases floral colour diversity and changes composition of plant communities in temperate grasslands. *Oecologia* **173**, 461–471.
- BIRD, C. M., BERENS, S. C., HORNER, A. J. & FRANKLIN, A. (2014). Categorical encoding of color in the brain. *Proceedings of the National Academy of Sciences of the United States of America* **111**, 4590–4595.
- BRADBURY, J. W. & VERHENCAMP, S. (1998). *Principles of Animal Communication*. Sinauer Associates, Sunderland.
- BRANDT, R. & VOROBYEV, M. (1997). Metric analysis of threshold spectral sensitivity in the honeybee. *Vision Research* **37**, 425–439.
- BRENNAN, E. J. (1987). Corresponding chromaticities for different states of adaptation to complex visual fields. *Journal of the Optical Society of America A* **4**, 1115–1129.
- BRISCOE, A. D. & CHITTKA, L. (2001). The evolution of color vision in insects. *Annual Review of Entomology* **46**, 471–570.
- BUCHSBAUM, G. & GOTTSCHALK, A. (1983). Trichromacy, opponent colour coding and optimum colour information transmission in the retina. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **220**, 89–113.
- BURCKHARDT, D. H. (1989). UV vision: a bird's eye view of feathers. *Journal of Comparative Physiology A* **164**, 787–796.
- BURD, M., STAYTON, C. T., SHRESTHA, M. & DYER, A. G. (2014). Distinctive convergence in Australian floral colours seen through the eyes of Australian birds. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **281**, 1–7.
- BURNS, K. C. & DALEN, J. L. (2002). Foliage color contrasts and adaptive fruit color variation in a bird-dispersed plant community. *Oikos* **96**, 463–469.
- CAZETTA, E., SCHAEFER, H. M. & GALETTI, M. (2009). Why are fruits colorful? The relative importance of achromatic and chromatic contrasts for detection by birds. *Evolutionary Ecology* **23**, 233–244.
- CHITTKA, L. (1992). The color hexagon: a chromaticity diagram based on photoreceptor excitations as a generalized representation of colour opponency. *Journal of Comparative Physiology A* **170A**, 533–543.
- CHITTKA, L. & BROCKMANN, A. (2005). Perception space – the final frontier. *PLoS Biology* **3**, e137.
- CHITTKA, L., FARUQ, S., SKORUPSKI, P. & WERNER, A. (2014). Colour constancy in insects. *Journal of Comparative Physiology A* **200**, 435–448.
- CHITTKA, L., SHMIDA, A., TROJE, N. & MENZEL, R. (1994). Ultraviolet as a component of flower reflections, and the colour perception of Hymenoptera. *Vision Research* **34**, 1489–1508.
- CIE Publication (1986). *Technical Report 15.2-1986: Colorimetry*. Second Edition. CIE Central Bureau, Vienna.
- COHEN, J. (1964). Dependency of the spectral reflectance curves of the munsell-color chips. *Psychonomic Science* **1**, 369–370.
- COHEN, J. A. (1984). Sexual selection and the psychophysics of female choice. *Zeitschrift für Tierpsychologie* **64**, 1–8.
- CORTESI, F. & CHENEY, K. (2010). Conspicuousness is correlated with toxicity in marine opisthobranchs. *Journal of Evolutionary Biology* **23**, 1509–1518.
- CRONIN, T. W., JOHNSEN, S., MARSHALL, N. J. & WARRANT, E. J. (2014). *Visual Ecology*. Princeton University Press, Princeton.
- CROTHERS, L. R. & CUMMINGS, M. E. (2013). Warning signal brightness variation: sexual selection may work under the radar of natural selection in populations of a polytypic poison frog. *American Naturalist* **181**, E116–E124.
- CUMMINGS, M. E. (2007). Sensory trade-offs predict signal divergence in surfperch. *Evolution* **61**, 530–545.
- DEFRIZE, J., THÉRY, M. & CASAS, J. (2010). Background colour matching by a crab spider in the field: a community sensory ecology perspective. *Journal of Experimental Biology* **213**, 1425–1435.
- DE VALOIS, R. L., SMITH, C. J., KITAI, S. K. & KAROLY, S. J. (1958). Responses of single cells in different layers of the primate lateral geniculate nucleus to monochromatic light. *Science* **127**, 238–239.
- DYER, A. G. (1999). Broad spectral sensitivities in the honeybee's photoreceptors limit colour constancy. *Journal of Comparative Physiology A* **185**, 445–453.
- DYER, A. G. (2006). Discrimination of flower colours in natural settings by the bumblebee species *Bombus terrestris* (Hymenoptera: Apidae). *Entomologia Generalis* **28**, 257–268.
- DYER, A. G. (2012). The mysterious cognitive abilities of bees: why models of visual processing need to consider experience and individual differences in animal performance. *Journal of Experimental Biology* **215**, 387–395.
- DYER, A. G., BOYD-GERNY, S., MCLOUGHLIN, S., ROSA, M. G. P., SIMONOV, V. & WONG, B. B. M. (2012). Parallel evolution of angiosperm colour signals: common evolutionary pressures linked to hymenopteran vision. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **279**, 3606–3615.
- DYER, A. G. & CHITTKA, L. (2004). Biological significance of distinguishing between similar colours and in spectrally variable illumination: bumblebees (*Bombus terrestris*) as a case study. *Journal of Comparative Physiology A* **190**, 105–114.
- DYER, A. G. & NEUMEYER, C. (2005). Simultaneous and successive colour discrimination in the honeybee (*Apis mellifera*). *Journal of Comparative Physiology A* **191**, 547–557.
- EATON, M. D. (2007). Avian visual perspective on plumage coloration confirms rarity of sexually monochromatic North American passerines. *Auk* **124**, 155–161.
- ENDLER, J. A. (1980). Natural selection on color patterns in *Poecilia reticulata*. *Evolution* **34**, 76–91.
- ENDLER, J. A. (1993). The color of light in forests and its implications. *Ecological Monographs* **63**, 1–27.
- ENDLER, J. A. & BASOLO, A. L. (1998). Sensory ecology, receiver biases and sexual selection. *Trends in Ecology and Evolution* **13**, 415–420.
- ENDLER, J. A., BASOLO, A., GLOWACKI, S. & ZERR, J. (2001). Variation in response to artificial selection for light sensitivity in guppies (*Poecilia reticulata*). *The American Naturalist* **158**, 36–48.
- ENDLER, J. A. & MIELKE, P. W. (2005). Comparing entire colour patterns as birds see them. *Biological Journal of the Linnean Society* **86**, 405–431.
- ENDLER, J. A. & THÉRY, M. (1996). Interacting effects of lek placement, display behaviour, ambient light and colour patterns in three neotropical forest-dwelling birds. *American Naturalist* **148**, 421–452.
- ENDLER, J. A., WESTCOTT, D. A., MADDEN, J. R. & ROBSON, T. (2005). Animal visual systems and the evolution of color patterns: sensory processing illuminates signal evolution. *Evolution* **59**, 1795–1818.
- FAIRCHILD, M. D. (2005). *Color Appearance Model*. Second Edition. Wiley-IS&T, Chichester.
- FARUQ, S., MCOWAN, P. W. & CHITTKA, L. (2013). The biological significance of colour constancy: an agent-based model with bees foraging from flowers under varied illumination. *Journal of Vision* **13**, 1–14.
- FECHNER, G. T. (1860). *Elemente der Psychophysik*. Breitkopf und Härtel, Leipzig.
- FEENEY, W. E., STODDARD, M. C., KILNER, R. M. & LANGMORE, N. E. (2014). “Jack-of-all-trades” egg mimicry in the brood parasitic Horsfield's bronze-cuckoo? *Behavioral Ecology* **25**, 1365–1373.
- FIEBERG, J. (2007). Kernel density estimators of home range: smoothing and the autocorrelation red herring. *Ecology* **88**, 1059–1066.
- FLAMARIQUE, I. N. (2013). Opsin switch reveals function of the ultraviolet cone in fish foraging. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **280**, 20122490.
- FOSTER, D. H. (2011). Color constancy. *Vision Research* **51**, 674–700.
- FULLER, R. C. & NOA, L. A. (2010). Female mating preferences, lighting environment, and a test of the sensory bias hypothesis in the bluefin killifish. *Animal Behaviour* **80**, 23–35.
- GERALD, M. S., AYALA, J., RUÍZ-LAMBIDES, A., WAITT, C. & WEISS, A. (2010). Do females pay attention to secondary sexual coloration in vervet monkeys (*Chlorocebus aethiops*)? *Naturwissenschaften* **97**, 89–96.
- GIURFA, M., VOROBYEV, M., BRANDT, R., POSNER, B. & MENZEL, R. (1997). Discrimination of coloured stimuli by honeybees: alternative use of achromatic and chromatic signals. *Journal of Comparative Physiology A* **180**, 235–243.
- GIURFA, M., VOROBYEV, M., KEVAN, P. & MENZEL, R. (1996). Detection of coloured stimuli by honeybees: minimum visual angles and receptor specific contrasts. *Journal of Comparative Physiology A* **178**, 699–709.
- GOLDSMITH, T. H. (1990). Optimization, constraint, and history in the evolution of eyes. *Quarterly Review of Biology* **65**, 281–322.
- GOTO, T. & KONDO, T. (1991). Structure and molecular stacking of anthocyanins—flower color variation. *Angewandte Chemie International Edition English* **30**, 17–33.
- GRILL, C. P. & RUSH, V. N. (2000). Analysing spectral data: comparison and application of two techniques. *Biological Journal of the Linnean Society* **69**, 121–138.
- GUILFORD, T. & DAWKINS, M. S. (1991). Receiver psychology and the evolution of animal signals. *Animal Behaviour* **42**, 1–14.
- GUMBERT, A., KUNZE, J. & CHITTKA, L. (1999). Floral colour diversity in plant communities, bee colour space and a null model. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **266**, 1711–1716.
- HAM, A. & OSORIO, D. (2007). Colour preferences and colour vision in poultry chicks. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **274**, 1941–1948.
- HAMILTON, D. G., WHITING, M. J. & PRYKE, S. R. (2013). Fiery frills: carotenoid-based coloration predicts contest success in frillneck lizards. *Behavioral Ecology* **24**, 1138–1149.
- HANLEY, D., STODDARD, M. C., CASSEY, P. & BRENNAN, P. L. (2013). Eggshell conspicuousness in ground nesting birds: do conspicuous eggshells signal nest location to conspecifics? *Avian Biology Research* **6**, 147–156.

- HASLER, D. & SUESSTRUNK, S. E. (2003). Measuring colorfulness in natural images. In *Electronic Imaging 2003*, pp. 87–95. International Society for Optics and Photonics, Baitimore.
- HAUSER, F. E., VAN HAZEL, I. & CHANG, B. S. (2014). Spectral tuning in vertebrate short wavelength-sensitive 1 (SWS1) visual pigments: can wavelength sensitivity be inferred from sequence data? *Journal of Experimental Zoology Part B* **322**, 529–539.
- HAYFIELD, T. & JEFFREY, S. R. (2008). Nonparametric econometrics: the *np* package. *Journal of Statistical Software* **27**(5), 1–32.
- HEBETS, E. A. & PAPA, D. R. (2005). Complex signal function: developing a framework of testable hypotheses. *Behavioral Ecology and Sociobiology* **57**, 197–214.
- HEMPEL, D. I., GIURFA, M. & VOROBYEV, M. V. (2001). Detection of coloured patterns by honeybees through chromatic and achromatic cues. *Journal of Comparative Physiology A* **187**, 215–224.
- HOFMANN, C. M., O'QUIN, K. E., SMITH, A. R. & CARLETON, K. L. (2010). Plasticity of opsin gene expression in cichlids from Lake Malawi. *Molecular Ecology* **19**, 2064–2074.
- HOPKINS, R. & RAUSHER, M. D. (2012). Pollinator-mediated selection on flower color allele drives reinforcement. *Science* **335**, 1090–1092.
- HYVÄRINEN, A. & OJA, E. (2000). Independent component analysis: algorithms and applications. *Neural Networks* **13**, 411–430.
- INGLE, D. J. (1985). The goldfish as a retinal animal. *Science* **227**, 651–654.
- JACOBS, G. (1993). *Comparative Color Vision*. Elsevier, Amsterdam.
- JACOBS, G. H. (2008). Primate color vision: a comparative perspective. *Visual Neuroscience* **25**, 619–633.
- DE JAGER, M. L., DREYER, L. L. & ELLIS, A. G. (2011). Do pollinators influence the assembly of flower colours within plant communities? *Oecologia* **166**, 543–553.
- JAMESON, D. & HURVITZ, L. M. (1964). Theory of brightness and color contrast in human vision. *Vision Research* **4**, 135–154.
- JOHANSSON, J.-O. (2000). Measuring homogeneity of planar point-patterns by using kurtosis. *Pattern Recognition Letters* **21**, 1149–1156.
- JONES, C., OSORIO, D. & BADDELEY, R. (2001). Colour categorization by domestic chicks. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **268**, 2077–2084.
- JUNKER, R. R., BLÜTHGEN, N., BREHM, T., BINKENSTEIN, J., PAULUS, J., SCHAEFER, H. M. & STANG, M. (2013). Specialisation on traits as basis for the niche-breadth of flower visitors and as structuring mechanism of ecological networks. *Functional Ecology* **27**, 329–341.
- KATZENBERGER, T. D., LUNAU, K. & JUNKER, R. R. (2013). Salience of multimodal flower cues manipulates initial responses and facilitates learning performance of bumblebees. *Behavioral Ecology and Sociobiology* **67**, 1587–1599.
- KELBER, A. & OSORIO, D. (2010). From spectral information to animal colour vision: experiments and concepts. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **277**, 1617–1625.
- KELBER, A., VOROBYEV, M. & OSORIO, D. (2003). Animal colour vision—behavioural tests and physiological concepts. *Biological Reviews* **78**, 81–118.
- KOSHITAKA, H., KINOSHITA, M., VOROBYEV, M. & ARIKAWA, K. (2008). Tetrachromacy in a butterfly that has eight varieties of spectral receptors. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **275**, 947–954.
- VON KRIES, J. (1904). Die Gesichtsempfindungen. In *Handbuch der Physiologie des Menschen* (Volume 3, ed. W. NAGEL), pp. 109–282. Vieweg und Sohn, Braunschweig.
- KUEHNI, R. G. (2003). *Color Space and its Divisions*. John Wiley & Sons, Hoboken.
- LANCASTER, J. E., LISTER, C. E., READY, P. F. & TRIGGS, C. M. (1997). Influence of pigment composition on skin color in a wide range of fruit and vegetables. *Journal American Society for Horticultural Science* **122**, 594–598.
- LAND, E. H. (1977). The retinex theory of color vision. *Scientific American* **237**, 108–128.
- LANDE, R. (1981). Models of speciation by sexual selection on polygenic traits. *Proceedings of the National Academy of Sciences of the United States of America* **78**, 3721–3725.
- LANGMORE, N. E., STEVENS, M., MAURER, G., HEINSOHN, R., HALL, M. L., PETERS, A. & KILNER, R. M. (2011). Visual mimicry of host nestlings by cuckoos. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **278**, 2455–2463.
- LEAL, M. & FLEISHMAN, L. J. (2004). Differences in visual signal design and detectability between allopatric populations of Anolis lizards. *American Naturalist* **163**, 26–39.
- LENZ, R., ÖSTERBERG, M., HILTUNEN, J., JAASKELAINEN, T. & PARKKINEN, J. (1996). Unsupervised filtering of color spectra. *Journal of the Optical Society of America A* **13**, 1315–1324.
- LIND, O. & KELBER, A. (2009). Avian colour vision: effects of variation in receptor sensitivity and noise data on model predictions as compared to behavioural results. *Vision Research* **49**, 1939–1947.
- LIPETZ, L. E. (1971). The relation of physiological and psychological aspects of sensory intensity. In *Principles of Receptor Physiology* (ed. W. R. LOEWENSTEIN), pp. 191–225. Springer, Berlin.
- LONG, F., YANG, Z. & PURVES, D. (2006). Spectral statistics in natural scenes predict hue, saturation and brightness. *Proceedings of the National Academy of Sciences of the United States of America* **103**, 6013–6018.
- LOTTO, R. B. & WICKLEIN, M. (2005). Bees encode behaviorally significant spectral relationships in complex scenes to resolve stimulus ambiguity. *Proceedings of the National Academy of Sciences of the United States of America* **102**, 16870–16874.
- LYNN, S. K., CNAANI, J. & PAPA, D. R. (2005). Peak shift discrimination learning as a mechanism of signal evolution. *Evolution* **59**, 1300–1305.
- MACLEOD, D. I. A. & BOYNTON, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *Journal of the Optical Society of America A* **69**, 1183–1186.
- MADDOCKS, S. A., CHURCH, S. C. & CUTHILL, I. C. (2001). The effects of the light environment on prey choice by zebra finches. *Journal of Experimental Biology* **204**, 2509–2515.
- MAIA, R., RUBENSTEIN, D. R. & SHAWKEY, M. D. (2013). Key ornamental innovations facilitate diversification in an avian radiation. *Proceedings of the National Academy of Sciences of the United States of America* **110**, 10687–10692.
- MALONEY, L. T. (1986). Evaluation of linear models of surface spectral reflectance with small numbers of parameters. *Journal of the Optical Society of America A* **6**, 318–322.
- MC EWEN, J. & VAMOSI, J. C. (2010). Floral colour versus phylogeny in structuring subalpine flowering communities. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **277**, 2957–2965.
- MCGHEE, G. R. (2007). *The Geometry of Evolution: Adaptive Landscapes and Theoretical Morphospaces*. Cambridge University Press, New York.
- MCGRAW, K. J., NOLAN, P. M. & CRINO, O. L. (2011). Carotenoids bolster immunity during moult in a wild songbird with sexually selected plumage coloration. *Biological Journal of the Linnean Society* **102**, 560–572.
- MENZEL, R. & SCHMIDA, A. (1993). The ecology of flower colours and the natural colour vision of insect pollinators: the Israeli flora as a study case. *Biological Reviews* **68**, 81–120.
- MERILAITA, S. & RUXTON, G. D. (2007). Aposematic signals and the relationship between conspicuousness and distinctiveness. *Journal of Theoretical Biology* **245**, 268–277.
- MERILAITA, S. & STEVENS, M. (2011). Crypsis through background matching. In *Animal Camouflage—Mechanisms and Function* (eds M. STEVENS and S. MERILAITA), pp. 17–33. Cambridge University Press, Cambridge.
- MUCHHALA, N., JOHNSEN, S. & SMITH, S. D. (2014). Competition for hummingbird pollination shapes flower color variation in Andean Solanaceae. *Evolution* **68**, 2275–2286.
- Munsell Color Company, Inc. (1976). *Munsell Book of Color. Matte Finish Collection*. Munsell Color, Baltimore.
- NEUMEYER, C. (1981). Chromatic adaptation in the honeybee: successive color contrast and color constancy. *Journal of Comparative Physiology A* **144**, 543–553.
- NEUMEYER, C. (1998). Comparative colour constancy. In *Perceptual Constancy: Why Things Look as They Do* (eds V. WALSH and J. KULKOWSKI), pp. 352–372. Cambridge University Press, Cambridge.
- NIGGEBRÜGGE, C., LÉBOULLE, G., MENZEL, R., KOMISCHKE, B. & DE IBARRA, N. H. (2009). Fast learning but coarse discrimination of colours in restrained honeybees. *Journal of Experimental Biology* **212**, 1344–1350.
- OSORIO, D., HAM, A. D., GONDA, Z. & ANDREW, R. J. (2009). Sensory generalization and learning about novel colours by poutry chicks. *Quarterly Journal of Experimental Psychology* **62**, 1249–1256.
- OSORIO, D. & VOROBYEV, M. (2005). Photoreceptor spectral sensitivities in terrestrial animals: adaptations for luminance and colour vision. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **272**, 1745–1752.
- OSORIO, D. & VOROBYEV, M. (2008). A review of the evolution of animal colour vision and visual communication signals. *Vision Research* **48**, 2042–2051.
- PAPADOPULOS, A. S., POWELL, M. P., PUPULIN, F., WARNER, J., HAWKINS, J. A., SALAMIN, N., CHITTKA, L., WILLIAMS, N. H., WHITTEN, W. M. & LOADER, D. (2013). Convergent evolution of floral signals underlies the success of Neotropical orchids. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **280**, 20130960.
- PIKE, T. W. (2012). Preserving perceptual distances in chromaticity diagrams. *Behavioral Ecology* **23**, 723–728.
- PORTER, S. (2013). Adaptive divergence in seed color camouflage in contrasting soil environments. *New Phytologist* **197**, 1311–1320.
- PRUM, R. O. (2012). Aesthetic evolution by mate choice: Darwin's really dangerous idea. *Philosophical Transactions of the Royal Society B* **367**, 2253–2265.
- RAMANATH, R., KUEHNI, R. G., SNYDER, W. E. & HINKS, D. (2004). Spectral spaces and color spaces. *Color Research and Application* **29**, 29–37.
- RAUSHER, M. D. (2008). Evolutionary transitions in floral color. *International Journal of Plant Sciences* **169**, 7–21.
- REGAN, B., JULLIOT, C., SIMMEN, B., VIENOT, F., CHARLES-DOMINIQUE, P. & MOLLON, J. D. (1998). Frugivory and colour vision in *Alouatta seniculus*, a trichromatic platyrrhine monkey. *Vision Research* **38**, 3321–3327.
- REGAN, B. C., JULLIOT, C., SIMMEN, B., VIENOT, F., CHARLES-DOMINIQUE, P. & MOLLON, J. D. (2001). Fruits, foliage and the evolution of primate colour vision. *Philosophical Transactions Royal Society of London, Series B: Biological Sciences* **356**, 229–283.
- RENOULT, J. P., COURTIOL, A. & KJELLBERG, F. (2010). When assumptions on visual system evolution matter: nestling colouration and parental visual performance in birds. *Journal of Evolutionary Biology* **23**, 220–226.
- RENOULT, J. P., COURTIOL, A. & SCHAEFER, H. M. (2013a). A novel framework to study colour signaling to multiple species. *Functional Ecology* **27**, 718–729.

- RENOULT, J. R., SCHAEFER, H. M., SALLÉ, B. & CHARPENTIER, M. J. E. (2011). The evolution of the multicoloured face of mandrills: insights from the perceptual space of colour vision. *PLoS One* **6**, e29117.
- RENOULT, J. P., THOMANN, M., SCHAEFER, H. M. & CHEPTOU, P.-O. (2013b). Selection on quantitative colour variation in *Centaurea cyanus*: the role of the pollinator's visual system. *Journal of Evolutionary Biology* **26**, 2415–2427.
- RICK, I. P., MEHLIS, M. & BAKKER, T. C. M. (2011). Male red ornamentation is associated with female red sensitivity in sticklebacks. *PLoS One* **6**, e25554.
- ROSENTHAL, G. G. & RYAN, M. J. (2011). Conflicting preferences within females: sexual selection versus species recognition. *Biology Letters* **7**, 525–527.
- RYAN, M. J. & CUMMINGS, M. E. (2013). Perceptual biases and mate choice. *Annual Review of Ecology and Evolution* **44**, 437–459.
- SCHAEFER, H. M., MCGRAW, K. & CATONI, C. (2008). Birds use fruit colour as honest signal of dietary antioxidant rewards. *Functional Ecology* **22**, 303–310.
- SCHEMSKE, D. W. & BRADSHAW, H. D. (1999). Pollinator preference and the evolution of floral traits in monkeyflowers (*Mimulus*). *Proceedings of the National Academy of Sciences of the United States of America* **96**, 11910–11915.
- SCHLUTER, D. & PRICE, T. (1993). Honesty, perception and population divergence in sexually selected traits. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **253**, 117–122.
- SCHMIDT, V., SCHAEFER, H. M. & WINKLER, H. (2004). Conspicuousness, not colour as foraging cue in plant-animal signalling. *Oikos* **106**, 551–557.
- SECONDI, J. & THÉRY, M. (2014). An ultraviolet signal generates a conflict between sexual selection and species recognition in a newt. *Behavioral Ecology and Sociobiology* **48**, 1049–1058.
- SHRESTHA, M., DYER, A. G., BOYD-GERNY, S., WONG, B. B. M. & BURD, M. (2013). Shades of red: bird-pollinated flowers target the specific colour discrimination abilities of avian vision. *New Phytologist* **190**, 301–310.
- SIDDIQI, A., CRONIN, T. W., LOEW, E. R., VOROBYEV, M. & SUMMERS, K. (2004). Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. *Journal of Experimental Biology* **207**, 2471–2485.
- SKORUPSKI, P. & CHITTKA, L. (2009). Is colour cognitive? *Optics & Laser Technology* **43**, 251–260.
- SMITH, V. C. & POKORNY, J. (1975). Spectral sensitivity of the foveal cone photopigments between 400 and 500 nm. *Vision Research* **15**, 161–171.
- SPAETHE, J., TAUTZ, J. & CHITTKA, L. (2001). Visual constraints in foraging bumblebees: flower size and color affect search time and flight behavior. *Proceedings of the National Academy of Sciences of the United States of America* **98**, 3898–3903.
- SPOTTISWOODE, C. N. & STEVENS, M. (2012). Host-parasite arms races and rapid changes in bird egg appearance. *American Naturalist* **179**, 633–648.
- STEVENS, S. S. (1961). To honor Fechner and repeal his law. *Science* **133**, 80–86.
- STEVENS, M. (2013). *Sensory Ecology, Evolution, & Behaviour*. Oxford University Press, Oxford.
- STEVENS, M., HARDMAN, C. J. & STUBBINS, C. L. (2008). Conspicuousness, not eye mimicry, makes "eyespot" effective antipredator signals. *Behavioral Ecology* **19**, 525–531.
- STEVENS, M., LOWN, A. E. & WOOD, L. E. (2014a). Camouflage and individual variation in shore crabs (*Carcinus maenas*) from different habitats. *PLoS One* **9**, e115586.
- STEVENS, M., LOWN, A. E. & WOOD, L. E. (2014b). Color change and camouflage in juvenile shore crabs *Carcinus maenas*. *Frontiers in Ecology and Evolution* **2**, 14.
- STEVENS, M., PÁRRAGA, C. A., CUTHILL, I. C., PARTRIDGE, J. C. & TROSCIANKO, T. S. (2007). Using digital photography to study animal coloration. *Biological Journal of the Linnean Society of London* **90**, 211–237.
- STEVENS, M., STODDARD, M. C. & HIGHAM, J. P. (2009). Studying primate color: towards visual system-dependent methods. *International Journal of Primatology* **30**, 893–917.
- STILES, S. (1946). A modified Helmholtz line element in brightness-colour space. *Proceedings of the Physical Society of London* **58**, 41–51.
- STOBBE, N. & SCHAEFER, H. M. (2008). Enhancement of chromatic contrast increases predation risk for striped butterflies. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **275**, 1535–1541.
- STODDARD, M. C. (2012). Mimicry and masquerade from the avian visual perspective. *Current Zoology* **58**, 630–648.
- STODDARD, M. C. & PRUM, R. O. (2008). Evolution of avian plumage color in a tetrahedral color space: a phylogenetic analysis of new world buntings. *American Naturalist* **171**, 755–776.
- STODDARD, M. C. & PRUM, R. O. (2011). How colorful are birds? Evolution of the avian plumage color gamut. *Behavioral Ecology* **22**, 1042–1052.
- STODDARD, M. C. & STEVENS, M. (2011). Avian vision and the evolution of egg color mimicry in the common cuckoo. *Evolution* **65**, 2004–2013.
- STOURNARAS, K. E., LO, E., BÖHNING-GAESE, K., CAZETTA, E., DEHLING, D. M., SCHLEUNING, M., STODDARD, M. C., DONOGHUE, M. J., PRUM, R. O. & SCHAEFER, H. M. (2013). How colorful are fruits? Limited color diversity in fleshy fruits on local and global scales. *New Phytologist* **198**, 617–629.
- STOURNARAS, K. E., PRUM, R. O. & SCHAEFER, H. M. (2015). Fruit advertisement strategies in two Neotropical plant-seed disperser markets. *Evolutionary Ecology* **29**, 489–509.
- STUART, Y. E., DAPPEN, N. & LOSIN, N. (2012). Inferring predator behavior from attack rates on prey-replicas that differ in conspicuousness. *PLoS One* **7**, e48497.
- STUART-FOX, D. & MOUSSALLI, A. (2008). Selection for social signalling drives the evolution of chameleon colour change. *PLoS Biology* **6**, 22–29.
- SVAETICHIN, G. (1956). Spectral response curves from single cones. *Acta Physiologica Scandinavica* **39**, 17–46.
- TASTARD, E., ANDALO, C., GIURFA, M., BURRUS, M. & THÉBAUD, C. (2008). Flower colour variation across a hybrid zone in *Antirrhinum* as perceived by bumblebee pollinators. *Arthropod-Plant Interactions* **2**, 237–246.
- TEMPLE, S. (2011). Why different regions of the retina have different spectral sensitivities: a review of mechanisms and functional significance of intraretinal variability in spectral sensitivity in vertebrates. *Visual Neuroscience* **28**, 281–293.
- THÉRY, M. & CASAS, J. (2002). Predator and prey views of spider camouflage. *Nature* **415**, 133.
- THÉRY, M., DEBUT, M., GOMEZ, D. & CASAS, J. (2005). Specific color sensitivities of prey and predator explain camouflage in different visual systems. *Behavioral Ecology* **16**, 25–29.
- TZENG, D. Y. & BERNS, R. S. (2005). A review of principal component analysis and its applications to color technology. *Color Research & Application* **30**, 84–98.
- UCHIKAWA, K. & IKEDA, M. (1981). Temporal deterioration of wavelength discrimination with successive comparison method. *Vision Research* **21**, 591–595.
- VOGEL, E. R., NEITZN, M. & DOMINY, N. J. (2007). Effect of color vision phenotype on the foraging of wild white-faced capuchins, *Cebus capucinus*. *Behavioral Ecology* **18**, 292–297.
- VOROBYEV, M. (2003). Coloured oil droplets enhance colour discrimination. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **270**, 1255–1261.
- VOROBYEV, M., BRANDT, R., PEITSCH, D., LAUGHLIN, S. B. & MENZEL, R. (2001). Colour thresholds and receptor noise: behaviour and physiology compared. *Vision Research* **41**, 639–653.
- VOROBYEV, M. & OSORIO, D. (1998). Receptor noise as a determinant of colour thresholds. *Proceedings of the Royal Society of London, Series B: Biological Sciences* **265**, 351–358.
- VOROBYEV, M., OSORIO, D., BENNETT, A. T. D., MARSHALL, N. J. & CUTHILL, I. C. (1998). Tetrachromacy, oil droplets and bird plumage colours. *Journal of Comparative Physiology A* **183**, 621–633.
- WALSH, V. & KULIKOWSKI, J. (1998). *Perceptual Constancy: Why Things Look as They Do*. Cambridge University Press, New-York.
- WHIBLEY, A. C., LANGLADE, N. B., ANDALO, C., HANNA, A. I., BANGHAM, A., THÉBAUD, C. & COEN, E. (2006). Evolutionary paths underlying flower color variation in *Antirrhinum*. *Science* **313**, 963–966.
- WYSZECKI, G. & STILES, W. S. (1982). *Color Science: Concepts and Methods, Quantitative Data and Formulae*. Second Edition. Wiley, New-York.

XI. APPENDIX

(1) Equations for modelling psychophysical colour spaces

The following equations allow calculating coordinates of coloured stimuli with different models of colour space. We assumed that input data are reflectance spectra, but the models can be used with photon catches directly retrieved from calibrated digital images (e.g. Stevens *et al.*, 2007; Porter, 2013; Stevens, Lown & Wood, 2014b). The different photoreceptor types in a given organism are labelled using subscript i , with i increasing with the wavelength of maximal photoreceptor sensitivity. In all but the colour opponent coding model of bee colour vision (Backhaus, 1991), chromatic distances between two stimuli can then be estimated in the colour space using Pythagorean distance formulae.

(a) The four main steps of psychophysical models

All models start by calculating the number Q of photons reflected by stimulus n and caught by photoreceptor type i

(step 1 in Section II.3):

$$Q_{p,i} = \int_{\lambda} R_n(\lambda) S_i(\lambda) d(\lambda) \quad (\text{A1.1})$$

where $S_i(\lambda)$ is the sensitivity function of photoreceptor i and $R_n(\lambda)$ is the reflectance spectrum of stimulus n . Thus defined, the photon catch is based on the assumption of an ideal, perfectly white illuminant. A photon catch version accounting for the coloured nature of the illuminant is given by:

$$Q_{p,i} = \int_{\lambda} R_n(\lambda) S_i(\lambda) I(\lambda) d(\lambda) \quad (\text{A1.2})$$

where $I(\lambda)$ is the illuminant spectrum. If the influence of background colouration is disregarded, then the normalised photon catch $q_{n,i}$ is (normalisation by 1)

$$q_{n,i} = Q_{p,i}. \quad (\text{A1.3})$$

Alternatively, photon catches from the studied item can be normalised by the photon catch from the background $R_{back}(\lambda)$ to model chromatic adaptation (step 1 in Section II.3). Following the von Kries transformation:

$$q_{n,i} = \frac{Q_{p,i}}{Q_{back,i}} \quad (\text{A1.4})$$

where $Q_{back,i}$ is the photon catch from the background. If no further transformation is applied to $q_{n,i}$, photoreceptor signals $s_{n,i}$ are linearly related to photon catches:

$$s_{n,i} = q_{n,i}. \quad (\text{A1.5})$$

Alternatively, photoreceptor signals can be nonlinearly related to photon catches (step 3 in Section II.3). A nonlinear relationship is modelled using a logarithmic (Weber–Fechner law):

$$s_{n,i} = \ln(q_{n,i}) \quad (\text{A1.6})$$

or hyperbolic transformation:

$$s_{n,i} = \frac{q_{n,i}}{1 + q_{n,i}}. \quad (\text{A1.7})$$

Eventually, opponent mechanisms can be coded by combining $s_{n,i}$ from the different photoreceptors (step 4 in Section II.3).

(b) *Basic models without chromatic adaptation, nonlinear transformation and opponent receptor processing*

$s_{n,i}$ is first calculated using Equations A1.1 + A1.3 + A1.5. Then, the chromaticity diagram is extracted by removing

the achromatic dimension ($\sum_i s_{n,i} = 1$), which gives intensity-normalized photoreceptor signals $s_{n,i}^c$:

$$s_{n,i}^c = \frac{s_{n,i}}{\sum_i s_{n,i}}. \quad (\text{A1.8})$$

For dichromatic vision, the chromaticity diagram is a segment, along which the coordinate of stimulus n is calculated as:

$$\{x_n\} = \left\{ \frac{1}{\sqrt{2}} (s_{n,2}^c - s_{n,1}^c) \right\} \quad (\text{A1.9})$$

with end points coordinates:

$$\{x_{i=1}\} = \left\{ \frac{-1}{\sqrt{2}} \right\}; \{x_{i=2}\} = \left\{ \frac{1}{\sqrt{2}} \right\}. \quad (\text{A1.10})$$

For trichromatic vision, the diagram is the Maxwell triangle (MacLeod & Boynton, 1979), in which coordinates are calculated as (Kelber *et al.*, 2003):

$$\{x_n, y_n\} = \left\{ \frac{1}{\sqrt{2}} (s_{n,3}^c - s_{n,2}^c), \frac{\sqrt{2}}{\sqrt{3}} \left(s_{n,1}^c - \frac{s_{n,3}^c + s_{n,2}^c}{2} \right) \right\} \quad (\text{A1.11})$$

with the apex coordinates:

$$\begin{aligned} \{x_{i=1}, y_{i=1}\} &= \left\{ 0, \frac{\sqrt{2}}{\sqrt{3}} \right\}; \\ \{x_{i=2}, y_{i=2}\} &= \left\{ -\frac{1}{\sqrt{2}}, \frac{-\sqrt{2}}{2\sqrt{3}} \right\}; \\ \{x_{i=3}, y_{i=3}\} &= \left\{ -\frac{1}{\sqrt{2}}, \frac{-\sqrt{2}}{2\sqrt{3}} \right\}. \end{aligned} \quad (\text{A1.12})$$

Equation A1.8 is intended to define a subspace of constant luminance within the photoreceptor excitation space. Because the equation gives equal weight to all photoreceptors, in humans where the first photoreceptor almost does not contribute to luminance, the subspace is not isoluminant. MacLeod & Boynton (1979) proposed a different coordinate system that deals with this issue, by normalizing intensity with signals from the second and third photoreceptors only (note the use of $s_{n,i}$ instead of $s_{n,i}^c$):

$$\{x_n, y_n\} = \left\{ \frac{s_{n,3}}{s_{n,3} + s_{n,2}}, \frac{s_{n,1}}{s_{n,3} + s_{n,2}} \right\}. \quad (\text{A1.13})$$

Regan *et al.* (1998) applied the MacLeod and Boynton diagram to non-human trichromatic monkeys. Their model differs from the original model only by assuming different photoreceptor sensitivity curves and by accounting for the illuminant spectrum (Equation A1.2 instead of Equation A1.1). Regan *et al.* (2001) further adapted the

model to the dichromatic vision of New World primates. The coordinate along the chromatic line is then given by:

$$\{x_n\} = \left\{ \begin{matrix} s_{n,1} \\ s_{n,2} \end{matrix} \right\}. \tag{A1.14}$$

Be careful that with our notation, for primates $s_{n,2}$ describes the so-called ‘receptor M’ in Equations A1.9 and A1.10 and Equation A1.14, and ‘receptor L’ in Equations A1.11–A1.13.

For tetrachromatic vision, the diagram is the Goldsmith tetrahedron (Goldsmith, 1990), in which coordinates are calculated as (Kelber *et al.*, 2003):

$$\{x_n, y_n, z_n\} = \left\{ \begin{matrix} \frac{1}{\sqrt{2}} (s_{n,4}^c - s_{n,3}^c), \\ \frac{\sqrt{2}}{\sqrt{3}} \left(s_{n,2}^c - \frac{s_{n,4}^c + s_{n,3}^c}{2} \right), \\ \frac{\sqrt{3}}{2} \left(s_{n,1}^c - \frac{s_{n,3}^c + s_{n,2}^c + s_{n,1}^c}{3} \right) \end{matrix} \right\} \tag{A1.15}$$

with the vertex coordinates:

$$\begin{aligned} \{x_{i=1}, y_{i=1}, z_{i=1}\} &= \left\{ 0, 0, \frac{\sqrt{3}}{2} \right\}; \\ \{x_{i=2}, y_{i=2}, z_{i=2}\} &= \left\{ 0, \frac{\sqrt{2}}{\sqrt{3}}, \frac{-1}{2\sqrt{3}} \right\}; \\ \{x_{i=3}, y_{i=3}, z_{i=3}\} &= \left\{ -\frac{1}{\sqrt{2}}, \frac{-\sqrt{2}}{2\sqrt{3}}, \frac{-1}{2\sqrt{3}} \right\}; \\ \{x_{i=4}, y_{i=4}, z_{i=4}\} &= \left\{ \frac{1}{\sqrt{2}}, \frac{-\sqrt{2}}{2\sqrt{3}}, \frac{-1}{2\sqrt{3}} \right\}. \end{aligned} \tag{A1.16}$$

Stoddard & Prum (2008) proposed a different derivation from Equation A1.8 to build the Goldsmith tetrahedron. The difference is purely arbitrary and has no biological meaning:

$$\{x_n, y_n, z_n\} = \left\{ \begin{matrix} \frac{\sqrt{3}}{\sqrt{2}} \left(\frac{1 - 2s_{n,2}^c - s_{n,3}^c - s_{n,1}^c}{2} \right), \\ \frac{-1 + 3s_{n,3}^c - s_{n,1}^c}{2\sqrt{2}}, s_{n,1}^c - \frac{1}{4} \end{matrix} \right\} \tag{A1.17}$$

with the vertex coordinates:

$$\begin{aligned} \{x_{i=1}, y_{i=1}, z_{i=1}\} &= \left\{ 0, -\frac{1}{\sqrt{2}}, \frac{3}{4} \right\}; \\ \{x_{i=2}, y_{i=2}, z_{i=2}\} &= \left\{ -\frac{\sqrt{3}}{2\sqrt{2}}, -\frac{1}{2\sqrt{2}}, -\frac{1}{4} \right\}; \\ \{x_{i=3}, y_{i=3}, z_{i=3}\} &= \left\{ 0, \frac{1}{\sqrt{2}}, -\frac{1}{4} \right\}; \\ \{x_{i=4}, y_{i=4}, z_{i=4}\} &= \left\{ \frac{\sqrt{3}}{2\sqrt{2}}, -\frac{1}{2\sqrt{2}}, -\frac{1}{4} \right\}. \end{aligned} \tag{A1.18}$$

(c) *Basic models with chromatic adaptation and nonlinear transformation, without opponent receptor processing*

Endler & Mielke (2005) proposed a chromaticity diagram that models bird colour vision using Equations A1.2 + A1.4 + A1.6 + A1.8 + A1.17. The tetrahedron models general and widespread mechanisms of chromatic adaptation and nonlinear transformation and thus can be used with any tetrachromatic organism. More generally, all models detailed above can be adapted to account for these two physiological mechanisms.

(d) *Basic opponent model*

An example of the basic opponent model is given by the bee colour hexagon (Chittka, 1992). The model first calculates photoreceptor signals while accounting for the illuminant, chromatic adaptation and nonlinear transformation (Equations A1.2 + A1.4 + A1.7). Receptor signals are then combined to define two opponent coordinate axes:

$$\{x_n, y_n\} = \left\{ \begin{matrix} \sqrt{\frac{3}{2}} (s_{n,3} - s_{n,1}) ; \\ s_{n,2} - 0.5 (s_{n,1} + s_{n,3}) \end{matrix} \right\} \tag{A1.19}$$

with the vertex coordinates:

$$\begin{aligned} \{x_{i=1}, y_{i=1}\} &= \left\{ -\frac{\sqrt{3}}{2}, -\frac{1}{2} \right\}; \\ \{x_{i=1+2}, y_{i=1+2}\} &= \left\{ -\frac{\sqrt{3}}{2}, \frac{1}{2} \right\}; \\ \{x_{i=2}, y_{i=2}\} &= \{0, 1\}; \\ \{x_{i=2+3}, y_{i=2+3}\} &= \left\{ \frac{\sqrt{3}}{2}, \frac{1}{2} \right\}; \\ \{x_{i=3}, y_{i=3}\} &= \left\{ \frac{\sqrt{3}}{2}, -\frac{1}{2} \right\}; \\ \{x_{i=3+1}, y_{i=3+1}\} &= \{0, -1\}. \end{aligned} \tag{A1.20}$$

where $x_{i=1+2}$ gives the x coordinate of a stimulus maximally stimulating photoreceptors 1 and 2 simultaneously.

(e) *Scaled opponent models*

In these models, additional transformations are applied to photoreceptor signals such that the estimated colour distances match the psychophysical data. In the colour opponent coding model of bee colour vision (Backhaus, 1991), for example, $s_{n,i}$ is first calculated using Equations A1.2 + A1.4 + A1.7. The coordinates of stimulus n are then calculated along two opponent axes as:

$$\{x_n, y_n\} = \{-9.86s_{n,1} + 7.7s_{n,2} + 2.16s_{n,3}; -5.17s_{n,1} + 20.25s_{n,2} - 15.08s_{n,3}\}. \quad (\text{A1.21})$$

Here, the weights associated with each receptor signal have been estimated by multidimensional scaling of colour similarity experiments (Backhaus *et al.*, 1987). The chromatic distance D_n between two stimuli A and B is estimated using the city-block metric:

$$D_n = |x_A - x_B| + |y_A - y_B|. \quad (\text{A1.22})$$

The receptor noise limited (RNL) colour opponent models (Vorobyev *et al.*, 1998) assume that discrimination thresholds are set by receptor noise, which is thus used to scale chromatic distances. $s_{n,i}$ is first calculated using Equations A1.2 + A1.4 + A1.6. The coordinate of stimulus n along a chromatic segment (dichromatic vision) is then calculated as:

$$\{x_n\} = \left\{ \sqrt{\frac{1}{e_2^2 + e_3^2}} (s_{n,3} - s_{n,2}) \right\} \quad (\text{A1.23})$$

where e_i is the standard deviation of the noise in photoreceptor i . Coordinates within the triangle (trichromatic vision) are calculated as Hempel *et al.* (2001):

$$\{x_n, y_n\} = \left\{ \sqrt{\frac{1}{e_2^2 + e_3^2}} (s_{n,3} - s_{n,2}); \sqrt{\frac{e_2^2 + e_3^2}{(e_1e_2)^2 + (e_1e_3)^2 + (e_2e_3)^2}} \left(s_{n,1} - \left(s_{n,3} \frac{e_2^2}{e_2^2 + e_3^2} + s_{n,2} \frac{e_3^2}{e_2^2 + e_3^2} \right) \right) \right\} \quad (\text{A1.24})$$

and for tetrachromatic vision:

$$\{x_n, y_n, z_n\} = \left\{ \sqrt{\frac{1}{e_3^2 + e_4^2}} (s_{n,4} - s_{n,3}); \sqrt{\frac{e_3^2 + e_4^2}{(e_2e_3)^2 + (e_2e_4)^2 + (e_3e_4)^2}} \left(s_{n,2} - \left(s_{n,4} \frac{e_3^2}{e_3^2 + e_4^2} + s_{n,3} \frac{e_4^2}{e_3^2 + e_4^2} \right) \right); A(s_{n,1} - (as_{n,4} + bs_{n,3} + cs_{n,2})) \right\} \quad (\text{A1.25})$$

with

$$A = \sqrt{\frac{(e_3e_4)^2 + (e_2e_4)^2 + (e_2e_3)^2}{(e_2e_3e_4)^2 + (e_1e_3e_4)^2 + (e_1e_2e_4)^2 + (e_1e_2e_3)^2}} \quad (\text{A1.26})$$

$$a = \frac{(e_2e_3)^2}{(e_3e_4)^2 + (e_2e_3)^2 + (e_2e_4)^2} \quad (\text{A1.27})$$

$$b = \frac{(e_2e_4)^2}{(e_3e_4)^2 + (e_2e_3)^2 + (e_2e_4)^2} \quad (\text{A1.28})$$

$$c = \frac{(e_3e_4)^2}{(e_3e_4)^2 + (e_2e_3)^2 + (e_2e_4)^2} \quad (\text{A1.29})$$

The photoreceptor noise e_i has two components: the neural noise and the photon noise, which describe random neural stimulations that are independent of any external stimulation and the uncertainty for photoreceptors to capture photons striking the retina, respectively. In bright illumination, the photon noise is marginal (many photons) and the photoreceptor noise approximately equals the neural noise: $e_i = \omega/\sqrt{\eta_i}$, with ω the Weber fraction and η_i the relative density of photoreceptor i . In conditions of dim light, however, both the neural noise and the photon noise are important: $e_i = \sqrt{\omega^2/\eta_i + 1/Q_{n,i}}$, with $Q_{n,i}$ given by Equation A1.2. Critically, the Weber fraction is known for only a very limited number of species and seems quite variable among species. Thus, it is good practice to validate results using different Weber fractions.

Vorobyev & Osorio (1998) present a version of the RNL model with a linear phototransduction process (Equation A1.5 instead of Equation A1.6). With this model, colour distances are independent of the intensity of the stimulus in the vicinity of the achromatic point only, not throughout the colour space as with the log-linear version of the model (Kelber *et al.*, 2003).

The CIE $L^*a^*b^*$ model of human colour vision (CIE Publication, 1986) has the specificity of using the CIE XYZ tristimulus values as input data. This is because most devices in colour engineering measure colours in XYZ coordinates.

The tristimulus values can be calculated from reflectance and illuminant spectra as:

$$X_n = K \int_{\lambda} I(\lambda) x(\lambda) R_n(\lambda) d(\lambda); \quad (\text{A1.30})$$

$$Y_n = K \int_{\lambda} I(\lambda) y(\lambda) R_n(\lambda) d(\lambda); \quad (\text{A1.31})$$

$$Z_n = K \int_{\lambda} I(\lambda) z(\lambda) R_n(\lambda) d(\lambda); \quad (\text{A1.32})$$

$$K = 100 / \int_{\lambda} I(\lambda) y(\lambda) d(\lambda); \quad (\text{A1.33})$$

$x(\lambda), y(\lambda), z(\lambda)$ are the so-called matching functions, which can be retrieved in tabular form from <http://www.cvrl.org/cmfs.htm> and K is a normalising constant.

The model then includes a chromatic adaptation:

$$X'_n = X_n/X_{back}; Y'_n = Y_n/Y_{back}; Z'_n = Z_n/Z_{back} \quad (\text{A1.34})$$

where X_{back}, Y_{back} and Z_{back} are the tristimulus values for the background spectrum. This step is frequently termed the ‘wrong von Kries transformation’ because normalisation is performed on tristimulus values, not on photoreceptor responses. $L^*a^*b^*$ coordinates are eventually calculated as:

if $X'_n, Y'_n, Z'_n > 0.008856$:

$$L^* = 116Y_n'^{\frac{1}{3}} - 16; \quad (\text{A1.35})$$

$$a^* = 500 \left(X_n'^{\frac{1}{3}} - Y_n'^{\frac{1}{3}} \right); \quad (\text{A1.36})$$

$$b^* = 200 \left(Y_n'^{\frac{1}{3}} - Z_n'^{\frac{1}{3}} \right); \quad (\text{A1.37})$$

or if $X'_n, Y'_n, Z'_n \leq 0.008856$:

$$L^* = 903.29Y_n'^{\frac{1}{3}}; \quad (\text{A1.38})$$

$$a^* = 500 \left(7.787 \left(X_n' + \frac{16}{116} \right) - 7.787 \left(Y_n' + \frac{16}{116} \right) \right); \quad (\text{A1.39})$$

$$b^* = 200 \left(7.787 \left(Y_n' + \frac{16}{116} \right) - 7.787 \left(Z_n' + \frac{16}{116} \right) \right). \quad (\text{A1.40})$$

The cubit roots model the nonlinear transformations of receptor signals. L^* is correlated with the perceived lightness. The chromaticity diagram is given by the plane a^*b^* , with the two opponent axes a^* and b^* approximately describing

green to red (green in negative values) and blue to yellow (blue in negative values) variations, respectively.

(2) Chromatic adaptation and colour diversity

The von Kries transformation is used in two different ways in ecological literature. In the first approach, the signal spectrum is multiplied by the illuminant spectrum to compute signal photon catches. Signal photon catches are then normalised by catches of the illuminant photons (central equation in Fig. A1). This approach disregards the fact that photoreceptors adapt to the light arising from the whole visual scene (Land, 1977; Neumeyer, 1981), not only to the illuminating overhead light as modelled in the first approach. Adaptation to the average radiance spectra arising from the scene surrounding a target stimulus can be modelled normalising signal photon catches by background and illuminant photon catches (upper equation in Fig. A1; see also Hempel *et al.*, 2001; Kelber *et al.*, 2003). Crucially, the two approaches can yield different results regarding the study of colour diversity. Figure A1 illustrates this issue by mapping 32 colour stimuli in a chromaticity diagram (Equation A1.11), using both approaches of von

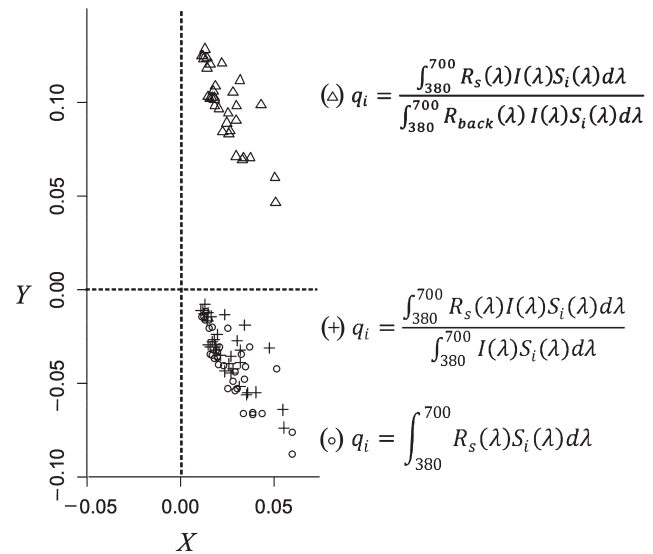


Fig. A1. Effect of chromatic adaptation on colour loci in a chromaticity diagram. For a given symbol, each point represents the location in the diagram of the average reflectance spectrum $R_s(\lambda)$ of the red face of one male mandrill (*Mandrillus sphinx*; $N = 32$; for details, see Renoult *et al.* (2011)). The chromaticity diagram is extracted from a photoreceptor excitation (without chromatic adaptation) or contrast (with chromatic adaptation) space. X and Y coordinates were calculated with quantum catches q_i computed without von Kries transformation and completely discounting the effect of the illuminant (circles), with a von Kries transformation modelling chromatic adaptation to the illuminant only (crosses), or with a von Kries transformation modelling chromatic adaptation to both the illuminant and the background (triangles). $I(\lambda)$ is an irradiance spectrum of forest shade (Endler, 1993) and the background $R_{back}(\lambda)$ an average reflectance spectrum of Marantaceae leaves.

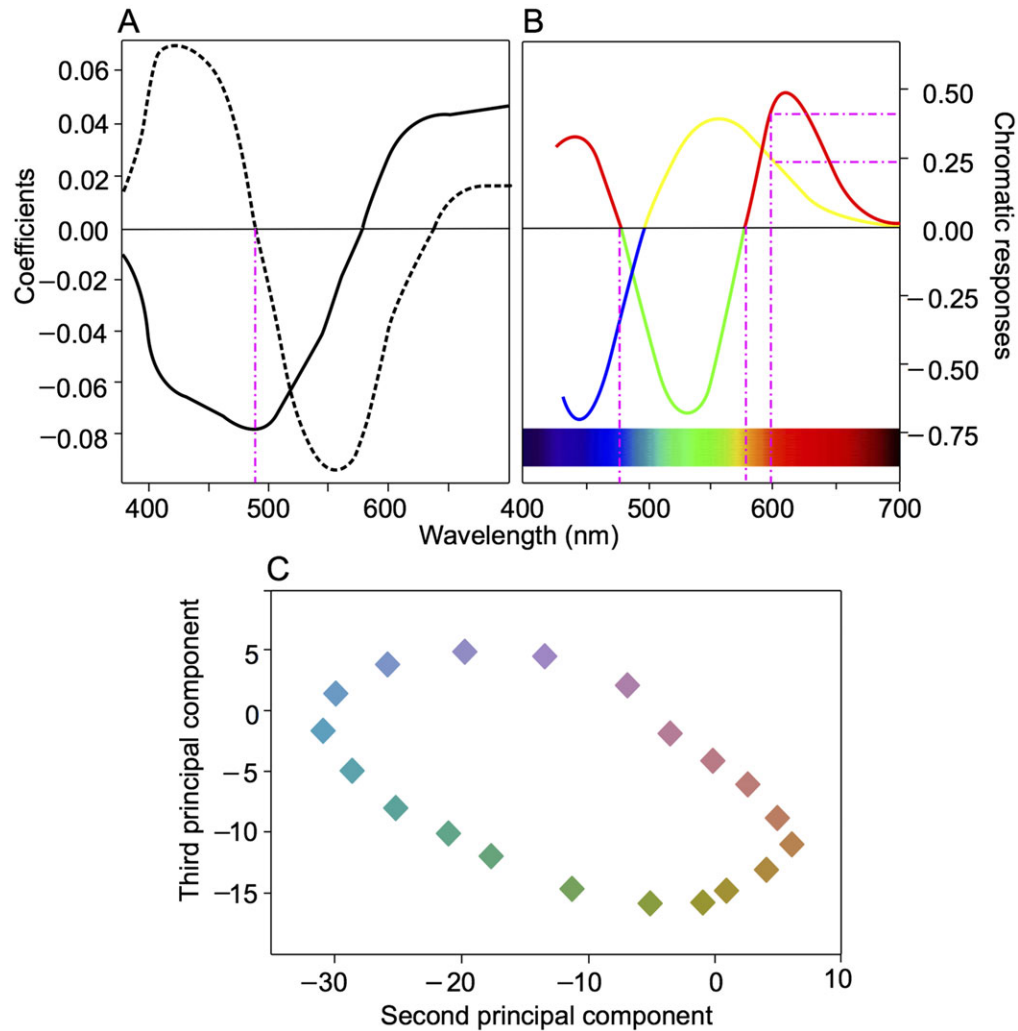


Fig. A2. Similarities between principal components and opponent functions. (A) Second (solid line) and third (black dashed line) principal components fitted to reflectance spectra of 1269 Munsell colour chips (redrawn from Lenz *et al.*, 1996). The graph reads as follows: stimuli rich in 490 nm-long light waves (see pink dashed line) have highly negative scores and null scores at the second and third principal components, respectively, in the spectral space. (B) Opponent colour functions for the CIE 2° standard observer (redrawn from Jameson & Hurvitch, 1964). All spectral hues can be matched by mixing either unique red or unique green to either unique blue or unique yellow. For example, an orange-reddish light peaking at approximately 600 nm can be matched by mixing unique yellow of intensity 0.25 with unique red of intensity 0.4. Unique blue and unique yellow are hues that contain neither red nor green; they peak at 475 and 580 nm, respectively. (C) Plot of 20 colour stimuli having hue evenly spaced in the Munsell colour system (chroma and lightness are constant) in a subspace defined by the two principal components represented in (A) (redrawn from Kuehni, 2003).

Kries transformation or no transformation at all (lower equation in Fig. A1). The 32 spectra are located similarly independent of whether the illuminant spectrum is accounted for (crosses and circles). Normalising for both the illuminant and the background spectra (triangles), however, shifted colours markedly. Importantly, colour stimuli vary in hue as much as in chroma when normalising photon catches for the background, but they vary almost exclusively in chroma otherwise. Modelling chromatic adaptation, and the way it is modelled thus has a strong influence on estimates of hue and chroma diversity.

(3) Spectral spaces: proxy to colour spaces?

Although the spectral space is an objective characterisation of colour trait variation, whether or not it encodes information on the perception of colours is an important topic in visual science (Ramanath *et al.*, 2004). Lenz *et al.* (1996) pointed out a resemblance between the second and third principal components of a PCA applied to hundreds of colour spectra and human opponent curves. The authors showed that these two components described variation in red–green and yellow–blue variation, respectively (Fig. A2A), which mirrors the two red–green and yellow–blue opponent channels

(Fig. A2B; see figure legend for details). The resemblance indicates that the principal components encode information on the human perception of the studied colour stimuli. This appears clearly when plotting in a spectral space equally light and equally saturated stimuli that gradually and evenly differ in hue (Fig. A2C). In the Munsell perceptual space, these stimuli would be arranged regularly in a circle. The elliptical shape visible in Fig. A2C means that the spectral space is not uniform, and thus that distances in a spectral space do not inform on perceptual distances. However, stimuli are organised in a proper ordinal manner. Correct ordination also occurs for stimuli varying in lightness and chroma (not shown; Kuehni, 2003).

Rather than saying that spectral spaces encode information on perception, a more correct interpretation of Lenz *et al.* (1996)'s results is that the evolution of human colour vision has been primarily driven by the physical characteristics of visual stimuli. Then the discrepancies between the spectral space and the Munsell psychological space (in particular, non-circularity in Fig. A2C) could originate from the fact that the spectral space was built

from stimuli that have not all been influential in the evolution of colour vision. In particular, the stimuli used by Lenz *et al.* (1996) are disproportionately saturated in comparison to natural stimuli (Kuehni, 2003). Although it remains to be tested, we anticipate that discrepancies would be reduced by retrieving principal components from a data set representative of the statistical distribution of colour stimuli constituting a typical forest scene, the visual environment that mainly contributed to shaping colour vision in Old World primates (see also Long, Yang & Purves, 2006).

It is likely that the visual systems of other animals also have been tuned in relation to the spectral characteristics of a subset of relevant visual stimuli. Thus, a principal or independent component space obtained with reflectance spectra relevant to studied species (e.g. of flowers visited by an insect) could represent a rough model of colour space when no or approximate data on colour vision are available, and when a correct ordination of stimuli only is necessary (e.g. when identifying innovative signals).

(Received 30 January 2015; revised 14 September 2015; accepted 17 September 2015)