

Studying Primate Color: Towards Visual System-dependent Methods

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Abstract Primates exhibit a striking diversity of colors and patterns in their pelage and skin markings, used in functions as diverse as camouflage to sexual signaling. In studying primate colors, it is important to adopt approaches not based on human assessment wherever possible, and that preferably take account of the visual system of the appropriate receiver(s). Here, we outline some of the main techniques for recording the colors exhibited and encountered by primates, including the use of digital photography and reflectance spectrometry. We go on to discuss the main approaches for analyzing the data obtained, including those not linked to a particular visual system, such as direct analyses of reflectance spectra. We argue that researchers should strive for analyses based on the visual system of the relevant receiver, and outline some of the main modeling approaches that can be used, such as color space and discrimination threshold modeling. By analyzing color measures with respect to specific visual systems, field studies can link behavioral ecology to the visual and cognitive sciences, and move toward descriptions of signal information content that incorporate elements of receiver psychology. This in turn should lead to a greater understanding of the detection and interpretation of signals by receivers, and hence their likely use in decision making.

Keywords coloration · color measurement · photography · primates · reflectance

Introduction

Adaptive coloration has provided numerous examples of both natural and sexual selection, and has revealed a great deal about adaptation and the evolution of

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signaling and sensory systems. The majority of studies of animal color have centered on comparatively striking animal groups, such as birds and insects. In comparison, relatively few studies have addressed ultimate and proximate questions of primate coloration, despite the fact that primates have a diverse range of visual signals involved with skin and pelage coloration, used in a variety of functions, from camouflage to sexual signaling, often have good color vision, and have a range of signal receivers, from conspecifics to predators (Bradley and Mundy 2008). Since early studies of primate color, which relied on human assessment of coloration (e.g., Bercovitch 1996; Isbell 1995; Setchell and Dixson 2001; Wickings and Dixson 1992), the more recent development of digital methods for color measurement, analysis, and stimuli production has heralded an increase in the number of studies that include color measures (Gerald *et al.* 2006a, 2007; Higham *et al.* 2008; Setchell *et al.* 2006). In studying primate color it is important to find methods to quantify color without using human subjectivity wherever possible, and preferably that consider the perception of color by the appropriate receiver's visual system (Ender 1990). Here, we discuss the principal ways that researchers can study the coloration of primates and other animals. We outline the different techniques that can be used to acquire data on coloration, with an emphasis on practical considerations, and then focus on how researchers can analyze and interpret this information.

Color and Luminance Perception

To find the most appropriate ways to study animal coloration, it is important to understand how vision works. In particular, two aspects of visual perception are likely to be crucial in assessing primate color signals: color and luminance (perceived lightness), which many animals use for different functions (Osorio and Vorobyev 2005). How color and luminance vision work, and their functions in different taxa, are by no means simple issues, and readers should consult Kelber *et al.* (2003) and Osorio and Vorobyev (2005, 2008) for more detailed discussion than is given here. Color vision involves the ability to discriminate between different light spectra irrespective of their relative intensity and necessitates the possession of two or more receptor types sensitive to different parts of the spectrum (Kelber *et al.* 2003). In humans, we can think of color vision as involving two attributes: hue, meaning the actual color type itself, (e.g., red as opposed to green, blue, and so on) and saturation, essentially the amount of the color compared to white light; (e.g., red is highly saturated and pink is unsaturated). Whether nonhuman animals categorize colors based on hue is unclear, but it seems likely that, at least in some instances, they do (Ham and Osorio 2007).

Animals can have a range of photoreceptor and pigment types, with not all of these used in color vision. Humans are trichromatic, with color vision based on three cone types, sensitive to relatively long (LWS; "red"), medium (MWS; "green"), and short (SWS; "blue") wavelengths of light. Essentially, color vision is defined psychophysically by the number of primaries (of different proportions) needed to match all the colors that the animal can see. The number of these indicates the presence of di-, tri-, or tetrachromatic vision (2, 3, or 4 primaries needed respectively; Kelber *et al.* 2003). The number of primaries needed will not exceed

the number of receptor types present, but may be lower. However, in vertebrates, the dimensions of color space do seem to match the number of cone pigments present, with one exception being some human females who have 4 cone pigments, but still seem to have trichromatic vision (Jordon and Mollon 1992). Other animals have different numbers of receptors used in color vision (different dimensions of color space), such as dichromats using 2 cone types, (e.g., many mammals) and tetrachromats using 4 cone types, (such as diurnal birds). For color vision, it is not the absolute stimulation of any receptor type that matters, but rather a comparison between the relative stimulation between two or more of the photoreceptors. As such, the presence of, for example 4 receptor types does not prove the presence of tetrachromatic vision; this can only really be inferred from behavioral tests (Kelber *et al.* 2003).

Color vision results from comparing the outputs of different receptor types, by the process of color opponency, involving excitatory and inhibitory connections between the receptor classes, with antagonistic color pairs being processed in separate neural channels (Rolls and Deco 2002). In humans, these include yellow versus blue, and red versus green pathways (Chatterjee and Callaway 2003; Chichilnisky and Wandell 1999), with either member of the color pair perceived depending upon excitation or inhibition of the pathway. Different types of color opponent channels are not just present in humans, but appear to be found in the visual system of other primates, (e.g., macaques (Dacey 2000)), birds (Osorio *et al.* 1999), and turtles (Ammermüller *et al.* 1998; Ventura *et al.* 1999). Because color vision involves discriminating between the relative outputs of receptor types, it provides information about differences in reflectance between objects or patches, and is important in object detection and classification (Osorio and Vorobyev 2005). Overall, while color perception is also affected by a number of other factors, there are various models of color perception that predict behavioral data effectively.

Luminance is an achromatic signal arising from the sum of photoreceptor outputs, and relates to some measure of achromatic intensity (white through gray to black with decreasing luminance; Osorio and Vorobyev 2005). The mechanisms underlying luminance vision differ between animals. For example, in humans and other trichromatic primates, it is based on the summed outputs of the LWS and MWS cones, whereas in other animals, such as birds, it may stem from another class of receptors, such as the double cones (Kelber *et al.* 2003). In contrast to measures of brightness (the amount of light reflected from an object), luminance is not defined by appearance but is closely associated with physiological mechanisms (Lennie *et al.* 1993; Stockman and Plummer 2005). As with color, luminance is not just a simple matter of light intensity but also depends on the state of adaptation of the photoreceptors, (i.e., changes in receptor sensitivity due to ambient light levels) and the contrast of neighboring patches (Gregory 1998). Luminance signals in primates are often used for tasks involving motion, pattern, and texture detection and discrimination (Osorio and Vorobyev 2005).

Researchers studying the coloration of nonprimate animals such as birds, fish, reptiles, and insects have for some time acknowledged the importance of considering the visual systems of receivers, perhaps because species in these taxa are well known to have very different color perception from humans (Kelber *et al.* 2003; Osorio and Vorobyev 2005, 2008). Most mammals have a dichromatic visual system, including many primates. However, in Old World monkeys, apes, and howlers, color vision appears always to be trichromatic, due to a duplication of the LWS/MWS gene to

give LWS and MWS pigments (Osorio and Vorobyev 2008). The spectral sensitivities of these 3 photopigment types appear to be close to those of humans (Bowmaker *et al.* 1991; Jacobs and Deegan 1999): λ_{\max} values *ca.* 430, 530, and 560 nm for the SW, MW, and LW pigments, respectively (Dartnall *et al.* 1983). However, it is becoming increasingly apparent that even in groups such as catarrhines, in which spectral sensitivities of cone pigments are highly conservative (Jacobs and Deegan 1999), differences in, for example the relative proportions of cone types, may lead to species differences in overall wavelength sensitivity. For example, macaques (*Macaca* spp.) and chimpanzees (*Pan troglodytes*) have increased SW sensitivity but reduced LW sensitivity compared to humans (Jacobs and Deegan 1999; Waite and Buchanan-Smith 2006). In other primate groups, vision can differ markedly, including mono- and dichromacy, often linked to environment and life-history traits (Sumner and Mollon 2003; Waite and Buchanan-Smith 2006). Variation can also exist within species, with many New World primates and some lemurs having sex-linked polymorphisms for the LWS/MWS gene, leading to either di- or trichromacy within the same species but differing between individuals (Jacobs 1996; Surrige *et al.* 2003; Tan and Li 1999). This can mean that some females in a population can be trichromatic, whereas other individuals can have a dichromatic system with the SWS cone and either the MWS or the LWS cone (Osorio and Vorobyev 2008). Objective methods for studying colors enable assessments that are independent of human vision (Sumner and Mollon 2003).

Data Acquisition

Though we discuss data acquisition separately from analytical techniques, the two processes will often be closely linked. There is a range of ways to acquire data, with two methods likely to be especially useful for allowing objective analysis or models of visual processing: spectrophotometry and digital imaging.

Color Charts

Color charts have often been used in the past to record the colors of animals by a human observer (including by primatologists, e.g., Setchell and Dixson 2001), essentially by matching or ranking the color of the marking to the closest value on a chart of different colors. Partly due to the ease of this technique color charts were widely used to assess the colors of other animals and natural objects, especially before objective techniques, such as spectrometers and digital cameras, became more affordable and available. However, there are numerous drawbacks in using color charts to study nonhuman colors, including low inter- and intra-observer reliability, even under controlled lighting conditions (exacerbated under field conditions), effects of neighboring color patches on perception, and most importantly that color matching is based entirely on the vision of the human observer and not that of the appropriate receiver, which may perceive the signal differently (Endler 1990; Stevens and Cuthill 2005). For nonhumans, available color spaces are likely to be nonuniform where differences in the recorded values (such as between two values on a color chart) do not equate to equal differences in perception to the receiver, and

some spaces, such as RGB space, are inappropriate because they are both nonuniform and cannot represent all perceivable colors even to humans (Stevens and Cuthill 2005). Some color spaces such as CIELAB (Commission Internationale d'Eclairage) are broadly uniform, and more appropriate for recording color values for humans or primates with human-like visual systems (Wyszecki and Stiles 1982). Overall, color charts should only be used to study animal coloration if access to objective methods is not possible, and even then, only with well defined high-quality color charts, such as Macbeth color checker charts, and perceptually uniform color spaces, such as CIELAB space. In addition, regular intra and interobserver reliability tests in the range of light conditions and habitats in which data will be collected, and standardization of measurements for time of day, should help to improve accuracy.

Spectrometry

Perhaps the most common approach taken to obtain objective measures of the properties of a color signal is to measure its reflectance spectra with a spectrometer to provide precise information on the intensity of light reflected over a range of wavelengths (Andersson and Prager 2006; Cuthill *et al.* 1999; Endler 1990; Endler and Mielke 2005). Studies of many animal taxa, particularly those of birds, have been based on spectrometry. In contrast, the approach has rarely been used by primatologists (*cf.* Sumner and Mollon 2000b, 2003). This may stem partly from the difficulties of acquiring spectra from study specimens. However, reflectance spectra would be easy to obtain from museum pelts and samples of hair (e.g., Sumner and Mollon 2003), or for other features of the environment important to primates, such as fruit and leaves (e.g., Sumner and Mollon 2000b). The process of acquiring reflectance spectra is outlined in detail by Andersson and Prager (2006), and so we do not repeat it here. Generally, spectra can be acquired either from specimens or samples brought into the laboratory, or by taking a portable spectrometer into the field. Portable spectrometers are usually also used to acquire measurements of the ambient light under which a signal may usually be viewed (irradiance), which involves calibrating the spectrometer with a light source of known output. It is also possible to measure radiance directly, using a radiometer, and this can be an ideal way of directly recording the spectrum of light that would reach the receiver by simultaneously including reflectance and irradiance, rather than measuring the two separately and then calculating an estimate of radiance later.

One common problem with spectrometry is that it is a poor method for studying complex patterns, generally only being able to record spectra from a single point on a color patch at a time. The other main drawback is that it often requires a static object in close proximity, which is often not possible when studying wild animals. Further, measurements taken in the field can be strongly affected by fluctuating light conditions, meaning that standard measurements often have to be taken repeatedly, or the probe has to be fitted with a custom sheath that comes into contact with the specimen and excludes all the ambient light. Teleradiometers, in contrast, are useful because they directly measure the spectral radiance from an object from afar, and by design include the light conditions under which the signal is viewed (e.g., Sumner *et al.* 2005). Finally, the recordings that are obtained with a spectrometer can also be strongly affected by the angle of measurement (Andersson and Prager 2006; Osorio

and Ham 2002; Santos *et al.* 2007). Ultimately what matters is the angle that the signal will be observed from, and this is what researchers should consider more when choosing the angle(s) of measurement.

Digital Imaging

The aforementioned drawbacks mean that spectrometry can be poorly suited to measuring animals or stimuli in the field. An alternative and increasingly popular approach is the use of digital imaging. This has become more common in studies of primate coloration (e.g., Bergman and Beehner 2008; Gerald *et al.* 2001; Higham 2006; Higham *et al.* 2008; Setchell *et al.* 2006; Marty *et al.*, Clough *et al.*, Dubuc *et al.*, Setchell *et al.*, Bergman *et al.*, Kamilar, this issue), and the function of primate vision (e.g., Lovell *et al.* 2005; Párraga *et al.* 2002), and has numerous advantages over methods such as spectrometry, including that data acquisition in the field is easier, non-invasive, and that the images include both pattern and color information (Stevens *et al.* 2007a). That images are 2-dimensional means they can be used to study not just the color of a single patch, but the entire signal or visual scene, enabling, such as the size and color of a signal to be analyzed from the same image (e.g., Higham *et al.* 2008). An additional advantage of digital images is that samples can be taken and averaged over a large area (many pixels), rather than from a limited number of point samples, as in spectrometry, for example and we recommend that investigators take this approach. One can then either analyze images as visual system independent data, or incorporate them into specific models of visual processing (Párraga *et al.* 2002; Stevens and Cuthill 2006). Finally, digital imaging and manipulation also provides a powerful tool for creating carefully defined stimuli for use in behavioral experiments. However, drawbacks to digital image approaches include that images need to be calibrated before accurate data can be obtained. In addition, cameras capture color information in a manner similar to real visual systems, by transforming radiance spectra over all wavelengths into usually 3 color channels. Though this is often an efficient way of capturing relevant information in a visual scene, some information can be lost in the process, which does not occur to the same extent when using spectrometry or radiometry because intensity information is captured over the entire visual range at fine scales, e.g., around 1-nm intervals.

Field Methods for Acquiring Images Many researchers will wish to acquire images of animals in the field, for which there are a range of factors to consider to obtain accurate data. They are outlined in detail in Stevens *et al.* 2007a, but here we highlight the key methodological points.

- 1) Selecting an appropriate camera: Key features include the ability to store RAW or TIFF files, manual settings for exposure times and white balancing, good image resolution, and quick image storage times. Manual white-balancing is important to prevent incorrect balances between the R, G, and B channels, and manual exposure times are crucial to capture images that are neither over- or underexposed.
- 2) Light conditions and standardization: Ideally, where light conditions fluctuate, a standard should be included in each image. However, this is often impractical or

impossible depending on the species investigated, and an alternative approach is to take a second image of a standard when the subject has moved away in the same location, under the same light conditions, and with the same camera settings. This sequential method has recently been adopted in a number of primate studies (Bergman and Beehner 2008; Higham 2006; Higham *et al.* 2008; Bergman *et al.*, Clough *et al.*, Dubuc *et al.*, Marty *et al.*, this issue), and is outlined in Bergman and Beehner (2008) and Higham (2006). If taking photographic measurements under controlled conditions (e.g., Kamilar, this issue), then it may only be necessary to take photographs of a set of standards at the start and end of a photography session.

- 3) File type: It is important that one records the images as either RAW or TIFF files; JPEGs and other file types often use lossy compression techniques to reduce the file size, which can result in artifacts in the data (Stevens *et al.* 2007a). JPEGs may introduce only small errors if the color patches are relatively simple and measurements are averaged over large areas (Bergman and Beehner 2008). However, the level of error introduced is difficult to predict because it will depend on the level of compression and the actual pattern being photographed. For spatially complex markings, errors may be significant.
- 4) Avoiding saturation (overexposure): One of the most important factors in obtaining accurate data is to achieve a suitable exposure time for the signal being studied, and in particular to avoid saturation or overexposure, where the light reaching the sensors hits an upper limit and additional photons are not recorded, so that the true value that the signal produced is not measured. In general, saturation is easily avoided by marginally underexposing images with respect to the brightest regions of interest. However, one should also be careful not to underexpose the images with respect to any dark regions. For some animal color patches, >1 photograph may be needed to record both light and dark signal regions accurately.

Image Calibration Once images have been acquired, several calibrations are required because images will be affected by the combination of ambient light and camera settings on which they were taken, plus biases inherent in the camera's processing. Further, each camera will differ in its attributes, and so standardization allows the data obtained to be compared across studies (Westland and Ripamonti 2004). The main issues are outlined in Stevens *et al.* (2007a), and include:

- 1) Linearization: Almost all digital cameras have a nonlinear response to changes in light levels in terms of the image value recorded, which needs to be linearized. The nonlinearity of a camera can be calculated by taking images of a set of reflectance standards, which reflect light equally across all relevant wavelengths, of different values.
- 2) Equalization: The problem of variability in the color and luminance of ambient light in the field is compounded by the fact that most digital cameras show a bias in favor of certain wavelengths of light, meaning that some colors may be overrepresented. This may not be a problem if mapping directly to another color space because the exact sensitivity of the camera's sensors is known (though there may be cases in which equalization is still advantageous). However, one of

the principal data types that can be obtained with digital imaging is reflectance information in the respective color channels, i.e., RGB gray-score values. To correct for both ambient light, and camera biases toward specific wavelengths, one wishes to ensure that pixel values are the same in each color channel with respect to a grey standard (Stevens *et al.* 2007a). A recent alternative approach is to use a technique whereby reflectance spectra can be estimated from the content of the digital images themselves, using Colourworker™ (<http://www.chrometrics.com>). This requires the user only to include a standard such as a Macbeth chart in the image (or a subsequent image under the same light and camera conditions), and to have a small sample of reflectance spectra from the type of object of interest. The spectra should cover the range of the signal of interest (or similar objects). If obtaining sample spectra is difficult, then some databases do exist with sample spectra for downloading, such as of primate skin and pelage, and fruits and foliage (<http://vision.psychol.cam.ac.uk/spectra/>), and the program itself comes with a small sample of spectra of a limited number of objects. The approach is based on evidence that reflectance spectra from natural images are often restricted to a few types, allowing an estimation of reflectance spectra from the content of the RGB channels of a camera (Chiao *et al.* 2000). Though the software is relatively new, the approach seems to be able to accurately recover reflectance spectra from digital images of objects including fruit, bird plumage colors, and human skin. Following this process, reflectance spectra can be obtained from images that resemble those that would be acquired with a spectrometer, and can then be analyzed in the same way.

- 3) Software: There is a range of available software programs that can be used to analyze and to calibrate the content of digital images, including MATLAB (The Mathworks Inc. Natick, MA), with its Image Processing toolbox, and Image J (Abrámoff *et al.* 2004; Rasband 1997–2009), a free Java-based program. Both programs allow a range of associated image analysis functions, have supporting books (Efford 2000; Gonzalez *et al.* 2004; Westland and Ripamonti 2004), often with available functions for downloading, and have the significant advantage that their associated programming language enable self-made programs and functions to be written. Adobe Photoshop (Adobe Systems Inc., San Jose, CA) also offers a plug-in that both equalizes and linearizes the content of digital images automatically (inCamera: <http://www.pictocolor.com/incamera.htm>) and requires the user only to select areas of a standard, such as a GretagMacbeth ColorChecker chart to do this (Bergman and Beehner 2008).

Ultraviolet It is worth noting that while primates seem generally unable to perceive ultraviolet (UV) light, many other animals can (Tovée 1995). For most studies, this makes studying primate coloration and signaling easier because it negates the need for UV light-recording specialized equipment. However, there may be occasions when considering UV is important. For example, if one wishes to study how raptors that feed on primates, such as crowned hawk-eagles (*Stephanoaetus coronatus*), find their prey, UV information could be important because birds are sensitive to UV light (Cuthill 2006). For this, there are some digital SLR cameras that have sensors that can record UV light, either fortuitously (such as some Nikons in the DX range)

or those that are designed for UV sensitivity (such as the Fujifilm IS Pro). Generally, UV imaging is possible because one or more of the sensors has sensitivity to part of the human visible spectrum, (e.g., the “red” sensor to relatively LW light) but also has a second peak in the ultraviolet, such as around 360 nm. By using filters that either transmit or block UV or human-visible wavelengths, one can generate four images, in the UV, SW, MW, and LW part of the spectrum, using one of the sensors twice to capture the UV. However, the crucial factor for incorporating UV effectively is to use a quartz lens, as “standard” glass lenses do not transmit UV light effectively. Otherwise the same issues apply to UV images as to RGB ones, such as linearization and RGB-UV equalization.

Data Analysis

Once suitable data have been acquired there is a range of different methods that can be used to analyze and interpret it. Broadly, we can divide these into visual system independent techniques, where the data are not linked to any particular visual system, and visual system dependent techniques, where the data are analyzed with respect to how they would be processed by the visual system of the receiver. Visual system independent methods can include measurements such as reflectance, and have the advantage that the data stand alone as a specific property of the object itself. This means that data can be compared across studies/specimens when the visual system of the receiver is unknown or poorly understood. However, we advocate strongly that researchers use methods where the signal is analyzed with respect to the appropriate visual system wherever possible, because how the signal is processed by the receiver is ultimately what matters. For many primates, there are good data on the visual system possessed. Furthermore, simply considering reflectance, for example, can be misleading because a high reflectance value in one part of the spectrum is irrelevant if the receiver is unable to perceive those wavelengths.

Visual System Independent Techniques

Essentially, most visual system independent techniques are based on reflectance or radiance information. However, simply analyzing reflectance spectra can be highly error prone, and here we consider two of the most common objective methods for analyzing spectral results, though there are various others.

Principle Component Analysis One way to use all of the information from reflectance data is to enter the data from each spectrum (or a sample of images of different wavebands) into a principal component analysis (PCA; Cuthill *et al.* 1999; Endler 1990). PCA can summarize complex data in a few orthogonal variables, the principle components (PCs), and can therefore give measures of statistical differences in spectra (Cuthill *et al.* 1999). PCA can also be used for data reduction, where multiple original measures can be transformed into PCs with only relatively minor loss of information (Higham *et al.* 2008). It can also be used to assess whether different aspects of a signal appear to covary, or whether they might vary differentially, and hence possibly contain different information (by assessing whether

different measures load onto different axes; Higham *et al.* 2008). PCA axis scores can also be analyzed using most modern statistical techniques, including General Linear Mixed Models (GLMMs) and multivariate analysis of variance (MANOVA), often used in studies that feature multiple observations of the same individuals (Cuthill *et al.* 1999; Higham *et al.* 2008). In order to eliminate achromatic differences and examine just the differences in color (spectral shape), some studies remove brightness from the PCs (Cuthill *et al.* 1999; Endler 1990).

There are, however, a number of notable drawbacks to PCA, specifically, that the PCs are defined by the data originally included (Cuthill *et al.* 1999). As such, one could not compare PCs derived from different data sets directly, only the general findings. This could be particularly problematic for studies assessing color development over time (e. g., through adolescence); results deriving from separate PCA analyses of the same animals from different eras would not be comparable. Also, though PCA is excellent for using all data, the results do not correspond to hue, saturation, or luminance, but rather to various aspects of the average geometrical shape of the spectra, and these depend on the shape of the spectra present in the data set (Endler 1990). Most often, PCs rarely correspond to spectral sensitivities of photoreceptors, so relating PCs from reflectance spectra to visual systems and visual tasks is problematic.

Measuring Spectral Shape A relatively common way to interpret reflectance spectra has been to derive measurements of “hue,” “saturation,” and “brightness” (HSB) based on aspects of the reflectance spectra (Montgomerie 2006). Here, hue describes the ‘color’ of the signal (e.g. red, blue, green, and so on), saturation is a measure of the degree to which a color appears to be pure compared to white light, (e.g. red as opposed to pink), and brightness is a measure of the total amount of light, (i.e., achromatic information). Though an array of different measures have been used to obtain these variables, most frequently hue is measured as a position (wavelength) along the spectrum where the reflectance is highest, saturation is often the reflectance in a particular part of the spectrum divided by the reflectance of the entire visible spectrum, and brightness is usually the total area under the reflectance curve (Montgomerie 2006).

However, like PCA, analysis of spectral shape has significant drawbacks. First, measurements of hue are strongly affected by random noise in the spectrum, and are unhelpful when there is >1 significant peak in the spectrum. More importantly, color perception does not stem simply from which wavelength is most common, but rather by comparisons between the outputs of the receptors and opponency mechanisms. Likewise, brightness (luminance) is not a sum of all the wavelengths present but rather stems from a particular pathway or receptor output. Therefore, while HSB has been used widely to describe the shape of reflectance/radiance spectra in birds, it is a method that is potentially misleading because it implies some relationship to how a spectrum is perceived by the receiver, which may often not be the case. RGB color space also has notable problems, most importantly that 1) RGB color space is not uniform and so differences in RGB do not necessarily equate to equivalent differences in perception and 2) even for humans, RGB values are not capable of reproducing all the perceptual colors that we can see (Stevens and Cuthill 2005). If a color space is to be used instead of calculating measurements based on receptor information of the observer, then for humans and animals with a very similar visual systems the CIELAB is likely the best because it is essentially perceptually uniform (Wyszecki and Stiles 1982).

Visual System Dependent Techniques

Analyzing visual signals in a way that is linked to the receiver's visual system requires certain information about that system. In particular, one needs to know the relative spectral sensitivity of the receptor types, but more information, such as potential color opponent and luminance channels, allows more sophisticated modeling of the signal. For many primates, much of this information is available, allowing a range of techniques to be used, with the most useful ones often depending on the specific research question being asked. In general, because primates have fewer receptor types involved in color vision (fewer dimensions of color space) compared to many other vertebrates, lack UV vision, and have often been well studied in terms of their visual capabilities, primatologists are ideally placed to use visual system dependent techniques. We discuss a range of the most widely used and useful models, which almost always begin with calculating the predicted quantal (or photon) catches of the receptors; i.e., how stimulated each receptor type is by the signal entering the eye. Many of the programs (self-written MATLAB functions) are available from the authors on request, and some data on primate sensitivity functions, receptor abundances, and Weber fractions are available from the Colour and Vision Database, run by the Colour and Vision Research Laboratories, Institute of Ophthalmology, UCL (<http://cvrl.ucl.ac.uk/index.htm>). See also the text that follows for some specific references containing the raw data needed for different primate species and groups.

Modeling Animal Quantal (Photon) Catches Calculating the degree of stimulation of the different receptor types of an animal, the quantal or photon catch, is usually based on the assumption that the light entering an animal's eye is a product of the reflectance spectra of the object being viewed, and the irradiant light in the environment. This radiance spectra is then multiplied by the spectral sensitivity of each of the different cone types to determine the quantal catch of each cone type (Endler and Mielke 2005; Maddocks *et al.* 2001; Sumner and Mollon 2003). A stimulus is therefore defined by receptor quantal catches by,

$$q_i = \int_{\min \lambda}^{\max \lambda} R_i(\lambda) S_i(\lambda) d(\lambda) \quad (1)$$

where q_i is the quantal catch of receptor type i , λ is the wavelength (for the range over which the signal is measured, e.g., from *ca.* 400–750 nm for many primates), S_i is the spectral sensitivity of receptor i , (e.g., the LWS, MWS, and SWS cones for trichromatic primates), and $R(\lambda)$ is the spectrum of light entering the eye (a product of the reflectance and irradiance spectra, or radiance directly measured). The code $d(\lambda)$ means to integrate over the visible spectrum. The spectral sensitivity of the animal's receptors should not just be the absorbance of the visual pigment, but also include how the light passing through the eye will be affected by factors such as the ocular media, to give absorptance. Spectral sensitivities for a wide range of primates are available in the published literature, including values for lemurs (e.g., Jacobs and Deegan 1993), many African (e.g., Jacobs and Deegan 1999) and Asian Old World primates (e.g., Deegan and Jacobs 2001), and assorted New World monkeys (e.g., Jacobs 2007; Jacobs and Deegan 2003). Finally, most models based on estimating photoreceptor stimulation

rescale the quantal catch measurements with respect to either a spectrally flat white standard, or some measure of the background. This has 2 purposes: 1) Because color vision also relies on color constancy, where colors appear similar despite changes in the total flux and composition of the ambient light, this process is a simple way of accounting for this phenomenon (Cuthill 2006; Kelber *et al.* 2003). 2) The process of standardizing the cone captures to a standard or the background accounts for adaptation, where the receptor outputs respond to differences from their current state of adaptation rather than absolute values (Cuthill 2006). Once quantal catch data have been obtained, this can then be used in a range of potential analyses.

Using Cameras to Map to Other Color Spaces A powerful use of digital images as an alternative to spectrometry is to convert the pixel data to correspond to a specific color space relevant to the receiver in question, obtaining data corresponding to quantal catches of the animal's receptor types, and incorporating these into advanced models of vision. However, it is also possible to map directly across to other color spaces, e.g., CIELAB space for human vision (Westland and Ripamonti 2004). One way to convert from camera color space to another requires knowing the spectral sensitivity of the camera's sensors. Unfortunately, this is not straightforward, because manufacturers rarely publish this information, and it can vary even between specific cameras of the same model. Another approach involves taking photographs of a reflectance standard through a set of bandpass filters, each of which only transmits light of specific wavebands, (e.g., in 10-nm intervals), and concurrently measuring the amount (radiance) of light of different wavelengths that is transmitted through the filters with a radiometer (see Lovell *et al.* 2005; Párraga *et al.* 2002 for details). Doing so allows a calculation of how sensitive each of the camera's sensor types is to specific wavelengths of light. Once this information is known, it is possible to produce a mathematical transformation from the camera to another color space (Párraga *et al.* 2002; Stevens *et al.* 2007a). This approach can be very accurate with a low error (<2%) in predicting quantal catches compared to using a spectrometer to measure reflectance and irradiance spectra (Stevens and Cuthill 2006), though further tests of the level of error with different objects are needed. An alternative approach is to use software such as ColourworkerTM to obtain reflectance spectra from images and then model quantal catches using these.

Modeling Receptor Stimulation in Color Space Once a measure of quantal catch has been obtained, a range of approaches allows analyses of the data to be undertaken, including comparisons between two or more stimuli, or obtaining visual system dependent measures of color by hue and saturation. One of the most widespread and intuitive ways to analyze quantal catch data is to plot them in a color space, whereby the receptor catches are converted into a set of coordinates corresponding to a given color space (Fig. 1). This method provides a quantitative map of color perception that is based on the visual system of the receiver, and is generally easy to calculate. A color can be defined by a set of n quantal catches and represented in an $n - 1$ dimensional color space that contains information about a color's hue and saturation. For example, the quantal captures of a trichromat's SWS, MWS, and LWS cones can be plotted in a 2-dimensional space, with each set of cone captures corresponding to a given stimulus being represented by a single point. Such colors mapped in color space are

independent of the achromatic signal because they are defined by relative rather than absolute quantal capture (each cone capture is represented as the proportion of the total quantal catches of all cones and so changes in absolute quantal catch are removed).

For a dichromat, any color can be mapped as a point on a line, with its position on the line determined by the proportionate cone captures of the SWS and MWS/LWS

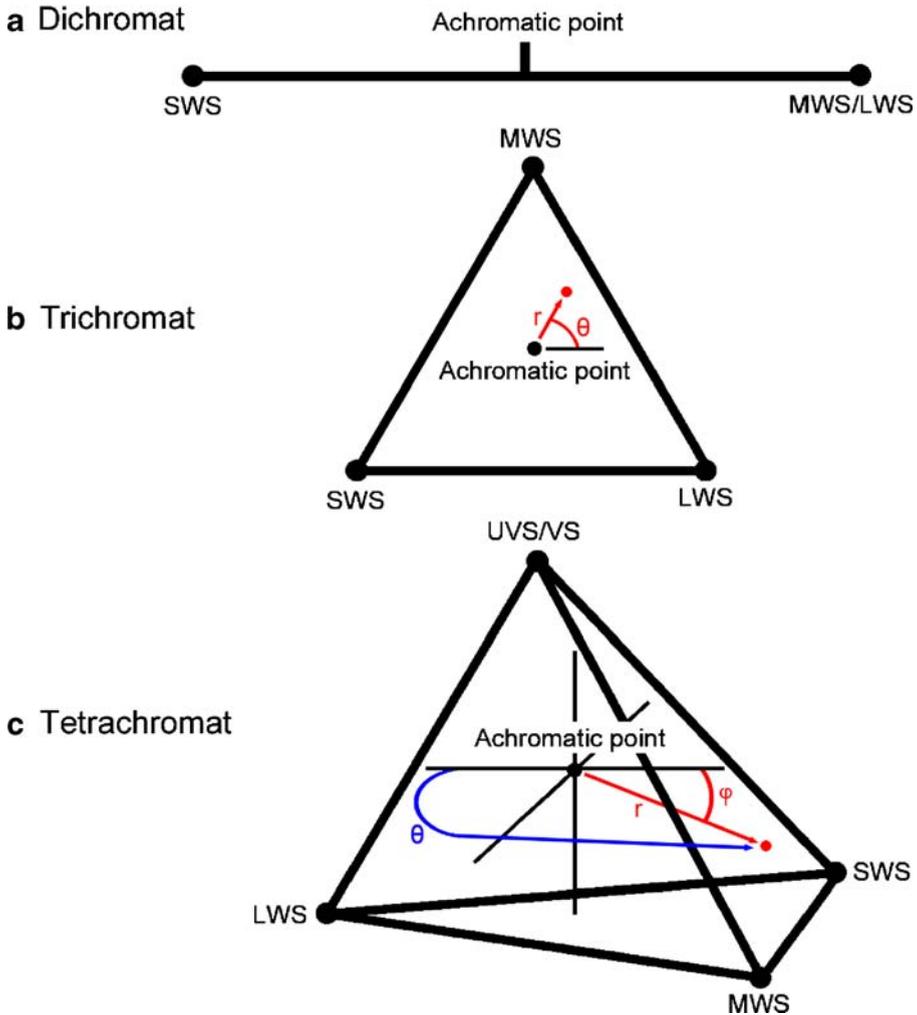


Fig. 1 Representations of color space, with the achromatic point of equal stimulation shown at the origin. **(a)** Dichromatic color space can be represented by a line on which a color's position is determined by the relative stimulation of the SWS and MWS/LWS cone types. **(b)** Trichromatic color space can be represented by a triangle in which a color is represented by the proportionate cone captures of the SWS, MWS, and LWS cone types. A color can be described by its polar coordinates θ and r . Hue is measured by θ , the angular displacement of the color vector from the positive x -axis, and chroma, or saturation, is given by the magnitude of r , which is the distance from the achromatic point at the origin. **(c)** Tetrachromatic color space can be represented by a tetrahedron in which a color is a point determined by the relative stimulation of the UVS (or VS), SWS, MWS, and LWS cone types. Here, hue is measured by two angles, θ and ϕ , which are analogous to longitude and latitude, respectively.

color cones, such that dichromatic color space is 1-dimensional (Fig. 1). The trichromatic color space is a 2-dimensional triangle with vertices corresponding to the SWS, MWS, and LWS photoreceptors (Fig. 1). A color's position in the tristimulus color space (the Maxwell triangle; Kelber *et al.* 2003) is determined by the relative stimulation of the 3 cone types. In tetrachromatic color space, a color is a point in a tetrahedron determined by the relative stimulation of 4 color cone channels: UVS (or VS), SWS, MWS, and LWS (Fig. 1). The achromatic point of equal cone stimulation—white, black, or gray—is usually placed at the origin of the tri- and tetrachromatic color spaces. Multiple orientations for tri- and tetrachromatic color spaces have been proposed, with full details and equations for plotting, available elsewhere (Endler and Mielke 2005; Goldsmith 1990; Kelber *et al.* 2003).

Trichromatic and tetrachromatic color spaces have many useful properties for describing the variation and distribution of colors. In trichromatic color space, a color point can be described by its polar coordinates, θ and r , which define a color vector and provide measures of hue and saturation (Fig. 1). As in the 2D human-based Munsell and CIELAB color spaces, hue is defined as the direction of the color vector and is measured via θ , which is the angular displacement of the color vector from the positive x -axis. The saturation (often called chroma) of a color is given by the magnitude of r , which is its distance from the achromatic origin. In both tri- and tetrachromatic color space, colors of the same hue that differ in saturation fall on a single line at different lengths from the origin. The functions that describe how variation in the relative stimulation of color cones varies as a function of saturation r for any hue can be calculated (Stoddard and Prum 2008). Different hues vary in their potential maximum saturation. It may be more important to define the achieved saturation of a color, i.e., saturation relative to the maximum saturation possible for its hue, rather than its absolute saturation (Stoddard and Prum 2008). Redefining hue and saturation in the context of visual system dependent color spaces provides a major advantage over analyses based directly on reflectance spectra. Because spectra vary widely in their shape, traditional measures of hue and saturation have failed to characterize animal colors accurately (Montgomerie 2006). In contrast, color space measurements are standardized, generalizable, and suitable for colors with complex reflectance spectra, though with some analyses careful attention needs to be paid to the type of statistics that should be used (Endler and Mielke 2005).

A set of quantitative and broadly comparable measures can be used to characterize multiple colors plotted together in color space, (e.g., all of the colors of a pelage or plumage). For example, the Euclidean distance, or span, between two colors can be calculated to provide a measure of visual contrast (but such a measure does not include the effects of photoreceptor noise). A cloud of several color points can be described by measures of overall color contrast (average span), color diversity (occupied area for trichromatic space, occupied volume for tetrachromatic space, average hue disparity), and overall saturation (average saturation). Recent studies on bowerbird plumage and ornamentation (Endler *et al.* 2005) and plumage color evolution in a clade of New World buntings (Stoddard and Prum 2008) have used the avian tetrahedral color space to describe and analyze bird colors in this way. Custom-designed computer programs such as TriColorSpace and TetraColourSpace (available on request from the author; Stoddard and Prum 2008) are designed for the analysis of reflectance

spectra or photon catch data, (e.g., from digital photographs), and provide an assortment of quantitative analyses and graphical tools for describing color stimulus variation and diversity.

As an alternative to the Maxwell triangle described in the preceding text, many color spaces based on primate vision use axes corresponding to opponency mechanisms. Unlike in bird vision, for which opponent channels have not been described fully, the red-green and yellow-blue opponency pathways in humans and trichromatic primates are fairly well understood. Accordingly, primate color space coordinates can be defined in a way that has greater physiological significance. In such diagrams, which resemble the MacLeod-Boynton chromaticity diagram for humans (MacLeod and Boynton 1979), the x -value is given by $q_L/(q_L+q_M)$ and the y -value is given by $q_S/(q_L+q_M)$, where q_S , q_M , and q_L denote the quantal catches of the SWS, MWS, and LWS color cones, respectively (Sumner and Mollon 2000a, b, 2003). Depending on the question at hand, it may be important to define axes in a way that incorporates information about known neural channels (Cuthill 2006). However, this type of representation lacks the intuitive appeal of a triangular color space and its geometry cannot be used to define hue and saturation in a convenient way.

In many studies of varied taxa, including nonhuman primates, color signals have been mapped to color space with excellent results. Several of these studies have investigated the hypothesis that primate trichromacy evolved to help frugivorous primates detect fruit among leaves (Regan *et al.* 1998, 2001; Sumner and Mollon 2000a). Others have explored the ecology of color vision by comparing colors of natural objects as seen by different groups of land animals (Osorio and Vorobyev 2008). In a departure from studies focused on frugivory, Sumner and Mollon (2003) mapped fur and skin colors of 31 primate species in color space to provide a survey of pelage colors found in primates.

The Vorobyev-Osorio Receptor Noise Model Because color vision is a product of opponent coding between receptor types, as well as the possession of >1 spectrally distinct photoreceptor type, models that concentrate solely on cone stimulation or color space approaches may not reflect visual perception in discrimination between stimuli accurately. The Vorobyev and Osorio (1998) model gives a measure of whether color variation is likely to be discriminable by the specific visual system of the receiver. The model is based on evidence that color discrimination thresholds are determined by noise that arises in the photoreceptors, rather than in the subsequent neural processing, which influences the accuracy of color vision and discrimination (Vorobyev and Osorio 1998; Vorobyev *et al.* 1998, 2001). The model assumes that in a visual system with n receptor types, color is coded by $n - 1$ color opponent mechanisms, which are assumed to give no signal for stimuli that differ in luminance only (the achromatic signal is disregarded). Stimuli are therefore detectable as different in the model only if the calculated distance between them is larger than a threshold distance, ΔS . The threshold distance can be determined from the difference in quantal catch between the stimuli (Δq_i) and an estimate of noise in the receptor channel e_i . Under many circumstances, it is standard to use a log form of the model, primarily because differences in perceptual discrimination often

seem to occur on a log rather than a linear scale. As such, the difference between the receptor catches for a given receptor type for a pair of stimuli is given by

$$\Delta q_i = \log \frac{q_{i1}}{q_{i2}} \quad (1)$$

Receptor noise, e_i , is calculated for each cone type as

$$e_i = \frac{w_i}{\sqrt{n_i}} \quad (2)$$

where w_i is taken as a Weber fraction value and n_i is the relative proportion of cone type i in the retinal integration area. The value of w_i is often taken as between 0.02 and 0.05 for the most abundant cone type, though this is often a best estimate and other more appropriate values may be used. Information on Weber (sometimes called Fechner) fractions and receptor noise are available in Wyszecki and Stiles (1982), Osorio and Vorobyev (1996), and the appendix of Vorobyev and Osorio (1998). Estimates of cone ratios vary, and for humans can be obtained from the aforementioned references and, for example Kremers *et al.* (2000), Brainard *et al.* (2008), and <http://cvr1.ucl.ac.uk/index.htm>. Estimates of nonhuman primate cone ratios are available for numerous and varied species, with examples including macaques (Knoblauch *et al.* 2006), baboons (Marc and Sperling 1977), strepsirrhines such as mouse lemurs (Dkhissi-Benyahya *et al.* 2001), and many New World monkeys (Jacobs and Williams 2006). Color discrimination values are then calculated according to the following:

For a dichromat:

$$(\Delta S)^2 = \frac{(\Delta q_1 - \Delta q_2)^2}{e_1^2 + e_2^2} \quad (3)$$

For a trichromat:

$$(\Delta S)^2 = \frac{e_1^2(\Delta q_3 - \Delta q_2)^2 + e_2^2(\Delta q_3 - \Delta q_1)^2 + e_3^2(\Delta q_1 - \Delta q_2)^2}{(e_1 e_2)^2 + (e_1 e_3)^2 + (e_2 e_3)^2} \quad (4)$$

For a tetrachromat:

$$(\Delta S)^2 = \frac{\left((e_1 e_2)^2 (\Delta q_4 - \Delta q_3)^2 + (e_1 e_3)^2 (\Delta q_4 - \Delta q_2)^2 + (e_1 e_4)^2 (\Delta q_3 - \Delta q_2)^2 + (e_2 e_3)^2 (\Delta q_4 - \Delta q_1)^2 + (e_2 e_4)^2 (\Delta q_3 - \Delta q_1)^2 + (e_3 e_4)^2 (\Delta q_2 - \Delta q_1)^2 \right)}{(e_1 e_2 e_3)^2 + (e_1 e_2 e_4)^2 + (e_1 e_3 e_4)^2 + (e_2 e_3 e_4)^2} \quad (5)$$

The units of ΔS are in “just noticeable differences” (jnds), where a jnd value of <1.00 indicates that 2 stimuli are likely to be indistinguishable by the observer even under optimal light conditions, with values >1.00 indicating how much above threshold the difference between 2 stimuli is, with increasing values indicating more

rapid discrimination under less optimal conditions (Siddiqi *et al.* 2004). Modeled discrimination values fit many experimental data well, and the model accounts for the consideration that chromatic signals are often more reliable than achromatic ones (Kelber *et al.* 2003), and predicts discrimination and behavioral sensitivity data for various animals, including birds, mammals, and bees (Kelber *et al.* 2003; Vorobyev and Osorio 1998; Vorobyev *et al.* 1998, 2001). One of the principle advantages of the Vorobyev-Osorio model is that, unlike modeling in color space, it can be used to compare discrimination thresholds for animals with different dimensions of color space. This could be especially useful in systems where there are sex-linked differences in color vision (as in some New World monkeys) or if wanting to model how both conspecifics and predators perceive the same signal.

Perhaps the main limitation of the “standard” model above is its relatively poor performance in predicting behavior in dim light, presumably because the model disregards the achromatic signal (Vorobyev and Osorio 1998). However, there are two extensions/modifications to the model that can address this issue. First, it is possible to model the achromatic difference between two stimuli based on the likely method of luminance perception of the relevant animal’s visual system. For example, Siddiqi *et al.* (2004) modeled the achromatic mechanism in birds based on the output of the double cones; similar modeling could be undertaken for the achromatic channel of many primates. Second, a more advanced version of the model can utilize information on how discrimination values vary under different light levels. The standard Vorobyev-Osorio (Vorobyev and Osorio, 1998) model assumes that, according to Weber’s law, threshold contrast between two stimuli is independent of light intensity. However, at low light intensities noise also arises due to actual variations in quantal catch, where noise is proportional to the square root of this quantal catch (Osorio *et al.* 2004; Rovamo *et al.* 2001). At high light levels contrast thresholds follow Weber’s law and are independent of intensity. It seems likely that under many natural conditions where a signal will be viewed, both these types of noise will be important, and so both photon- and Weber-type noise should be modeled to give a more accurate discrimination value (Osorio *et al.* 2004).

Researchers studying systems involving the receiver potentially making comparisons between two color signals have widely used the Vorobyev-Osorio model. For example, it has been used to show that some birds may signal in the ultraviolet (UV) part of the spectrum for intra- or intersexual communication, because UV signals may be less detectable from mammalian predators and birds of prey (Håstad *et al.* 2005; Stevens and Cuthill 2007), and to investigate the toxicity and conspicuousness of poison frogs to birds (Darst *et al.* 2006) as well as conspecifics (Siddiqi *et al.* 2004). However, the model has rarely been applied in studies of primate visual signals. One exception is the study of Osorio *et al.* (2004), who investigated the ability of different types of primate visual systems in detecting fruit, including how different systems may be related to differing aspects of visual ecology.

Finally, most models investigating animal color vision and behavioral tasks, including the Vorobyev-Osorio model, address whether the receiver can distinguish between two objects for color or luminance, and by how much they differ. However, such discrimination values/distances may not account for how the stimulus is responded to by the animal because they do not account for if and how an animal may categorize colors; i.e., they take into account the sensory systems of the receiver, but not the

subsequent cognitive processing. Categorization by nonhumans is poorly studied, but there is evidence that birds may categorize suprathreshold stimuli (stimuli above discrimination threshold differences) in a manner according to what category they fall into, rather than how different they are in discrimination values (Ham and Osorio 2007). Though the importance of categorization is currently difficult to determine, it is something to consider if discrimination threshold models fail to predict behavior accurately.

Developing More Advanced Models of Perception While the techniques discussed in the preceding text can be powerful in addressing how visual signals are used in a task, there are many instances when it may become useful to adopt further modeling of perceptual processes. For example, here we have dealt almost exclusively with the task of analyzing color or luminance, yet pattern and texture are also crucial aspects of many visual signals; that is, one should not ignore the 2- (or 3-) dimensional aspect of the signal. Recently, statistical methods have been outlined to cope with the problem of analyzing whole patterns in an avian color space (Endler and Mielke 2005), which could be adapted for other color spaces. However, digital images offer even greater opportunities, given that these capture color, luminance, and pattern information simultaneously, and in great detail. Developing models that incorporate images allows a suite of powerful approaches to be used (Stevens *et al.* 2007a). For example, Párraga *et al.* (2002) calibrated digital images to estimated primate (human) cone stimulation values, and the luminance, red-green, blue-yellow opponent channels (Fig. 2). They showed that the spatiochromatic (color and pattern) properties of visual scenes containing red-yellow fruit and green leaves are encoded well by the red-green opponent color system at a typical grasping distance, supporting the idea that the evolutionary significance of trichromacy may lie in the advantage it gives to detect ripe fruit or young leaves against a background of mature green leaves (Regan *et al.* 2001; Surridge *et al.* 2003). For example, researchers have used similar models to investigate the relative costs and benefits of different types of opponent color channels (Fig. 2) in resisting noise from changes in environmental illumination (Lovell *et al.* 2005). Other models using digital images have investigated how certain types of camouflage patterns found in nature may exploit the way in which visual systems encode the boundaries between objects (such as a prey item and the background) by edge information based on sharp changes in intensity within a scene (Stevens and Cuthill 2006), and related this to behavioral experiments in the field (Cuthill *et al.* 2005; Stevens *et al.* 2009). Such models enable researchers to test the underlying mechanisms of particular color patterns, and are particularly tractable in vertebrates, especially mammals, as much is known about how various stages of “low-level” vision may work, such as the presence and function of receptive fields and lateral inhibition, and spatial frequency and edge processing (Graham 1989; Rolls and Deco 2002).

Designing Stimuli for Behavioral Experiments

For many purposes, an ideal method to determine the function and value of a visual signal is to conduct a behavioral experiment with relevant stimuli or manipulations.

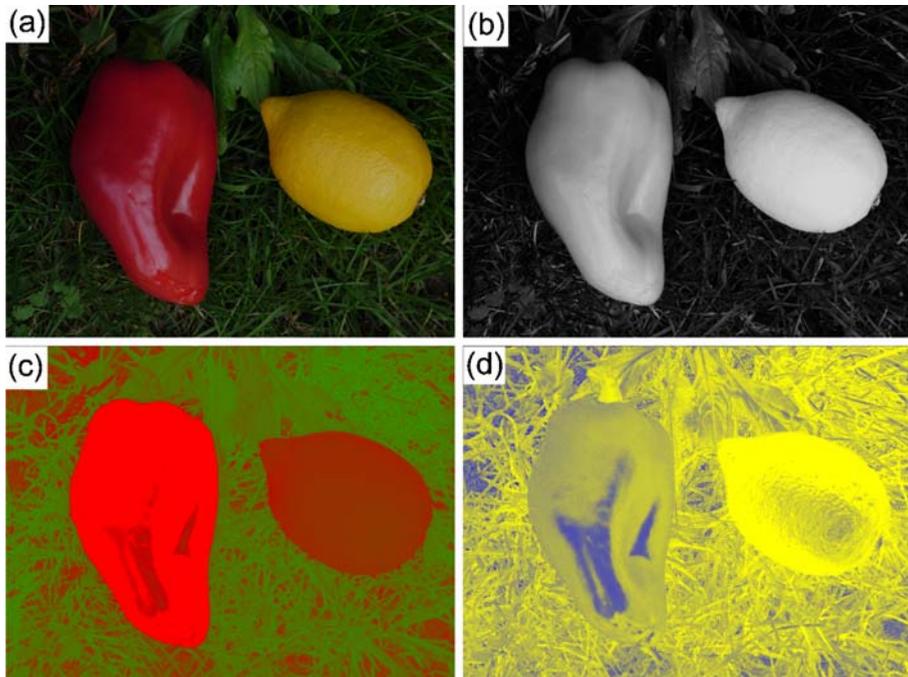


Fig. 2 Calibrated digital images (similar to Párraga *et al.* 2002) of red and yellow food objects (a red pepper and a lemon) against a background of grass and leaves, showing the original image **(a)**, and the red-green **(c)**, blue-yellow **(d)** opponent color channels, and the luminance channel **(b)** present in trichromatic primates. The images are calculated as: red – green = $\frac{LWS - MWS}{LWS + MWS}$, blue – yellow = $\frac{SWS - \left(\frac{LWS + MWS}{2}\right)}{SWS + \left(\frac{LWS + MWS}{2}\right)}$, luminance = $LWS + MWS$.

Experimental stimuli and manipulation are significant subjects in themselves, and here we offer only some broad suggestions. Essentially, many of the conceptual points that apply to modeling color signals also apply here, specifically that one needs to consider the visual system of the receiver when producing or modifying the stimuli. Simply creating stimuli that look accurate to human eyes is likely to be error prone at best. To do so, one can use many of the modeling approaches described earlier. Broadly, we can think about 3 types of goal: to modify existing stimuli, to create entirely new stimuli, and to use video displays simulating real or artificial stimuli.

Modifying existing colors and patterns is a common manipulation in avian biology. For example, many studies investigating the role of ultraviolet vision and signal components in mate choice involved enhancing or reducing the UV aspect of a signal. This has been done by, for example, applying sun-lotions to alter the UV reflectance from a color patch, and then measuring subsequent changes in behavior (e.g., Andersson and Amundsen 1997; Siitari *et al.* 2002), or conducting behavioral experiments with subjects tested under filters selectively removing different wavelengths of the ambient light spectra (e.g., Maddocks *et al.* 2001; Osorio *et al.* 1999). In primates, for practical and ethical reasons, experimental alterations of individual color are rare, though some studies have performed such manipulations successfully (e.g., Gerald 2001; Gerald *et al.* 2006a). The crucial factors with such experiments are to ensure that effective controls are used, that the animals still

behave normally, and that the manipulation is not so unnatural as to make the animal look “odd.”

An array of approaches can be used to make artificial stimuli. These can include creating prey items made from pastry dyed to have different colors and luminances with respect to the receiver’s vision, (e.g., to investigate foraging behavior (e.g., Rowland *et al.* 2007)), calibrating the outputs of printers to produce artificial targets that look like natural backgrounds or objects to the receiver (Cuthill *et al.* 2005), or creating carefully controlled backgrounds with respect to specific luminances and pattern, to determine how the animal responds (e.g., Zylinski *et al.* 2009). The advantage of artificial stimuli is that they can be modified carefully with respect to a few specific visual features, allowing greater control over their exact properties. Calibration of a printer output, changing the levels of dye, balance of print toner, or spatial attributes, and modeling of the animal’s visual system enable the researcher to ensure that manipulations are well defined. For example, Cuthill *et al.* (2005) produced artificial prey items based on digital images of natural backgrounds calibrated to bird vision, and required the targets to look natural to the avian predators. As such, they calibrated the artificial prey such that modeled quantal catches of the stimuli for the bird’s single and double cones fell within the natural range of cone captures from samples of the background. Authors of similar studies have controlled the level of contrast of stimuli markings based on luminance channels (e.g., Stevens *et al.* 2007b), or in terms of color discrimination thresholds (e.g., Stobbe and Schaefer 2008). The actual calibration of the stimuli values can be achieved in a number of ways, but perhaps the most straightforward is to begin with measuring the properties of the object that is to be matched in the appropriate color space. Then, one can produce a set of self-made calibration charts by printing patches of different colors and luminances from the printer, and check these by measuring the properties of each patch by photography or spectrometry, and comparing the stimuli values measured to those from the original signal. This process can be repeated by modifying the closest color matches in turn iteratively to obtain the closest match possible from the printer output. Assessing which color patches are best can be achieved by using color space comparisons or discrimination models. For example, if one wishes to produce artificial stimuli that match a natural object as closely as possible for color, then one can calculate which colors when printed give a discrimination contrast of less than or as close to 1.00 jnd as possible. This should mean that the observer cannot tell the difference between the real and artificial object for color or luminance, though it is important to remember that comparisons may be made based on other attributes too, such as texture.

Finally, a number of studies have now utilized video display units to present artificial stimuli to primates in experiments investigating the significance of color variation (e.g., Gerald *et al.* 2006b, 2007; Waitt *et al.* 2006). A significant amount of attention has been given to the use of such units for conducting behavioral experiments, and so we recommend that readers consult this literature for the relevant information regarding how to calibrate displays for color, luminance, flicker, motion, and other attributes (see for example Baldauf *et al.* 2008; D’Eath 1998; Fleishman *et al.* 1998; Fleishman and Endler 2000). It is also important to note that though many of the criticisms aimed at the use of display units have stemmed from their use for animals with very different visual systems from our own,

(e.g. birds and fish), many of the associated problems also need careful consideration when dealing with a range of primates (Waite and Buchanan-Smith 2006).

Conclusion

The diversity in both primate coloration and visual systems make them a potentially valuable group for testing proximate and ultimate questions of animal coloration. However, in doing so, it is important to use appropriate methods to quantify the signals involved objectively. There are a range of methodological approaches, the most appropriate being dictated by the exact question in hand and practical constraints. Measuring color data in terms of the quantal catch of the photoreceptors of specific receivers, and hence incorporating color measurements into models of visual perception, can be highly accurate in quantifying coloration in a manner relevant to the appropriate visual system, and in predicting behavior. By analyzing color measures with respect to specific visual systems, field studies can link behavioral ecology to the visual and cognitive sciences, and move toward descriptions of signal information content that incorporate elements of receiver psychology. This in turn should lead to a greater understanding of the detection and interpretation of signals by receivers, and hence their likely use in decision making.

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Note: A range of self-written MATLAB files for undertaking modeling of quantal catch data and camera calibration are available on request from the corresponding author (ms726@cam.ac.uk).

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