American Journal of Primatology 59:67–91 (2003)

RESEARCH ARTICLE

Colors of Primate Pelage and Skin: Objective Assessment of Conspicuousness

PETROC SUMNER[1,2*] AND J.D. MOLLON[1]
[1]*Department of Experimental Psychology, Cambridge, United Kingdom*
[2]*Department of Cognitive Neuroscience, Faculty of Medicine, Imperial College, London, United Kingdom*

We present a quantitative means of assessing the conspicuousness of animal coats or other objects in terms of the color vision of each possible observer. We measured reflectance spectra from the fur and skin of many primate species in order to provide an objective survey of the possibilities of pelage coloration found in extant primates. We show that the orange coloration displayed by many platyrrhine and some strepsirhine primates, while being conspicuous to humans, would be cryptic amongst foliage to all males and many females of their own species. In relation to this finding, we briefly review what is known of the color vision of birds that prey on primates, and assess how conspicuous the orange pelage would be to these predators. Am. J. Primatol. 59:67–91, 2003.

Key words: trichromacy; dichromacy; coat color; *Leontopithecus*; *Mandrillus*

INTRODUCTION

The importance of colors of animal fur, skin, and plumage–in camouflage, signaling, and mate choice–has long been scientifically recognized [e.g., Darwin, 1794], but there have been surprisingly few studies of the behavioral significance of pelage colors in primates [Kingdon, 1980]. Moreover, existing studies have generally used color names and categories based solely on subjective human judgments [Ross & Regan, 2000; Treves, 1997]. However, within the animal kingdom the form of color vision possessed by humans is rare, and is not even shared by all primates [e.g., Bowmaker, 1998; Hart, 2001; Jacobs, 1993; Mollon et al., 1984]. An animal's coloration, whether for display or crypsis, cannot be understood without an appreciation of the color vision of conspecifics and the other animals, especially predators, with which that species interacts. We must also take into account the natural environment in which the animal would be

*Correspondence to: P. Sumner, Department of Cognitive Neuroscience, Faculty of Medicine, Imperial College, St. Dunstan's Road, London W6 8RF, UK. E-mail: p.sumner@ic.ac.uk.

Received 6 August 2002; revision accepted 2 December 2002

DOI 10.1002/ajp.10066
Published online in Wiley InterScience (www.interscience.wiley.com).

seen [Endler, 1990]. Here we propose a quantitative method for assessing the conspicuousness of colors, and we argue that an approach of this kind must be adopted when assessing the ecological role of pelage color.

In a range of wild and captive primates, and in preserved pelts, we measured the spectral reflectance (i.e., the proportion of incident light reflected at each wavelength) of the pelage. Many catarrhine, platyrrhine, and diurnal strepsirhine species were included in the study, but special attention was given to *Mandrillus sphinx*, since ''no other member in the whole class of mammals is colored in so extraordinary a manner as the adult male mandrill'' [Darwin, 1888]. We emphasize also the orange coloration displayed by many platyrrhine species and by some species of Madagascan strepsirhines, because these primates have an interesting pattern of sex-linked polymorphism in their color vision. We show that these orange colorations, although conspicuous to humans, would be cryptic amongst foliage to all male and to some female conspecifics. What is the selective advantage in a pelage that may advertise your presence to a predator but is cryptic to most members of your own species? We assess this apparent paradox in terms of what is known about the color vision of the predators, and in terms of the gamut of possible pelage coloration that a primate may exhibit.

The goals of this study were threefold: 1) to provide objective spectral measurements of a range of primate pelage; 2) to set out a generic method for assessing colors in terms of any particular animal's color vision; and 3) to draw attention to, and as far as possible assess, the ecological puzzle that the seemingly conspicuous pelage of some primates is in fact not conspicuous to many conspecifics. First, we briefly review the color vision of primates in the context of the less sophisticated color vision of other mammals.

Brief Review of Mammalian Color Vision

Retinal photoreceptors signal only the total number of photons they absorb per unit time, and thus they cannot intrinsically distinguish colors. Any color can be made to match any other by a suitable adjustment of luminance [Rushton, 1972]. In order to have color vision, an animal must possess at least two types of photoreceptor, which differ in their absorption spectra (that is, in their sensitivity to different wavelengths of light). If an animal has two types of cone photoreceptor, the creature can discriminate lightness and one dimension of hue, and its vision is said to be dichromatic. For example, human dichromats may be able to distinguish colors varying along a yellow-violet axis, but not those varying on the green-red dimension. Most placental mammals have dichromatic color vision. When three distinct types of photoreceptor are active together, trichromacy results, and the color vision now has two chromatic dimensions. Many vertebrates have four distinct types of cone, and thus the potential for tetrachromatic color vision.

All catarrhines (Old World monkeys and apes) appear to share a form of trichromacy that is exemplified by normal human vision. In the retinas of these primates there are three types of cone photoreceptor, termed S, M, and L cones according to which region of the visible spectrum (short, middle, or long wavelength) they are maximally sensitive. The wavelengths to which the S, M, and L cones are most sensitive lie close to 430 nm, 530 nm, and 560 nm, respectively, for all catarrhines that have been tested [Bowmaker et al., 1991; Jacobs, 1993] (see Fig. 1C). The spectral tuning of photoreceptors is determined by opsin proteins, and in the case of the M and L cones these differ from each

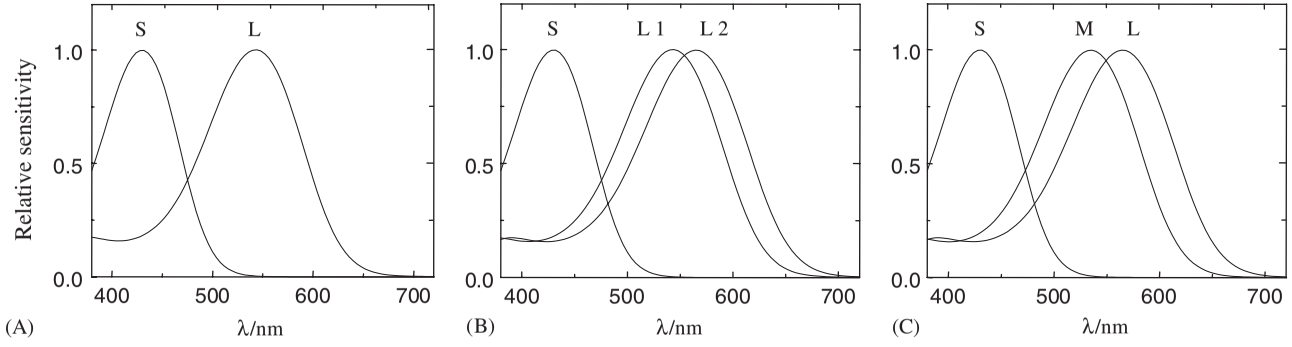


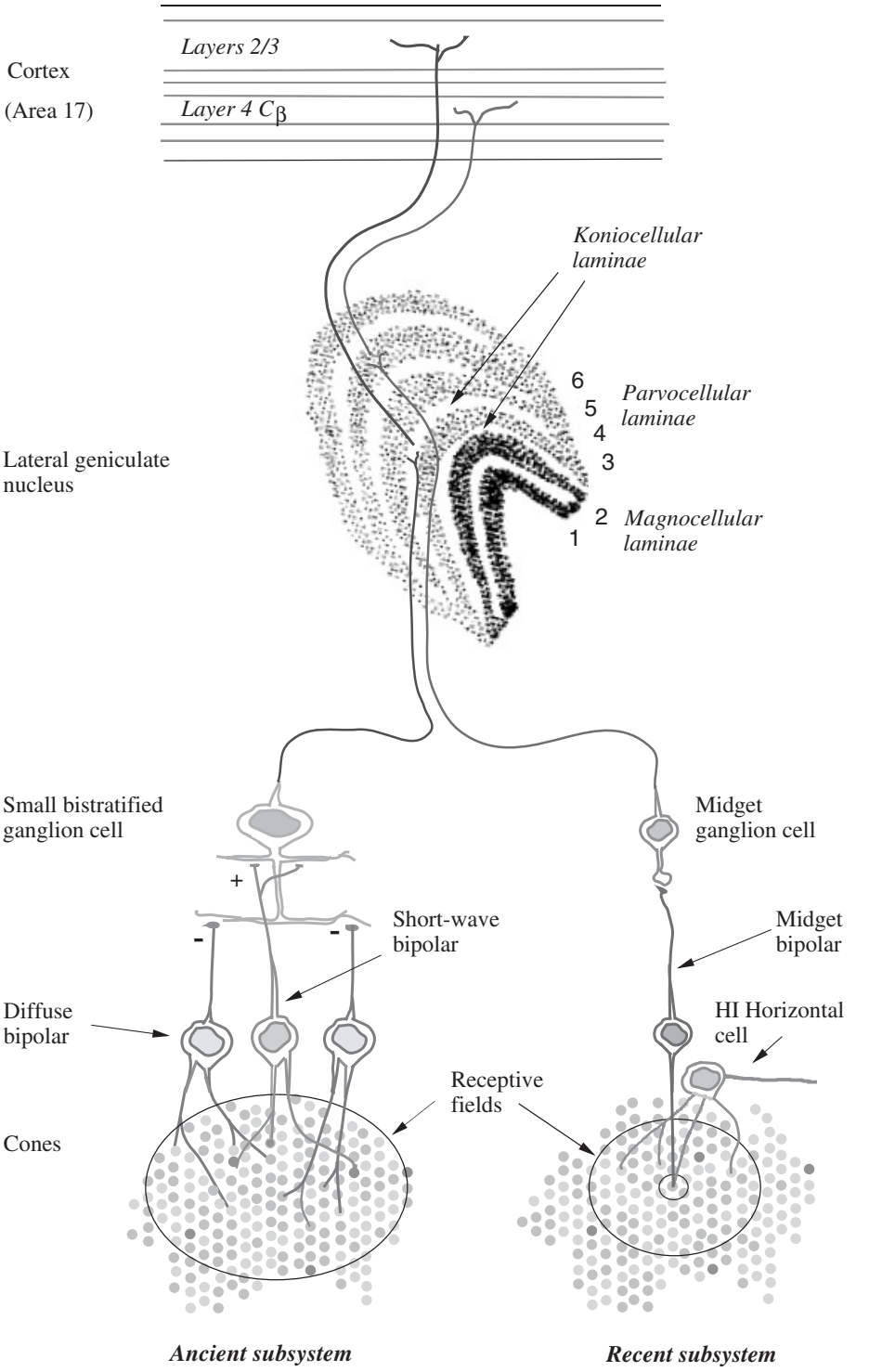
Fig. 1. Spectral sensitivity of primate cone pigments. Part **A** represents the dichromatic condition of most mammals, including all males and some females of the platyrrhine and strepsirhine primate species that exhibit sex-linked polymorphism. In the polymorphic species, LWS pigments with peak sensitivity (λ_{max}) values of 536, 543, 550, 556, and 563 nm have been recorded, and in most species at least three of these are present in the population. Part **B** represents the trichromatic condition of a heterozygous female platyrhine or lemur (the λ_{max} values are 430, 543, and 563 nm in this diagram). Part **C** represents the catarrhine primates, which are uniformly trichromatic. Following a gene duplication in this lineage, the two LWS pigments, L and M, are produced by separate genes (rather than different alleles at the same locus, as in the case of the primates with polymorphic vision). The λ_{max} values for all catarrhines are about 430, 530, and 560 nm. The platyrrhine genus *Alouatta*, the howler monkey, also possesses this form of uniform trichromacy, following a separate duplication of the LWS gene in their lineage.

other only by 15 amino acids. Both belong to the same class of vertebrate photopigments (called LWS, long-wavelength-sensitive). The S cone opsin belongs to a separate class (termed SWS1, short-wavelength-sensitive class 1), or violet-UV after the avian members of the group), which diverged from the LWS class before the divergence of tetrapods and teleost fish [Bowmaker, 1998]. The only nonprimate mammals so far discovered to have trichromatic color vision are two species of marsupial [Arrese et al., 2002]. Their trichromacy, which may be shared by other species of marsupial that remain unstudied, is of a form closer to that of reptiles than that of primates [Arrese et al., 2002]. Most placental mammals possess only one type of LWS cone and a few S cones [Jacobs, 1993], and so exhibit dichromatic color vision rather like that found in ''red-green color-blind'' humans (Fig. 1A). Some mammals, including aquatic species [Peichl et al., 2001] and nocturnal animals such as the owl monkey (*Aotus trivirgatus*) [Jacobs et al., 1993a], have only LWS cones and no S cones, and thus have no color vision (unless they compare rod signals with the signals from their single class of cones).

The neural pathway subserving the dichromatic comparison of S and LWS cone signals is called herein the ''ancient mammalian color subsystem.'' This pathway is thought to be similar in dichromatic and trichromatic primates [Dacey & Lee, 1994; Ghosh et al., 1997; Silveira et al., 1999]. A separate neural pathway, the ''recent color subsystem,'' exists in trichromatic primates to compare the signals from M and L cones, and is probably parasitic on neural machinery (the parvocellular pathway) that is already present in both dichromats and trichromats for making fine spatial comparisons [Ghosh et al., 1996; Goodchild et al., 1996; Mollon & Jordan, 1988; OKeefe et al., 1998; Silveira et al., 1998; Wilder et al., 1996; Yamada et al., 1996, 1998]. Thus it seems that all diurnal primates with three types of cone have the potential to be trichromatic without the need for changes in retinal processing. The two separate neural pathways of primate color vision are shown diagramatically in Fig. 2.

In contrast to the catarrhines, most platyrrhine species display a sex-linked polymorphism, in which there are two or more types of LWS cone present in the population. The color vision of all males and some females is dichromatic, whereas some females possess trichromacy [Jacobs, 1993]. This is explained by the ''single X-chromosome locus model'' proposed by Mollon et al. [1984]: A single locus encodes an opsin sensitive to middle-to-long wavelengths, but this gene is polymorphic. Males inherit only one copy of the gene because it is on the X chromosome; therefore, all of their LWS cones must be identical and they can only be dichromatic (all individuals also possess S cones). Females inherit two copies of the gene, only one of which is expressed per cell owing to X chromosome inactivation [Lyon, 1972]. All the LWS cones of a homozygous female will be identical, but heterozygous females will possess two types of LWS cone and thus have the potential for trichromacy (Fig. 1B).

Fig. 2. The two separate color subsystems that subserve primate trichromacy. The ancient system (left) compares the signal from S cones to that from the cones of the LWS class. If distinct M and L cones are present in the retina, the recent subsystem (right) compares the signals from these. This latter system is thought to be embodied in the parvocellular pathway, which is specialized for spatial acuity and is present in both dichromatic and trichromatic primates. The source of the surround input to the midget ganglion cell is not yet known for certain, and may be mediated by horizontal cells.


Cortex
(Area 17)
Layers 2/3
Layer 4 Cβ
Koniocellular laminae
6
5
4
3
2
1
Parvocellular laminae
Magnocellular laminae
Lateral geniculate nucleus
Small bistratified ganglion cell
Midget ganglion cell
+
-
-
Short-wave bipolar
Midget bipolar
Diffuse bipolar
HI Horizontal cell
Receptive fields
Cones
Ancient subsystem
Recent subsystem

As a result of a genetic study [Tan & Li, 1999] and electrophysiological measurements [Jacobs & Deegan, 2002; Jacobs et al., 2002] it is now thought that the color vision of at least some, and conceivably all, diurnal Madagascan strepsirhines displays a sex-linked polymorphism similar to that seen in platyrrhines. The polymorphic condition may also have existed in catarrhines, ancestral to the uniform trichromacy found in all extant species. In one platyrrhine genus, *Alouatta* (howler monkeys), there has been a gene duplication that has separately produced uniform trichromacy almost identical to that of the catarrhines [Jacobs et al., 1996]. For a fuller account of the evolution of primate color vision, see Mollon [2000].

METHODS

General Method for Specifying Color for a Known Observer

One cannot rely upon instruments or metrics designed for human color vision to represent in any meaningful way what colors would look like to other animals. The exception is when an animal's ocular filtering characteristics are known to be highly similar to those of man and its cone sensitivities are the same as, or a subset of, those found in normal human vision (as in the case of human dichromats). In all other cases it is necessary to begin with full spectral measurements (i.e., of the photon flux at each potentially visible wavelength) rather than measurements made using standard cameras, video cameras, colorimeters, and other instruments that extract the information in terms of three primaries. It is impossible to know the exact nature of the full spectrum from three primaries, and thus impossible to reconstruct what another animal might see. Two colors that look identical to humans might appear different to another animal if its cone sensitivities were different from those of humans, and, conversely, two colors that look different to most humans might be indistinguishable to other animals. Lucas et al. [2001] have described an apparatus suitable for measuring the reflectance spectra of small collected samples. If measurements are required from larger or uncollected surfaces (as in this case of primate pelage), a telespectroradiometer is most suitable. Outlined below are the steps that are necessary for quantitatively assessing the conspicuousness of an object's reflectance to an observer whose color vision is known (see Fig. 3).

1. For each object of interest (e.g., an area of fur or skin) one must obtain the ''stimulus spectrum'' that might reach the observer's eye in a natural environment (e.g., a primate in the forest canopy). (See Endler [1990] for a comprehensive discussion of stimulus spectra.) The measurements can be made directly in situ – for example, in a forest canopy – but this is not always possible. Alternatively, the stimulus spectrum can be calculated by measuring the reflectance spectrum of the object elsewhere, and combining it with a measurement of the illumination in the appropriate natural environment (Fig. 3, top panels). For objects, such as fur, whose reflectance properties differ for different angles of illumination and observation, extra care must be taken to obtain realistic estimates of the stimulus spectra that would present themselves to observers in the natural environment. If the measurements are made in units of energy (or power), they must be converted to photon flux, since photoreceptors respond in proportion to the number of photons they absorb, not the amount of energy [Endler, 1990].

2. Each stimulus spectrum must be filtered as it would be by the optical properties of the animal's eye, before it reached the photoreceptors. Mathema-

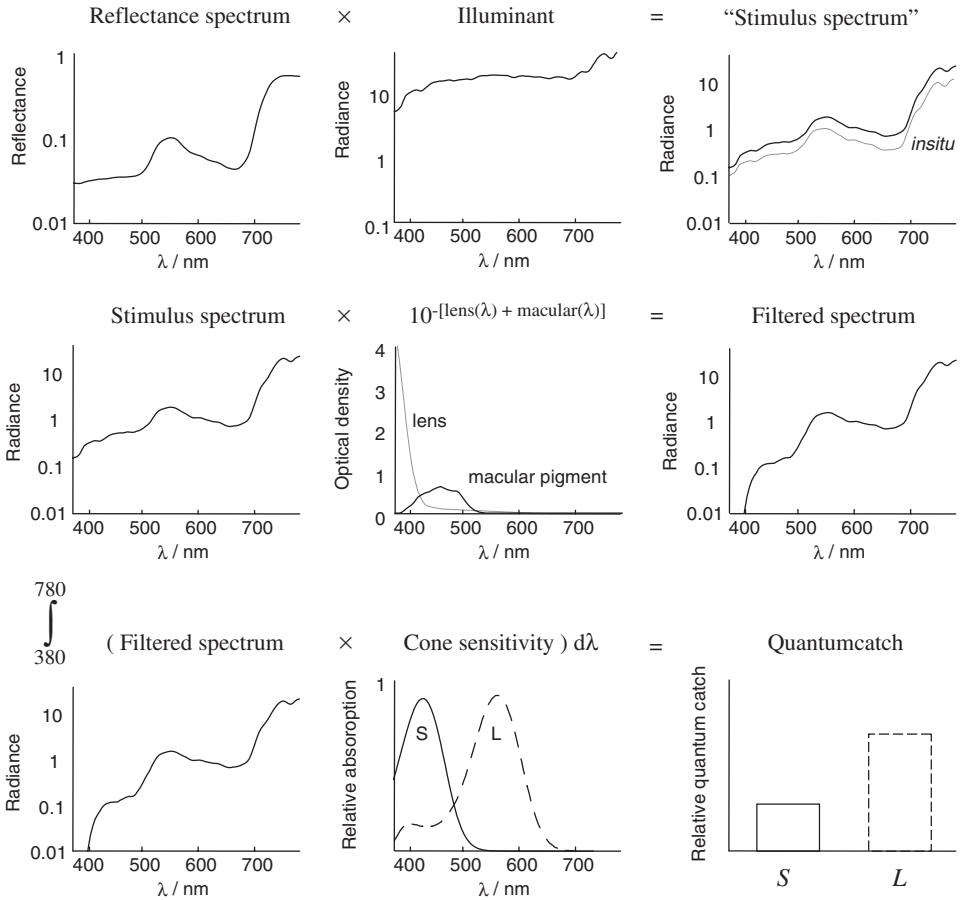


Fig. 3. Diagrammatic representation of the stages in calculating the relative quantum catch (*L* or *S*) of primate L and S cones for a particular stimulus. The stimulus spectra (of leaves in this case, top right panel) are obtained in one of two ways: by measuring in situ in the appropriate environment (gray line), or by multiplying a reflectance spectrum measurement by a suitable illuminant measurement (black lines, top row). The middle panels show the filtering of the stimulus spectrum by ocular media (in this case the filtering for the optical media is applied to the stimulus spectrum rather than to the cone-sensitivity curve, an operation that is mathematically equivalent). Lens(λ) is the optical density of the lens, and Macular(λ) is the optical density of macular pigment. The bottom panels show the calculation of each quantum catch from the filtered spectrum, using the appropriate sensitivity function for each cone. See text for more details.

tically, the stimulus spectrum must be multiplied by the transmission spectra of the ocular media that have significant absorption in the range of wavelengths to which the animal's retinal receptors are sensitive. The important ocular media for primates are the lens and macular pigment, which absorb at short wavelengths (Fig. 3, middle panels). If appropriate measurements are not available (there may be differences between species, individuals, or ages), one can take the approach, as we do here, of choosing the best available measurements and testing the effects on the results of simply varying these values beyond the plausible range.

3. The filtered stimulus spectra must be multiplied by cone sensitivity functions and integrated over the visible range of wavelengths in order to calculate the quantum catch (*S*, *M*, or *L*, for primates) in each class of cone (Fig. 3,

bottom panels). First one needs to determine the appropriate sensitivity functions for the cone pigments; we calculate these by using the empirically derived polynomial equation of Baylor et al. [1987]. This takes advantage of the fact that all photopigments have a sensitivity of a similar shape if they have 11-cis-retinal as the chomophore (as all mammalian rods and cones do), and thus the whole sensitivity function can be generated by knowing only the wavelength of peak sensitivity (λ_{max}). For completeness, the sensitivity functions should be adjusted for the self-screening properties of the receptors themselves (before the light can reach a certain layer of pigment, it is filtered by the preceding layers). For birds, the sensitivity functions must be adjusted also for the colored oil droplets that reside in their cones and sharpen the spectral tuning. Sometimes steps 2 and 3 are combined: Instead of filtering the incoming spectra by absorption properties of the lens and macular pigment, one can adjust the cone sensitivity functions for these properties (or this can be done directly by measuring the spectral sensitivity functions of an animal at the cornea).

4. Once the photon/quantum catch in each of the animal's photopigments is known, any given surface can be plotted in terms of the ratios of quantum catches in different classes of photoreceptor. Such a plot is called a ''chromaticity diagram.'' In the case of primates, it is convenient to use as ordinates the two ratios $S/(L+M)$ and $L/(L+M)$. The former corresponds to the signal in the phylogenetically ancient subsystem, and the latter corresponds to the signal in the newer subsystem. Physical stimuli of different spectral composition but the same chromaticity are those that will produce the same ratios of quantum catches in the photoreceptors. Chromaticity is the objective correlate of perceived hue, but the relationship is not an invariant one, since subjective appearance depends also on the adaptive state of the eye and on the surrounding context. Sometimes human observers give different color names to light and dark colors that have similar chromaticities, for example orange and brown.

5. Finally, there are two types of approaches to assess conspicuousness: 1) If one is interested in how different two or more colors look, a measure of the contrast or spread of the chromaticities is appropriate. The colors might be from patches of fur or plumage, and we have previously taken this approach to calculate the distinguishability of unripe and ripe fruit [Sumner & Mollon, 2000b]. 2) If one is interested in how detectable a color is amongst a certain environmental background (as when the target is a fruit or a primate, and the distractors are leaves in the forest), one can calculate a signal-to-noise ratio, such that the signal is the difference between target and background, and the noise is the variation in the background. This approach has been taken for calculating the detectability of fruit or young leaves in the canopy by Regan et al. [1998, 2001] and Sumner and Mollon [2000a]. In the case of the first approach, statistical tests that compare means of populations may be appropriate (such as applying the *t*-test to discover, for example, whether two species of flower have significantly different chromaticity distributions). However, comparing means of target and background chromaticity distributions will not determine whether targets are conspicuous. To be camouflaged, a class of objects does not have to display the whole range of visual appearances found in their surroundings; they need only appear like a subset of their surroundings. If targets are rare compared to distractors (as when the targets are fruits or primates, and the distractors are leaves in the forest), the targets must lie outside the distribution of distractors if they are to be detected [Sumner & Mollon, 2002].

Specific Methods

We gathered 223 measurements from 18 species of primate held in British zoological parks (see Acknowledgments); 15 from free-ranging *Cercopithecus ascanius* and *C. aethiops* in the Entebbe Wildlife Center, Uganda; and 132 from the fur of preserved pelts of 20 species at the Natural History Museum, London. All spectra were measured at 4-nm intervals between 380 nm and 780 nm, using a portable PhotoResearch PR650 telespectroradiometer. Reflectance spectra were calculated by dividing a radiance measurement of pelage by a measurement of the prevailing illuminant made by placing a white barium sulfate plaque in the same place as the measured pelage. Standard illumination and standard measuring angles were used for the skins at the Natural History Museum. Each part of each pelt was measured twice – in line with, and at 90° to – the lie of the fur. However, for live animals, this degree of control was impossible to achieve. The animals were never restrained, and thus the illumination of the measured pelage may not always have been identical to the illumination measurement. It was not always possible to position the white plaque at exactly the same angle in exactly the same position as the part of the animal measured, and the time delay between pelage and plaque measurement was not always as short as would be desirable. However, most measurements were made under an overcast sky, and thus the differences in illumination due to time delays or plaque positioning were minimized.

As explained in section 1 above, the reflectance spectra were multiplied by an illuminant spectrum to produce a ''stimulus spectrum'' that might reach a primate's eye in a natural environment. The illuminant chosen as the standard was measured in the canopy of a Ugandan rainforest under an overcast sky. It represents approximately the midpoint in chromaticity and luminance of 66 measurements of illumination made in various forest and savanna locations under varying weather conditions, and is similar to measurements made under cloudy conditions in other forests by Endler [1993] and Regan et al. [2001]. We have tested the effects of using illuminants from the extremes of the range, and found that this did not affect any conclusions presented here. The numerical values of the results changed, but the patterns did not.

The chromaticities of the stimulus spectra were specified in color spaces appropriate for a particular primate in question, taking into account the exact cone sensitivities possessed. Each stimulus spectrum (in quantum units) was adjusted for the filtering effects of the ocular media (see section 2 above). The spectral optical density distribution of the lens and macular pigment has been measured for only a few primate species. In the case of the lens, we had available human, baboon, macaque, and marmoset data [Cooper & Robson, 1969; Tovée et al., 1992; Wyszecki & Stiles, 1982]. These lens measurements are all very similar. For macular pigment we used human data from Wyszecki and Stiles (1982), which are similar to Snodderly et al.'s [1984] measurements for macaques. We tested the effects of changing the lens and macular pigments densities beyond the plausible range, and found that it made no difference to the conclusions presented herein. The filtered stimulus spectra were multiplied by cone sensitivity functions and integrated over the visible range of wavelengths in order to calculate the quantum catch (S, M, or L) in each class of cone. The cone sensitivity functions were calculated for the different spectral tuning of each photopigment by using the empirically derived polynomial equation of Baylor et al. [1987] (see section 3 above). For trichromatic primates, the chromaticity

coordinates $S/(L+M)$ and $L/(L+M)$ were calculated, representing the signals in the two color subsystems. The resulting chromaticity diagram is similar in form to the Macleod-Boynton chromaticity diagram for humans [MacLeod & Boynton, 1979]. Luminance was represented as $L + M$. For dichromatic primates, which possess no distinct M cone and therefore no recent color subsystem, luminance was simply L, and the one chromaticity value was S/L, representing the signal of the ancient mammalian color system.

The full reflectance spectra (and also CIE 1931 chromaticity coordinates) for all measurements are available from http://vision.psychol.cam.ac.uk/spectra. The species for which we have measurements are listed in Table I.

TABLE I. Species of Primate From Which Reflectance Spectra Have Been Measured

Infraorder	Species	Common name	Live/pelt
Catarrhini			
	Cercopithecus aethiops	Vervet monkey	l
	Cercopithecus ascanius	Red-tailed monkey	l,p
	Cercopithecus patas	Patas monkey	l
	Colobus badius	Red colobus	p
	Hylobates concolour	Crested or white cheeked gibbon	p
	Macaca fascicularis	Crab-Eating macaque	l
	Mandrillus sphinx	Mandrill	l,p
	Pongo pygmaeus	Orangutan	p
	Presbytis melalophos	Black-Crested sureli	p
	Presbytis rubicunda	Red sureli	p
	Semnopithecus obscurus	Dusky leaf monkey	l
	Trachypithecus auratus	Ebony langur	l
Platyrrhini			
	Alouatta seniculus	Red howler monkey	l,p
	Aotus trivirgatus	Owl or night monkey or douroucouli	p
	Cacajao calvus rubicundus	Bald or red uakari	l,p
	Callicebus moloch	Dusky titi	p
	Callicebus personatus	Masked titi	p
	Callithrix argentata	Silvery marmoset	l
	Chiropotes satanus	Bearded or black saki	p
	Lagothrix flavicauda	Yellow-tailed woolly monkey	p
	Leontopithecus rosalia	Golden lion tamarin	l,p
	Leontopithecus chrysomelas	Golden headed tamarin	l
	Saguinus midas	Red handed tamarin	l
	Saguinus nigricollis	Spix's black-mantled tamarin	p
	Saguinus oedipus	Cotton top tamarin	l
	Saimiri sciureus	Squirrel monkey	l,p
Lemuriformes			
	Avahi laniger	Woolly lemur	p
	Lemur fulvus collaris	Collared lemur	l
	Lemur fulvus sanfordi	Sanford's lemur	l
	Lemur mongoz	Mongoose lemur	p
	Varecia variagata rubra	Red-ruffed lemur	l,p

The last column indicates whether the measurements were of live animals in zoos or wildlife parks (see Acknowledgments), or of preserved pelts at the Natural History, London.
Tables of full spectra, body part measured and location of animal can be found at http://vision.psychol.cam.ac.uk/spectra.

RESULTS

Gamut of Chromaticities Presented by Primate Pelage

Figure 4 shows a chromaticity diagram for the fur and skin of all primates measured. The vertical axis represents, for a trichromatic catarrhine, the signal in the ''ancient mammalian color subsystem,'' and the horizontal axis represents the signal in the recently evolved color subsystem. Included for comparison, marked by a dashed triangle, is the gamut of chromaticities available from a typical computer monitor (the apices are the chromaticities of the blue (top), green (bottom left), and red (right) phosphors). The curved line represents the chromaticitites of single wavelengths of the spectrum.

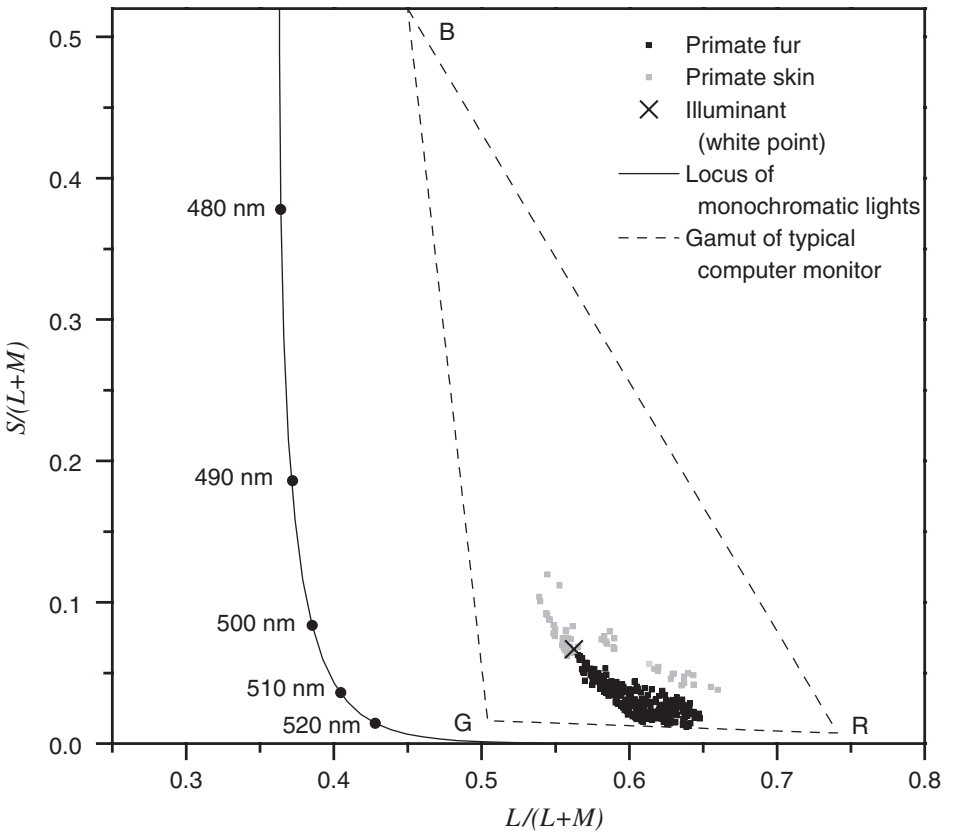


Fig. 4. Primate fur and skin plotted in a chromaticity diagram constructed to be most appropriate for catarrhines. The signals of the ancient and recent subsystems of color vision, which together produce trichromacy, are represented by the vertical and horizontal axes, respectively. The primate fur has a restricted range of chromaticities that lie in a white-yellow/orange color direction. Lying on roughly the same chromaticity axis, close on the opposite side of white, is the blue skin displayed by some catarrhines. Notice that the difference between this and other pelage or skin colors is manifested in the signals of both color subsystems; thus it is not simply the case that blue is detected by ''blue'' cones (S cones). Also separate from the fur lies the purple and pink/red skin displayed by catarrhines, measured mainly in *Mandrillus sphinx*. The dashed triangle shows, for comparison, the gamut of chromaticities available from a typical computer monitor, delineated by the blue (top), green (bottom left), and red (right) phosphors. The solid curve marks part of the locus of monochromatic lights (the chromaticities of individual wavelengths).

These are the most saturated lights possible. Notice that the whole gamut of primate fur occupies a restricted area of chromaticity space, lying roughly on a line between white (marked by a cross) and yellow-orange. If more exhaustive measurements had been made, and we had not concentrated on examples of clearly colored fur, there would be more data points around the cross, representing ''white'' and the various light and dark grays exhibited by many primates.

Figure 5 shows the measurements of pelage divided into categories of primate infraorder and type of measurement (live animal or pelt). Figure 5A and C are chromaticity plots for trichromatic primates, whereas Fig. 5B and D are plots of the signals in the luminance pathways and the ancient color subsystem of a dichromat, which are similar to the signals in the equivalent pathways of a trichromat. The plots show in more detail the restricted gamut of fur colors displayed by primates, and indicate that there are no systematic differences between the furs of catarrhines, platyrrhines, and lemuriformes. A comparison of Fig. 5A and C indicates that there is good agreement between the chromaticities calculated from measurements of live animals and pelts, and indeed, the results from individual species measured in more than one location (Natural History Museum, different zoos, or Uganda) were always found to be in good agreement (the chromaticity differences were generally as small as the variation between individuals; reasons for the poorer agreement between the luminances are outlined in the Discussion). Lying outside the limited range of fur colors are the skin colors of some catarrhines. Our measurements include the blue scrotum of the vervet monkey (*Cercopithecus aethiops*); the face of the dusky leaf monkey (*Semnopithecus obscurus*); and the blue, red, and purple of the rump, snout, and scrotum of the mandrill (*Mandrillus sphinx*). Measurements from the different body parts of *M. sphinx* are shown in more detail in Fig. 6A. Notice that the blue produces a large contrast to yellow/orange fur and red skin in both color subsystems, not just in the S cone subsystem (often misleadingly referred to as the ''blue-yellow'' channel). The chromaticities of the mandrill's purple-colored skin plot between the chromaticities of red and blue skin, and Fig. 6B shows that this is because the purple coloration is produced by a reflectance spectrum that is approximately a sum of the blue and red reflectances. A likely reason for this is proposed in the Discussion below.

Also plotted in Fig. 5 are measurements of foliage from rainforest canopy, which allow us to assess how conspicuous the primate pelage might be in the forest to trichromats or dichromats. This issue is dealt with below in the context of the polymorphic color vision of platyrrhines and lemurs.

Conspicuous and Cryptic Primates

Figure 7 shows the chromaticity measurements of the coat of the golden lion tamarin (*Leontopithecus rosalia*) compared to measurements of rain forest foliage and bark. The leaves and bark were measured in Uganda, but show a nearly identical chromaticity distribution to those measured in South America by Regan et al. [2001]. A recent genetic study [Surridge & Mundy, 2002] indicates that these tamarins have polymorphic color vision like that of the species *Callithrix jacchus*, *Saguinus fuscicolis*, and *S. oedipus*, whose color vision has previously been examined by microspectrophotometry [Tovée et al., 1992; Travis et al., 1988] and electroretinography [Jacobs, 1994; Jacobs et al., 1987] as well as molecular

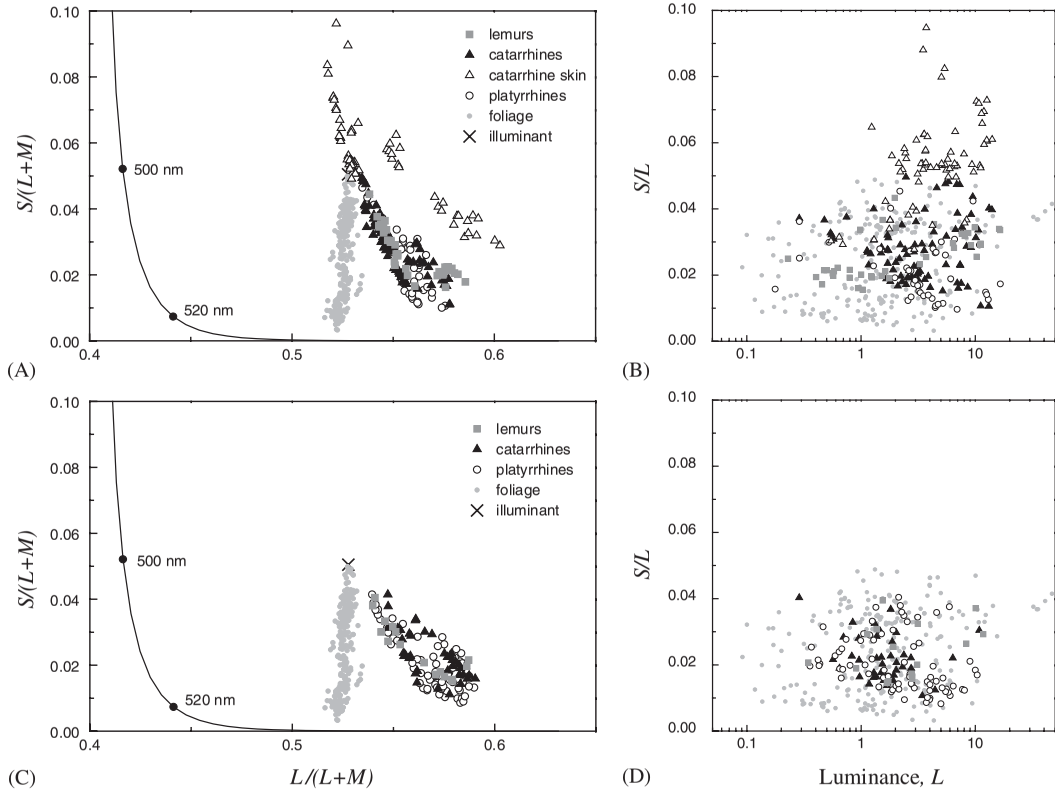


Fig. 5. **A:** Pelage of live primates plotted in a chromaticity diagram appropriate for a trichromatic platyrrhine, using cone λ_{max} values of 423, 543, and 563 nm, and marmoset lens data (see Methods). Part **B** shows, for the same spectra, a luminance (L) vs. chromaticity (S/L) plot for a dichromatic platyrrhine with cone λ_{max} values of 423 and 556 nm. The luminance axis is logarithmic and relative (the absolute values have no meaning here, since they will change with the brightness of the illuminant). Also plotted are forest leaves (measured in situ in the canopy under cloudy conditions), demonstrating which pelage colorations would be conspicuous amongst foliage to trichromatic or dichromatic individuals. **C** and **D:** Corresponding plots for pelts in the Natural History Museum, London. Platyrrhine spaces were used in this figure to allow direct comparison to Fig. 7, but the data look very similar when plotted in color spaces for catarrhines with cone λ_{max} values of 430, 530, and 560 nm. In parts A and C, as in Figs. 4, 6A, and 7A, the solid curve marks part of the locus of monochromatic lights.

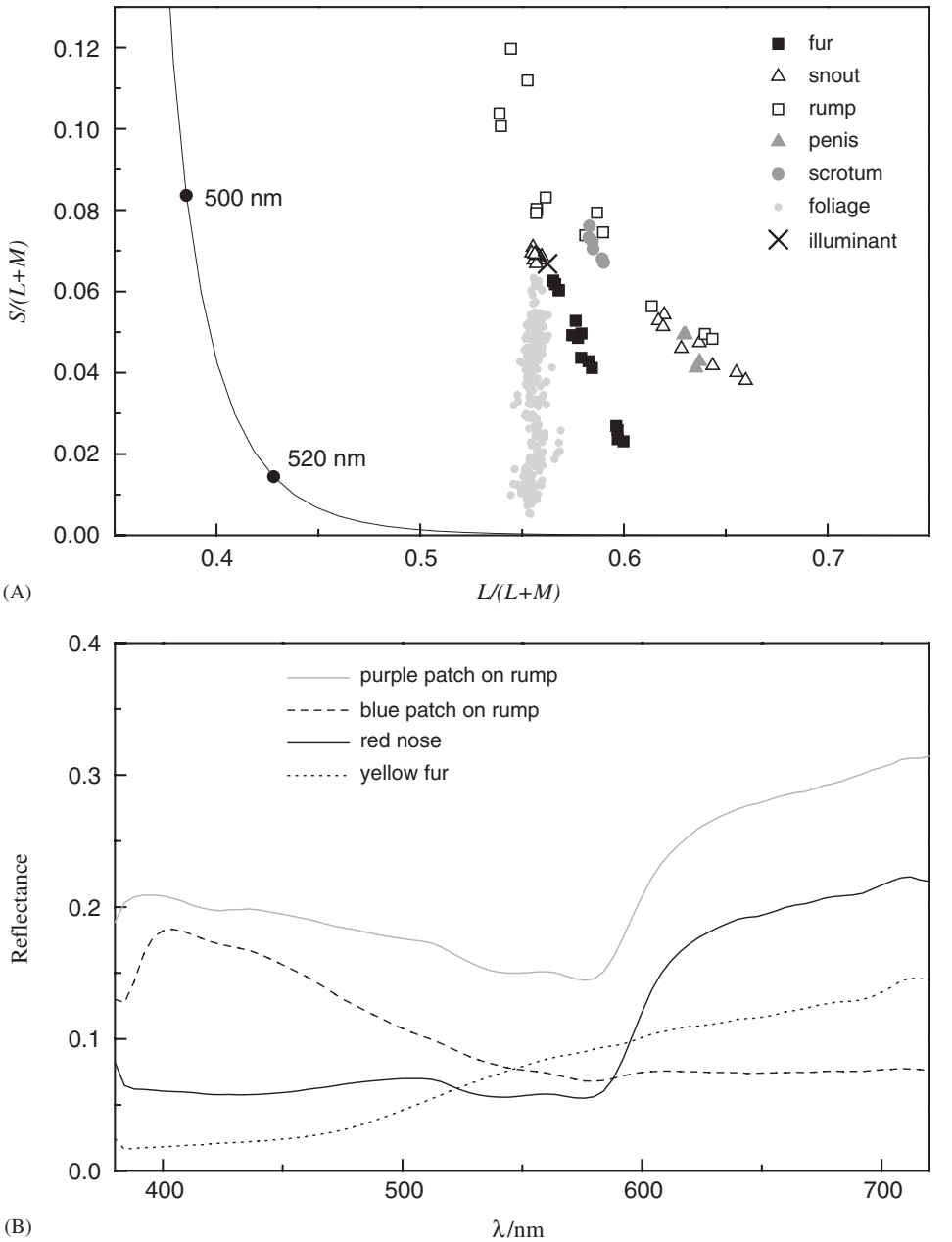


Fig. 6. **A**: Chromaticities of a *Mandrillus sphinx* breeding male (high-ranking in a multimale group in Colchester Zoo) plotted in a chromaticity diagram for a catarrhine, using cone λ_{max} values of 430, 531, and 561 nm, and an average of macaque and baboon lens data (see Methods). The beard of this primate is yellow, and much of the rest of the fur consists of black and yellow flecks, producing chromaticities that lie within the gamut displayed by other primates. However, the mandrill is most celebrated for its dramatic and rare utilization of red, blue, and purple on the snout and rump, the reflectance spectra for which are shown in **B**.

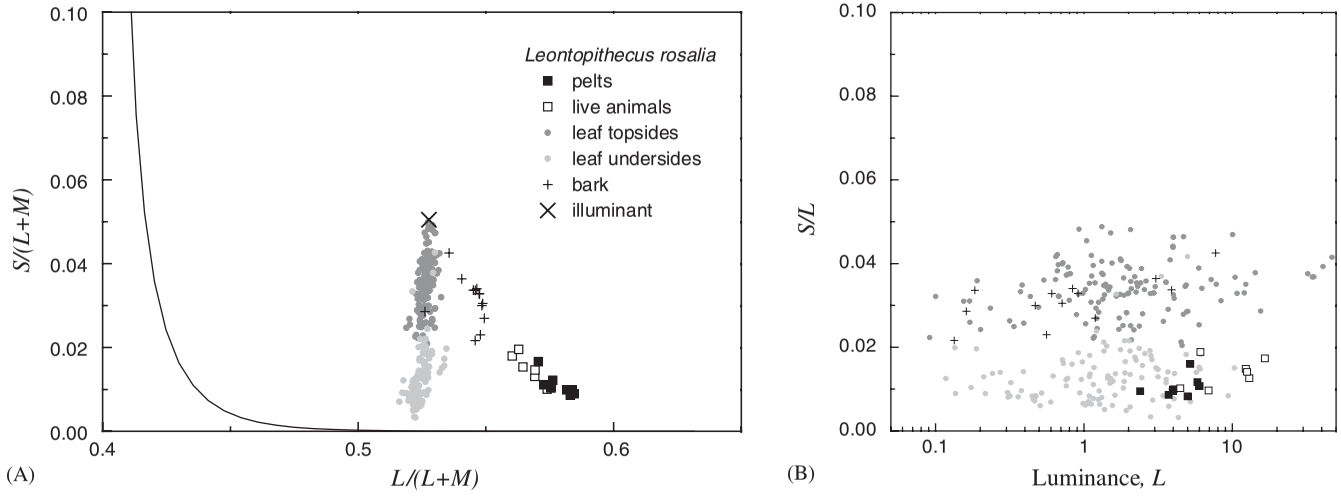


Fig. 7. A: Measurements of the golden lion tamarin (*Leontopithecus rosalia*) plotted in a chromaticity diagram appropriate for a trichromatic platyrrhine, using cone λ_{max} values of 423, 543, and 563 nm, and marmoset lens data. B: The same measurements plotted in a luminance/chromaticity diagram appropriate for a dichromatic platyrrhine with cone λ_{max} values of 423 and 556 nm. Also plotted are forest leaves (measured in situ in the canopy under cloudy conditions) and some examples of bark to demonstrate whether the pelage colorations would be conspicuous amongst foliage in the forest canopy to trichromatic or dichromatic individuals. The results for the alternative M/L λ_{max} value combinations of 543/556 and 556/563 nm are highly similar and lead to the same conclusions.

genetics [Jacobs et al., 1993b; Williams et al., 1992]. All individuals possess an S cone with a peak sensitivity (λ_{max}) value of about 425 nm, and there are (at least) three LWS cone opsin alleles in the population, producing λ_{max} values of 543, 556, and 563 nm. Most individuals possess only one of these L cone types, which makes them dichromatic. However, about two-thirds of the females are heterozygous (possessing two distinct L cone types), which allows them to be trichromatic. Thus Fig. 7A is a chromaticity diagram for trichromatic platyrrhine primates possessing cones with λ_{max} values of 423, 543, and 563 nm. It can be seen that the golden lion tamarin's coat stands out well from the background of foliage and bark for the recent color subsystem (i.e., horizontally in the diagram). Chromaticity diagrams for the alternative LWS cone pairings of 543/556 nm and 556/563 nm produce very similar results. Figure 7B is a diagram of luminance vs. the single dimension of color for a dichromatic platyrrhine possessing cones with λ_{max} values of 423 and 556 nm. The tamarin's pelage falls within or on the edge of the distribution of leaves, and our modeling shows that this is also true for the alternative LWS opsin alleles (543 and 563 nm). The calculated luminance of the fur is in fact the upper limit to the luminance that would present itself in the forest, and the values from the pelts measured in controlled conditions should be taken as a better representative of the true upper limit than the values from the live animals (the reasons for this are elaborated in the Discussion). Since the leaves were measured in situ in the canopy, their luminance values represent the true range in the forest, not an upper limit. In the forest, therefore, the pelage would lie within the distribution of foliage for a dichromat, and thus would be difficult to detect.

Golden lion tamarins are not the only primates with polymorphic color vision that display pelage of this orange coloration on part of the body. Plotted in Fig. 5 are several other examples: *Saimiri sciureus* (squirrel monkey), *Cacajao calvus rubicundus* (bald or red uakari), *Chiropotes satanus* (bearded or black saki), *Lagothrix flavicauda* (yellow-tailed woolly monkey), *Callicebus moloch* (dusky titi), *Callicebus personatus* (masked titi), *Saguinus midas* (red-handed tamarin), *S. nigricollis* (Spix's black-mantled tamarin), *Leontopithecus chrysomelas* (golden-headed tamarin), and *Avahi laniger* (the woolly lemur). Figure 5A and C are chromaticity diagrams identical to Fig. 7A, appropriate for a trichromatic platyrrhine possessing cones with λ_{max} values of 423, 543, and 563 nm. Likewise, Fig. 5B and D are luminance/chromaticity diagrams identical to Fig. 7B, for a dichromatic platyrrhine with λ_{max} values of 423 and 556 nm. It can be seen that for these dichromatic individuals, most primate pelage lies within the distribution of leaf chromaticities and luminances, which makes the animal inconspicuous. However, Fig. 5A and C show that much of the fur stands out in the recently evolved color subsystem of a trichromat. The same observations are true for the alternative dichromatic and trichromatic phenotypes found in platyrrhines. The pelage of *L. rosalia* combines a high chromatic signal with high luminance, lying at the lower right of the distributions in Fig. 5A–D. Thus, out of any existing primate fur, that of *L. rosalia* is maximally conspicuous to trichromats.

It is interesting that our results show no example of blue skin in a platyrrhine or lemuriforme species. Yet, such skin would be conspicuous to dichromatic primates, since it would lie outside the distribution of forest leaves and bark (Fig. 5B).

DISCUSSION

Gamut of Chromaticities Presented by Primate Pelage

The range of fur chromaticities displayed by primates is restricted because mammalian coloration is determined chiefly by melanin pigments. Different combinations of pheomelanin and eumelanin (or their absence) can supply a small range of colors from reddish-brown or orangish-yellow to white, gray, or black. In nature, orange coloration is often produced by carotenoids [Nassau, 1983], but these pigments do not appear to be used in mammalian fur. It has been reported that there are no detectable concentrations of carotenoids even in the very orange fur of lion tamarins and orangutans [Slifka et al., 1999]. In addition, the good agreement between the measurements of pelts and live animals indicates that pelage chromaticities do not change much with the environment or the diet of captive animals. However, it is undeniable that direct sunlight does cause some bleaching of fur color, which moves the fur's chromaticity toward white, and raises its luminance.

As Fig. 5 shows, chromaticities of catarrhine skin can deviate from this restricted distribution of fur. The blue coloration displayed by species such as *Mandrillus sphinx* and *Cercopithecus aethiops* is caused by Rayleigh scattering [Nassau, 1983], whereby small particles scatter short-wavelength (blue) light more strongly than longer-wavelength (red) light. The blue caused by Rayleigh scattering is often called ''Tyndall blue'' (blue sky is an example). Thus the range of blues in the mandrill and vervet have very similar chromaticities to the blues of the sky. In these primates, the incident light of shorter wavelengths is scattered toward the observer by small particles in the skin, whereas the longer wavelengths pass through and are absorbed by an underlying dark layer of melanin. The larger the scattering particles, the less saturated the blue color will be, because more middle wavelengths will also be scattered. It is interesting to note in Fig. 6A how close to white are the chromaticities of the mandrill's ''blue'' snout, yet they still appear blue owing to the contrast with adjacent colors, especially the red of the nose (the same is true of the desaturated ''blue'' of the scrota of some other cercopithecines, adjacent to a red penis). A more saturated color, like that on the mandrill's rump, inevitably limits the lightness possible, because a surface of saturated color is one that reflects a narrow spectral range and thus can never reflect a large proportion of a natural illuminant. This might make the coloration less visible, not more visible, in the dim conditions of the forest understorey.

The cause of the blue coloration explains why purple skin can be created with a reflectance spectrum that is approximately a sum of the reflectances of the blue and red skin (Fig. 6B). Since the blue is caused by scattering, not by pigmentation, another color can be superimposed by reflection from an underlying layer (e.g., red hemoglobin pigmentation). These two colors can be approximately additive, behaving more like mixed lights than mixed pigments (the colors are in fact not truly additive, because the reflected light from the underlying layer is filtered by the scattering layer before being added to the scattered light). For the same reason, green skin cannot be created by adding a yellowish melanin backing to the blue. This mixture would be primarily additive and the resulting spectrum would still contain both short and long wavelengths (green can be created from yellow and blue only by subtractive mixture, as in the mixing of paints [Helmholtz, 1852]).

Conspicuous and Cryptic Primates

Figures 5 and 7 show that the orange coloration displayed by many primates stands out from background foliage in the recently evolved color subsystem of

trichromatic primates, but not in the color or luminance channels of dichromatic primates. The calculated luminance of some measurements of live animals' fur did come out higher than the leaves, but the upper limit of the fur luminance is better represented by the measurements of pelts, for the following reasons. First, as mentioned above, sun-bleaching may be one reason why the fur from zoo animals has in some cases produced higher luminance values than those from pelts. Another reason for the luminance differences is that in order to obtain a reflectance spectrum of primate pelage, two measurements must be made: one of the pelage itself and one of a reference plaque, which gives the incident illumination on the pelage for each pelage measurement. In the case of live animals, this reference plaque could not be guaranteed to be in exactly the same conditions as the animals when measured, and thus there is an error in the calculated luminance of live animals. We have calculated that the luminance value may change by up to a factor of 4 owing to slight differences, such as the angle of the surface of the fur to the illuminant, whereas the chromaticity values are far more robust to the possible inconsistencies in the measurements. Thus the calculated luminance of pelts measured in standard conditions should be taken as a better indicator of the true luminance of the fur, and in fact these actually represent an upper limit to the luminance that would present itself in the forest. This is because the luminance of each fur measurement has been calculated from its reflectance spectrum as if it were horizontally placed in direct illumination, whereas in a natural environment surfaces are subject to oblique illumination, patches of shade, and shading from the animal's own body (especially in the case of the belly, from which come some of the measurements with greatest luminance). The leaves, on the other hand, were measured in situ in the canopy, and the luminance values calculated already encompass a wide range of blade angles to the illuminant as well as to leaves in shade. In the forest, therefore, the pelage would lie within the luminance distribution of foliage, and would be difficult to detect for a dichromat.

For a dichromatic individual, the chromaticity distribution of *Leontopithecus* (Fig. 7B) has a different mean and variance from the chromaticities of mature leaves. However, as discussed in section 5 of Methods, in order to be camouflaged, a class of objects does not have to display the whole range of visual appearances found in their surroundings; they need only appear as a subset of their surroundings. Thus to a dichromatic viewer, an individual monkey could not be easily distinguished by its color or lightness from the colors and lightnesses of the much more numerous leaves. However, to a trichromatic viewer, the pelage stands well outside the range of the background leaves in the color subsystem that compares the L to M cone signal. Therefore we have the extremely interesting situation that in these primates with polymorphic color vision, the orange pelage is highly conspicuous to conspecific trichromatic females but not to the dichromatic majority (who might have to rely on shape or movement to distinguish a monkey from its surroundings).

Figure 8 illustrates the different appearance of these orange pelage markings to trichromatic and dichromatic primates. Figure 8A shows a photograph of *L. rosalia* reproduced with the chromaticity of every pixel altered to represent the appearance to dichromats. Figure 8B shows a similarly altered photograph of *Saimiri sciureus* (squirrel monkey), the species for which the pattern of polymorphic color vision characteristic of platyrrhines was first worked out [Mollon et al., 1984]. It can be seen that the monkeys are not very conspicuous. Figure 8C–D show the original photographs, in which the monkeys are highly conspicuous for trichromatic observers (if the printing could perfectly reproduce

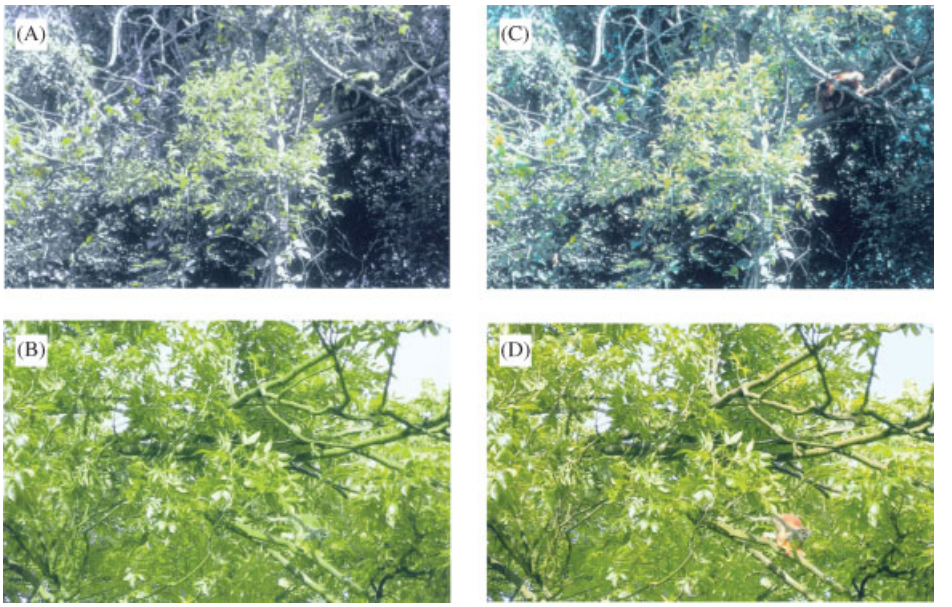


Fig. 8. Photographs of (**A**) *L. rosalia* and (**B**) *Saimiri sciureus* (squirrel monkey), in which the chromaticities have been adjusted to represent the appearance to a dichromatic primate lacking M cones. For each pixel, L-cone and S-cone activation levels were calculated from the original RGB values. Then, in order to calculate new RGB values to be printed and viewed by normal human trichromats, the M-cone activation level (which the dichromat lacks) was set to be equal to the L-cone activation. Since photographs do not contain full spectral information, the illustrations are strictly applicable only to human observers. However, the dichromacy and trichromacy present in other primates are similar enough to those in humans that we can gain an idea of how the scenes might appear to them. **C** and **D:** The original photographs (i.e., the view for a trichromatic observer). If the printing could reproduce the exact chromaticities, a human deuteranope (who lacks M cones) would perceive these images as identical to A and B, respectively. The photograph of *L. rosalia* was kindly provided by J. Dietz.

the correct chromaticities, Fig. 8A and C would appear identical to human deuteranopes, who lack M cones. Similarly, B and D would appear identical.)

It is worth noting that although for a dichromat the orange pelage is not conspicuous amongst foliage, it is distinguishable from all other primate pelage colors. Thus all individuals could use it to distinguish between conspecifics and other species (or subspecies); they could also discriminate against any individuals born without it, thus maintaining the pelage once it is established. But why might such a potentially costly pelage become established in the first place? To further assess the nature of the puzzle, we must know whether there is a cost to being potentially conspicuous. Without a cost there is no need for a benefit.

Predation Risk

The cost of the orange pelage in the context of predation depends on whether the color vision of the predators makes the pelage conspicuous. The mammalian carnivores (such as jaguars, pumas, and margays in South America, and the fossa in Madagascar) that prey on monkeys are almost certainly dichromatic or monochromatic in their color vision [Jacobs, 1993], and thus the orange pelage would be cryptic to this group of important predators. Snake predators may enjoy trichromacy or tetrachromacy [Bowmaker, 1998], but probably the most

significant threat would come from raptors, such as harpy eagles, crested eagles, or ornate hawk eagles [Peres, 1993; Robinson, 1994]. The color vision of these diurnal hunters is not known, but virtually every other diurnal avian species tested has shown four different cone pigments and is therefore presumably tetrachromatic (the four pigments are labeled SWS1 or UV, SWS2, RH2 or MWS, and LWS; see Bowmaker [1998] and Hart [2001] for more details). If eagles share the refined color apparatus of other birds, it would be costly for their primate prey to offer a glimpse of orange in the green forest canopy (see Fig. 9).

However, none of the birds that have been tested for the photopigment complement were raptors, and an animal that attacks moving targets from a distance would have good reason to dispense with color vision in favor of better spatial acuity (for example, although the eagles mentioned above generally do not soar, they make long, flying attacks through foliage). The presence of photoreceptors of different spectral sensitivities must always reduce spatial acuity. If only one class of receptor is used to provide spatial information, clearly the density of this class must be reduced. However, if more than one class is used, the difference in their signals adds noise to spatial information. There is also the problem of chromatic aberration (different wavelengths cannot concurrently be in focus on the retina) [Osorio et al., 1998; Regan et al., 2001].

The retinal structure of red-tailed hawks (*Buteo jamaicensis*) was examined by Braekevelt [1993], and the results certainly suggest that they possess some color vision. The oil droplets in their double and single cones are different. However, the number of single cones (which are thought to provide the color sense of birds) is small relative to double cones. The ratio is 1:5, whereas in other birds nearly equal numbers of single and double cones are the norm [Bowmaker & Knowles, 1977; Hart et al., 1998; Jane & Bowmaker, 1988; Wilkie et al., 1998]. All of their cone photoreceptors are of smaller diameter than is normally reported for avian species, consistent with the high spatial acuity associated with raptors. It is known that kestrels (*Falco tinnunculus*) have not lost all color vision, since they show ultraviolet sensitivity [Viitala et al., 1995], but they are thought to use this for the specific purpose of seeing the urine of voles, and therefore this does not necessarily imply that all raptors have maintained their SW1 (UV) cones. In any case, as Fig. 9 shows, it would be the comparison of avian LWS and RH2 (MWS) cones that would make the orange pelage highly conspicuous amongst foliage. Thus the question of whether raptors have retained RH2 cones becomes an interesting topic for future research, as does the relative rate of attack by raptors on primate species with and without orange pelage.

Potential Benefits

If raptors can compare the signals from RH2 and LWS cones, then the pelage of *L. rosalia*, and many other primates, will be conspicuous to these predators and thus entail a cost. In that case we must ask what might be the benefit of such orange pelage?

Sexual selection.

If the origin of orange pelage lies in sexual selection, we might expect a sexual dichromatism in pelage in which only males have any orange coloration, because in a visually polymorphic species only females can have trichromatic vision. For example, male mongoose lemurs (*Lemur mongoz*) have orange cheeks, whereas

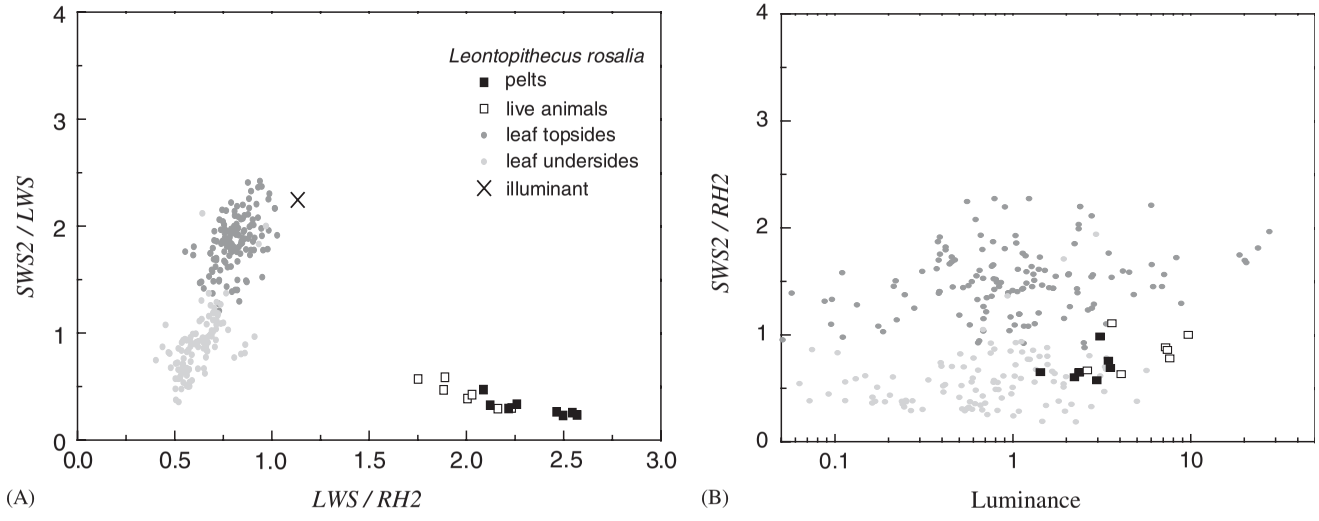


Fig. 9. *L. rosalia* and forest leaves represented in avian chromaticity and luminance diagrams. The λ_{max} values for the LWS, RH2 (or MWS), and SWS2 cone pigments of most birds are remarkably conserved [Hart, 2001]; we chose typical values of 565, 505, and 450 nm. Our spectral measurements do not extend below 380 nm, and so we do not model the quantum catch of avian SW1 (UV) cones. Avian single cones have characteristic oil droplets that filter the light before it reaches the photopigment, so the sensitivity functions of the LWS, RH2, and SWS2 pigments were adjusted for the transmission spectra of red-, yellow-, and clear-type oil droplets, respectively. The microspectro-photometric measurements of the oil droplets were provided by J. Bowmaker. There are two main types of clear oil droplet–one with much less transmission below 450 nm–but this difference did not affect the form of the results in any important way, and we present the data for the more transparent type. Chromatic signals were calculated as simple ratios of the quantum catches of each type of single cone. **A:** The axes correspond to the ratios *LWS*/*RH*2 and *SWS*2/*LWS*, and it is clear that the former offers a large signal from the primate's pelage relative to the foliage. The *SWS*2/*LWS* ratio does not offer such a clear distinction between pelage and foliage, but a bird that lacked RH2 cones could use this channel to detect the primate if the background were formed only by the tops of leaves. **B:** The variation the stimuli produces in the ratio *SWS*2/*RH*2, and in luminance. On neither of these axes does the pelage signal stand out from the foliage. Since the double cones, which contain LWS pigment, are thought to provide a luminance signal for birds, we estimated luminance by using the LWS pigment without oil droplet filtering. (The avian P-type oil droplet, which is typically present in front of one of the two members of the double cone, absorbs significantly only at short wavelengths [Hart et al., 1999], and would not substantially alter the pattern of results.)

the females have white cheeks. It is not known whether this species is among those strepsirhines with polymorphic color vision, but on this evidence we would predict that it is. Strangely, however, this kind of pelage dichromatism between the sexes has not occurred in most platyrrhine species.

Visibility to other group members.

If the advantage lies in adults being conspicuous to other group members, for example to aid group cohesion while foraging or moving, three predictions can be made: First, it should be possible to observe behavioral differences (differences that are not explained by the trichromat's better ability to detect fruit, young leaves, or insects) between trichromatic and dichromatic individuals while the group is foraging or moving. For example, dichromatic females may have a smaller maximum distance to which they will stray from other individuals, or may utilize vocalizations more to maintain contact with other group members. Note that whereas in the case of sexual selection the coat-wearer would benefit directly by being seen, in these examples it is only the trichromats that directly gain from being able to see other individuals, and other individuals may benefit indirectly from the behavior of the trichromats. Thus the second prediction would be that the indirect benefit should reveal itself in behavioral differences between foraging or traveling groups that contain trichromatic individuals and those that do not. Third, there should be behavioral differences between groups of closely related species with and without orange pelage. For example, golden lion tamarin individuals may not maintain as close proximity to each other compared to other species.

Conspicuousness of young.

It may be that of special importance is the visibility of young, rather than adults, to trichromatic females. In some catarrhine species, infants have a more conspicuous coat than adults, possibly to encourage allocare [Hrdy, 1976; Ross & Regan, 2000], to guard against infanticide [Treves, 1997], or simply to allow monitoring by parents. However, in most visually polymorphic species there is no age-related difference in pelage, and in those species that do show a difference, it is nearly always in the direction of making the infants less conspicuous [Ross & Regan, 2000; Treves, 1997]. This is consistent with the idea that sporting a conspicuous pelage entails a cost, and seems to rule against the possibility that the benefit lies especially in young individuals being conspicuous to adult females.

Visibility to other groups.

The benefit of the pelage may in fact not depend on trichromatic individuals within the group, but on trichromatic individuals in other groups. If all members of a group are highly visible, competing groups may be less likely to encroach on territory or a given food resource. In this case we would also predict behavioral differences between groups with trichromats and those without, between the trichromatic and dichromatic females within a group, and between species with and without orange pelage. However, these differences would be seen not while foraging, but when the group gets within potential sight of another group. For example, we might predict that in golden lion tamarins, groups approach each other less closely than in other species, and that groups containing no trichromats would approach more closely to other groups than would groups with trichromats. We might also predict that in a group with trichromats, when another group is

nearby, the trichromats would make more vocalizations, and would more often make the first vocalizations, than would the dichromats (note that this contrasts with the prediction that dichromats might vocalize more if the benefit of the pelage lies in the visibility of other group members).

Aposematic advertisement or Batesian mimicry.

For completeness, we note that conspicuous coloration may act as a warning that an animal is noxious to the predator. Although relatively rare, such signals do occur in mammals, the best example being the white tail of a skunk [Cott, 1940]. In invertebrates, salient colors, especially yellow and orange, are widely used as aposematic advertisements [Poulton, 1890]. If the primates are themselves not noxious, there remains the logical possibility that the protective effect relies on an association of the color with the noxiousness of another animal (living or extinct).

As shown in Fig. 5, many uniformly trichromatic primates (e.g., the red howler monkey (*Alouatta seniculus*) and the red-tailed monkey (*Cercopithecus ascanius*) also display orange or reddish pelage without the ecological puzzle presented by the species with visual polymorphism, although in many cases the exact benefits of the conspicuous pelage (e.g., conspicuous natal coats [Ross & Regan, 2000; Treves, 1997]) remain to be determined. It is likely that the benefits and costs of orange, reddish, or yellowish pelage in each species will have to be considered separately, and there may be no general explanation of its presence in platyrrhines or other primates.

ACKNOWLEDGMENTS

We owe thanks to the Natural History Museum, London; Entebbe Wildlife Centre, Uganda; Colchester Zoo, Colchester; Drayton Manor Park, Tamworth; Hamerton Wildlife Park, Hamerton; Twycross Zoo, Atherstone; and Willers Mill Wild Animal Sanctuary, Shepreth. We are grateful to J. Bowmaker for providing the transmission spectra of avian oil droplets, and to J. Dietz for the photograph of *L. rosalia* used in Fig. 8.

REFERENCES

Arrese CA, Hart NS, Thomas N, Beazley LD, Shand J. 2002. Trichromacy in Australian marsupials. Curr Biol 12:657–660.

Baylor DA, Nunn BJ, Schnapf JL. 1987. Spectral sensitivity of cones of the monkey *Macaca fascicularis*. J Physiol Lond 390:145–160.

Bowmaker JK, Knowles A. 1977. The visual pigments and oil droplets of the chicken, *Gallus gallus*. Vision Res 17:755–764.

Bowmaker JK, Astell S, Hunt DM, Mollon JD. 1991. Photosensitive and photostable pigments in the retinae of Old World monkeys. J Exp Biol 156:1–19.

Bowmaker JK. 1998. Evolution of colour vision in vertebrates. Eye 12:541–547.

Braekevelt CR. 1993. Retinal photoreceptor fine-structure in the red-tailed hawk (*Buteo jamaicensis*). Anat Histol Embryol J Vet Med C 22:222–232.

Cooper GF, Robson JG. 1969. The yellow colour of the lens of man and other primates. J Physiol Lond 203:411–417.

Cott HB. 1940. Adaptive coloration in animals. London: Methuen.

Dacey DM, Lee BB. 1994. The 'blue on' opponent pathway in primate retina originates from a distinct bistratified ganglion cell type. Nature 367:731–735.

Darwin C. 1888. The descent of man and selection in relation to sex. 2nd ed. London: John Murray.

Darwin E. 1794. Zoonomia. London: J. Johnson.

Endler JA. 1990. On the measurement and classification of colour in studies of animal colour patterns. Biol J Linn Soc 41: 315–352.

Endler JA. 1993. The color of light in forests and its implications. Ecol Monogr 63:1–27.

Ghosh KK, Goodchild AK, Sefton AE, Martin PR. 1996. Morphology of retinal ganglion cells in a New World monkey, the marmoset *Callithrix jacchus*. J Comp Neurol 366: 76–92.

Ghosh KK, Martin PR, Grunert U. 1997. Morphological analysis of the blue cone pathway in the retina of a New World monkey, the marmoset *Callithrix jacchus*. J Comp Neurol 379:211–225.

Goodchild AK, Ghosh KK, Martin PR. 1996. Comparison of photoreceptor spatial density and ganglion cell morphology in the retina of human, macaque, cat and the marmoset *Callithrix jacchus*. J Comp Neurol 366:55–75.

Hart NS, Partridge JC, Cuthill IC. 1998. Visual pigments, oil droplets, cone photoreceptor distribution in the European starling (*Sturnus vulgaris*). J Exp Biol 201:1433–1446.

Hart NS, Partridge JC, Cuthill IC. 1999. Visual pigments, cone oil droplets, ocular media and predicted spectral sensitivity in the domestic turkey (*Meleagris gallopavo*). Vision Res 39:3321–3328.

Hart NS. 2001. The visual ecology of avian photoreceptors. Prog Retin Eye Res 20: 675–703.

Helmholtz H. 1852. Über die Theorie der zusammengesetzten Farben. Annalen Physik 87:45–66.

Hrdy SB. 1976. Care and exploitation of primate infants by conspecifics other than the mother. In: Rosenblatt JS, Hinde RA, Shaw E, Bier C, editors. Advances in the study of behaviour. Vol. VI. New York: Academic Press. p 101–158.

Jacobs GH, Neitz J, Crognale MA. 1987. Color vision polymorphism and its photopigment basis in a callitrichid monkey (*Saguinus fuscicollis*). Vision Res 27:2089–2100.

Jacobs GH. 1993. The distribution and nature of colour vision among the mammals. Biol Rev 68:413–471.

Jacobs GH, Deegan JF, Neitz J, Crognale MA, Neitz M. 1993a. Photopigments and color vision in the nocturnal monkey, *Aotus*. Vision Res 33:1773–1783.

Jacobs GH, Neitz J, Neitz M. 1993b. Genetic basis of polymorphism in the colour vision of platyrrhine monkeys. Vision Res 33: 269–274.

Jacobs GH. 1994. Photopigment polymorphism in cotton-top tamarins (*Saguinus oedipus*). Am J Primatol 33:217.

Jacobs GH, Neitz M, Deegan JF, Neitz J. 1996. Trichromatic colour vision in New World monkeys. Nature 382:156–158.

Jacobs GH, Deegan JF. 2002. Photopigment polymorphism in prosimians and the origins of primate trichromacy. In: Mollon JD, Pokorny J, Knoblauch K, editors. Normal and defective colour vision. Oxford: OUP.

Jacobs GH, Deegan JF, Tan Y, Li W-H. 2002. Opsin gene and photopigment polymorphism in a prosimian primate. Vision Res 42:11–18.

Jane SD, Bowmaker JK. 1988. Tetrachromatic colour vision in the duck (*Anas platyrhynchos*): microspectrophotometry of visual pigments and oil droplets. J Comp Physiol A 165:225–235.

Kingdon JS. 1980. The role of visual signals and face patterns in African forest monkeys (guenons) of the genus *Cercopithecus*. Trans Zool Soc Lond 35:425–475.

Lucas PW, Beta T, Darvell BW, Dominy NJ, Essackjee HC, Lee PK, Osorio D, Ramsden L, Yamashita N, Yuen TD. 2001. Field kit to characterize physical, chemical and spatial aspects of potential primate foods. Folia Primatol (Basel) 72:11–25.

Lyon MF. 1972. X-chromosome inactivation and developmental patterns in mammals. Biol Rev 47:1–35.

MacLeod DIA, Boynton RM. 1979. Chromaticity diagram showing cone excitation by stimuli of equal luminance. J Opt Soc Am 69:1183–1186.

Mollon JD, Bowmaker JK, Jacobs GH. 1984. Variations of colour vision in a New World primate can be explained by polymorphism of retinal photopigments. Proc R Soc Lond B 222:373–399.

Mollon JD, Jordan G. 1988. Eine evolutionäre Interpretation des menschlichen Farbensehens. Die Farbe 35/36:139–170.

Mollon JD. 2000. Cherries among the leaves: the evolutionary origins of colour vision. In: Davis S, editor. Color perception: philosophical, psychological, artistic, and computational perspectives. Oxford: Oxford University Press.

Nassau K. 1983. The physics and chemistry of color. New York: John Wiley & Sons.

O'Keefe LP, Levitt JB, Kiper DC, Shapley RM, Movshon JA. 1998. Functional organization of owl monkey lateral geniculate nucleus and visual cortex. J Neurophysiol 80:594–609.

Osorio D, Ruderman DL, Cronin TW. 1998. Estimation of error in luminance signals encoded by primate retina resulting from sampling of natural images with red and green cones. J Opt Soc Am A 15: 16–22.

Peichl L, Behrmann G, Kroger RHH. 2001. For whales and seals the ocean is not blue: a visual pigment loss in marine mammals. Eur J Neurosci 13:1520–1528.

Peres CA. 1993. Anti-predation benefits in a mixed-species group of Amazonian tamarins. Folia Primatol (Basel) 61:61–76.

Poulton EB. 1890. The colours of animals. Their meaning and use. London: Kegan Paul, Trench and Trübner.

Regan BC, Julliot C, Simmen B, Viénot F, Charles-Dominique P, Mollon JD. 1998. Frugivory and colour vision in *Alouatta seniculus*, a trichromatic platyrrhine monkey. Vision Res 38:3321–3327.

Regan BC, Julliot C, Simmen B, Viénot F, Charles-Dominique P, Mollon JD. 2001. Fruits, foliage and the evolution of the primate colour-sense. Phil Trans R Soc Lond B 356:229–283.

Robinson SK. 1994. Habitat selection and foraging ecology of raptors in Amazonian Peru. Biotropica 26:443–458.

Ross C, Regan G. 2000. Allocare, predation risk, social structure and natal coat colour in anthropoid primates. Folia Primatol (Basel) 71:67–76.

Rushton WAH. 1972. Pigments and signals in colour vision. J Physiol 220:1–31P.

Silveira LCL, Lee BB, Yamada ES, Kremers J, Hunt DM. 1998. Post-receptoral mechanisms of colour vision in New World primates. Vision Res 38:3329–3337.

Silveira LCL, Lee BB, Yamada ES, Kremers J, Hunt DM, Martin PR, Gomes FL. 1999. Ganglion cells of a short-wavelength-sensitive cone pathway in New World monkeys: morphology and physiology. Vision Neurosci 16:333–343.

Slifka KA, Bowen PE, Stacewicz-Sapuntzakis M, Crissey SD. 1999. A survey of serum and dietary carotenoids in captive wild animals. J Nutr 129:380–390.

Snodderly DM, Brown PK, Delori FC, Auran JD. 1984. The macular pigment. I. Absorbance spectra, localization, and discrimination from other yellow pigments in the primate retina. Invest Ophthalmol Visual Sci 25:660–673.

Sumner P, Mollon JD. 2000a. Catarrhine photopigments are optimised for detecting targets against a foliage background. J Exp Biol 203:1963–1986.

Sumner P, Mollon JD. 2000b. Chromaticity as a signal of ripeness in fruits taken by primates. J Exp Biol 203:1987–2000.

Sumner P, Mollon JD. 2002. Did primate trichromacy evolve for frugivory or folivory? In: Mollon JD, Pokorny J, Knoblauch K, editors. Normal and defective colour vision. Oxford: OUP.

Surridge AK, Mundy NI. 2002. Trans-specific evolution of opsin alleles and the maintenance of trichromatic colour vision in Callitrichine primates. Mol Ecol 11: 2157–2169.

Tan Y, Li W-H. 1999. Trichromatic vision in prosimians. Nature 402:36.

Tovée MJ, Bowmaker JK, Mollon JD. 1992. The relationship between cone pigments and behavioural sensitivity in a New World monkey (*Callithrix jacchus jacchus*). Vision Res 32:867–878.

Travis DS, Bowmaker JK, Mollon JD. 1988. Polymorphism of visual pigments in a callitrichid monkey. Vision Res 28:481–490.

Treves A. 1997. Primate natal coats: a preliminary analysis of distribution and function. Am J Phys Anthropol 104:47–70.

Viitala J, Korpimaki E, Palokangas P, Koivula M. 1995. Attraction of kestrels to vole scent marks visible in ultraviolet light. Nature 373:425–427.

Wilder HD, Grunert U, Lee BB, Martin PR. 1996. Topography of ganglion cells and photoreceptors in the retina of a New World monkey: the marmoset *Calithrix jacchus*. Vision Neurosci 13:335–352.

Wilkie SE, Vissiers PMAM, Das D, DeGrip WJ, Bowmaker JK, Hunt DM. 1998. The molecular basis for UV vision in birds: spectral characteristics, cDNA sequence and retinal localization of the UV-sensitive pigment of the budgerigar (*Melopsittacus undulatus*). Biochem J 330:541–547.

Williams AJ, Hunt DM, Bowmaker JK, Mollon JD. 1992. The polymorphic photopigments of the marmoset: spectral tuning and genetic basis. EMBO J 11:2039–2045.

Wyszecki G, Stiles WS. 1982. Color science. New York: Wiley.

Yamada ES, Silveira LCL, Perry VH. 1996. Morphology, dendritic field size, somal size, density, and coverage of M and P retinal ganglion cells of dichromatic Cebus monkeys. Vision Neurosci 13:1011–1029.

Yamada ES, Marshak DW, Silveira LCL, Casagrande VA. 1998. Morphology of P and M retinal ganglion cells of the bush baby. Vision Res 38:3345–3352.