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CATARRHINE PHOTOPIGMENTS ARE OPTIMIZED FOR DETECTING TARGETS AGAINST A FOLIAGE BACKGROUND

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Summary

The colour vision of many primates is trichromatic, whereas that of all other mammals is thought to be dichromatic or monochromatic. Moreover, the triplets of cone pigments in different catarrhines (Old World apes and monkeys) are strikingly similar in their spectral positions. We ask whether the selective advantage of trichromacy lies in an enhanced ability to find edible leaves or fruit. Further, we ask whether any factor in these two search tasks has constrained the particular set of cone spectral sensitivities observed in all catarrhines. We measured the spectral properties of the natural environments of six primate species in Uganda: *Pan troglodytes*, *Cercopithecus mitis*, *Cercopithecus ascanius*, *Lophocebus albigena*, *Colobus guereza* and *Colobus badius*. We concentrated on the fruit and leaves in their diets and the leaves of the trees that make up the background against which these diet items must be found. We plotted these measured stimuli in colour spaces appropriate for each primate species, and found that both frugivory and folivory are facilitated by the extra dimension of colour vision found in catarrhines but lacking in most other mammals. Furthermore, by treating the task of searching for food as a signal-detection task, we show that, of all possible combinations of cone sensitivities, the spectral positions of the actual primate pigments are optimal for finding fruit or young leaves against the background of mature leaves. This is because the variance of the chromaticities of the mature leaves is minimised in one channel of the primate's colour vision, so allowing anything that is not a mature leaf to stand out.

Key words: colour vision, trichromacy, opsin, visual ecology, Old World primate, frugivory, folivory, evolution, Kibale, Uganda.

Introduction

The only mammals known to possess three types of cone, and therefore to enjoy trichromatic colour vision, are primates. The trichromacy of catarrhine primates (Old World monkeys and apes) depends on two separate dichromatic subsystems (Mollon and Jordan, 1988). The older one almost certainly predates the divergence of mammals (Bowmaker, 1998) and compares the signal in a sparse population of short-wavelength-sensitive cones to the signal in a class of cones with peak sensitivity in the range 493–570 nm. In most mammals, there is only one type of cone in the latter range (Jacobs, 1993), but early in the catarrhine lineage there arose two distinct middle- (M) and long-wavelength-sensitive (L) cones, so that a second neural subsystem that compares their signals became possible (Dulai et al., 1999; Mollon, 1991; Nathans, 1999; Nathans et al., 1986).

The spectral sensitivities of cones of many catarrhine species have been measured by microspectrophotometry (e.g. Bowmaker et al., 1991; Dartnall et al., 1983), by suction-pipette electrophysiology (Baylor et al., 1987; Schnapf et al., 1987) or by electroretinographic flicker photometry (e.g. Deegan and Jacobs, 1997; Jacobs et al., 1996a) or have been inferred from the genetic sequence (e.g. Dulai et al., 1994; Ibbotson et al., 1992), and all seem to have an M cone pigment with a peak sensitivity (λ_{max}) near 530 nm and an L cone pigment with λ_{max} near 560 nm. This remarkable consistency would seem to be at odds with the finding that the absorbance spectra of photopigments are not difficult to change: *in vitro* studies of the opsin proteins have shown that λ_{max} can be altered by single base-pair mutations in the relevant exon sequence (Asenjo et al., 1994), and λ_{max} values between 493 and 570 nm have been reported for mammalian long-wavelength-sensitive cones (e.g. Jacobs, 1993). The mutagenesis technique has not yet been systematically used to test whether rhodopsins of the long-wavelength type could lie outside this range.

We here test quantitatively whether trichromacy offers an advantage over dichromacy in foraging tasks that face certain primates and whether there are ecological factors that favour the spectral positions that the M and L pigments have taken. Our modelling takes advantage of the fact that the absorbance curves of rhodopsins are all of a similar shape, so that their spectral sensitivity can be predicted from only the wavelength of peak sensitivity (λ_{max}) (Baylor et al., 1987; MacNichol, 1986; Mansfield, 1985). Of the two chromophores found in

vertebrate photopigments, only retinal has been found in mammals (e.g. Bowmaker, 1991), and thus it seems that mammalian photopigments are always rhodopsins rather than porphyropsins. This means that we can calculate the response of a primate visual system that contains any hypothetically possible set of cone sensitivities. The present study assumes that primate photopigments could have evolved to have any λ_{max} between approximately 400 nm and 650 nm, and asks which combination of pigments would be optimal for performing the two ecologically important tasks of detecting fruits amongst their background of forest canopy leaves and of detecting young edible leaves among mature leaves. We regard these tasks as natural versions of the laboratory visual search paradigm. In the accompanying paper (Sumner and Mollon, 2000), we examine the separate task of discriminating amongst ripe and unripe fruits.

The hypothesis that primate trichromacy evolved for frugivory is more than a century old and has been developed into a theory of co-evolution between primate vision and fruit signals (Allen, 1879; Polyak, 1957). Spotting fruits in foliage is one of the few natural tasks at which human dichromats are impaired (Mollon, 1989; Steward and Cole, 1989): colour vision becomes especially important when a target item is embedded in a background that varies unpredictably in lightness and in form (see Fig. 1). Many primates rely heavily on fruit, and in the case of those that do not, specialised folivory may be a secondary adaptation that has followed the more frugivorous habits of ancestors. Research on platyrrhine monkeys in French Guiana has found that the photopigments of *Alouatta seniculus* and the trichromatic individuals of *Ateles paniscus* and *Cebus apella* are optimised for detecting the fruits in the diet of these monkeys against the natural background of forest leaves (Regan, 1997; Regan et al., 1998; B. C. Regan, C. Julliot, B. Simmen, F. Viénot, P. Charles-Dominique and J. D. Mollon, in preparation). Using a different analysis and measuring cultivated fruits, Osorio and Vorobyev (1996) found that, for trichromatic primates with pigments at 430 and 565 nm, a third pigment with λ_{max} between 490 and 530 nm would maximise the number of fruits that could be distinguished from leaves. Our present study builds on the work of Regan (1997) and Regan et al. (1998) and uses methods of analysis similar to theirs: to estimate what possible photopigments might be optimal for certain tasks, signal-to-noise ratios in one 'chromatic channel' have been calculated for certain sets of 'target' stimuli that must be detected against sets of 'background' stimuli (e.g. fruit targets against foliage background). The present study has extended the earlier work in two ways: first, we have studied catarrhines, whose trichromacy is thought to have evolved separately from the trichromacy found in some platyrrhines (Dulai et al., 1999). Second, the study has encompassed not only the fruit diet of the primates, but also the leaves they eat. Most primates are folivorous to some degree, and some rely heavily on young leaves; so we might expect that this also has moulded primate colour vision.

Materials and methods

The fieldwork was mainly carried out at Makerere University Biological Field Station (MUBFS) in Kibale Forest, Western Uganda. Data were also collected at four other sites within Kibale Forest (which also lie within the same reserve: 0°13′ to 0°41′N and 30°19′ to 30°32′E), at Budongo Forest and in Queen Elizabeth National Park. The primates studied were *Pan troglodytes* (chimpanzee), *Cercopithecus mitis* (blue monkey), *Cercopithecus ascanius* (red-tailed monkey), *Lophocebus albigena* (grey-cheeked mangabey), *Colobus guereza* (black and white colobus or guereza) and *Colobus badius* (red colobus). There have been 25 years of research on the primates in Kibale Forest, and their diets are well-established (e.g. Baranga, 1983; Barrett, 1994; Chapman and Chapman, 1996; Clutton-Brock, 1975; Freeland, 1979; Isabirye-Basuta, 1989; Isbell, 1983; Oates, 1977; Olupot, 1998; Olupot et al., 1998; Rudran, 1978a,b; Struhsaker, 1978a,b; Waser, 1975, 1977, 1984; Wrangham et al., 1994a). The primates were being continuously studied while this field work was carried out, and so there was also available unpublished information about the current diets during the period of fieldwork for this study. The chimpanzees in the same area of forest were being followed every day by researchers of

Fig. 1. Fruits of *Ficus asperifolia*, a fig species known to be eaten by *Pan troglodytes* and *Cercopithecus ascanius* in Kibale Forest, Uganda. The fruits are much more conspicuous in the coloured than in the black-and-white version of the photograph, illustrating the importance of colour in a visual search task where lightness and form vary unpredictably.

the 'Kibale Chimp Project' from whom regular reports were received on what the chimpanzees were eating and where to find these fruiting trees. Elsewhere in the forest, at Kanyanchu and Ngogo, the chimpanzees were also being tracked, and periodic reports were sent on their present diet. The 'Kibale Monkey Project' researchers supplied an unpublished dietary list for all five monkey species and also gave directions to, or occasionally brought samples from, fruiting trees that either they had observed monkeys feeding in recently or were included in their phenology studies at three sites: Kanyawara (where the field station is), 'Dura-mid' and 'Power lines'. William Olupot and his field assistants were engaged in a radio tracking study of mangabeys. He also provided his then unpublished diet list and supplied information every day on the mangabeys' movements and present diet, and sometimes brought fruit samples.

Introduction to the six species of primate studied

Cercopithecus mitis is a medium-sized guenon, with adults normally weighing 3–4 kg. Their diet in Kibale contains approximately 60 % fruit and 20 % leaves. [These figures, from Rudran (1978b), are the percentage of feeding observations on specific food items over a 1 year period. Most researchers in Kibale have measured diet using methods similar to those of Rudran (1978b).] Few fruits are taken unripe, and leaves are preferred when young. *Cercopithecus ascanius* is closely related to *Cercopithecus mitis* and has a very similar diet. The main differences between the two species in Kibale are that red-tails live in larger groups and are significantly smaller, adults weighing 2–3 kg. Mangabeys are canopy-dwelling cousins of the baboons, and the closest relatives in this study of the macaques, which have been the subject of much research in vision. The grey-cheeked mangabeys (*Lophocebus albigena*) in Kibale eat approximately 80 % fruit and 10 % leaves. They are large monkeys, with adults often weighing over 7 kg. The black and white colobus, or guereza (*Colobus guereza*), in Kibale have the most specialised diet of any of the primates in the present study. Between half (Oates, 1977) and 75 % (Clutton-Brock, 1975) of it is made up by leaves of only two tree species. Only 10–20 % of their diet is fruit and virtually all of this is taken unripe. Guereza are medium to large monkeys (5–6 kg), tend to live in small family groups and spend most of their time in the highest branches of trees. *Colobus badius* has the highest population density of all the (diurnal) primates in Kibale; they are found in groups of dozens of individuals. Adults are large, weighing approximately 6 kg. Nominally folivorous, they have a diverse diet, about 30 % of which is young leaf blades (they eat a lot of buds and petioles that could not be measured spectroradiometrically). Fruit, mostly unripe, constitutes only 10 % or less of their diet.

We have adopted 430 nm, 531 nm and 561 nm (from Baylor et al., 1987) as the best estimates of the cone λ_{max} values for all the catarrhine monkeys. Microspectrophotometric studies (e.g. Bowmaker et al., 1991; Dartnall et al., 1983) give λ_{max} values nearer 535 nm and 565 nm, but this difference may reflect the difference between the curve-fitting techniques used, rather than a real difference between the cones measured; since in our analysis we employ the polynomial expression from Baylor et al. (1987), we use their λ_{max} values.

The closest living relative of *Pan troglodytes*, with the exception of *Pan paniscus* (the bonobo), is *Homo sapiens*. *Pan troglodytes* is considered to have changed little in the last five million years and may be a fair approximation to the common ancestor of humans, chimpanzees and gorillas (Wrangham et al., 1994b). Chimpanzees weigh on average approximately 35 kg and consume mostly fruit (85 % of diet in Kibale), but also rely on young leaves and other plant material, especially at times when major fruit crops (e.g. *Ficus* sp.) are absent. They eat many items that grow in the understorey and are absent from the diets of the monkeys. This reflects the fact that the chimpanzees do most of their travelling on the ground, whereas the monkeys, which are much lighter, jump from tree to tree in the canopy. We have not assumed that chimpanzees possess the same photopigment set as the catarrhine monkeys, and have taken our best estimates for the λ_{max} of the cones of *Pan troglodytes* as 430 nm, 531 nm and 563 nm (Jacobs et al., 1996a).

Spectroradiometry

In total, 1540 reflectance spectra were measured of fruits (51 species) and young leaves (48 species) in the diets of the six primate species and 530 reflectance measurements were made of the mature leaves of these plant species. Radiance spectra from leaves were also measured directly in the forest canopy (N=625), and 66 spectral irradiance measurements of different natural illuminants were collected. The spectra were measured at 4 nm intervals between 380 nm and 780 nm using a PhotoResearch PR650 telespectroradiometer, and the illuminant measurements were made using a white, barium sulphate plaque. Climbing by the 'single rope technique' allowed access to the canopy to collect samples and make measurements. Samples were also collected from the ground when they were dropped or dislodged by the primates themselves or by the wind. Virtually all of each primate's diet during the period of the fieldwork was covered.

The question of which samples would be eaten by a primate is not easy to answer. Ideally, the samples to measure would be the ones actually selected by the primate, and this was possible in the case of fruits that had a hard outer shell that was discarded and could be collected (e.g. *Aframomum* sp.). Very few of the fruits were of this nature, and so a method of defining ripeness had to be adopted. Many studies of primate diet distinguish between 'ripe' and 'unripe' fruits, but rarely do they mention on what criteria this distinction was made. Observations made at a distance through binoculars can allow only informal classification.

There are several ways one could define 'ripe', and no way is obviously better than all others. In this study, it was important to have a definition based on a measurement independent of the surface reflectance properties. From the point of view of a tree, a fruit is ripe when the seed has an

optimal chance of germinating. This study takes the point of view of the primates, that a fruit could be said to be most ripe when maximum nutritional value is available and physical barriers (such as toughness of flesh or a hard shell) are absent or reduced. However, different animals require a different balance of nutrients at different times, and so which nutrients should be chosen and what level would constitute ripeness depend on both the plant species and the primate species. In addition, different animals have different levels of tolerance of toxins and different abilities to cope with physical barriers, and so there can be no universal way of defining ripeness. The main method chosen in this study was a quantitative measurement of the force needed to punch through 1 mm^2 of the fruit surface (using a 'penetrometer' originally designed for testing the ripeness of tomatoes before shipment). This measurement is assumed to correlate with nutrient and toxin changes. 'Ripe' was defined as requiring less than half the maximum force required for any of the fruit samples of the same species (it was important to have collected a range of samples). If no fruits of a species met this criterion (as was the case for those with hard shells that do not split open on ripening), 'ripe' could be defined as having above the median diameter of all fruits of that species. If the diameters of all samples did not differ by more than 20 %, none was classed as ripe (because when ripe fruits are present normally unripe ones will be also).

In the case of leaf diet, the information included in the studies listed above normally distinguished between 'young leaves' and 'mature leaves', and the primates were always found to prefer the former category. This distinction was again informal, and the criteria on which it was based were not discussed. In the present study, it was occasionally possible to collect a leaf out of which a chimpanzee had actually taken a bite, but for the majority of samples the young/mature classification was made using a combination of size and position on the stem. To be classified as 'young', the leaf had to be fewer than three leaves from the end and also less than half the length of the largest leaves on that sample branch. The thickness of all leaves was measured using a micrometer, but this proved unsatisfactory for young leaves because their veins were often too close together. The penetrometer was used to estimate the toughness of every leaf, but the results did not correlate well with the position-and-size method of classification, probably again because of the closeness of veins in the young leaves.

Calculating the quantum catches in a cone class

The sensitivity of the cone pigment, $S_{\text{pigment}}(\lambda)$, was calculated using a polynomial curve derived empirically by Baylor et al. (1987) for the cone pigment sensitivities of *Macaca fascicularis*:

$$\log S_{\text{pigment}}(\lambda) = \sum_{n=0}^{6} a_n \left[\log \left(\frac{\lambda_{\max}}{561} \, \frac{1}{\lambda} \right) \right]^n , \qquad (1)$$

where $\lambda_{\max}$ is the desired wavelength of peak sensitivity (in nm). The wavenumber $1/\lambda$ is expressed in μm^{-1}, and a_0–a_6 are −5.2734, −87.403, 1228.4, −3346.3, −5070.3, 30881 and −31607. This formula, being a polynomial, actually causes the curve to rise again after $\lambda_{\max}$+250 nm. This does not reflect real cone pigments, and absorbance was therefore set to zero at all wavelengths beyond $\lambda_{\max}$+250 nm. This polynomial has no theoretical significance: it is the expression that Baylor et al. (1987) found fitted best their suction electrode measurements for all three cone classes of *Macaca fascicularis*. It had already been found that all measured rhodopsins have the same shape on a relative frequency abscissa (MacNichol, 1986; Mansfield, 1985). There are two advantages in having an expression that enables any primate photopigment absorbance spectrum to be constructed from its $\lambda_{\max}$. First, for many primates, full sensitivity curves have not been measured, but peak sensitivities have been. Second, curves can easily be generated for all putative possible pigments a primate might possess, and this was a necessary part of the present analysis.

The polynomial produces a sensitivity curve for a thin layer of pigment. This has to be adjusted to produce an estimate of the true sensitivity of the cone at the retina, $S_{\text{retina}}(\lambda)$, because the light reaching the pigment in a certain part of the cone outer segment will have been filtered by the pigment it has already passed through. The adjustment for this self screening was:

$$S_{\text{retina}}(\lambda) = 1 - 10^{-a S_{\text{pigment}}(\lambda)} , \qquad (2)$$

where a, the optical density of the cone to axial illumination at $\lambda_{\max}$, was assumed to be 0.3. This value was based on the following calculation: the length of the outer segment was taken to be 30 μm, the width 2 μm and the transverse absorbance was taken to be 0.02 (Bowmaker et al., 1985). Multiplying this latter value by length/width, we calculate the longitudinal optical density of 0.3. The optical density within the central 0.5 ° of the fovea may be as great as 0.8 (Pokorny and Smith, 1976), but using this value in the analysis did not affect the pattern of the results or conclusions drawn.

The sensitivity of the cone at the retina was adjusted for the filtering effects of the optic media to calculate the sensitivity of the cone at the cornea, $S_{\text{cornea}}(\lambda)$:

$$S_{\text{cornea}}(\lambda) = 10^{-[\text{Lens}(\lambda)+\text{Macular}(\lambda)]} S_{\text{retina}}(\lambda) . \qquad (3)$$

In all cases, Macular(λ) was the optical density of human macular pigment given by Wyszecki and Stiles (1982), which is very similar to the data of Snodderly et al. (1984b) for macaques. In the analysis for chimpanzees, Lens(λ) was the optical density of human lens given by Wyszecki and Stiles (1982). For mangabeys, the optical density for a baboon lens (Cooper and Robson, 1969) was used, and an average of the baboon and macaque data from Cooper and Robson (1969) was used for the guenons and colobus monkeys. The properties of these three lenses, and also lens data from *Callithrix jacchus* (Tovée et al., 1992), *Saimiri sciureus* and *Galago crassicaudatus* (Cooper and Robson, 1969), are very similar: they are high-pass filters, blocking wavelengths below 400 nm and slightly attenuating longer wavelengths. The present results were little affected by which of these lenses was used, and even leaving the lens filtering out of the analysis altogether

made virtually no difference. The effect of changing the macular pigment density was slightly greater and will be discussed again below, but it did not change the form of the results or the conclusions drawn.

Each measured reflectance spectrum was converted into a 'stimulus spectrum' (an estimate of the light that would actually reach the eye of a primate) by multiplying it by an illuminant measurement (see section on illuminants below for a discussion of which illuminants were chosen). The quantum catch of a cone, Q, for any stimulus, was calculated by multiplying the stimulus spectrum, stim(λ), (in quantum units) by the sensitivity of the cone at the cornea, S_{cornea}.

$$Q = \int_{380}^{780} \text{stim}(\lambda) S_{\text{cornea}}(\lambda) \text{d}\lambda \,, \qquad (4)$$

Fig. 2 illustrates the stages in calculating the quantum catch, from any stimulus, of hypothesized cones containing photopigments with any chosen λ_{max}. It is mathematically equivalent to apply the lens and macular pigment filtering to the stimulus spectrum or to the cone sensitivity curve.

From the position of being able to estimate the quantum catch of a cone with any λ_{max} for any of the stimulus spectra, the analysis took two forms. First, the stimuli have been plotted in colour spaces appropriate for the relevant primates (see below). Regan (1997) and Regan et al. (1998) have done this for some platyrrhines, and they were the first to construct chromaticity diagrams for non-human mammals. Second, to estimate what possible photopigments might be optimal for detecting objects against their backgrounds, signal-to-noise ratios in one 'chromatic channel' have been calculated for certain sets of 'target' stimuli against sets of 'background' stimuli.

Catarrhine colour space

For each relevant stimulus spectrum, quantum catches were calculated for three putative cone sensitivities of the trichromatic primate in question. These quantum catch values, S, M and L, were converted into coordinates, $L+M$, $S/(L+M)$ and $L/(L+M)$, of a three-dimensional colour space whose axes represent the putative inputs to the luminance channel and to the ancient mammalian and recent catarrhine colour subsystems. A three-dimensional graph would lack clarity, so the data are plotted in two diagrams: a chromaticity diagram of $L/(L+M)$ *versus* $S/(L+M)$, resembling the MacLeod–Boynton chromaticity diagram for man (MacLeod and Boynton, 1979), and a plot of $S/(L+M)$ *versus* luminance $(L+M)$, which on its own roughly represents the two-dimensional colour space of the putative platyrrhine–catarrhine ancestor (see Fig. 3). The $S/(L+M)$ axis is vertical in both diagrams to aid comparison of the chromaticity and luminance coordinates of the stimuli. When referring to non-human

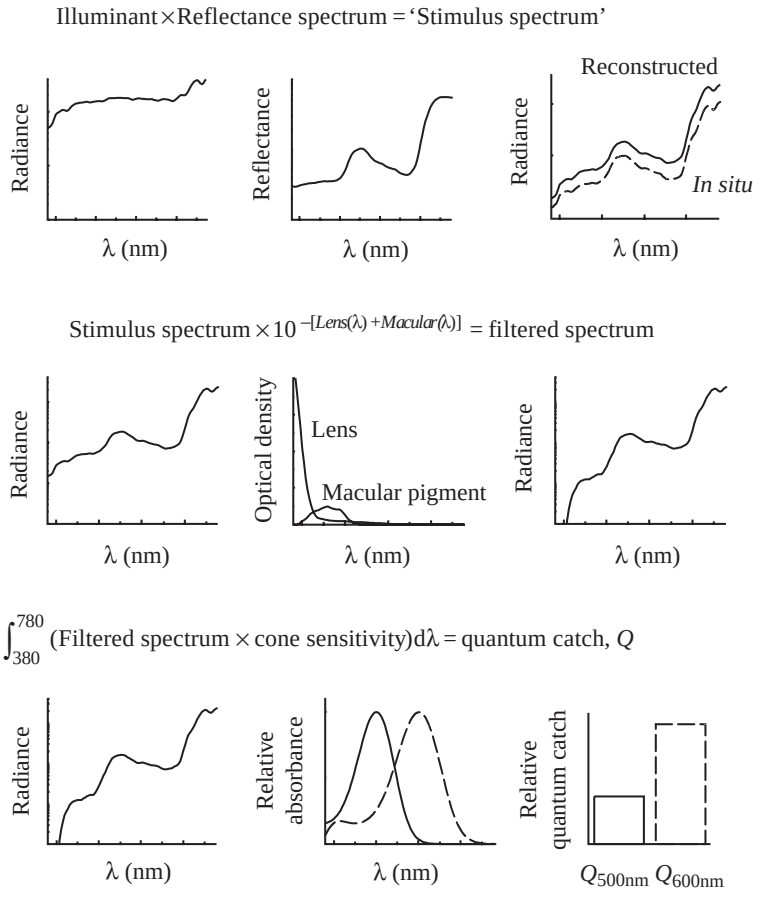

Fig. 2. The stages in calculating the relative quantum catch (Q) in a cone with any chosen wavelength of peak sensitivity (λ_{max}). In this case, the filtering for the optical media is applied to the stimulus spectrum rather than to the cone sensitivity curve, an operation that is mathematically equivalent. *Lens*(λ) is the optical density of the lens and *Macular*(λ) is the optical density of macular pigment (see text for details). Since the graphs are shown only to represent the method diagrammatically, the scales are unimportant here.

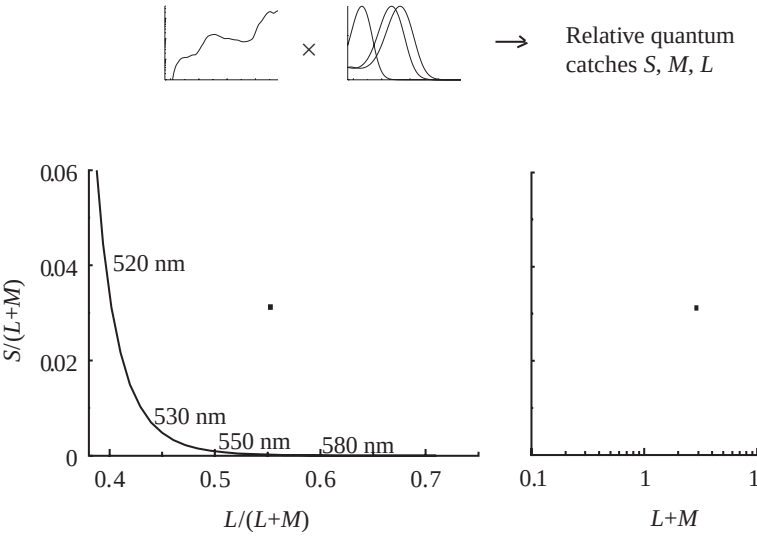

Fig. 3. Calculating the colour space coordinates and plotting the chromaticity diagram (left-hand panel) and luminance *versus* ancient colour subsystem diagram (right-hand panel) from the quantum catches, *S*, *M* and *L*, in the short- (S), middle- (M) and long-wavelength-sensitive (L) cone classes. The vertical axes in the two panels are identical. The same mature leaf stimulus is plotted in both panels as a black square. The solid line shows the chromaticity locus of monochromatic lights. The *L*+*M* axis is logarithmic, and the scale is relative (for reference, 500 cd m^{-2} corresponds to approximately 10 on this scale).

primates, we use the word luminance interchangeably with *L*+*M*, but it is possible that luminance in catarrhines would better be represented by a non-unitary ratio of *L* to *M*. It has been suggested that humans normally have more L cones than M cones (Cicerone and Nerger, 1989), and V_λ, the psychophysically measured expression for luminance, is approximately 2*L*+*M*. However, the ratio of L and M cones in other catarrhines has been found not to deviate significantly from 1:1 (Bowmaker et al., 1991; Mollon and Bowmaker, 1992). In fact, the precise ratio did not matter in this study: the form of the colour space distributions remained the same and the results of the signal-to-noise ratio analysis (described below) were unaffected by making the L cone class twice as sensitive as the M cone class.

In the chromaticity diagram, only the relative quantum catches of the cones are important, and we do not discuss until later the constants in the analysis that affect the absolute quantum catches without altering the relative values of S, M and L. For this reason, *L*+*M* is a relative axis and the absolute values have little significance here (10 corresponds to approximately 500 cd m^{-2}). Note also that this axis has a logarithmic scale in our diagrams.

Optimal cone pigments for detecting objects against their natural background

The analysis described in this section, which was developed by Regan and Mollon (Regan 1997; Regan et al., 1998), is primarily concerned only with the more recent subsystem of primate colour vision that no other mammals are thought to possess. Assuming that the peak sensitivities of the L and M cones could have evolved to be anywhere between 420 nm and 650 nm, the aim is to discover which pair of possible pigments would be optimal for detecting important items against their natural backgrounds. In this case, 'optimal' is defined as maximum possible signal-to-noise ratio, where, for each target item, the 'signal' is the difference between the target chromaticity [*L*/(*L*+*M*)] and the average background chromaticity, and the 'noise' is the sum of noise from two sources: variation in background chromaticity and the inherent stochastic variation of quantum catches.

The steps in the signal-to-noise ratio analysis

(1) The peak sensitivities were chosen for the putative L and M cones, and their corneal sensitivity curves were calculated as previously detailed.

(2) For each chosen 'background' (i.e. mature leaf) stimulus spectrum, the quantum catches ('*L*' and '*M*') were calculated. For the calculation of colour space coordinates, only relative values of quantum catch are important, but in this analysis the absolute values become important, and so the constants used are discussed below.

(3) Using these quantum catches, the chromaticity value *L*/(*L*+*M*) was calculated for each background leaf spectrum, and the mean, $\overline{B}$, and the variance, $Var_{\overline{B}}$, of all these chromaticity values were calculated. (Each chromaticity value is called $\overline{B}$ because it is actually a mean chromaticity value for the reason explained in step 4 below.)

(4) Also using these quantum catches, the variance in each chromaticity value due to quantum fluctuations was calculated. Photons arrive and are absorbed in a probabilistic way, and the actual quantum catch in any given interval will vary as a Poisson distribution around the mean quantum catch for that interval length. When the mean quantum catch is large enough (in this case *L* or *M*, as calculated in step 2), this Poisson distribution approximates a Gaussian distribution with a variance the same as the mean, i.e. *L* or *M*. The variance of a sum, *x*+*y*, is var_x+var_y, and the variance of a quotient, *x*/*y*, is $(var_x/x^2+var_y/y^2)(x/y)^2$. Therefore, the variance of the chromaticity value *L*/(*L*+*M*), due to quantum fluctuation, will be $[L^{-1}+(L+M)^{-1}][\,L/(L+M)]^2$. This variance, Var_B, was calculated for every background spectrum, and the mean, $\overline{Var_B}$, of these variances was found.

(5) For one 'target' (i.e. fruit or young leaf) stimulus spectrum, following the same method as for each background spectrum, the quantum catches (*L* and *M*) were calculated, then the *L*/(*L*+*M*) chromaticity value $\overline{T}$, and lastly

the variance in this chromaticity due to quantum fluctuations, Var_T.

(6) The 'signal' for that target was calculated as the difference between its chromaticity value and the mean chromaticity value of the background: $\bar{T}-\bar{\bar{B}}$.

(7) The 'noise' was a combination of 'background chromaticity noise', target 'quantum noise' and mean background 'quantum noise': $\sqrt{Var_{\bar{B}}+Var_T+\overline{Var_B}}$.

(8) The signal-to-noise ratio for this target was calculated and multiplied by the weighting of the target (see next section).

(9) Steps 5–8 were repeated for every other chosen target stimulus spectrum, and the weighted mean signal-to-noise ratio for all these targets was calculated.

(10) All above steps were repeated for a different pair of putative cone sensitivities. The first analyses started with λ_{max} of 420 nm and 422 nm for the putative L and M cones, and proceeded in steps of 2 nm (next using 420 nm and 424 nm, etc.) to 648 nm and 650 nm, so 6670 different mean signal-to-noise ratios were calculated in all, one for each pair of pigments. The largest of these ratios was found, and all others were scaled as a percentage of this one. The results are plotted as a contour map, the axes being the λ_{max} values of the hypothetical pigments (see Fig. 8B for an example).

Target weightings

For some plant species, many target fruits or leaves were measured, but for some other species we obtained only a few measurements. To overcome this bias, each calculated signal-to-noise ratio for each target was weighted in the calculated average ratio by dividing it by the number of targets of that species included in that analysis. This would make every measured species in the diet of a certain primate equally important in determining what its optimal pigments should be. However, for each primate, some fruits and leaves are much more important than others, so each target signal-to-noise ratio was also multiplied by the proportion that target species made up of the diet of the primate in question, using the dietary information in the sources listed previously.

Details of constants used in the quantum catch calculation

The stimulus spectra were converted from energy units ($J\,s^{-1}\,sr^{-1}\,m^{-2}\,nm^{-1}$) to quantum units ($s^{-1}\,sr^{-1}\,m^{-2}\,nm^{-1}$) by multiplying by λ/hc, where λ is wavelength (m), h is Planck's constant (6.6×10^{-34} J s) and c is the speed of light (3×10^{8} m s^{-1}).

To calculate the number of quanta ($s^{-1}\,nm^{-1}$) that would reach the retina from a stimulus, we need to multiply by the area of the stimulus (m^2) and by the solid angle the pupil subtends (sr^{-1}). This solid angle is the area of the pupil divided by the square of the viewing distance. We chose a pupil diameter of 3 mm, a viewing distance of 10 m and a stimulus size of 30 mm (which corresponds to 10 min of arc). All the mature leaves were much larger than this, as were most young leaves. Many fruits (and some young leaves) were smaller, but they grow in clumps, so the colour signal would not be from a single target. Only when the monkey is much closer do single fruits (or young leaves) need to be distinguished.

Next, we need to calculate the proportion of these quanta that is available for capture by a cone class. Geisler (1989) estimates that the sampling aperture of a cone is approximately 80 % of its inner segment diameter. If, at the fovea, the majority of the receptor layer is taken up by L and M cones, and we assume equal numbers of these types, then the proportion of the incident quanta available to one class will be close to 0.64×0.5. The sampling time was taken to be 0.1 s (Hood and Finkelstein, 1986).

Some other minor adjustments were made. It was assumed that 5 % of the light was reflected at the anterior surfaces of the eye (Hecht et al., 1942). The quantum efficiency of cones was taken to be 0.67 (Knowles and Dartnall, 1977). The correction for the Stiles–Crawford effect was 0.86 (Applegate and Lakshminarayanan, 1993). These corrections are included for completeness, but will affect the analysis very little. They are of much less importance than the variables that can range over orders of magnitude, such as viewing distance, stimulus area and illuminant intensity.

Results and discussion

Reflectance spectra

Some examples of reflectance spectra are shown in Fig. 4. For further fruit reflectance spectra, see the accompanying paper (Sumner and Mollon, 2000). The spectra from mature leaves (drawn in black) closely resembled those from previous measurements (e.g. Gates et al., 1965; Regan, 1997), showing characteristic maxima between 500 and 600 nm and rising reflectance beyond 700 nm. This results from the absorbance peaks of chlorophyll at approximately 450 nm and 650 nm. Two

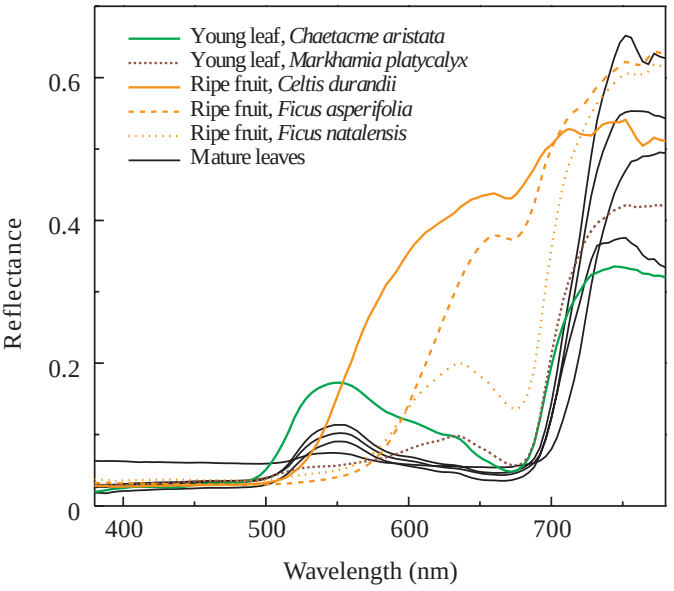

Fig. 4. Sample reflectance spectra of items in the diets of primates in Kibale Forest, Uganda. Spectra are given for three different fruit, two young leaves and representative mature foliage (see text for more details).

types of young leaf are shown. *Chaetacme aristata*, Ulmaceae, is representative of most species: the young leaves (solid green line) have similar-shaped reflectance spectra to the mature leaves, but overall greater reflectance. *Markhamia platycalyx*, Bignoniaceae, (dashed brown line) is representative of several species whose young leaves have relatively more long-wavelength reflectance than do the mature leaves. The fruits of *Celtis durandii*, Ulmaceae, and the fruits of *Ficus natalensis*, Moraceae, both feature highly in the diets of primates in Kibale, but they show different patterns of spectral change as they ripen. *Ficus asperifolia* is a fig species whose fruits display another different ripening pattern (for further details, see the accompanying paper; Sumner and Mollon, 2000).

Illuminants

To represent the stimuli that would actually be presented to an animal, the measured reflection spectra of surfaces must be combined with an appropriate illuminant that would be incident on these surfaces when the animal naturally viewed them.

Fig. 5 shows the measurements of the white barium sulphate plaque made in Uganda under natural illumination. They are similar to those measured in French Guiana by Regan (1997) and also to measurements made by Endler (1993). Depending on the proportions of blue sky, sunshine and reflection from cloud it contains, the chromaticity of each illuminant lies on a line that runs from blue sky to sun yellow. These changes in illumination show up more in the colour subsystem whose input sensitivities are further apart, i.e. the 'ancient mammalian' one. Endler (1993) predicted that the illumination in forest environments should fall into four categories during daylight hours. The bluer end of the chromaticity distribution

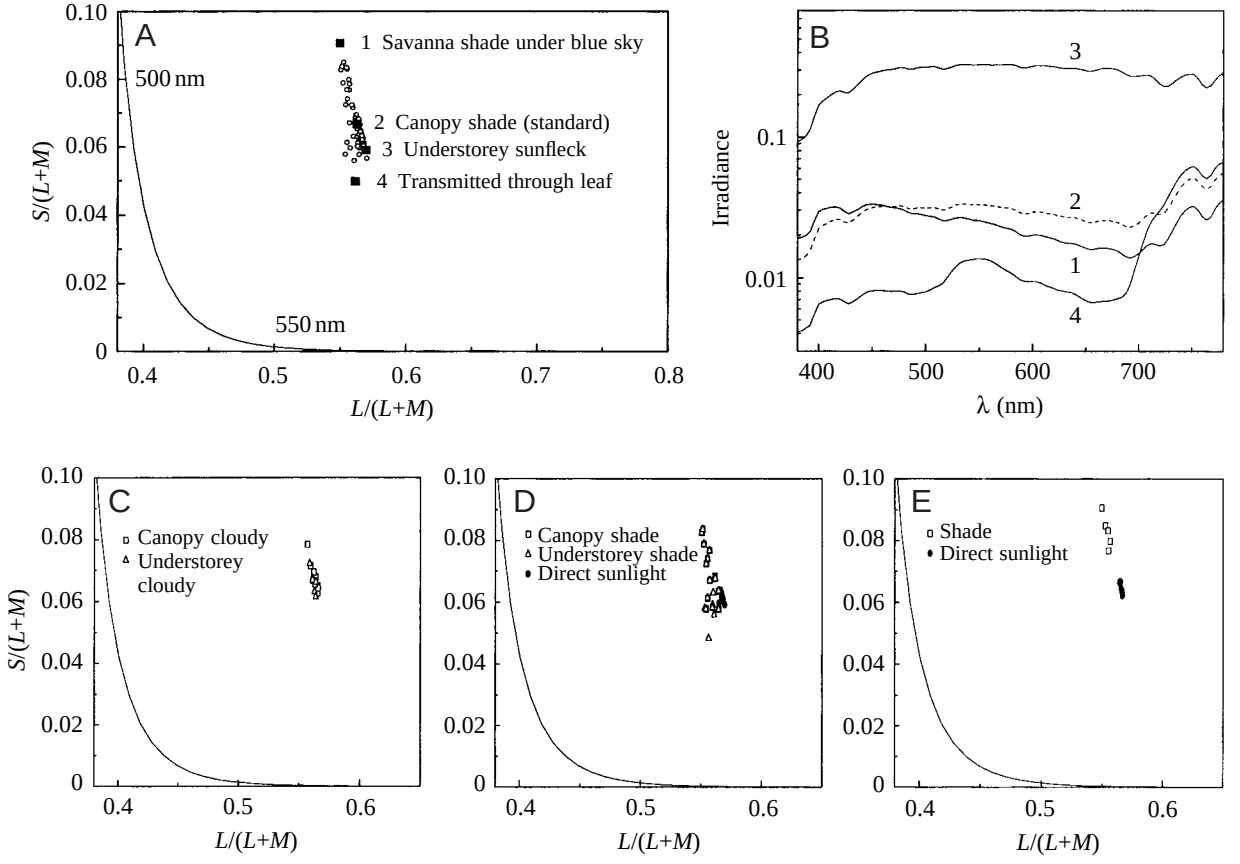

Fig. 5. (A) Measurements of the natural illuminant plotted in a chromaticity diagram appropriate for catarrhine monkeys (the peak sensitivities, λ_{max}, of the cone pigments were taken to be 430, 531 and 561 nm, and the mean of the lens data from a baboon and a macaque was used). The diagram plots $S/(L+M)$ against $L/(L+M)$ (see Materials and methods) and thus is similar to the Macleod–Boynton chromaticity diagram: the vertical axis represents the 'ancient mammalian' colour subsystem, and the horizontal axis represents the second catarrhine colour subsystem. The solid line shows the locus of monochromatic lights for reference. The filled black squares mark the four illuminants used to reconstruct the reflectance spectra into stimulus spectra. They were measured (1) in the shade of an *Acacia siberiana* in the savanna in Queen Elizabeth National Park [highest $S/(L+M)$ value, low luminance], (2) in the canopy (of *Lovoa synnertonii*) at Kanyawara, Kibale Forest, on a cloudy day (middle of chromaticity and luminance distributions, chosen as standard illuminant), (3) in a sunfleck at ground level under a closed canopy of *Cynometra alexandri* at 'Power Lines', Kibale Forest [highest $L/(L+M)$ value, and high luminance] and (4) directly under a leaf of *Ficus dawei* that was in full sunlight [lowest $S/(L+M)$ value and low luminance]. (B) The irradiance spectra of the four illuminants described above. (C) Illuminants measured in cloudy conditions in Kibale and Budongo Forests. (D) Illuminants measured in sunny conditions in Kibale and Budongo Forests. (E) Illuminants measured in the savanna of Queen Elizabeth National Park.

shown in Fig. 5 corresponds to Endler's 'woodland shade', the middle to his 'large gaps' or 'open/cloudy', and the yellow end to his 'small gaps'. If the illuminant contains a significant amount of light reflected or transmitted by leaves, its spectrum contains less of the wavelengths that chlorophyll absorbs, so its chromaticity drops below the 'blue–yellow' line, becoming more green, corresponding to Endler's 'forest shade'.

The illuminant marked as number 2 in Fig. 5A is the one chosen as standard for reconstructing the reflectance spectra into stimulus spectra. It was chosen for two reasons: it lies in the centre of the population of our illuminant measurements on both chromaticity axes and in luminance, and it was measured in typical canopy in cloudy conditions. Under cloudy illumination, the individual illuminants of leaves and fruits in the canopy are much more alike than in sunshine, when there are large differences between sunflecks and shade, and the angle of the reflecting surface to the sun also makes a large difference. Therefore, an analysis that combines all reflection spectra with the same illuminant is more realistic if it uses an illuminant measured under roughly uniform cloud.

The effects of changing the illuminant have been tested using the measurements marked 1, 3 and 4 in Fig. 5A. They were chosen to represent the extreme possible differences in illumination that primates might encounter during daylight hours. The only major sources of light in these extreme illuminants, respectively, were blue sky, sunlight and light transmitted through a leaf, and the only major source in the standard illuminant, number 2, was cloud. Since all natural illuminants in the forest canopy (in daylight hours) might be considered as some combination of light from sun, cloud, blue sky and leaf transmission or reflectance, the results produced by these selected measurements will represent the gamut of possibilities for almost any natural forest canopy illuminant. The colour space diagrams and the signal-to-noise ratio results presented below were not affected in any important way when the illuminants were swapped. Therefore, we can be confident that our conclusions are independent of variations in natural illumination in the environments of the primates.

Mature leaves

The background from which fruit or leaf food items must be detected in the forest is made up chiefly of mature leaves. The *in situ* measurements of leaf surfaces are shown in Fig. 6.

The chromaticity distribution for the catarrhine monkey is strikingly vertical, i.e. there is little variation on the $L/(L+M)$ axis and there is little correlation between the axes. This pattern of results for Ugandan forest leaves is very similar to that of Regan et al. (1998) for their sample from French Guiana, so the distribution of leaf chromaticities may be the most important universal influence on what cone sensitivities are

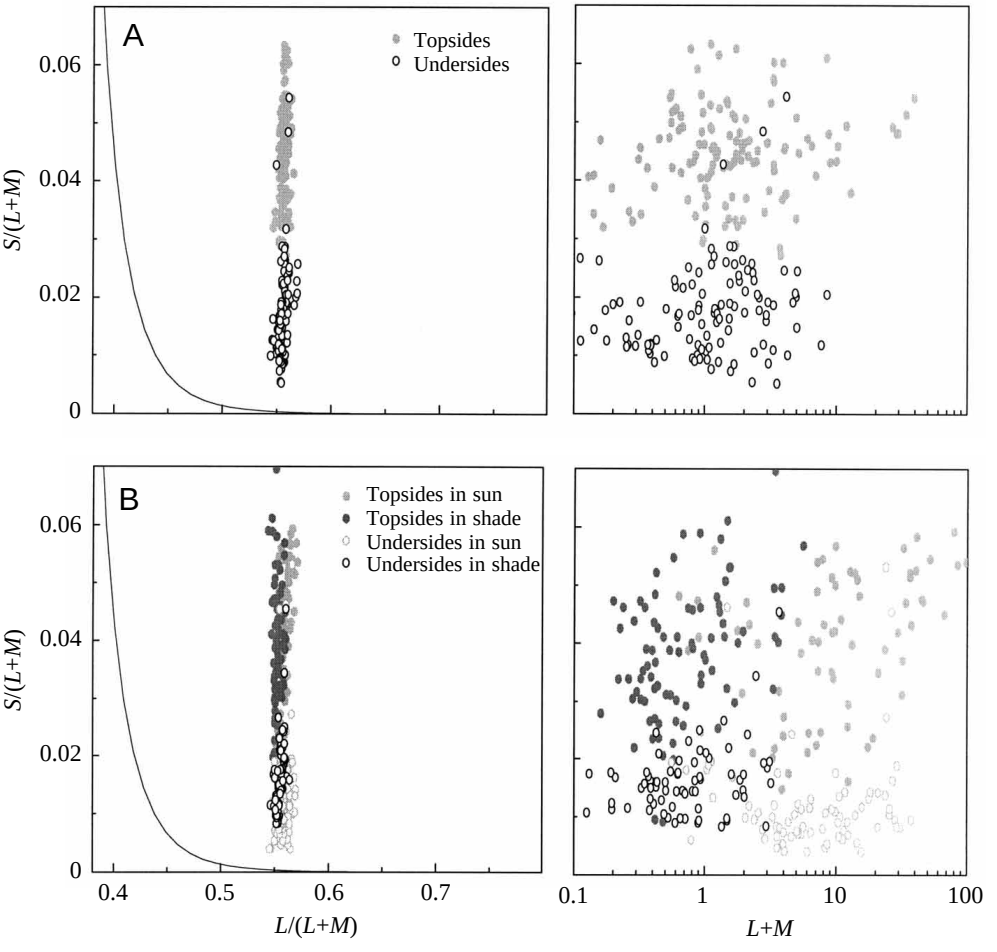

Fig. 6. Chromaticity (left) and luminance (right) values for mature leaves of Kibale forest plotted in catarrhine monkey colour space. (A) *In situ* measurements made in cloudy conditions. (B) *In situ* measurements made in sunny conditions. For further details, see Materials and methods.

possessed by arboreal animals. If leaf pigmentation is due chiefly to chlorophyll, then it is not remarkable that the chromaticities of all the reflected and transmitted spectra should lie on a continuous locus in colour space, since all leaves would have similar absorption spectra, modified only according to the optical density of the pigment. It can be seen in Fig. 6B that, as would be expected, the distribution of leaves measured in direct sunlight points to the chromaticity of the white plaque measured in sunlight (Fig. 5), and the distribution measured in shade points to the chromaticity of the illuminants measured in shade. What is remarkable is that these lines should be so nearly parallel to an axis of colour space, because this depends on the properties of the animal's eye.

The luminance of leaves in the forest may vary over 3 log units at one time (although the *in situ* measurements shown were not all made at one time). This spread is mostly due to local differences in the illuminant caused by shadows. It would be very difficult to spot targets by their lightness against this range of dappled background luminances. There is also very little correlation between $S/(L+M)$ and $L+M$: the mature leaves spread over a large area in the colour space of a dichromatic monkey, leaving no opportunity for targets to stand out from this foliage background by a combination of signal in the luminance and $S/(L+M)$ channels.

Other habitats

Fig. 7 shows the measurements made of plants in the savanna environment of Queen Elizabeth National Park, Uganda. The data set is not large, but it seems clear that the chromaticity distribution of the leaves (*Acacia geradii*, *Acacia siberiana*, *Euphorbia candelabra* and unidentified *Capparis* sp. and *Ulmaceae* sp.) conforms to the pattern found in the rain forest. The grasses and the bark of the two acacia species give relatively more L cone absorption, and the bark seems to fall into two categories: to the human eye, the cluster lower on the S axis looks brownish, and the other group is lighter and whiter. The main difference is that the undersides of the leaves measured *in situ* in the savanna did not produce as low S cone absorption as the ones in the forest. This is presumably because there was no closed canopy, and plenty of light from all directions could fall on these leaves so that the majority of the light measured from the leaf surfaces was reflected, not transmitted, light.

Webster and Mollon (1997) have measured the spectral distributions of objects and of the illuminant in natural scenes in mountain and desert regions of Nevada, USA, in the Western Ghats in Maharashtra, India, and in the temperate rainforest of Washington Olympic Peninsula, USA. Their results were broadly similar to those reported here. In the desert environments, the measured illuminants formed a line from blue to yellow (the daylight locus), and illuminants in the forest lay to the green side of this line. The distribution of chromaticities in the scenes with blue sky and arid landscape lay close to the blue–yellow axis of the sky-light illuminants, and the distribution of chromaticities in the scenes containing mostly lush vegetation and no sky lay close to the $S/(L+M)$ axis (of the Macleod–Boynton chromaticity diagram for man, which is very similar to the catarrhine chromaticity diagram presented in the present study). The distribution of chromaticities in virtually all scenes lay between these axes, and there were high correlations between the $S/(L+M)$ and $L/(L+M)$ axes, but much weaker correlations between luminance and chromaticity.

Hendley and Hecht (1949) were the first to report that the colours in natural scenes occupy a very small area of the space of all possible colours. They matched (by eye) objects in

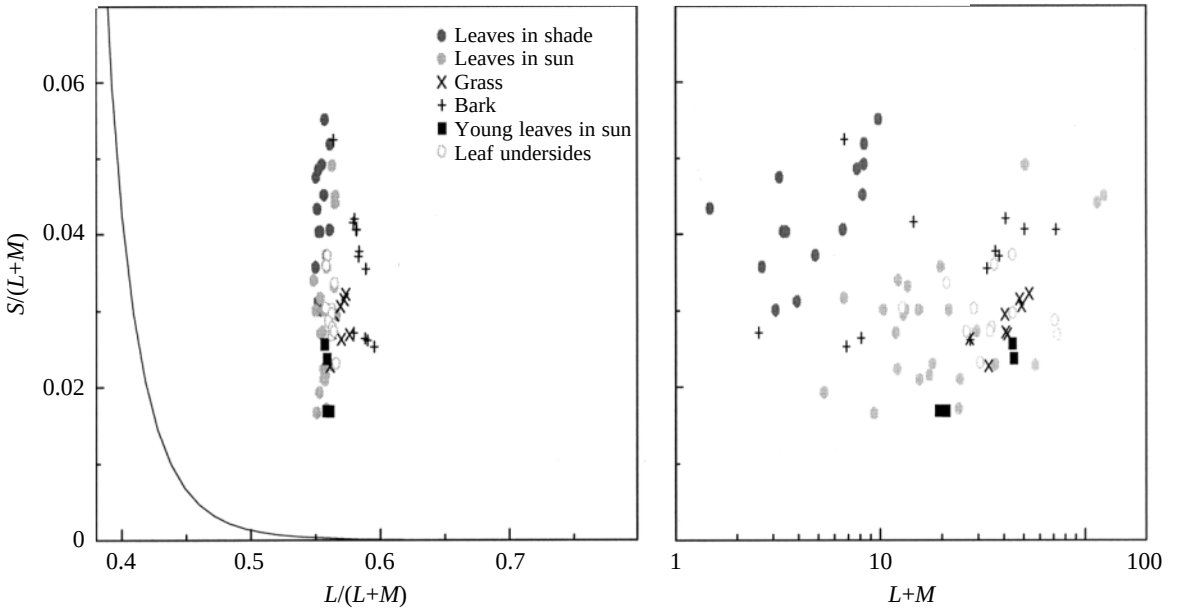

Fig. 7. Measurements of chromaticity (left) and luminance (right) for plants in the savanna environment of Queen Elizabeth National Park. For further details, see Materials and methods.

natural scenes to Munsell chips and found three important chromaticity groups [which they plotted in CIE 1931 colour space (Commission Internationale de l'Éclairage, 1932)]: yellow-greens of foliage, orange-yellows of earths and dried vegetation, and the blues of sky, distant objects and water. Although the authors do not comment on it, the distribution of the earths, water, distant objects and sky do in fact form a straight line through white (standard illuminant C), while the distribution of the foliage lies roughly in a different straight line and that line is indeed a tritan line [i.e. it would be parallel to the *S*/(*L*+*M*) axis in the catarrhine chromaticity diagram presented in this study].

Detecting target food items in the canopy

Mature leaves

Fig. 8A shows the chromaticities of reconstructed stimulus spectra of the ripe fruits eaten by *Cercopithecus mitis* and the mature leaves from the same trees, plotted in the 'standard catarrhine monkey colour space'. These leaves, whose reflectance spectra were all measured in the same standard conditions, display the same vertical chromaticity distribution that has already been discussed for the *in situ* measurements shown in Fig. 6. This shows that the spread in chromaticity is due to the properties of the different leaf surfaces and not just to the differences in local illuminant and leaf surface angle when measured *in situ*. The reflectance measurements of only the top sides of the leaves are included because these conform well to the *in situ* measurements of the top sides of the leaves (except that the *in situ* measurements show much more spread in luminance because of variation in local illuminant and leaf blade angle). The stimulus spectra reconstructed from reflectance measurements of leaf undersides did not match *in situ* measurements and do not, therefore, represent the stimuli that would naturally reach the eye of a primate. This is because a large proportion of the light from leaf undersides in the forest is transmitted light, not reflected light.

Ripe fruit

The fruits eaten by *Cercopithecus mitis* (*N*=292, 24 species) all lie to the right of the leaves in the chromaticity diagram (i.e. all have higher *L*-to-*M* ratios). The second catarrhine colour subsystem would, therefore, be useful for detecting these fruits against their background of leaves. The right-hand panel of Fig. 8A seems to show that both the luminance signal and the

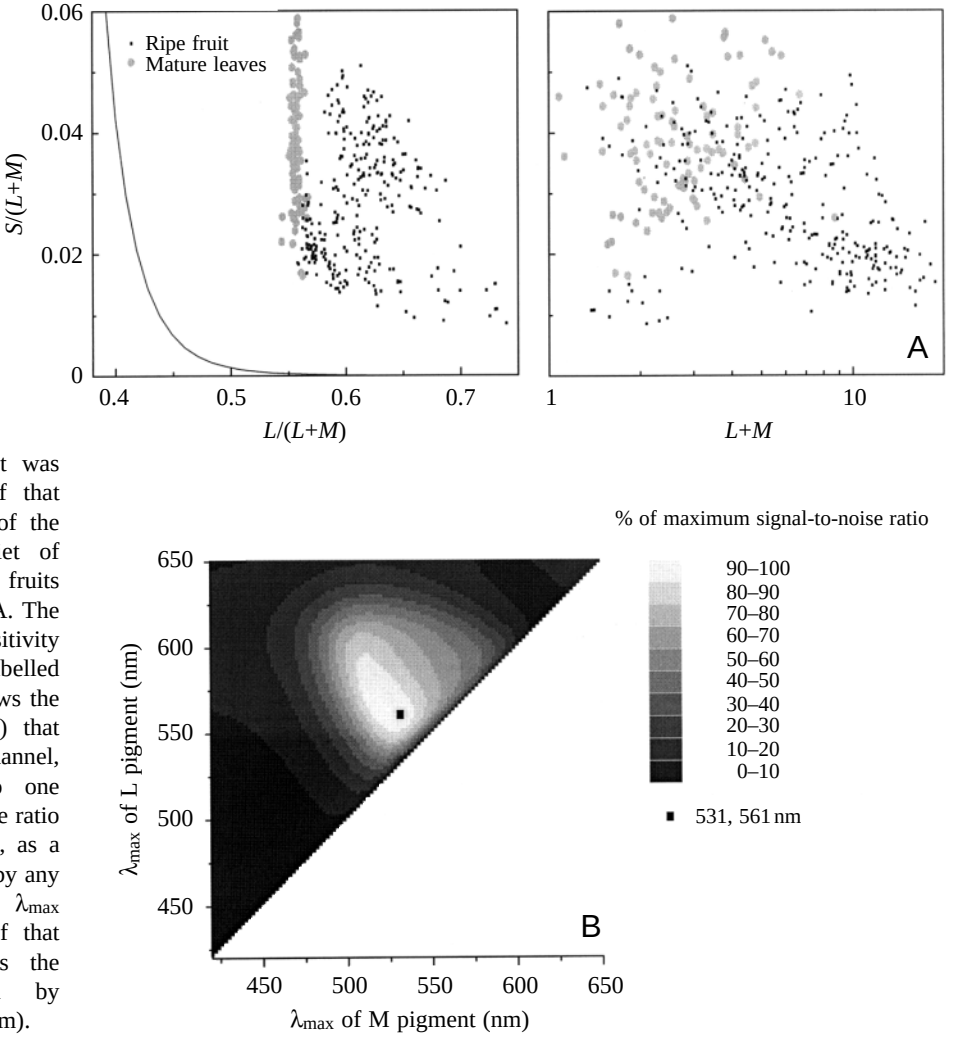

Fig. 8. (A) Chromaticity (left) and luminance (right) values for the fruits in the diet of *Cercopithecus mitis* (black symbols, *N*=292) and the mature leaves from the same trees (grey symbols, *N*=98) plotted in catarrhine monkey colour space (see Materials and methods for further details). Only the ripe fruits are included. The distribution shows the full gamut of the fruit chromaticities, but the density of the dots is biased because each measurement is plotted and the species for which more measurements were obtained are therefore over-represented. However, the number of measurements made of a species of fruit was highly correlated with the importance of that species to the primates. (B) The results of the signal-to-noise analysis for the fruit diet of *Cercopithecus mitis*. The 'targets' were the fruits and the 'background' the leaves shown in A. The abscissa shows the wavelength of peak sensitivity (λ_{max}) of one putative cone photopigment (labelled 'M' for convenience), and the ordinate shows the λ_{max} of the other putative pigment ('L') that subserves the dichromatic colour channel, *L*/(*L*+*M*). Each pixel, corresponding to one pigment pair, shows the mean signal-to-noise ratio for all targets against the leaf background, as a proportion of the maximum ratio produced by any pigment pair. The white area shows the λ_{max} combinations that produced over 90% of that maximum, and the filled square marks the pigments thought to be possessed by *Cercopithecus mitis* (λ_{max}: 531 nm and 561 nm).

ancient mammalian colour signal and luminance would also be useful for this task since the fruits lie below and to the right of the leaf distribution. However, comparison with the *in situ* leaves plotted in Fig. 6 will show that in the forest the luminance spread of the leaves is much larger, and leaf undersides occupy low $S/(L+M)$ values. It seems unlikely, therefore, that these signals are very useful for finding the fruits amongst the leaves.

Fig. 8B shows 6670 average signal-to-noise ratios for possible pairs of pigment sensitivities at 2 nm intervals from 420 nm to 650 nm. The abscissa shows the peak sensitivity of one pigment, which we call 'M', and the ordinate shows the peak sensitivity of the other pigment, labelled 'L'. The grey level of each pixel shows the signal-to-noise ratio for that pair of pigments relative to the maximum signal-to-noise ratio yielded by any of the pigment pairs. The target and background spectra used in this case were those of the fruits and leaves plotted in Fig. 8A. The weighting for each target was taken from the diet percentage data of Rudran (1978b) divided by the number of measurements of that fruit species.

The maximum signal-to-noise ratio was produced by pigments with λ_{max} values of 524 nm and 564 nm, and the white area shows the pigment combinations that yielded over 90 % of this maximum. The black square shows the pigments that *Cercopithecus mitis* is thought to possess (531 nm and 561 nm), which yielded 98 % of the maximum. Therefore, the sensitivities of the L and M cones of this monkey seem well-adjusted for detecting important fruits against their natural background. If the monkey were dichromatic, possessing one pigment with peak sensitivity near 430 nm and one other pigment, these data show that, no matter what the peak sensitivity of the second pigment, the signal-to-noise ratio would never exceed 20 % of what is possible. As soon as the primate has two cones with λ_{max} anywhere between 520 and 600 nm, there is an advantage over the ancient mammalian subsystem, even if the M and L pigments have very similar sensitivities, as they may have done immediately after the gene duplication. [The labels M and L are used for convenience, but the analysis could equally well apply to S cones and L cones, and we can substitute the label S for M. Strictly, we should not draw conclusions about dichromatic primates from the analysis of $L/(L+S)$, because the single colour channel (common to many mammals) of a dichromatic primate would be better represented as S/L, not $L/(L+S)$. Therefore, the analysis was repeated for S/L. The results were virtually identical.]

The fruit diets of the other five primate species have been analysed in the same way and, in addition, the analyses have been performed using the *in situ* measurements of mature leaves

Table 1. *Summary of optimal peak sensitivity (λ_{max}) values for different data sets*

	Optimal λ_{max} (nm)				*N*	
Target type	Mean	Separation	M, L	*P*	Targets	Background
Ripe fruits eaten by *Cercopithecus mitis*	544	40	524, 564	0.98	292	98
Ripe fruits eaten by *Cercopithecus ascanius*	543	42	522, 564	0.96	452	126
Ripe fruits eaten by *Lophocebus albigena*	544	36	526, 562	0.98	393	108
Unripe fruits eaten by *Colobus guereza*	544	44	522, 566	0.96	224	56
All fruits eaten by *Colobus guereza*	544	40	524, 564	0.97	396	56
Unripe fruits eaten by *Colobus badius*	543	46	520, 566	0.96	302	88
All fruits eaten by *Colobus badius*	543	42	522, 564	0.97	515	88
Top 10 fruit species eaten by *Pan troglodytes*	545	42	524, 566	0.98	195	54
Ficus species ripe fruits	539	42	518, 560	0.92	249	37
Canopy non-*Ficus* ripe fruits	541	42	520, 562	0.90	122	57
Understorey ripe fruits	540	36	522, 558	0.94	124	110
Non-chimpanzee ripe fruits	552	44	530, 574	0.97	59	44
Young leaves eaten by *Cercopithecus mitis*	542	56	514, 570	0.89	192	131
Young leaves eaten by *Cercopithecus ascanius*	543	50	518, 568	0.93	158	114
Young leaves eaten by *Lophocebus albigena*	546	52	520, 572	0.93	172	117
Young leaves eaten by *Colobus guereza*	546	52	520, 572	0.93	144	97
Young leaves eaten by *Colobus badius*	543	54	516, 570	0.91	222	160
Young leaves eaten by *Pan troglodytes*	541	58	512, 570	0.83	188	124
Background of mature leaves measured *in situ*						
Sunny conditions; fruit targets	548	52	522, 574	0.95	292	305
Sunny conditions; *in situ* young leaf targets	547	54	520, 574	0.95	56	305
Cloudy conditions; fruit targets	546	56	518, 574	0.92	292	246
Cloudy conditions; *in situ* young leaf targets	544	56	516, 572	0.87	61	246

In all cases, the background was mature leaves of the same trees as the targets. All stimulus spectra were reconstructed from reflectance spectra except where specified as *in situ*. *P*, proportion of maximum signal-to-noise yielded by the pigments possessed by the primate; *N*, number of measured reflectance spectra; M, middle-wavelength-sensitive pigment; L, long-wavelength-sensitive pigment.

(both top- and undersides) as background instead of the reconstructed stimulus spectra (the targets were reconstructed spectra of fruits because it was not possible to obtain many *in situ* measurements). In the analyses of the fruit diets of the colobines, only unripe fruit samples were included, so the target sets were completely different from those of the other analyses (which included only ripe samples). All the results were almost identical to those for *Cercopithecus mitis* discussed above. The results are strikingly similar also to those obtained by Regan (1997), Regan et al. (1998) and B. C. Regan, C. Julliot, B. Simmen, F. Viénot, P. Charles-Dominique and J. D. Mollon (in preparation) in French Guiana for *Alouatta seniculus* and for the trichromatic individuals of *Cebus apella* and *Ateles paniscus.* The optimal λ_{max} pairs produced by our analyses are shown in Table 1. Instead of considering the individual λ_{max} values of an M and L pigment pair, it is more appropriate for our present purpose to consider the mean of the λ_{max} pair, and the separation between the M and L values (the reasons for this are explained below). For example, the λ_{max} values of pigments possessed by catarrhine monkeys have a mean of 546 nm and a separation of 30 nm. Changes in the mean correspond to shifts parallel to the diagonal edge in the plots of signal-to-noise ratios, and a change in the separation corresponds to a move orthogonal to this diagonal edge. While the separation of the predicted optimal pigments from each analysis was always significantly more than 30 nm, the mean λ_{max} value was consistently close to 546 nm.

Given the similarity of their diets, it is perhaps not surprising that the results for *Cercopithecus ascanius* and *Lophocebus albigena* were very close to those of *Cercopithecus mitis*, even though different target weightings and lens data were used. The diet of *Pan troglodytes* is much less similar. Percentage data were available only for the top ten species in the diet, but these species constitute over 80 % of the total fruit diet, and in some months the chimpanzees rely almost exclusively on a small subset of these species (Isabirye-Basuta, 1989). The results for these top ten fruit species are shown in Fig. 9. The mature leaves are a different set from those in Fig. 8, but their distribution in colour space is similar. It can be seen that the photopigments thought to be possessed by the primate are strikingly well-optimised for detecting these important fruits amongst their natural background of leaves: the pigments with λ_{max} values of 531 nm and 563 nm yielded 98 % of the maximum possible signal-to-noise ratio. (Note that the signal-to-noise ratios are plotted only between 480 nm and 630 nm: there were no high signal-to-noise ratios outside this region.)

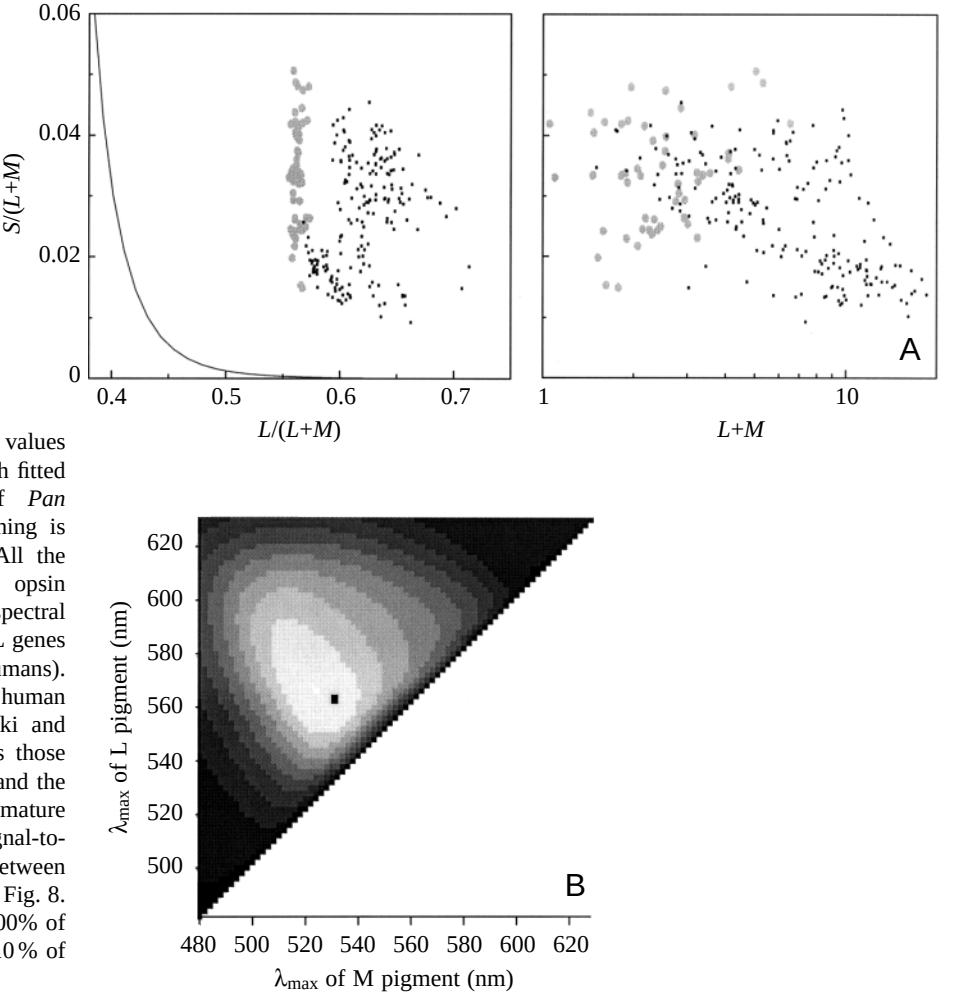

Fig. 9. (A) Chromaticity (left) and luminance (right) values for the top ten species of fruit in the diet of *Pan troglodytes* (black symbols) and mature leaves from the same trees (grey symbols). The pigments used to construct the colour space had wavelengths of peak sensitivity (λ_{max}) of 430 nm, 531 nm and 563 nm. Since no lens or macular pigment data are available for any apes other than humans, this would be a general colour space for all apes, except that measurements of S cone sensitivity for *Homo sapiens* (Asenjo et al., 1994; Dartnall et al., 1983; Merbs and Nathans, 1992; Oprian et al., 1991) have all found λ_{max} values at shorter wavelengths than the 430 nm which fitted the electroretinographic measurements of *Pan troglodytes* (Jacobs et al., 1996a), and nothing is known about the S cones of other apes. All the sequenced ape M genes have shown the opsin proteins to have the same amino acids at the spectral tuning sites, and the same is true for the ape L genes (excepting the known polymorphisms in humans). The signal-to-noise analysis (B) also used the human lens and macular pigment data of Wyszecki and Stiles (1982). The targets were the same as those plotted in the colour space (black symbols), and the background stimuli (grey symbols) were the mature leaves from the same trees. Note that the signal-to-noise ratios are plotted for λ_{max} values between 480 nm and 630 nm. For further details, see Fig. 8. The greyscale in B ranges from white (90–100% of maximum signal-to-noise ratio) to black (0–10 % of maximum signal-to-noise ratio).

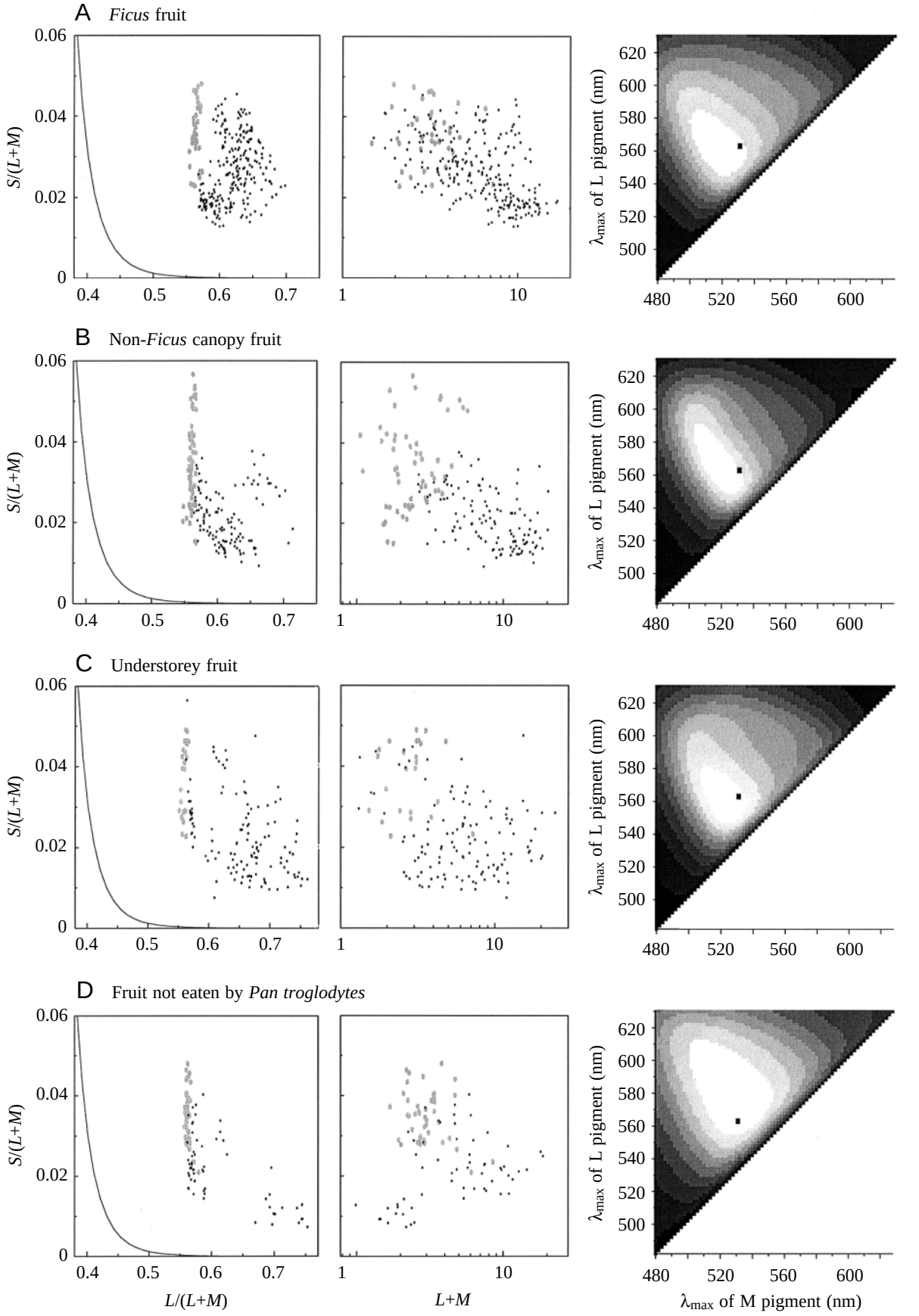
A Ficus fruit
B Non-Ficus canopy fruit
C Understorey fruit
D Fruit not eaten by Pan troglodytes
S/(L+M)
0.06
0.04
0.02
0
0.4
0.5
0.6
0.7
1
10
L/(L+M)
L+M
λmax of L pigment (nm)
620
600
580
560
540
520
500
480
520
560
600
λmax of M pigment (nm)

Fig. 10.

Fig. 10. (A) Chromaticity (left) and luminance values (centre) and the signal-to-noise analysis (right) for the ripe fruits only of *Ficus* species and for the mature leaves from the same trees. All these fruits are eaten by *Pan troglodytes*, and virtually all are also taken by *Cercopithecus mitis*, *Cercopithecus ascanius* and *Lophocebus albigena*. The analysis parameters are described in the legend for Fig. 9. (B) Results for (ripe) non-*Ficus* canopy fruits that are eaten by *Pan troglodytes* and for the mature leaves from the same trees. Most of these fruits are also taken by *Cercopithecus mitis*, *Cercopithecus ascanius* and *Lophocebus albigena*. (C) Results for fruits that grow in the understorey (i.e. under 5 m). Virtually none of these has been seen to be eaten by any of the monkeys in Kibale. (D) Results for (ripe) fruits that are not eaten by *Pan troglodytes* and for the mature leaves from the same trees. For further details, see Fig. 8. The greyscale in B ranges from white (90–100% of maximum signal-to-noise ratio) to black (0–10 % of maximum signal-to-noise ratio).

To test whether the similarities in the results discussed above were because the data sets shared some plant species, four mutually exclusive sets of ripe fruits and mature leaves have been similarly analysed: *Ficus* species (nine species), non-fig canopy fruits eaten by chimpanzees (18 species), understorey fruits (11 species) and fruits not eaten by chimpanzees but eaten by monkeys (15 species). The first three categories are subsets of the diet of *Pan troglodytes* and, for comparison, the analyses of all four categories used the same parameters as did the analysis of the top ten fruit species in the chimpanzee diet. The results are shown in Fig. 10. The colour space distributions of the four categories were very different from each other, especially on the $L/(L+M)$ axis (compare the average of the understorey fruits, 0.66, with the average of the canopy fruits, 0.61). In the understorey, the many fruits with high *L*-to-*M* ratios also have high luminance values (Fig. 10C). This large chromaticity difference from the leaf background, without a drop in lightness, would allow them to be visible in the lower illumination near the forest floor. In contrast, the canopy fruits having highest *L*-to-*M* ratio are very dark (Fig. 10D). They are also small (all less than 10 mm across), which may be why they are not eaten by the chimpanzees. Despite the differences between the data sets, all the signal-to-noise analyses produced remarkably similar results. The means of the pairs of λ_{max} values that produced maximum signal-to-noise ratios in the four analyses were 539 nm, 541 nm, 540 nm and 552 nm. The pigment pair probably possessed by *Pan troglodytes* (λ_{max} 531/563) yielded 92 %, 90 %, 94 % and 97 % of these maxima, respectively.

Young leaves

In Fig. 11 are plotted the results for the young leaves in the diet of *Colobus guereza* and for the mature leaves from the same trees (as before, only the topsides of leaves are used). The mature leaves are a different set from those used above, but again show a very similar distribution in colour space. The chromaticities and luminances of the young leaves (N=144, 17 species) seem to resemble a subset of the fruit distribution, except that a few young leaves lie just on the left side of the values for the mature leaves. Among the young leaves that differ from mature leaves in chromaticity, there is a continuous distribution of chromaticities between those that appear yellowish-green and those that are brown or reddish. The yellowish ones cluster at the bottom right of the mature leaf distribution in both panels of Fig. 11A, forming a clearly different distribution from mature leaves in the right-hand panel. Like many fruits, it seems they would be detectable by dichromats on account of their lightness, but *in situ* this would be made more difficult by the extended range in luminance of mature leaves. However, the position in which most young leaves are found (at the end of branches) would make them less likely to fall into the shadows of other leaves, and their lightness would therefore be less masked by the luminance spread of mature leaves than the lightness of fruits would be. The brownish young leaves spread up and right in the chromaticity diagram and tend to be darker than the other young leaves, so falling within the mature leaf distribution on the S cone and luminance axes. These browner leaves would therefore be cryptic to mammalian dichromats.

The maximum signal-to-noise ratio was for pigments with a mean λ_{max} of 546 nm and a separation of 52 nm, and was nearly five times less than the maximum for the fruits, because the average signal was much smaller (the chromaticities of the young leaves plot closer to those of the mature leaves than do the chromaticities of the fruits). The pair of pigments with λ_{max} of 531 nm and 561 nm gave 93 % of the maximum possible. The majority of the diet of *Colobus guereza* is provided by young leaves of *Celtis durandii*, Ulmaceae, and an analysis that included young and mature leaves of only this species (both top- and undersides included, measured *in situ*) produced results again remarkably similar to previous results: the optimal λ_{max} pair had a mean value of 553 nm and a separation of 38 nm, and the actual pigments of the monkeys produced 92 % of the maximum possible. Lucas et al. (1998) suggested that the ability to distinguish the reddish coloration of young leaves from the dark green of mature leaves may have driven the evolution of primate trichromacy, and it is clear from our results that the catarrhine photopigments are indeed optimised for spotting red/brown young leaves (e.g. those of *Markhamia platycalyx*, Bignoniaceae, the second most abundant food item in the diet of *Colobus guereza*) among mature leaves. However, the young leaves of *Celtis durandii* show no sign of being red or brown: they are pale green like those of *Chaetacme aristata*, a tree species of the same family, shown in Fig. 4. Therefore, our suggestion that primate trichromacy may have been selected for folivory (as well as for frugivory) does not rest only on plant species that colour their young leaves with a red/brown pigment.

The leaf diet of *Colobus guereza* is very different from that of the other primates, being chiefly made up of only two tree species. The leaf diets of the other five primate species have been analysed, and we have also used *in situ* measurements of mature leaves (both top- and undersides) instead of reconstructed stimulus spectra (using as targets *in situ* measurements of young leaves). The results were highly similar to the results for *Colobus guereza* discussed above. A

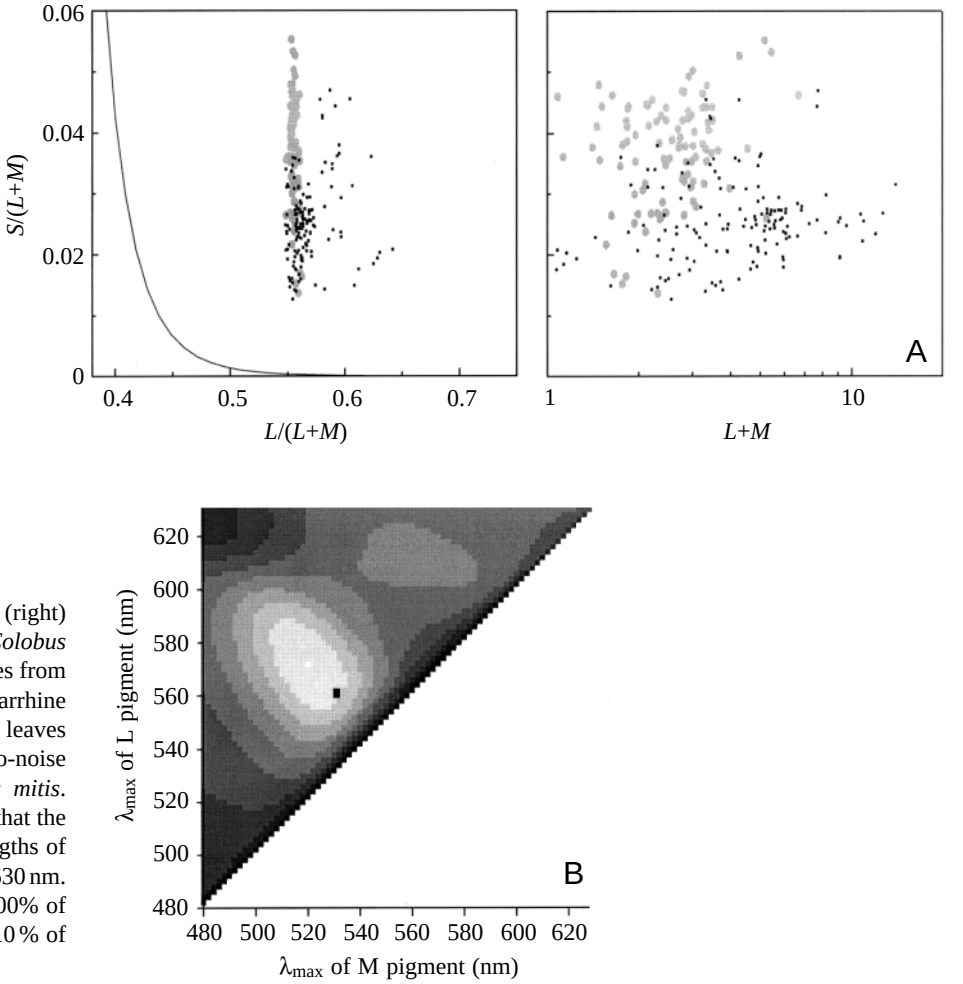

Fig. 11. Chromaticity (left) and luminance (right) values for the young leaves in the diet of *Colobus guereza* (black symbols) and the mature leaves from the same trees (grey symbols) plotted in catarrhine monkey colour space (only the topsides of leaves are included). (B) The results of the signal-to-noise analysis for the leaf diet of *Cercopithecus mitis*. Explanation and legend as for Fig. 8, except that the signal-to-noise ratios are plotted for wavelengths of peak sensitivity (λ_{max}) between 480 nm and 630 nm. The greyscale in B ranges from white (90–100% of maximum signal-to-noise ratio) to black (0–10 % of maximum signal-to-noise ratio).

summary of the results is included in Table 1. From the *P* values (proportion of maximum possible signal-to-noise ratio yielded by the pigments thought to be possessed by the primate), it would seem that catarrhine visual pigments are slightly better adapted to spotting ripe fruits than young leaves. However, this difference arises from the larger separation of the predicted optimal pigments, and this can be explained by the fact that the average signal was smaller for the young leaves (they are closer in chromaticity to the mature leaves than are the fruits). The mean λ_{max} values of the predicted optimal pigments are again close to 546 nm (the mean of 531 and 561 nm, the pigments that the primates are thought to possess), and we regard the similarities between the results for the fruit and young leaves as more important than the differences: for two completely different categories of target, the optimal sensitivities that primates could possess are nearly the same.

The effect of macular pigment

It was consistently found that the mean of the optimal pair of λ_{max} values was slightly less than 546 nm (i.e. the maximum signal-to-noise ratio is normally slightly closer to the bottom left-hand corner in the plots than is the black square marking the actual pigments of the primate). This pattern could be explained if the macular density used in the analysis were too high. If the optical density of the macular pigment is set to 0.8 times the standard value used, then, for most of the analyses, the predicted optimal pigments line up almost exactly with the pigments the primates are thought to possess. This adjustment, although *post hoc*, would make sense because the pigments may be optimised not just for an area of retina at the very centre of the fovea. The data of Wyszecki and Stiles (1982) have a peak optical density at 460 nm of approximately 0.5, which, by comparison with the distribution measurements of Snodderly et al. (1984a), corresponds to the area of fovea out to less than 1 ° eccentricity. Is it likely that cone sensitivities of primates would be optimised only within this area? It is also possible that the primates in this study have a lower macular pigment density than humans. It has already been reported by Mollon and Regan (1999), following their study on platyrrhine monkeys, that filtering by macular pigment has the effect of displacing to shorter wavelengths the optimal pigments for finding diet items amongst leaves. It may be that a selective advantage of having some macular pigment was to allow this task to be performed optimally without creating long-wavelength pigments that would be susceptible to thermal noise (or it may be just an alternative solution, adopted instead of the genetic changes required in the opsin gene to shift the λ_{max} beyond 561 nm). More likely, macular pigment exists for

other reasons and the evolutionary optimization of cone pigments has automatically taken it into account.

Synopsis

Colour space results

(i) Many fruits and young leaves are lighter than mature leaves. However, there is so much luminance variation in the background *in situ* (caused by local variation in illumination and angle of leaf blade) that this difference in reflectance would often be masked. So luminance would be a poor cue to rely upon to detect these targets (Mollon, 1989).

(ii) The chromaticity distributions of the fruits in the diet of each primate are broadly similar, but there are obvious large differences between understorey and canopy fruits, between figs and non-figs, and between those fruits that are not eaten by *Pan troglodytes* and those that are. Differences between unripe and ripe fruits are discussed in the accompanying paper (Sumner and Mollon, 2000).

(iii) The chromaticity distributions for young leaves in each primate's diet are also similar to each other and are more tightly clustered than the fruit distributions.

(iv) All fruits and many young leaves produce a higher *L*:*M* ratio than mature leaves (i.e. they lie to the right of the mature leaf chromaticity distribution). Therefore, the recently evolved primate colour channel would be useful for detecting these targets against their natural backgrounds.

(v) Some fruits, but few young leaves, also produce a higher (*L*+*M*):*S* ratio than the topsides of mature leaves (i.e. they lie below the chromaticity distribution of mature leaf tops). Therefore, in some circumstances (if only tops of leaves are visible), the ancient mammalian colour subsystem could be useful for distinguishing these targets from their natural backgrounds. However, none of the *S*/(*L*+*M*) chromaticity values of these targets lies outside the distribution for leaf topsides and undersides measured *in situ*.

Signal-to-noise analysis results

(i) The results across primates were very similar despite some large differences in target sets and target weightings. The results for four mutually exclusive sets of fruit target and background spectra were also remarkably similar. The results for young leaves were similar to those for fruits despite the completely different set of targets and the background sets having at most 30 % of samples in common with each other.

(ii) Whenever one cone had a peak sensitivity below 450 nm, very poor signal-to-noise ratios were obtained, indicating that the ancient mammalian colour channel has not been optimised for the task of distinguishing fruits or young leaves from mature leaves, and any animal with only one middle- or long-wavelength-sensitive cone would be at a severe disadvantage. Any two pigments between 520 nm and 600 nm produce higher signal-to-noise ratios for both fruit and young leaf targets, and so no matter what the exact sensitivities of the M and L cones after they first diverged, the initial selective advantage could have been in the search for any of these food items.

(iii) The two M and L pigments thought to be possessed by catarrhine primates produce close to optimal signal-to-noise ratios, and it is therefore likely that this natural visual search task of finding food items amongst foliage played a crucial role in the evolution of these pigments.

We conclude that there is a selective advantage in being trichromatic for both folivory and frugivory. Moreover, trichromacy offers a significant advantage over dichromacy for almost any M–L pigment combination within a large range. Once the primates are already trichromatic, we argue that there is further selective advantage in positioning the M and L λ_{max} values near 530 and 560 nm.

Mature leaves determine which pigments are optimal

In the calculation of the signal-to-noise ratios, there are three components: the difference between target and background chromaticities ('signal'), the variance in the background chromaticities ('background chromaticity noise') and the variance in the chromaticity of each stimulus due to the probabilistic arrival and absorption of photons ('quantum noise'). It is not immediately obvious how each of these components might affect the overall pattern of the results. In this section, the focus is on what determines which pigments are predicted as optimal for the task of finding food items amongst leaves.

Quantum noise

The calculation of the quantum noise is the only part of the analysis that requires estimates of the absolute numbers of photons absorbed in each class of cone, not just the relative numbers (see above). It is not claimed that our estimates are accurate to more than an order of magnitude, and changes in

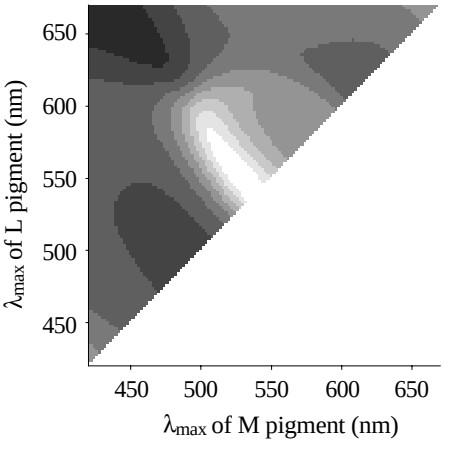

Fig. 12. The effect of leaving the quantum noise out of the analysis: the signal-to-noise results for young leaves in the diet of *Cercopithecus mitis*. The noise was leaf chromaticity noise alone. Compare this with the plot in which quantum noise was included (Fig. 13C). Note that the plot includes wavelengths of maximum sensitivity (λ_{max}) between 420 nm and 670 nm, and that each pixel was scaled relative to the maximum possible ratio in this case, which was a higher ratio than when the quantum noise was included. The greyscale ranges from white (90–100% of maximum signal-to-noise ratio) to black (0–10 % of maximum signal-to-noise ratio).

illumination would produce fluctuations much larger than this (see above). It is important, therefore, that the pattern of results should not be critically dependent on the influence of the quantum noise. Fig. 12 shows that the quantum noise greatly affects only the results for pairs of pigments with very similar sensitivity, because for these pigments both the signal and the variance in the background chromaticity were small. The peak signal-to-noise ratio, without the quantum noise included, was produced by pigments with λ_{max} values of 540 nm and 542 nm for the fruits and 538 nm and 540 nm for the young leaves. The magnitude of the quantum noise, therefore, determined how far apart were the λ_{max} values of the pigments that produced the maximum signal-to-noise ratios, but it did not much affect their average position in the spectrum.

Leaf chromaticity noise

Fig. 13A,B shows, for the leaf diet of *Cercopithecus mitis*, the 'signal' and the 'leaf chromaticity noise' plotted separately. Fig. 13C shows the signal-to-noise ratios. Comparison between these plots (and also with Fig. 12) reveals that the area of minimum noise corresponds to the area of maximum signal-to-noise ratios, but the area of maximum signal is at much

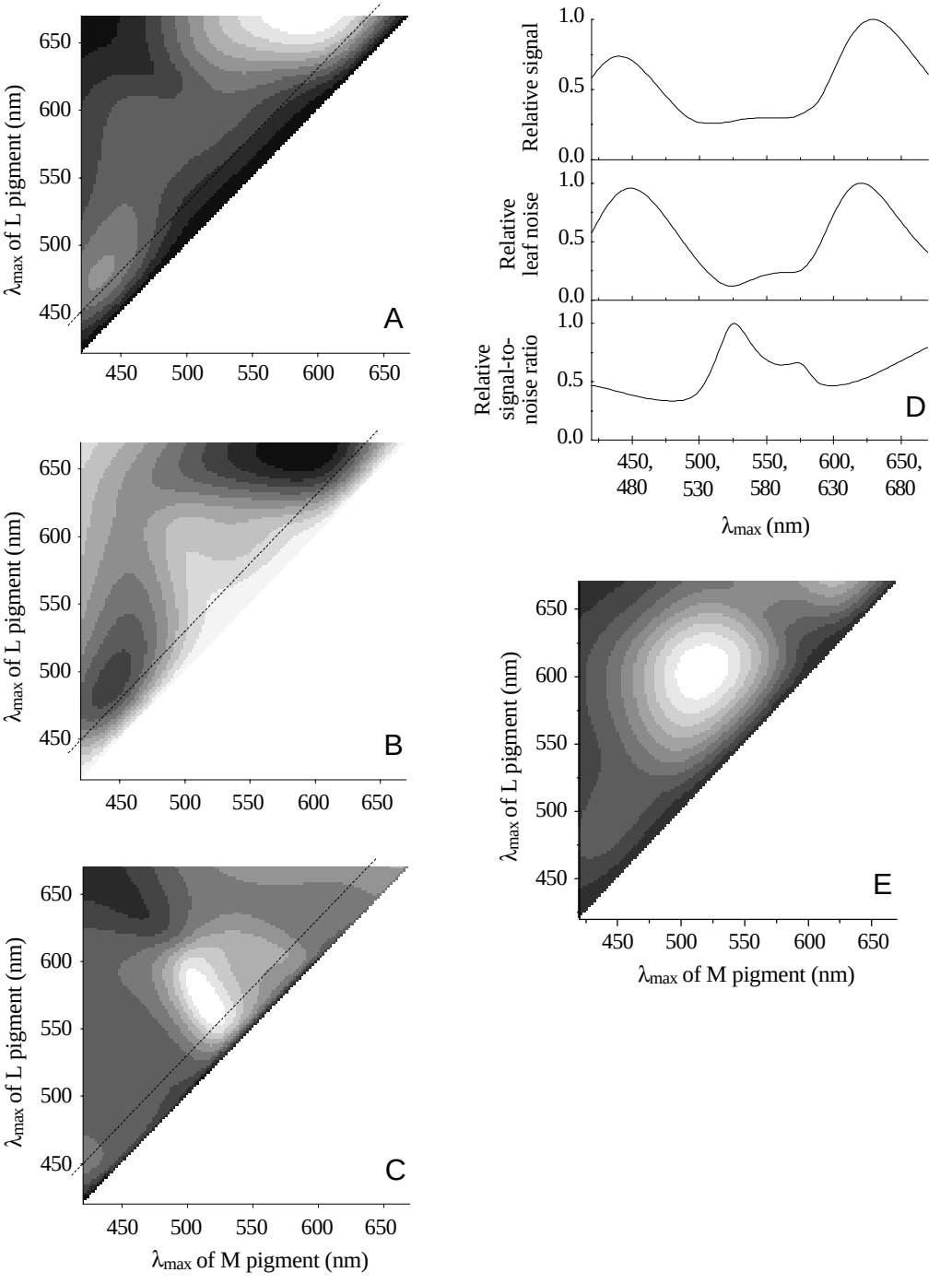

Fig. 13. (A) The average signal for the leaf diet of *Cercopithecus mitis* (the white area has the highest signal: >90 % of maximum). (B) The leaf chromaticity noise (i.e. standard deviation of leaf chromaticities) for the mature leaves used as background in the analysis leaf diet of *Cercopithecus mitis* (the white area has the lowest noise: <10 % of maximum). (C) Signal-to-noise ratios. The greyscale ranges from white (90–100% of maximum signal-to-noise ratio) to black (0–10 % of maximum signal-to-noise ratio). (D) The signal, leaf chromaticity noise and signal-to-noise ratios for pigment pairs with wavelengths of peak sensitivity (λ_{max}) separated by 30 nm for the leaf diet of *Cercopithecus mitis*. The curves are cross sections, parallel to the diagonal, of A, B and C (marked by the dashed lines). (E) The average signal for the fruit diet of *Cercopithecus mitis* (the white area has the highest signal: >90 % of maximum). See Fig. 8 for further details.

longer wavelengths. Fig. 13E shows that the pattern of signal for the fruit diet was very different from that for the leaf diet: the peak signal was produced by pigments with λ_{max} values of 516 nm and 606 nm for the fruits, but 592 nm and 670 nm for the young leaves. This large difference was not evident in the signal-to-noise ratios (as has been discussed above) because the pattern of leaf chromaticity noise was very similar in the two cases. When the quantum noise was omitted, the maximum signal-to-noise ratio was produced by exactly the same pigments as produced the minimum leaf chromaticity noise. These M and L pigments were very close together. When quantum noise was included, the maximum signal-to-noise ratio was produced by pigments with a greater separation. However, for any given fixed separation of pigments (up to 100 nm), the maximum possible signal-to-noise ratio was extremely close to the minimum leaf chromaticity noise and was a long way from the maximum signal. This is illustrated in Fig. 13D for pigments with a separation of 30 nm. The curves shown are slices through the grey-scale plots in Fig. 13A–C, indicated by the dashed lines.

Fig. 14 illustrates how the chromaticities of mature leaves change for different M and L pigments. The chromaticity diagrams show that, for pigments with λ_{max} values of 531 and 561 nm, the leaves form a vertical distribution. However, if the pigment sensitivities are moved to shorter or longer wavelengths, the distribution tilts and also broadens in the latter case, producing more variance on the horizontal axis and, therefore, more noise in the recent subsystem of catarrhine colour vision.

We conclude that, while the selective advantage of primate trichromacy may lie in finding edible fruits and leaves, the optimal cone pigments for the task are set not by the properties of the fruit or leaf targets themselves, but by the properties of the foliage background against which they must be detected. We argue that the chromaticities of mature leaves constrain the mean of the M and L cone λ_{max} values. Therefore, if the same mature leaf set is used as background in different analyses, the mean wavelength of the optimal λ_{max} pair should remain nearly constant regardless of which target set is used. The magnitude of the signal and the magnitude of the quantum noise do, however, affect the separation of the optimal pigments and put a limit on how similar the M and L pigments can be. Therefore, if the magnitude of the signal were larger for one target set, the quantum noise would have less effect and so the λ_{max} values of the optimal pigment pair would be closer together. These predictions were confirmed by simply repeating the analyses for the fruit and leaf diets of *Cercopithecus mitis* with the mature leaf background sets swapped. Similarly, if the brightness of the illuminant increases (more photons being available and quantum noise becoming less), the separation of the predicted optimal pigments decreases, but their mean λ_{max} value hardly changes. This is shown in Table 2 (the slight shift of 2 nm in the mean λ_{max} value is caused by the fact that, because of the shape of the reflectance spectra, longer-wavelength pigments catch more photons and thus are favoured as the brightness decreases and quantum noise becomes more important).

Colour vision interferes with spatial vision based on luminance

The robust and important result from our analyses is that the mean λ_{max} value of predicted optimal pigments for detecting targets against a background of forest leaves reliably falls very close to the mean λ_{max} value of catarrhine M and L pigments. The results of the present study do not predict that the photopigments optimal for finding diet items amongst foliage need to have their λ_{max} values as close together as 30 nm. For example, pigments with λ_{max} of 520 nm and 570 nm normally produced as high signal-to-noise ratios as did pigments with λ_{max} of 531 nm and 561 nm. However, spatial vision would deteriorate as the difference between the L and M cones increased, for two main reasons: (i) chromatic aberration and

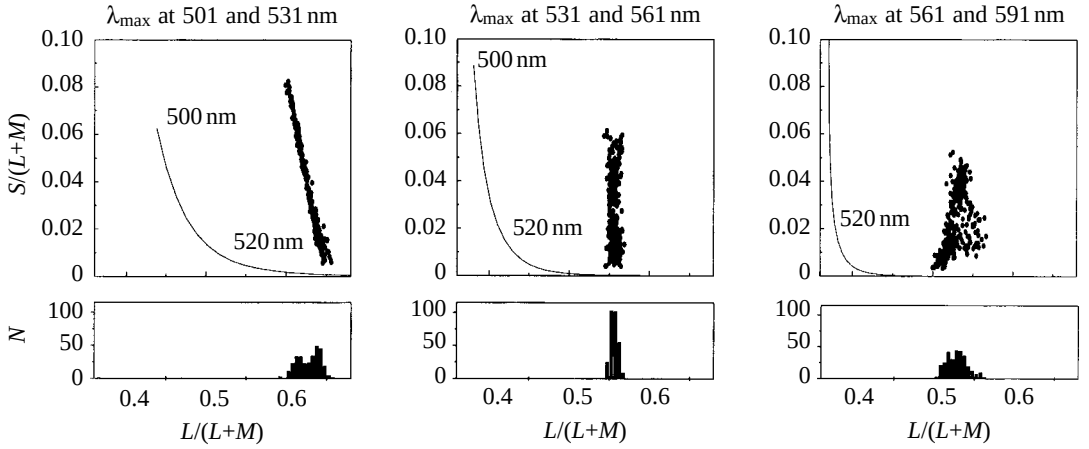

Fig. 14. Chromaticity distribution of mature leaves (measured *in situ* in sunny conditions) for three pairs of possible L and M pigments with wavelength of peak sensitivity (λ_{max}) separated by 30 nm. The λ_{max} of the S cone pigment was always 430 nm, and the lens and macular pigment data were as for our standard catarrhine colour space. The histograms show, for each set of pigments, the distribution of signals from mature leaves in the recent colour subsystem [represented by $L/(L+M)$, see Material and methods]. N is the number of leaves.

Table 2. *Summary of the effects of changing the intensity of the illuminant*

Illuminant	Optimal λ_{max} (nm) Mean	Separation	M, L	*P*
Standard multiplied by 0.5	546	48	522, 570	0.95
Standard multiplied by 1	545	42	524, 566	0.98
Standard multiplied by 2	544	36	526, 562	0.99
Standard multiplied by 4	544	28	530, 558	0.99

The data set was the top ten fruit species eaten by *Pan troglodytes*. Each analysis was identical in all respects except that the standard illuminant was multiplied by a different factor.

The range of intensities tested falls within the range that naturally occurs for cloudy illuminants.

P, proportion of maximum signal-to-noise yielded by the pigments possessed by the primate; λ_{max}, peak sensitivity; M, middle-wavelength-sensitive pigment; L, long-wavelength-sensitive pigment.

(ii) local ambiguities in the luminance signal. Since the eye is not corrected for chromatic aberration, only one wavelength band can be in focus, and the image sampled by a cone with sensitivity predominantly outside this band will necessarily be blurred. If L and M cones are to be used concurrently to extract high spatial frequencies, their λ_{max} values should not be widely separated in the spectrum. The second consequence of spatial vision using inputs from both cone classes is that ambiguity can arise at edges that are near equiluminance, because one class of cone will signal a luminance decrement in one direction while the other class signals the opposite. The range of luminance differences that would cause this 'contradiction of normally yoked signals' (Mollon, 1991) would be greater if the M and L pigments were more different. For further discussion, see Barlow (1982), Mollon (1991), Nagle and Osorio (1993) and Osorio et al. (1998).

Nagle and Osorio (1993) have previously reported a result similar to our observation that the chromaticity variance of mature forest leaves is minimised in the recent catarrhine colour subsystem. They measured the spectral reflectance (at 512×512 pixels) of 12 natural scenes of gardens and sclerophyll woodland in Canberra, Australia. They tested the effect on the L–M signal of moving both the (human) M and L cone sensitivities 10 or 20 nm to longer or shorter wavelengths, keeping their separation the same, and found that for the '11 scenes containing green leaves' the chromatic signal was least when there was no shift. They concluded that 'red–green vision has evolved for a specific task, such as finding fruits, whilst minimising interference by the chromatic signal in luminance vision'. Our conclusion, in contrast, is that the advantage of minimising the chromaticity distribution (in one colour subsystem) of most items in a primate's environment (i.e. leaves) is to allow the chromatic signal of important but rare items (fruits or young leaves) to stand out (in the same colour subsystem). The minimisation of the 'chromatic signal' of leaves is therefore understood in terms of an advantage within colour vision, without invoking any constraints set by luminance vision. (This is not to deny that chromatic signals do interfere with luminance vision, and this has certainly constrained the separation of L and M sensitivity, as mentioned above.) Second, the L/M dimension of colour vision may not have evolved for the specific task of finding fruits, but for a more general ability to spot anything that is not a mature leaf.

Are there other constraints on the tuning of catarrhine L and M cones?

The evidence presented is consistent with the idea that any similarity between the primate pigments and the optimal pigments for detecting targets against foliage is pure coincidence. Unfortunately, this is the nature of most arguments about evolutionary selective pressures: it is always possible that an unknown factor was actually more important than the one studied. In this case, since no rhodopsin has yet been found with a λ_{max} value significantly beyond that of the catarrhine L pigment at 561 nm, there are grounds for believing that such pigments are not actually possible, perhaps because the necessary mutations in the opsin proteins would make them unstable. However, there is no *a priori* reason why animals should possess the longest possible sensitivity (most dichromats do not); and why is the primate M pigment at 531 nm, producing a trichromacy with a very uneven spacing of its three pigments? The pigments of birds, for example, are much more evenly spaced in the spectrum. The primate L and M pigments diverged at least 30 million years ago, which we believe is ample evolutionary time for the M and L pigments to have shifted their λ_{max} to shorter wavelengths. For example, an English subspecies of the salmonid fish *Coregonus clupeoides* has a rhodopsin with a λ_{max} value of 520 nm, while a Welsh subspecies that is separated by only 20 000 years has a λ_{max} value of 510 nm (Bridges and Yoshikami, 1970). A possible answer to the question of uneven spectral spacing would be that a 30 nm separation between L and M pigments represents a balance between colour vision requiring a pigment far from L and spatial vision requiring M to be like L (as discussed above). This 30 nm spacing might then be placed with the L pigment at 561 nm because this may be the longest possible wavelength, conferring general advantages, such as maximising the visible spectrum, or more specific advantages such as discerning fruit ripeness (see Sumner and Mollon, 2000). The fact that this combination of L and M pigments minimises the spread of leaf chromaticities in one colour subsystem would then be a remarkable coincidence.

The S cone colour subsystem

The results of this study do not by themselves indicate that primates must be trichromatic to be able to discriminate diet items from their backgrounds. The analysis tested a dichromatic system and found that the optimal receptors would have λ_{max} values close to 530 nm and 560 nm. Instead of duplicating the L opsin gene to produce both M and L cones and a second colour subsystem, could the ancient mammalian colour system have done the job by shifting the S cone

sensitivity to longer wavelengths (and increasing the number of S cones)? This solution has not occurred in any known animal probably for two main reasons. First, the primate S cone opsin already has the longest wavelength sensitivity found in the 'ultraviolet/violet' class of vertebrate photopigments (Bowmaker, 1998; Yokoyama, 1994) and, since the gene shows only 40 % homology with the human M opsin gene, a λ_{max} beyond 500 nm probably could not be produced without many changes. Second, there are important ecological reasons for maintaining a dichromatic system with pigments well separated in the spectrum. For example, this channel is sensitive to differences between vegetable greens and to changes in the natural illuminant that signal changes in weather or time of day. The accompanying paper (Sumner and Mollon, 2000) shows that the S cone system is also useful for discriminating the ripeness of many species of fruit. Some primates (e.g. *Mandrillus sphinx*, *Cercopithecus aethiops*, *Cercopithecus hamlyni*) have developed signals using a vivid blue coloration that presents a large contrast from the surrounding pelage in both colour channels. These signals would not be as visible without S cones, although the signalling properties would be reduced, not lost.

Has there been co-evolution of fruit signals and primate vision?

Polyak (1957) revived a nineteenth century idea (Allen, 1879) that the fruit signals of the tree species dispersed by primates may have co-evolved with primate vision. In Africa, Asia and South America, some fruits are disproportionately or almost exclusively taken by primates, and these fruits tend to share characteristics: they weigh 5–50 g (or have a diameter larger than 14 mm), have few seeds, a succulent pulp and a hard external coat which is normally yellow or orange (Gautier-Hion et al., 1985; Janson, 1983; Julliot, 1996; McConkey, 1999). This set of traits can be interpreted as specialisations for seed dispersal by primates: a 'primate seed-dispersal syndrome' (Julliot, 1996). The fact that all these types of fruit occupy a small region of colour space (without exception in French Guiana), but come from diverse botanical families, makes it likely that the evolution of their colour signals has been influenced by primate trichromacy (Regan, 1997; B. C. Regan, C. Julliot, B. Simmen, F. Viénot, P. Charles-Dominique and J. D. Mollon, in preparation).

The present study took the point of view of the primates, asking what vision would be optimal for the signals in the forest. It was found that the mature leaf signals determined the optimal photopigments that a primate should possess, and so we conclude that the particular chromaticities of the fruits themselves have not determined the exact nature of primate trichromacy. However, important signals, be they fruits or young leaves, that would stand out from the mature leaves must have existed to confer an advantage on minimising the chromatic noise of mature leaves. Therefore, in addition to the advantage of being trichromatic, the actual absorbance spectrum of primate photopigments could be said to have been influenced by fruit signals (but not the exact nature of these signals, because the only requirement for there to be an advantage in minimising leaf chromaticity variance in the recently evolved second colour subsystem was that fruit chromaticities should be different from leaf chromaticities).

From the point of view of the tree species, the optimal fruit signals would be maximally visible to good dispersers (in this case primates), but cryptic to predators. If the potential predators are other mammals, which are dichromatic, the orange/yellow fruits would indeed be cryptic to them. However, birds are predators of some primate-dispersed fruits (e.g. *Mimusops bagshawei* in Kibale; P. Sumner, personal observations). Since these birds are probably tetrachromatic (Bowmaker, 1998), it will probably not be possible to make the fruits cryptic to them if they are to remain visible to primates. However, if bird colour vision does not minimise the background chromaticity noise in the same way, the yellow fruits may present low signal-to-noise ratios. In any case, conclusions about possible co-evolution between primate vision and fruit signals do not rest on how visible the fruits are to other animals.

In fact, in Kibale, there are few fruits that fit the primate dispersal syndrome described above (*Chrysophyllum* spp. are a notable exception; for more details, see Sumner and Mollon, 2000), and many of the species abundantly eaten and dispersed by the primates (e.g. *Ficus* sp., *Celtis* spp.) are also dispersed by birds (e.g. Struhsaker, 1978b). It is possible that some of these fruit have significant reflectance below 380 nm and may be specialised for avian ultraviolet sensitivity. Add this to the conclusion that primate trichromacy is optimised not for finding fruits *per se*, but for spotting anything that is not a mature leaf, and the present study cannot be taken in support of the co-evolution hypothesis that some fruit signals evolved specifically in response to primate vision and that primate colour vision evolved specifically in response to fruit signals. It is more likely in the case of the fruits in Kibale that there has been 'diffuse co-evolution' (Janzen, 1980) between a group of dispersers (that include primates and birds) and the plants whose seeds they disperse.

Platyrrhine polymorphism

In platyrrhines (South American monkeys), there is an interesting pattern of sex-linked polymorphism, so that in most species all the males are dichromatic and some females are trichromatic. Why this situation might be stable is still a mystery, and one of the aims of this study was to compare the visual environment of an Old World forest with that of the New World forest in French Guiana to find any differences that might lead to an ecological explanation of the different patterns of colour vision found in catarrhines and platyrrhines. In general, these data and results are strikingly similar to those from the South American study (Regan, 1997; B. C. Regan, C. Julliot, B. Simmen, F. Viénot, P. Charles-Dominique and J. D. Mollon, in preparation), but the fruits from Uganda tend to be smaller than those in French Guiana, and many darken as they ripen (see Sumner and Mollon, 2000), whereas in French Guiana nearly all lighten during ripening. Both these

differences would make the diet of the platyrrhines more visible to the dichromats than the diet of the catarrhines would be to a dichromat. So the selection pressure for trichromacy may be stronger in Africa than South America. Even if this is true, it still does not explain why platyrrhines do not display uniform trichromacy, since there is clearly an advantage for them to be trichromatic (Regan, 1997; B. C. Regan, C. Julliot, B. Simmen, F. Viénot, P. Charles-Dominique and J. D. Mollon, in preparation). It is possible that the platyrrhines have crucially different behaviour patterns that allow the dichromats to find fruits through their trichromatic conspecifics. There may be important advantages in dichromacy, for example in catching insects (it has been commented on above that colour vision impairs spatial vision). These possibilities are discussed more fully by B. C. Regan, C. Julliot, B. Simmen, F. Viénot, P. Charles-Dominique and J. D. Mollon (in preparation). It may be simply that the opsin gene duplication required to turn dichromacy into uniform trichromacy has only ever happened twice: in the catarrhine lineage and in the genus *Alouatta* (Jacobs et al., 1996b), and that the polymorphism in platyrrhines is maintained by pure heterozygous advantage (Mollon et al., 1984).

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References

Allen, G. (1879). *The Colour-Sense: Its Origin and Development.* London: Trubner & Co.

Applegate, R. A. and Lakshminarayanan, V. (1993). Parametric representations of Stiles–Crawford functions: normal variation of peak location and directionality. *J. Opt. Soc. Am.* A **10**, 1611–1623.

Asenjo, A. B., Rim, J. and Oprian, D. (1994). Molecular determinants of human red/green color discrimination. *Neuron* **12**, 1131–1138.

Baranga, D. (1983). Changes in the chemical composition of food parts in the diet of colobus monkeys. *Ecology* **64**, 668–673.

Barlow, H. B. (1982). What causes trichromacy? A theoretical analysis using comb-filtered spectra. *Vision Res.* **22**, 635–643.

Barrett, L. (1994). Feeding competition and patch use in the grey-cheeked mangabey (*Cercocebus albigena*) and the olive baboon (*Papio cyncephalus anubis*). *Report for MUBFS Management Research Fund Committee*.

Baylor, D. A., Nunn, B. J. and Schnapf, J. L. (1987). Spectral sensitivity of cones of the monkey *Macaca fascicularis*. *J. Physiol., Lond.* **390**, 145–160.

Bowmaker, J. K. (1991). The evolution of vertebrate visual pigments and photoreceptors. In *Evolution of the Eye and Visual System* (ed. J. R. Cronly-Dillon and R. L. Gregory), pp. 63–81. London: Macmillan.

Bowmaker, J. K. (1998). Evolution of colour vision in vertebrates. *Eye* **12**, 541–547.

Bowmaker, J. K., Astell, S., Hunt, D. M. and Mollon, J. D. (1991). Photosensitive and photostable pigments in the retinae of Old World monkeys. *J. Exp. Biol.* **156**, 1–19.

Bowmaker, J. K., Speigelhalter, D. J., Jacobs, G. H. and Mollon, J. D. (1985). Two types of trichromatic squirrel monkey share a pigment in the red–green spectral region. *Vision Res.* **25**, 1937–1946.

Bridges, C. D. B. and Yoshikami, S. (1970). Distribution and evolution of visual pigments in salmonid fishes. *Vision Res.* **10**, 609–626.

Chapman, C. A. and Chapman, L. J. (1996). Frugivory and the fate of dispersed and non-dispersed seeds of six African tree species. *J. Trop. Ecol.* **12**, 491–504.

Cicerone, C. M. and Nerger, J. L. (1989). The relative numbers of long-wavelength-sensitive to middle-wavelength-sensitive cones in the human fovea centralis. *Vision Res.* **29**, 115–128.

Clutton-Brock, T. H. (1975). Feeding behaviour of red colobus and black and white colobus in East Africa. *Folia Primatol.* **23**, 165–207.

Commission Internationale de l'Éclairage. (1932). *Recueil des Travaux et Compte Rendu de Séances du Huitième Session; Septembre 1931*. Cambridge: Cambridge University Press.

Cooper, G. F. and Robson, J. G. (1969). The yellow colour of the lens of man and other primates. *J. Physiol., Lond.* **203**, 411–417.

Dartnall, H. J. A., Bowmaker, J. K. and Mollon, J. D. (1983). Human visual pigments: microspectrophotometric results from the eyes of seven persons. *Proc. R. Soc. Lond. B* **220**, 115–130.

Deegan, J. F. and Jacobs, G. H. (1997). Photopigment basis for trichromatic color vision in colobine monkeys (Abstract). *Am. J. Primatol.* **42**, 104.

Dulai, K. S., Bowmaker, J. K., Mollon, J. D. and Hunt, D. M. (1994). Sequence divergence, polymorphism and evolution of middle-wave and long-wave visual pigment genes of great apes and Old World monkeys. *Vision Res.* **34**, 2483–2491.

Dulai, K. S., von Dornum, M., Mollon, J. D. and Hunt, D. M. (1999). The evolution of trichromatic color vision by opsin gene duplication in New World and Old World primates. *Genome Res.* **9**, 629–638.

Endler, J. A. (1993). The color of light in forests and its implications. *Ecol. Monogr.* **63**, 1–27.

Freeland, W. J. (1979). Mangabey (*Cercocebus albigena*): Social organization and population density in relation to food use and availability. *Folia Primatol.* **32**, 108–124.

Gates, D. M., Keegan, H. J., Schleter, J. C. and Weidner, V. R. (1965). Spectral properties of plants. *Appl. Optics* **4**, 11–20.

Gautier-Hion, A., Duplantier, J.-M., Quris, R., Feer, F., Sourd, C., Decoux, J.-P., Dubost, G., Emmons, L., Erard, C., Hecketsweiler, P., Moungazi, A., Roussilhon, C. and Thiollay, J.-M. (1985). Fruit characters as a basis of fruit choice and seed dispersal in a tropical forest vertebrate community. *Oecologia* **65**, 324–337.

Geisler, W. S. (1989). Sequential ideal-observer analysis of visual discriminations. *Psychol. Rev.* **96**, 267–314.

Hecht, S., Shlaer, S. and Pirenne, M. H. (1942). Energy, quanta and vision. *J. Gen. Physiol.* **25**, 819–840.

Hendley, C. D. and Hecht, S. (1949). The colors of natural objects and terrains and their relation to visual color deficiency. *J. Opt. Soc. Am.* **39**, 870–873.

Hood, D. C. and Finkelstein, M. A. (1986). Sensitivity to light. In *Handbook of Perception and Human Performance*, vol. 1, *Sensory Processes and Perception*, section 5 (ed. K. R. Boff, L. Kaufman and J. P. Thomas), pp. 1–66. New York: Wiley.

Ibbotson, R. E., Hunt, D. M., Bowmaker, J. K. and Mollon, J. D. (1992). Sequence divergence and copy number of the middle- and long-wave photopigment genes in Old World monkeys. *Proc. R. Soc. Lond. B* **247**, 145–154.

Isabirye-Basuta, G. (1989). Feeding ecology of chimpanzees in the Kibale Forest, Uganda. In *Understanding Chimpanzees* (ed. P. N. Heltne and L. Marquardt), pp. 116–127. Cambridge, MA: Harvard University Press.

Isbell, L. A. (1983). Daily ranging behaviour of red colobus (*Colobus badius*) in Kibale Forest, Uganda. *Folia Primatol.* **41**, 34–48.

Jacobs, G. H. (1993). The distribution and nature of colour vision among the mammals. *Biol. Rev.* **68**, 413–471.

Jacobs, G. H., Deegan, J. F. and Moran, J. L. (1996a). ERG measurements of the spectral sensitivity of common chimpanzee (*Pan troglodytes*). *Vision Res.* **36**, 2587–2594.

Jacobs, G. H., Neitz, M., Deegan, J. F. and Neitz, J. (1996b). Trichromatic colour vision in New World monkeys. *Nature* **382**, 156–158.

Janson, C. H. (1983). Adaptation of fruit morphology to dispersal agents in a neotropical forest. *Science* **219**, 187–189.

Janzen, D. H. (1980). When is it coevolution? *Evolution* **34**, 611–612.

Julliot, C. (1996). Fruit choice by red howler monkeys in a tropical rain forest. *Am. J. Primatol.* **40**, 261–282.

Knowles, A. and Dartnall, H. J. A. (1977). *The Photobiology of Vision*. *The Eye*, vol. 2B (ed. H. Davson). New York: Academic Press.

Lucas, P. W., Darvell, B. W., Lee, P. K. D., Yuen, T. D. B. and Choong, M. F. (1998). Colour cues for leaf food selection by long-tailed macaques (*Macaca fascicularis*) with a new suggestion for the evolution of trichromatic colour vision. *Folia Primatol.* **69**, 139–152.

MacLeod, D. I. A. and Boynton, R. M. (1979). Chromaticity diagram showing cone excitation by stimuli of equal luminance. *J. Opt. Soc. Am.* **69**, 1183–1186.

MacNichol, E. F. (1986). A unifying presentation of photopigment spectra. *Vision Res.* **26**, 1543–1556.

Mansfield, R. J. W. (1985). Primate photopigments and cone mechanisms. In *The Visual System* (ed. J. S. Levine and A. Fein), pp. 89–106. New York: Alan Liss.

McConkey, K. R. (1999). Gibbons as seed dispersers in the rain-forests of central Borneo. PhD thesis, Cambridge University.

Merbs, S. L. and Nathans, J. (1992). Absorption spectra of human cone pigments. *Nature* **356**, 433–435.

Mollon, J. D. (1989). 'Tho she kneel'd in that Place where they grew...'. *J. Exp. Biol.* **146**, 21–38.

Mollon, J. D. (1991). Uses and evolutionary origins of primate colour vision. In *Evolution of the Eye and Visual System* (ed. J. R. Cronly-Dillon and R. L. Gregory), pp. 306–319. London: Macmillan.

Mollon, J. D. and Bowmaker, J. K. (1992). The spatial arrangement of cones in the primate fovea. *Nature* **360**, 677–679.

Mollon, J. D., Bowmaker, J. K. and Jacobs, G. H. (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, J. D. and Jordan, G. (1988). Eine evolutionare Interpretation des menschlichen Farbensehens. *Die Farbe* **35/36**, 139–170.

Mollon, J. D. and Regan, B. C. (1999). Spectralnue svojstva kolbochek i makularnogo pigmenta primatov – soglasovanu s okrugajucshim murom. *Opticheskii Zhurnal* **66**, 3–9. [Translated in Mollon, J. D. and Regan, B. C. (1999). The spectral distribution of primate cones and of the macular pigment: Matched to properties of the world? *J. Opt. Technol.* **66**, 847–852].

Nagle, M. G. and Osorio, D. (1993). The tuning of human photopigments may minimize red–green chromatic signals in natural conditions. *Proc. R. Soc. Lond. B* **252**, 209–213.

Nathans, J. (1999). The evolution and physiology of human color vision: insights from molecular genetic studies of visual pigments. *Neuron* **24**, 299–312.

Nathans, J., Thomas, D. and Hogness, D. S. (1986). Molecular genetics of human color vision: The genes encoding blue, green and red pigments. *Science* **232**, 193–202.

Oates, J. F. (1977). The guereza and its food. In *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes* (ed. T. Clutton-Brock), pp. 275–321. New York: Academic Press.

Olupot, W. (1998). Long-term variation in mangabey (*Cercocebus albigena johnstoni* Lydekker) feeding in Kibale National Park, Uganda. *Afr. J. Ecol.* **36**, 96–101.

Olupot, W., Waser, P. M. and Chapman, C. A. (1998). Fruit finding by mangabeys (*Lophocebus albigena*): Are monitoring of fig trees and use of sympatric frugivore calls possible strategies? *Int. J. Primatol.* **19**, 339–353.

Oprian, D. D., Asenjo, A. B., Lee, N. and Pelletier, S. L. (1991). Design, chemical synthesis and expression of the genes for the three human color vision pigments. *Biochemistry* **30**, 11367–11372.

Osorio, D., Ruderman, D. L. and Cronin, T. W. (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.

Osorio, D. and Vorobyev, M. (1996). Colour vision as an adaptation to frugivory in primates. *Proc. R. Soc. Lond. B* **263**, 593–599.

Pokorny, J. and Smith, V. C. (1976). Effect of field size on red–green colour mixing equations. *J. Opt. Soc. Am.* **66**, 705–708.

Polyak, S. (1957). *The Vertebrate Visual System*. Chicago: University of Chicago Press.

Regan, B. C. (1997). Fruits, foliage and form: the roles of colour vision. PhD thesis, Cambridge University.

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

Rudran, R. (1978a). Socioecology of the blue monkeys (*Cercopithecus mitis stuhlmanni*) in the Kibale Forest, Uganda. *Smithson. Contr. Zool.* **249**, 1–88.

Rudran, R. (1978b). Intergroup dietary comparisons and folivorous tendencies of two groups of blue monkeys (*Cercopithecus mitis stuhlmanni*). In *The Ecology of Arboreal Folivores* (ed. G. G.

Montgomery), pp. 483–504. Washington, DC: Smithsonian Institution Press.

Schnapf, J. L., Kraft, T. W. and Baylor, D. A. (1987). Spectral sensitivity of human cone photoreceptors. *Nature* **325**, 439–441.

Snodderly, D. M., Auran, J. D. and Delori, F. C. (1984a). The macular pigment. II. Spatial distribution in primate retinas. *Invest. Ophthalmol. Vis. Sci.* **25**, 674–685.

Snodderly, D. M., Brown, P. K., Delori, F. C. and Auran, J. D. (1984b). The macular pigment. I. Absorbance spectra, localization and discrimination from other yellow pigments in the primate retina. *Invest. Ophthalmol. Vis. Sci.* **25**, 660–673.

Steward, J. M. and Cole, L. (1989). What do color vision defectives say about everyday tasks? *Optometry Vis. Sci.* **66**, 288–295.

Struhsaker, T. T. (1978a). Interrelations of red colobus monkeys and rain forest trees in the Kibale Forest, Uganda. In *The Ecology of Arboreal Folivores* (ed. G. G. Montgomery), pp. 397–422. Washington, DC: Smithsonian Institution Press.

Struhsaker, T. T. (1978b). Food habits of five monkey species in the Kibale Forest, Uganda. In *Recent Advances in Primatology*, vol 1, *Behaviour* (ed. D. J. Chivers and J. Herbert), pp. 225–248. London: Academic Press.

Sumner, P. and Mollon, J. D. (2000). Chromaticity as a signal of ripeness in fruits taken by primates. *J. Exp. Biol.* **203**, 1987–2000.

Tovée, M. J., Bowmaker, J. K. and Mollon, J. D. (1992). The relationship between cone pigments and behavioural sensitivity in a New World monkey (*Callithrix jacchus jacchus*). *Vision Res.* **32**, 867–878.

Waser, P. (1975). Monthly variations in feeding patterns of the mangabey, *Cercocebus albigena* (Lydekker). *E. Afr. Wildl. J.* **13**, 249–263.

Waser, P. M. (1977). Feeding, ranging and group size in the mangabey (*Cercocebus albigena*). In *Primate Ecology: Studies of Feeding and Ranging Behaviour in Lemurs, Monkeys and Apes* (ed. T. Clutton-Brock), pp. 183–222. New York: Academic Press.

Waser, P. M. (1984). Ecological differences and behavioral contrasts between two mangabey species. In *Adaptations for Foraging in Non-Human Primates* (ed. P. S. Rodman and J. G. H. Cant), pp. 195–216. New York: Columbia University Press.

Webster, M. A. and Mollon, J. D. (1997). Adaptation and the color statistics of natural images. *Vision Res.* **37**, 3283–3298.

Wrangham, R. W., Chapman, C. A. and Chapman, L. J. (1994a). Seed dispersal by forest chimpanzees in Uganda. *J. Trop. Ecol.* **10**, 355–368.

Wrangham, R. W., McGrew, W. C., de Waal, F. B. M. and Heltine, P. G. (1994b). *Chimpanzee Cultures*. Cambridge, MA: Harvard University Press.

Wyszecki, G. and Stiles, W. S. (1982). *Color Science*. New York: Wiley.

Yokoyama, S. (1994). Gene duplications and evolution of the short wavelength-sensitive visual pigments in vertebrates. *Mol. Biol. Evol.* **11**, 32–39.