# Frugivory and colour vision in *Alouatta seniculus*, a trichromatic platyrrhine monkey

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## Abstract

It is a long-standing hypothesis that primate trichromacy evolved to help fruit-eating primates find fruits amongst leaves. We measured the reflectance spectra of fruits eaten by a trichromatic primate, *Alouatta seniculus*, in the rainforest of French Guiana, as well as those of the leaves that form the natural background to fruits. We develop a method of specifying these natural colour signals in a chromaticity diagram appropriate for *A. seniculus*. By treating the task facing frugivorous monkeys as a signal detection task, we show that the spectral tuning of the L and M cone pigments in *A. seniculus* is optimal for detecting fruits amongst leaves. © 1998 Elsevier Science Ltd. All rights reserved.

*Keywords:* Alouatta seniculus; Trichromacy; Visual ecology; Frugivory; Evolution

## 1. Introduction

One of the few natural tasks that challenge colour-blind members of our own species is that of spotting fruit embedded in a background of foliage [1]. The disability of the daltonian tells us a primary advantage of colour vision: that of drawing attention to coloured targets against a dappled or variegated background, where lightness is varying randomly [2]. As early as 1879 it was suggested by Grant Allen [3] that the colour-sense of vertebrates evolved for frugivory, and the hypothesis was refined by Polyak (1957) [4], who suggested specifically that the trichromatic colour-sense of primates and the colour signals offered by a particular class of tropical fruits had reinforced each other's development, in a process of co-evolution.

Modern ecological studies lend strength to this hypothesis. Some tropical trees appear to depend almost exclusively on primates for dispersal of their seeds [5,6]. The fruits of such trees characteristically weigh between 5 and 50 g, often have a few large seeds (10–30 mm long) that can be ingested by primates without suffering damage, a nutritious pulp that is closely attached to the seeds, and a tough, indehiscent pericarp [5,7]. These specializations make such fruits inaccessible to most non-primate consumers, which do not have strong enough teeth to broach the hard protective tissues. When ripe, these fruits typically offer a yellow or orange colour signal to trichromatic disseminators [8,9]. Although primates are not the exclusive disseminators of all species whose fruits they consume, we are satisfied that at our study site there exist tree species (e.g. *Chrysophyllum lucentifolium*, *Pouteria guianensis*) for which primates are essentially the sole disseminators.

In this report we concentrate on the red howler monkey, *Alouatta seniculus* (Fig. 1a). Estimates of the proportion of fruit in the diet of this species in French Guiana range from 24.5 [10] to 47% [11], with some seasonal variation. The genus *Alouatta* is particularly interesting, for all individuals, both male and female, apparently possess trichromatic colour vision [12], in contrast to the polymorphism and sexual dimorphism that characterizes all the other diurnal platyrrhine genera that have been studied [13].
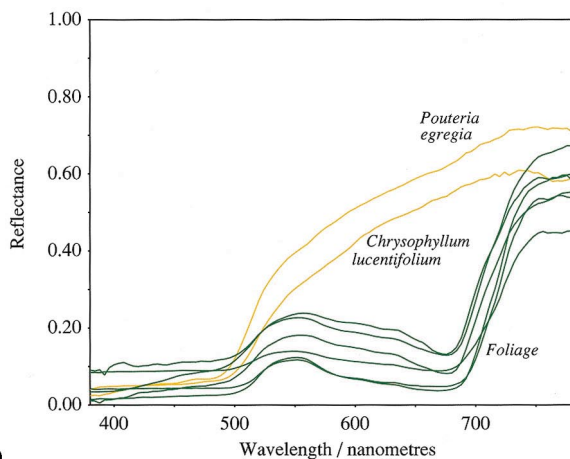
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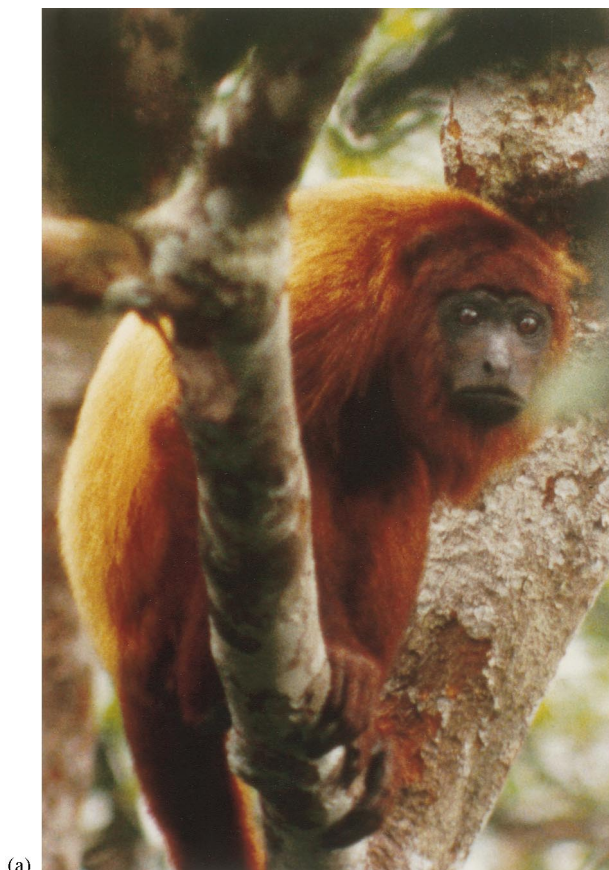
(a)



(b)



(c)

Fig. 1.

If trichromatic primate colour vision did indeed evolve for frugivory, then it should be optimized for detecting fruits in natural conditions. Such a conclusion has recently been reached by Osorio and Vorobyev (1996) [14], who measured cultivated fruits from supermarkets and leaves of various origins, and adopted an analysis different from the present one. In our own study, we have been concerned to use fruits taken by *A. seniculus* under natural conditions in intact rain forest, and we have measured at the same site the background foliage against which fruit signals must be discriminated. The principle of our analysis is to express the chromaticities of fruits and leaves in a chromaticity diagram calculated for a platyrrhine monkey possessing photopigments with arbitrary peak spectral sensitivities ($\lambda_{max}$ values). By repeating the analysis for every possible combination of $\lambda_{max}$ values, we find the set of photopigments that yields the largest signal-to-noise ratio for the natural signal-detection task of finding fruits amongst leaves in the rainforest.

## 2. Data collection

Data were collected at the Nouragues field station in French Guiana, 4° 5′ N, 52° 40′ W, situated in tropical lowland rainforest, and undisturbed by human activity for at least 200 years. By following troops of red howler monkeys, we were able to obtain fresh samples of fruits, or fragments of fruits, that were actually harvested by these monkeys. We also collected samples of leaves from the canopy. A PhotoResearch PR650 telespectroradiometer was used to measure the reflection spectra of the samples, at 4 nm intervals between 380 and 780 nm. We obtained a total of 247 reflectance spectra from 35 species of plant whose fruits were eaten by *A. seniculus*, and 155 reflectance spectra from leaves. The spectroradiometer was also used to measure the ambient illumination in the canopy, by measuring the spectrum of light reflected from a white barium oxide plaque. Some fruits eaten by *A. seniculus*, and sample reflection spectra of fruits and foliage, are illustrated in Fig. 1b and c.

## 3. Chromaticity diagrams for platyrrhine monkeys

Almost all previous ecological studies of natural colour signals have measured colour in terms appropriate for humans. However, it is improper to use human

Fig. 1. (a) The red howler monkey, *Alouatta seniculus*; (b) ripe and unripe samples of *Chrysophyllum lucentifolium*, a fruit common in the diet of *A. seniculus*; (c) examples of reflectance spectra measured at the field station. The green curves represent foliage, and the yellow curves, two fruits frequently eaten by *A. seniculus* at the site.

chromaticities to specify natural colour signals directed at non-human observers [15], since physiological colour signals depend upon the product of the spectral flux reaching the eye, the absorption by the ocular media, and the spectral sensitivities of the photoreceptors, all of which differ from species to species. We have developed a method of expressing natural colour signals in terms appropriate for platyrrhine monkeys: we calculated the quantum catches that would arise in the cones of a monkey viewing a fruit or a leaf in the rainforest canopy, and from these quantum catches we calculated chromaticity coordinates in a diagram analogous to the MacLeod-Boynton diagram for human vision [16]. The analysis had the following stages:

### 3.1. Reconstruction of stimulus spectra

Reflection spectra of fruit and foliage were multiplied by an illuminant spectrum, to obtain the radiance spectrum that would be presented to an observer in the rainforest canopy. The illuminant used in the present analysis was measured in the canopy at Les Nouragues on a typically overcast day, but we have used different illuminants (e.g. sunlit canopy, forest floor) with similar results.

### 3.2. Pre-receptoral filtering

The stimulus spectra were adjusted to allow for the filtering effect of the lens pigment and the macular pigment, which alter both the intensity and the spectral composition of the light incident on the photoreceptors. We used the lens absorption curve given by Tovée et al. (1992) [17] for the common marmoset, *Callithrix jacchus*, and, in the absence of platyrrhine data, we used the macular pigment curve for man given by Wyszecki and Stiles (1982)[18][1].

### 3.3. Numbers of quanta incident at each cone

In order to have an estimate of quantum noise, we calculated the number of quanta per second in each wavelength interval incident at a single cone, assuming a value of 3 mm for pupil diameter and 2.3 μm for the cone aperture[2]. The output of the model is not critically dependent on the exact values chosen for these parameters: quantum noise becomes significant in the model only when the photopigments have very similar spectral sensitivities.

### 3.4. Generation of cone absorptance spectra

The absorptance spectra of the cone pigments were generated using the polynomial formula of Baylor et al. (1987) [19], correcting for self-screening by assuming an axial optical density of 0.3 [20]. The strength of our method is that it allows the $\lambda_{\max}$ values for the cone pigments to be set to any arbitrary wavelength, to generate chromaticity diagrams for any colour vision phenotype.

### 3.5. Calculation of physiological signals and chromaticity coordinates

To calculate the quantum catches in the cones, we multiplied the stimulus spectra from Section 3.3 by the cone absorptance spectra from Section 3.4. For a trichromatic platyrrhine monkey, we denote the quantum catches in the S, M and L cones as $Q_S$, $Q_M$ and $Q_L$. For each stimulus spectrum, we calculated chromaticity coordinates that were analogues of the MacLeod-Boynton coordinates: the $x$ value was taken as $Q_L/(Q_L + Q_M)$, and the $y$ value as $Q_S/(Q_L + Q_M)$. These coordinates have physiological significance: they correspond to the inputs to the channels of colour vision that in the macaque monkey are subserved by the midget ganglion cells, and by the small bistratified ganglion cells, respectively.

This analysis allowed natural colour signals to be plotted in chromaticity diagrams appropriate for platyrrhine monkeys. We believe that this is the first time that natural colour signals have been plotted in chromaticity diagrams appropriate for non-human vertebrates. Although in this study we have applied the method to studying the interaction between primates and trees, it is equally appropriate for studying any other kind of natural colour signal for example, the colours of primate pelages. A similar method could be used to plot colour signals in chromaticity diagrams appropriate for human anomalous trichromats, if appropriate $\lambda_{\max}$ values were chosen, and the lens absorption spectrum of man were substituted for that of *Callithrix jacchus*.

### 3.6. Results for Alouatta seniculus

The two plots of Fig. 2 show, for alternative phenotypes, the chromaticities of all foliage samples (small solid points) and of a subset of fruits eaten by *Alouatta seniculus* (open symbols). The fruits chosen for illustration are the three most common in the diet of howler

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[1] Adopting a lower lens density has little effect on the output of the model, but omission of macular pigment increases by about 12 nm the optimum spectral positions of the middle- and long-wave pigments.

[2] The inner segments have a diameter of around 2.8 μm in many primates [28], and according to Geisler [26], the sampling aperture is about 80% of the inner segment diameter. We assumed a ratio of 223 μm in central retina to 1° of external visual angle (the ratio for the similarly-sized *Macaca fascicularis* [27]), and a reflection of 5% at the anterior surfaces of the eye.
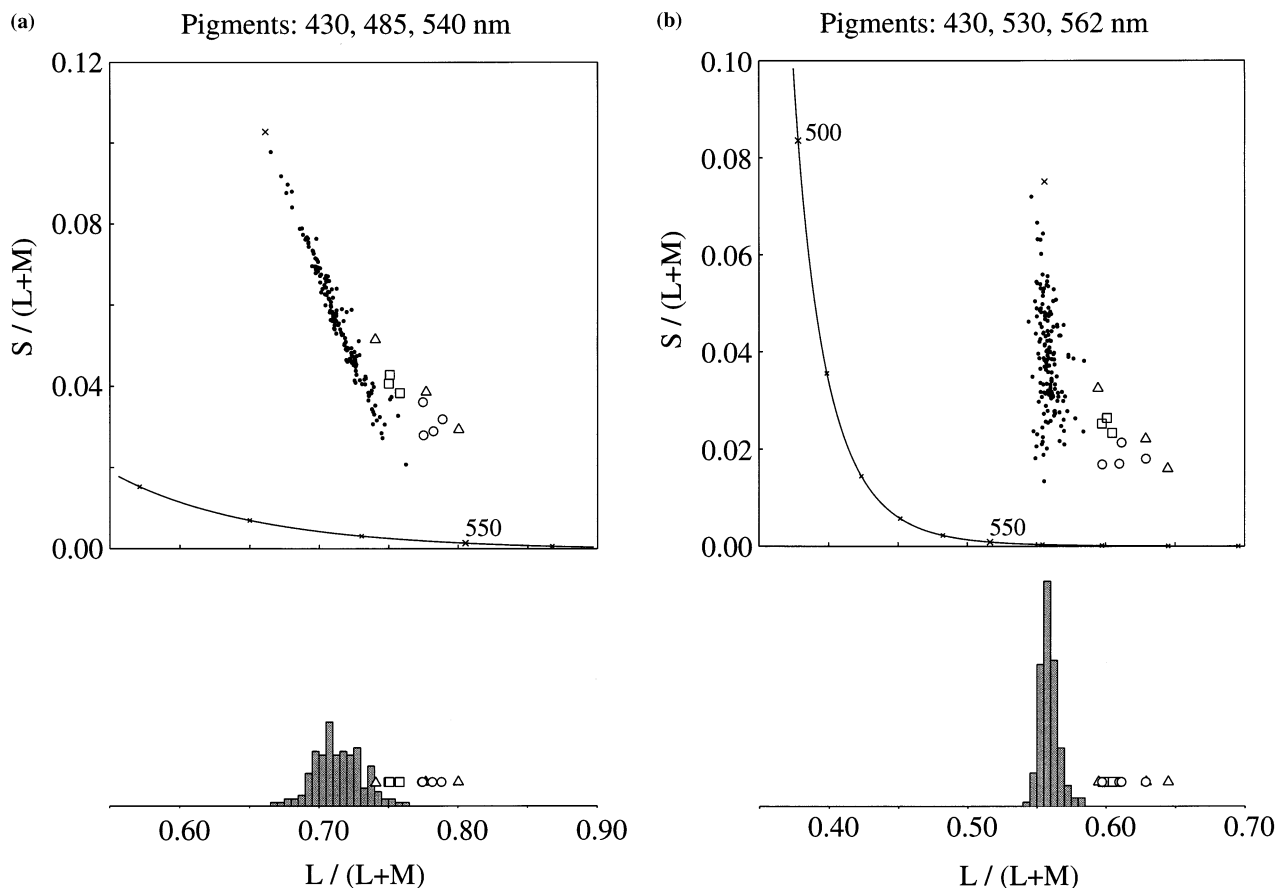
Fig. 2. Chromaticity diagrams analogous to that of MacLeod and Boynton, but for different sets of photopigments. The small solid circles show the chromaticities of foliage, and the open symbols those of the three fruits most commonly observed to be eaten by *Alouatta seniculus* at the field site: *Bagassa guianensis* (open triangles), *Chrysophyllum lucentifolium* (open circles) and *Vouacapoua americana* (open squares). (a) is for a triplet of pigments with $\lambda_{max}$ values evenly spaced in the spectrum, at 430, 485 and 540 nm—a set never observed in primates; (b) is for the set of pigments thought to be present in *A. seniculus*—430, 530 and 562 nm. Notice that the foliage distribution is tilted in (a), but that in (b) the foliage chromaticities fall on a near-vertical line. The small histograms below each diagram show the distribution of foliage chromaticities when projected on to the abscissa: note that fruit and foliage are better separated in (b) than in (a).

monkeys, the seeds of two of them being disseminated by monkeys, and those of the third (*Vouacapoua americana*) being predated. The plots are analogues of the MacLeod-Boynton chromaticity diagram for man: the ordinate corresponds to the relative short-wave cone excitation, and the abscissa to the ratio of excitations in the other two classes of cone. Fig. 2a shows chromaticities calculated for a phenotype with the photopigment $\lambda_{max}$ values evenly spaced in the spectrum, at 430, 485 and 540 nm—a triplet never observed in primates. Fig. 2b shows chromaticities calculated for the photopigments thought to be present in *A. seniculus*—430, 530 and 562 nm [12].

We believe that the phylogenetically older subsystem of colour vision, which compares the output of the short-wave cones with some combination of long- and middle-wave signals [2], is of little value in detecting fruit at a distance, because of its poor spatial resolution [21,22]. The signal in this channel is represented on our chromaticity diagrams by the ordinate. To compare the effectiveness of the two phenotypes in Fig. 2 at detecting fruits against a background of leaves, we have therefore

projected the chromaticities of fruits and leaves on to the abscissa. For the 430, 485, 540 phenotype, the distribution of foliage chromaticities lies along a tilted line, and when projected on to the abscissa, the fruit and foliage distributions overlap. In contrast, for the 430, 530, 562 photopigment complement of *A. seniculus*, the foliage chromaticities form a strikingly vertical distribution. In the context of human colour vision, the line of this distribution would be called a tritanopic confusion line. The distribution forms a tight cluster when projected on to the abscissa, overlapping little with the fruit distribution. For the task of detecting fruits amongst leaves, it is easy to see that the phenotype with the photopigment complement of *A. seniculus*, at 430, 530 and 562 nm, has the advantage.

## 4. The optimal photopigments for a frugivorous monkey

The task facing primates searching for fruits may be considered as a signal detection task: primates must
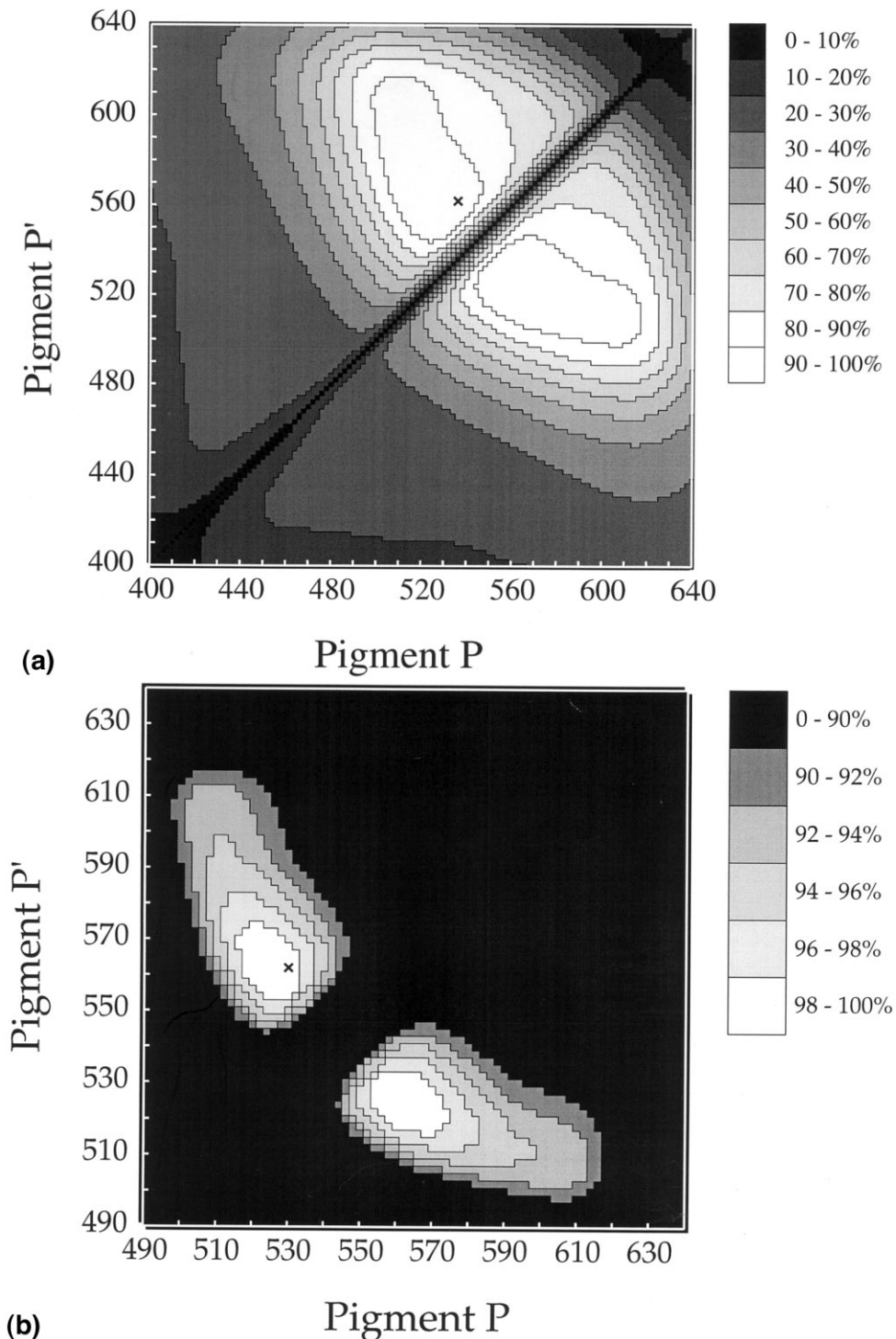
**(a)**



**(b)**

Fig. 3. Signal-to-noise ratios for detecting fruits against a background of leaves. The abscissa and the ordinate each show the peak sensitivity of one of the cone photopigments acting as an input to the phylogenetically more recent channel of colour vision. Signal-to-noise ratios are plotted as a percentage of the maximum value obtained for any pairing of photopigments. (a) shows signal-to-noise ratios for all pairings of photopigments with peak sensitivities between 400 and 640 nm; on this plot, the contours correspond to 10% intervals in signal-to-noise ratios; (b) shows the data from 90 to 100% of the maximum signal-to-noise ratio in greater detail; here, the contours represent 2% intervals in signal-to-noise ratios. Note that the abscissa on (b) runs only from 490 to 640 nm.

detect a signal (a fruit) embedded in noise. We now ask, 'what pair of photopigments, acting as inputs to the phylogenetically more recent channel of primate colour vision, maximizes the signal-to-noise ratio for detecting fruits against foliage?' In addition to the variability in the chromaticities of the leaves (the 'leaf noise'), we consider quantum noise, arising from constant small fluctuations in the numbers of quanta caught by the

different cone classes. We now refer to the photopigments as P and P', as they can take any arbitrary peak sensitivity. The modelling had the following steps:

## 4.1. Calculation of input to recent channel of colour vision from fruits and leaves

For each pair of photopigments P, P' with $\lambda_{max}$ in the range from 400 to 640 nm, a chromaticity $Q_P/(Q_P + Q_{P'})$ was calculated for the 247 spectra of fruit eaten by *A. seniculus* and the 155 spectra of leaves, using steps from Section 3.1 to Section 3.4 above.

## 4.2. Calculation of quantum noise

Photon capture is a poisson process. If the expected quantum catch in a cone over a given time interval is $Q$, and $Q$ is reasonably large, then the statistical distribution of $Q$ approximates a normal distribution, with mean and variance both equal to $Q$. The statistical distribution of a chromaticity calculated as in Section 3.5 above can be derived from this: the mean is $Q_P/(Q_P + Q_{P'})$, and the variance is $[Q_P^{-1} + (Q_P + Q_{P'})^{-1}] \cdot [Q_P/(Q_P + Q_{P'})]^2$. In order to calculate these variances, we assumed an integration time for the cones of 100 ms [23].

## 4.3. Calculation of signal-to-noise ratios

For each fruit spectrum, we calculated the 'signal' as the difference between the fruit chromaticity and the mean of the leaf chromaticities. The total noise for the detection task was calculated by adding together the variance in the distribution of leaf chromaticities (the 'leaf noise'), the variance in the chromaticity of the fruit due to quantum noise, and the mean variance in the chromaticities of leaves due to quantum noise. The signal-to-noise ratio was calculated as the signal divided by the square root of this sum of variances. The signal-to-noise ratio was calculated individually for each fruit spectrum, and the mean of these was taken.

The diagrams of Fig. 3 show, for the full sample of fruits, how the mean signal-to-noise ratio varies with the $\lambda_{max}$ values of P and P'. The signal-to-noise ratios are expressed as a percentage of the largest value obtained for any P, P' pairing. The lighter a region is, the higher the mean signal-to-noise ratio. Notice first that a combination of a short-wave pigment (say, 430 nm) with a long- or middle-wave pigment offers poor discrimination, confirming that the phylogenetically older channel of colour vision would be of little help to the frugivore. The highest signal-to-noise ratios are obtained with one pigment in the range 516–532 nm, and the other in the range 554–576 nm.

The cross on Fig. 3 shows the probable spectral positions of the L and M pigments of *A. seniculus* (530

and 562 nm). This pigment pair lies in the region of the space that offers a signal-to-noise ratio of at least 98% of the maximum possible, for the detection task we have empirically studied in the rainforest.

From this result alone, one cannot necessarily infer a co-evolution in the strict sense [24] between primate colour vision and the reflectance properties of fruits. It is also possible that trichromatic primate colour vision evolved for detection of pre-existing fruit signals, or that signalling fruits adapted themselves to pre-existing properties of primate colour vision. What our analysis does formally show is that the long- and middle-wave pigments of a particular trichromatic primate are very nearly optimal for discriminating fruit from foliage at a distance. Frugivory may be one answer to the classical question [25] of why primate photopigments occupy the spectral positions that they do. However, it remains a mystery why colour vision in so many other species of platyrrhine primate is polymorphic.

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