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The effect of colour vision status on the detection and selection of fruits by tamarins (*Saguinus* spp.)

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Summary

The evolution of trichromatic colour vision by the majority of anthropoid primates has been linked to the efficient detection and selection of food, particularly ripe fruits among leaves in dappled light. Modelling of visual signals has shown that trichromats should be more efficient than dichromats at distinguishing both fruits from leaves and ripe from unripe fruits. This prediction is tested in a controlled captive setting using stimuli recreated from those actually encountered by wild tamarins (*Saguinus* spp.). Dietary data and reflectance spectra of *Abuta fluminum* fruits eaten by wild saddleback (*Saguinus fuscicollis*) and moustached (*Saguinus mystax*) tamarins and their associated leaves were collected in Peru. *A. fluminum* leaves, and fruits in three stages of ripeness, were reproduced and presented to captive saddleback and red-bellied tamarins (*Saguinus labiatus*). Trichromats were quicker to learn the task and were more efficient at selecting ripe fruits than were dichromats. This is the first time that a trichromatic foraging advantage has been demonstrated for monkeys using naturalistic stimuli with the same chromatic properties as those encountered by wild animals.

Key words: polymorphic colour vision, trichromacy, dichromacy, sex differences, individual differences, tamarin, *Saguinus*.

Introduction

As an order, primates are among the most frugivorous of mammals. Indeed, with the exception of tarsiers (*Tarsius* spp.), all primate species have been recorded to eat fruit, and many eat it in large quantities (Richard, 1985); it even accounts for 25–50% of the diet of 'folivorous' species such as howler monkeys (*Alouatta seniculus*; Guillotin et al., 1994; Julliot, 1994). Whilst some species are specialized seed predators, the majority of primates act as dispersers for the species that they consume. Indeed, primate-mediated endozoochory may be the primary method of dispersal for many tropical plant species (Julliot, 1994). Given the importance of fruit to primates, and of primates to plant species in their dispersal, co-evolution has produced a suite of associated characteristics on both sides of this relationship. Trichromatic colour vision and the colour changes shown by fruits during maturation may be examples of such co-evolved characters.

Within placental mammals, trichromacy is unique amongst primates: all other species so far examined are either dichromats or monochromats (Jacobs, 1993; Ahnelt and Kolb, 2000; Arrese et al., 2002). It has been hypothesized that the evolution of trichromatic colour vision by the majority of primate species is a direct result of the chromatic signals produced by fruits (Regan et al., 2001) or leaves (Dominy and Lucas, 2001). For an animal to feed on fruits it has first to detect them against a background of leaves. Vision and olfaction are probably the principal senses employed. Theoretically, trichromacy has been predicted to be more efficient than dichromacy when detecting and identifying fruits against a leaf background (Osorio and Vorobyev, 1996; Sumner and Mollon, 2000a; Regan et al., 2001). In addition to detecting fruiting trees, an animal has to select ripe from unripe fruits. Physical and chemical defences may protect fruits until their seeds are ready to be dispersed. The ripening process is often characterized by a colour change that can give a clear visual signal to potential dispersers of the increased palatability of the ripe fruits (Regan et al., 2001). Theoretically, trichromats have also been predicted to be capable of distinguishing a greater number of ripe from unripe fruit species (Sumner and Mollon, 2000b; Regan et al., 2001).

Despite its theoretical advantages, trichromacy is not uniform within the primates. Whilst all catarrhines so far studied are trichromatic, all platyrrhines, with the two

exceptions of howler (*Alouatta* spp. – uniformly trichromatic; Jacobs et al., 1996a) and night monkeys (*Aotus* spp. – uniformly monochromatic; Jacobs et al., 1996b; Jacobs, 1984; Mollon et al., 1984), and some strepsirhines (Tan and Li, 1999; Jacobs et al., 2002) have a polymorphic colour vision system. All males and homozygous females are dichromats, whilst heterozygous females are trichromats. In platyrrhines, two loci code for the visual pigment proteins or opsins. The first, an autosomal locus, has a single allele that codes for the short wavelength (S) opsin and is common to all individuals. The second, on the X chromosome, codes for opsins within the long to medium wavelength (LM) range. A single X-linked locus model, with three alleles, explains the visual polymorphism observed in callitrichids (Mollon et al., 1984).

For non-human species it is necessary to take account of the animal's perceptual abilities. Thus, we should not relate our verbal classification of colours to colour discriminability or memorability for another species; even one with the same set of photopigments. A good starting point for understanding how other species might discriminate colours is to measure spectral stimuli and estimate the responses of their photoreceptors (Table 1).

The perceptual capabilities of various primate visual systems have been modelled to examine the potential advantages of trichromacy in detecting ripe fruits (e.g. Osorio and Vorobyev, 1996; Sumner and Mollon, 2000a,b; Regan et al., 2001) or flush leaves (Dominy and Lucas, 2001). The most pertinent stimuli for such modelling are those actually seen by the visual system of the primate in question in the wild. However, these models make (varying) assumptions about how photoreceptor signals are used to make behavioural decisions (e.g. Vorobyev and Osorio, 1998). For any given perceptual task we cannot be sure that model assumptions will hold. To examine whether an actual foraging advantage is conferred by trichromacy, the relative performance of actual subjects must be measured. For example, Caine and Mundy (2000) used artificially coloured food to show a trichromatic advantage for Geoffroy's marmosets (*Callithrix geoffroyi*) in a foraging task.

Whilst modelling and behavioural experiments imply that trichromacy is advantageous, this has yet to be demonstrated for a colour discrimination task that closely resembles that faced by primates foraging in their natural habitat. This is the goal of the present study. The relative efficiency of di- and trichromacy for tamarins (*Saguinus* spp.) is evaluated through an experimental protocol utilising captive monkeys and stimuli recreated from the reflectance spectra of actual fruits eaten (and their associated leaves) by wild tamarins in Peru and presented in a dappled naturalistic leaf canopy.

Materials and methods

Field observations

Field site and monkeys

Two mixed-species groups of saddleback (*Saguinus fuscicollis nigrifrons* I. Geoffroy 1850) (*N*=4 and 8 individuals) and moustached (*Saguinus mystax mystax* Spix 1823) tamarins (*N*=5 and 8 individuals) were observed (by A.C.S.) for 164 days (1612 h) from January 2000 until December 2000 at the Estación Biológica Quebrada Blanco II (4°21′ S, 73°09′ W) in northeastern Peru (for details, see Heymann and Hartmann, 1991). The tamarins were observed for approximately 14 days each month.

Data collection and analysis

All observed instances of fruit feeding were recorded. From these data, the number of 'tamarin feeding minutes' was calculated (where one 'tamarin feeding minute' equals one tamarin feeding for 1 min) and divided by the number of tamarins of the given species to account for differences in group size between groups, and species, and over the course of the study. Furthermore, each month's data were weighted equally to account for slight differences in the number of observation days.

Colour measurement

Colour measurements were taken using a portable S2000 spectrometer, HL2000 halogen light source (both Ocean Optics, Dunedin, FL, USA) and Satellite 4030CDT laptop computer (Toshiba) running SpectraWin 4.1 software (Top Sensor Systems, Eerbeek, The Netherlands). Reflectance spectra from a minimum of three fruits and three associated mature leaves were recorded for each species eaten. Where possible, spectra were recorded from parts of fruits discarded by tamarins as they fed and taken from both the upper and lower surfaces of leaf samples. Spectra were recorded on the day that the samples were collected.

Colour modelling

We estimated the responses of the tamarin's photoreceptors, and hence colour signals to spectral stimuli, as follows. We derived tamarin photoreceptor spectral sensitivities *in vivo* by fitting a standard exponential model of rhodopsin absorption (Stavenga et al., 1993) to spectral sensitivity maxima measured for common marmoset (*Callithrix jacchus*) cones with sensitivity maxima at 425 nm, 543 nm, 555 nm and 562 nm (Williams et al., 1992), which are close to those for *Saguinus* (Jacobs et al., 1987) assuming a maximum optical density of 0.4. Spectral absorption by the ocular media was also based on the common marmoset (Tovée et al., 1992). Recent work (Kawamura et al., 2001) lowers the estimated sensitivity maximum of the common marmoset 543 nm receptor to 539 nm; this difference is of negligible significance for the design and interpretation of our study.

Spectral stimuli reaching the eye depend upon the reflectance and illumination spectra. Reflectance was measured as described above, and the illumination spectrum was natural sunlight measured by a spectroradiometer calibrated with a known standard (LS1-cal; Ocean Optics). For an eye viewing the surface of an object, the (relative) quantum catch of the receptor *i* (Q_i) is given by the following expression:

$$Q_i = \int_{\lambda_{min}}^{\lambda_{max}} R_i(\lambda) S(\lambda) I(\lambda) d\lambda , \quad (1)$$

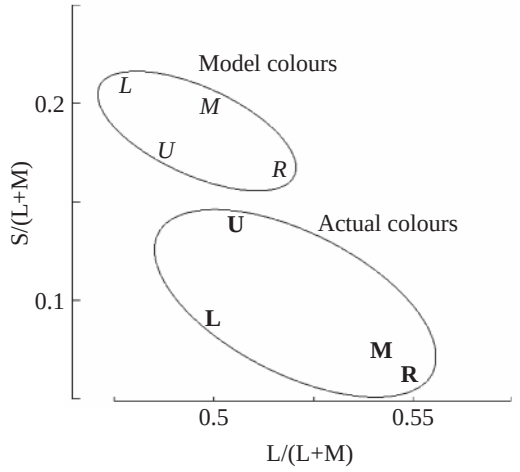

Fig. 1. Chromaticities of natural *Abuta fluminum* leaves and fruit and of the model colours used in this experiment, plotted in a standard chromaticity diagram modified for the common marmoset eye (see text; Macleod and Boynton, 1979; Regan et al., 1998). Colour differences on the horizontal axis are visible only to trichromats. Note that distance in this diagram does not directly predict colour discriminability. For example, in general, a given colour distance on the vertical axis will be less discriminable than on the horizontal. L, leaf; U, unripe; M, mid-ripe; R, ripe.

where λ denotes wavelength, λ_{min} and λ_{max} denote the lower and upper limits of the visible spectrum, respectively, $R_i(\lambda)$ is the spectral sensitivity of receptor i, $S(\lambda)$ is the reflectance spectrum and $I(\lambda)$ is the illumination spectrum. The receptor response normalised to the illuminant q_i is then given by: $q_i=Q_{i(t)}/Q_{i(i)}$, where $Q_{i(t)}$ and $Q_{i(i)}$ are estimated quantum catches for a target and the barium sulphate reflectance standard, respectively. Finally, stimulus chromaticities (Fig. 1) were given by Macleod and Boynton (1979) chromaticity co-ordinates based on outputs of marmoset 425 nm (S), 543 nm (M) and 562 nm (L) cone photoreceptors (see also Regan et al., 1998). The Cartesion coordinates are given by S/(L+M) and L/(L+M), which is convenient because S/(L+M) roughly represents the blue–yellow chromatic signal available to a dichromat, while the red–green parameter, L/(L+M), is available only to trichromats. Although the colours used for the experiments did not exactly match those of the plant (Fig. 1), the chromaticity differences between the leaf background and fully ripe fruit were very similar for the real and experimental colours, with the 'unripe' and 'mid-ripe' model fruit lying at intermediate locations on the red–green axis.

Results

Diet composition and choice of representative fruit species

The tamarins ate fruits from 833 plants from 167 species in 87 genera and 50 families during 164 days of observation. *Abuta* was chosen as representative of ripe fruit eaten by tamarins for which trichromatic colour vision may give an advantage in the detection and selection. It formed a significant part of the diet of both species in both groups. It was eaten in all months but two; no other genus was eaten in as many months. It was chosen over other important genera (i.e. *Parkia*, *Tapirira*, *Pourouma*, *Buchenavia*, *Unonopsis* and *Simaba*), as these genera typically ripened to a dark purple or black colour for which trichromacy has little benefit, and over *Inga*, as the bean-like fruit pods of many species of this genus may be deemed cryptic since they remain green even when mature. Six species of *Abuta* were eaten by the tamarins: *A. arborea*, *A. fluminum*, *A. imene*, *A. pahni*, *A. rufescens* and *A. solimoensis*. Of these, *A. fluminum* was chosen as representative as it accounted for the greatest number of feeding records. Fig. 2 shows the reflectance spectra of ripe and unripe *A. fluminum* fruit and leaves (upper surface).

The fruits and leaves of *A. fluminum* occupy roughly mid positions on the L/(L+M) axis (the red–green parameter available only to trichromats) of all the species sampled. Of the ripe fruits sampled, those of *A. fluminum* have a value of 0.5474±0.0052 (*N*=12 fruits), from a range spanning 0.5032–0.5914 (*N*=137 species), whereas the leaves of *A. fluminum* have a value of 0.5009±0.0021 (*N*=9 leaves), from a range of 0.4957–0.5147 (*N*=154 species). Their chromaticity is similar to that of other fruits eaten by tamarins and also by other primates (Sumner and Mollon, 2000b; Regan et al., 2001).

Table 1. *Sex and visual status of experimental animals*

Species	ID #	Sex	Visual status	Opsins (nm)
Saddleback tamarin	2422	Female	Trichromat	423, 543, 563
	3894	Female	Trichromat	423, 543, 563
	3948	Female	Trichromat	423, 543, 563
	2214	Female	Trichromat	423, 543, 563
	1045	Female	Dichromat	423, 543
	3895	Male	Dichromat	423, 543
	989	Male	Dichromat	423, 563
	2365	Male	Dichromat	423, 563
Red-bellied tamarin	3782	Female	Trichromat	423, 543, 563
	3873	Female	Trichromat	423, 543, 563
	2972	Female	Dichromat	423, 563
	2666	Female	Dichromat	423, 563
	657	Female	Dichromat	423, 563
	874	Male	Dichromat	423, 543
	3201	Male	Dichromat	423, 563
	3874	Male	Dichromat	423, 563

Captive experiment

Animals and housing

Eight captive adult saddleback (*S. fuscicollis weddelli* Deville 1849) and six red-bellied tamarins (*S. labiatus labiatus* Geoffroy in Humboldt 1812) held at the Belfast Zoological Gardens were observed (by A.C.S.) in the experiment. The numbers of each species are given for each sex and visual phenotype in Table 1. Effort was made to balance sex and visual status across species from the animals available.

The monkeys were housed in standard indoor/outdoor enclosures off-exhibit. Testing took place in the outside

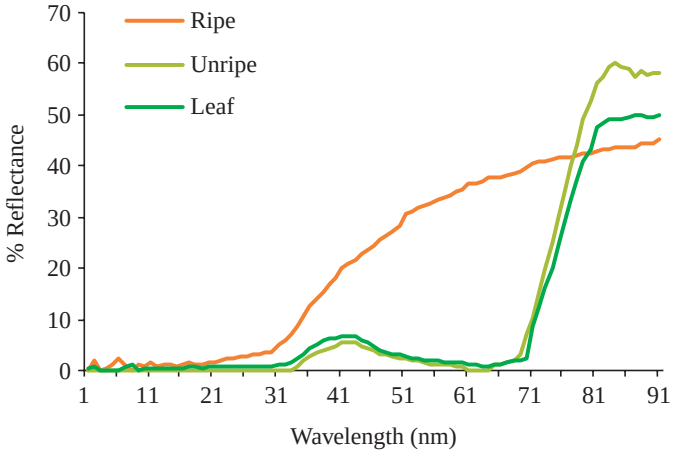

Fig. 2. Reflectance spectra of ripe and unripe *A. fluminum* fruit and leaves (upper surface).

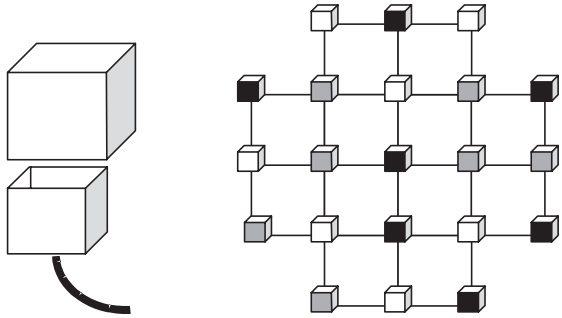

Fig. 3. Diagram of artificial fruit and its coloured lid, and the pattern of the 21 test fruits.

enclosures (1.95 m×1.55 m×3.50 m). Each was furnished with a network of approximately eight branches (5 cm to >10 cm diameter), with the three branches closest to the test apparatus placed in the same configuration. The monkeys were accustomed to being held individually in the outside enclosures.

Genotyping

Visual status was determined genetically (by A.K.S.), by amplification and sequencing of the X-linked opsin gene. Tamarin opsin alleles can be defined by four amino acid substitutions at positions 180 in exon 3, 229 and 233 in exon 4 and 285 in exon 5, which are important for spectral tuning (Shyue et al., 1998). DNA was extracted from plucked hair samples from each individual tamarin using a QIAamp DNA mini-kit (Qiagen, Crawley, UK). PCR and sequence analysis of exons 3, 4 and 5 were performed as previously described (Surridge and Mundy, 2002). Genotypes were assigned according to the combined sequence of the four important amino acids in each of the exons mentioned above. These are as follows for each of the three opsin alleles: 543 nm=Ala, Ile, Ser, Ala; 556 nm=Ala, Phe, Ser, Thr; 563 nm=Ser, Phe, Gly, Thr. Trichromatic females were identified by the presence of heterozygous sites in the DNA sequence at these important positions.

Test apparatus

The apparatus consisted of two rigid, wire grid panels. One was covered with laminated paper leaves (leaf background) and the other was unadorned (no background). The leaves, in the oval shape of *A. fluminum*, ranged from 70 mm×50 mm to 150 mm×115 mm. They were arranged to form a naturalistic canopy, giving dappled lighting from the incident daylight. The randomly varying degrees of illumination from the dappled light ensured that the task could not be solved by brightness cues of the targets alone. Twenty-one fruit bases, made from 1.5 mm card, were fixed at regular intervals as per Fig. 3. Each was covered with a lid, also made from 1.5 mm card that overhung and covered its sides. The lids were covered in one of three colours of paper corresponding to unripe, mid-ripe and ripe *A. fluminum* fruit. Ripe fruits contained 0.5 g fudge, mid-ripe contained 0.25 g fudge and unripe fruits contained no reward. The pattern of the fruit locations was varied systematically.

The leaves were made from a commercially available green paper, the reflectance spectrum of which roughly matched that of real *A. fluminum* leaves, although overall the colour was somewhat brighter than the real leaves (Table 2; Fig. 4). Fruit lid colours were calculated to differ in chromaticity from the model leaves in the same way that natural fruits differ from natural leaves (Fig. 1). This design, with dappled lighting, means that as a test of colour vision the experimental task closely resembles the task faced in natural foraging. We modelled ripe, mid-ripe and unripe *A. fluminum* fruit (Table 2). Colours were made in Adobe Photoshop and printed using an Epson Color 580 inkjet printer.

Fig. 4. A saddleback tamarin foraging for the artificial fruits when presented on a leaf background.

Table 2. *Quantum catches, relative to a barium sulphate white standard, of tamarin cones for* A. fluminum *fruit and leaves and recreated stimuli*

	Fruit and leaves							
	425 nm		543 nm		556 nm		562 nm	
Stimulus	Actual	Model	Actual	Model	Actual	Model	Actual	Model
Ripe fruit	0.0227±0.0088 (12)	0.0832	0.1666±0.0204 (12)	0.2415	0.1908±0.0247 (12)	0.2531	0.2017±0.0268 (12)	0.2577
Mid-ripe fruit	0.0181	0.1792	0.1071	0.4628	0.1201	0.4632	0.1257	0.4611
Unripe fruit	0.0136±0.0008 (2)	0.1349	0.0477±0.0018 (2)	0.3927	0.0494±0.0025 (2)	0.3834	0.0497±0.0028 (2)	0.3768
Leaf (upper side)	0.0087±0.0025 (9)	0.1583	0.0483±0.0133 (9)	0.3976	0.0489±0.0137 (9)	0.3767	0.0485±0.0138 (9)	0.3653

	Recreated stimuli									
	S 425nm		M 543nm		L 562nm		S/(L+M)		L/(L+M)	
Stimulus	Actual	Model	Actual	Model	Actual	Model	Actual	Model	Actual	Model
Ripe fruit	0.023	0.083	0.167	0.242	0.2017	0.259	0.0616	0.1667	0.5477	0.5163
Mid-ripe fruit	0.0181	0.179	0.1071	0.463	0.1257	0.461	0.0777	0.1940	0.5399	0.4991
Unripe fruit	0.0136	0.135	0.0477	0.393	0.0497	0.377	0.1396	0.1753	0.5103	0.4897
Leaf	0.0087	0.158	0.0483	0.398	0.0485	0.365	0.0899	0.2075	0.5010	0.4789

N is given in parentheses.

Protocol

Tamarins were tested individually in their outside enclosures. There were two conditions: condition 1, where 21 fruits, seven of each of three colours, were presented against no background (the plain wire mesh of the guide frame and cage wall), and condition 2, where the same fruits were presented against a leaf background (Fig. 4). Each tamarin received training trials until it had successfully located and taken six fruits. These trials were performed as for condition 2. The experiment was split into two phases: phase 1 was three trials of condition 1, and phase 2 was three trials of condition 2.

Trials were terminated either after the tamarin had taken all 21 fruits or after 15 min, whichever was sooner. During each trial, the time and colour of the fruit the tamarin took was continuously recorded using a hand-held computer running the Observer TM package (Tracksys Ltd., Nottingham, UK). General linear models run through SPSS were used for statistical comparisons.

Results

Trichromats required significantly fewer training trials than their dichromatic counterparts (1.83±1.33 *vs* 4.60±2.88, respectively: $F_{1,10}$=9.40, P<0.05) to reach the criterion of six fruits taken. Neither species (saddleback, 2.38±1.60; red-bellied, 4.75±3.20: $F_{1,10}$=1.29, P>0.05) nor sex (male, 3.17±2.64; female, 3.80±2.90: $F_{1,10}$=4.52, P>0.05) had a significant effect on number of trials to criterion, nor were the interactions of species and vision ($F_{1,10}$=0.97, P>0.05) and species and sex ($F_{1,10}$=0.01, P>0.05) significant.

To examine the efficiency with which fruits were selected, the number of ripe fruits within the first six fruits taken was

Table 3. *Mean number of ripe fruits (±S.D.) taken within the first six fruits*

		Fruits against no background			Fruits against leaf background		
Effect/interaction	Category (*N*)	Mean no. ripe fruits	$F_{1,10}$	P	Mean no. ripe fruits	$F_{1,10}$	P
Visual status	Trichromat (6)	3.28±0.49	7.71	0.02	3.06±0.80	8.08	<0.05
	Dichromat (10)	2.35±0.59			2.13±0.64		
Species	Saddleback (8)	2.75±0.61	0.51	>0.05	2.27±0.60	4.63	>0.05
	Red-bellied (8)	2.65±0.84			2.69±0.99		
Sex	Female (10)	2.80±0.77	0.78	>0.05	2.67±0.82	0.36	>0.05
	Male (6)	2.53±0.62			2.17±0.78		
Species × visual status			0.16	>0.05		0.16	>0.05
Species × sex			0.62	>0.05		0.22	>0.05

calculated. When the fruits were presented against both the no background and the leaf background, trichromats took significantly more ripe fruits than did dichromats (Table 3). There were no other significant effects.

Whether the fruits were presented against a leaf background or not had no significant effect on the number of ripe fruits within the first six fruits taken (no background 2.70±0.71; leaf background 2.48±0.82: $F_{1,14}$=1.41, P>0.05). There was no interaction of visual status and background ($F_{1,14}$=0.001, P>0.05) nor was there a difference between dichromats and trichromats in the total number of ripe fruits taken by the end of each trial, either when presented against no background (dichromat, 6.30±0.66; trichromat, 6.33±0.73: $F_{1,14}$=0.009, P>0.05) or a leaf background (dichromat, 5.43±1.29; trichromat, 6.05±0.53: $F_{1,14}$=1.25, P>0.05).

Discussion

The main finding is that trichromacy confers an advantage when selecting ripe fruits from those at various stages of maturity; both as a simple task and also when presented as a more naturalistic complex task against a background of distracting leaves. This is the first time that such an advantage has been demonstrated for primates using naturalistic stimuli. In addition, the patchy illumination falling on the fruit and leaves in our experiments resembles that of a natural forest canopy with areas of shadow and sun. These are conditions that might favour colour vision. Despite the benefits of trichromacy in the efficient detection and selection of ripe fruit, the selection of heterozygous trichromats will maintain both trichromacy and dichromacy within the population since, within the X-linked single-locus model, males are always dichromats irrespective of their mother's visual status (Mollon et al., 1984).

The three alleles of the single-locus model give three trichromat phenotypes and three dichromat phenotypes. The spectral tuning of the opsins of each phenotype may render them each more or less advantageous under different photic conditions. Even at a given time of day there are vast differences in illumination within a rain forest. It would repay investigation to examine the actual foraging efficiencies of the different phenotypes using real-world stimuli under a variety of naturalistic lighting conditions. Similarly, it would have been informative to examine differences in the relative performance of each of the three dichromatic and three trichromatic phenotypes, but distribution of the phenotypes of the available animals did not permit this. Indeed, all of the trichromats were 423 nm, 543 nm, 563 nm, and the small sample size did not permit examination of differences between the two dichromat phenotypes in the study, namely 423 nm, 563 nm and 423 nm, 543 nm.

Although we have found that trichromacy is advantageous for detection and selection of ripe fruit (at least for the phenotypes present in our study), this does not give a complete picture of the likely costs and benefits of colour vision. Nor does this result demonstrate that trichromacy originally evolved for foraging. For example, trichromacy has been suggested as being more efficient for detecting yellow predators against a green leafy background (Coss and Ramakrishnan, 2000). Examples might include the yellowish jaguar (*Panthera onca*), ocelot (*Leopardus pardalis*), margay (*L. wiedii*) and oncilla (*L. tigrina*), all of which live in the Neotropics. Dichromacy, however, may be advantageous in breaking camouflage (Morgan et al., 1992). This is relevant not only for detection of predators but also for the detection of insect and other prey items that are taken by many primate species. However, a recent study failed to find any evidence of a dichromat advantage in terms of the number of prey captured by wild and captive tamarins (H. M. Buchanan-Smith, A. C. Smith, A. K. Surridge, M. J. Prescott, D. Osorio and N. I. Mundy, manuscript in preparation).

The detection and discrimination of fruits is a complex task. Fruits must be distinguished from leaves, edible fruits must be discriminated from inedible or toxic fruits, and ripe fruits must be typically picked over unripe fruits. Colouration may aid in all of these tasks; indeed, as this study has shown, primate trichromacy is advantageous in the efficient selection of ripe fruits from an array of unripe, mid-ripe and ripe fruits. However, there are many subtle factors other than colour *per se* that can influence the choice of fruits by wild primates. As Savage et al. (1987) point out, discrimination may be most acute for those foods that are rarely consumed yet are an essential source of one or more nutrients.

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