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Demonstration of a foraging advantage for trichromatic marmosets (*Callithrix geoffroyi*) dependent on food colour

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It has been suggested that the major advantage of trichromatic over dichromatic colour vision in primates is enhanced detection of red/yellow food items such as fruit against the dappled foliage of the forest. This hypothesis was tested by comparing the foraging ability of dichromatic and trichromatic Geoffroy's marmosets (*Callithrix geoffroyi*) for orange- and green-coloured cereal balls (Kix®) in a naturalized captive setting. Trichromatic marmosets found a significantly greater number of orange, but not green, Kix® than dichromatic marmosets when the food items were scattered on the floor of the cage (at a potential detection distance of up to 6 m from the animals). Under these conditions, trichromats but not dichromats found significantly more orange than green Kix®, an effect that was also evident when separately examining the data from the end of the trials, when the least conspicuous Kix® were left. In contrast, no significant differences among trichromats and dichromats were seen when the Kix® were placed in trays among green wood shavings (detection distance < 0.5 m). These results support an advantage for trichromats in detecting orange-coloured food items against foliage, and also suggest that this advantage may be less important at shorter distances. If such a foraging advantage for trichromats is present in the wild it might be sufficient to maintain the colour vision polymorphism seen in the majority of New World monkeys.

Keywords: colour vision; marmoset; opsin; trichromacy; *Callithrix*; foraging

1. INTRODUCTION

Among the mammals, only human beings, apes, Old World monkeys and howler monkeys have habitual trichromatic colour vision (Jacobs 1993; Jacobs *et al*. 1996). Superimposed on the 'ancient' blue–yellow colour opponent system as shown by dichromatic mammals, individuals of these species have separate middle- and long-wave colour visual pigments (opsins) which enable far greater colour discrimination in the green to red part of the spectrum than in dichromats (Mollon 1991). Many New World monkeys, including marmosets, display an intriguing intermediate position in which populations are polymorphic for colour vision, with both dichromats and trichromats present (Mollon *et al*. 1984; Jacobs *et al*. 1987; Tovée *et al*. 1992). In such species there is a single X-linked locus encoding a middle- to long-wave opsin which is polymorphic. Together with the autosomally encoded invariant short-wave opsin, this means that all males and homozygous females are dichromats, whereas heterozygous females, which express two middle- to long-wave opsins, are trichromats. These species provide an ideal model for studying the ecology and evolution of trichromacy versus dichromacy.

The assumption is commonly made that the advantage of trichromacy is the ability to see ripe fruit (often orange or red) against a dappled green background (see also Lucas *et al*. (1998) concerning colour cues in edible leaves). This is a logical assumption that is supported indirectly by some empirical data and theoretical arguments. For example, Regan *et al*. (1996) used spectroradiometric data from neotropical fruit trees to model colour discrimination with an invariant short-wave opsin and a variable medium- to long-wave opsin and concluded that, 'no dichromatic phenotype . . . could distinguish the fruit from the foliage distribution on the basis of chromaticity' (p. S648). Likewise, Osorio & Vorobyev (1996) used spectra of fruits and leaves and receptor characteristics to confirm theoretical trichromatic superiority in fruit foraging contexts. That dichromatic and trichromatic New World monkeys have different spectral sensitivities and colour vision capacities has been shown in laboratory psychophysical tests in squirrel monkeys (Jacobs 1984), tamarins (Jacobs *et al*. 1987) and marmosets (Tovée *et al*. 1992). However, no one has demonstrated the superiority of trichromacy among animals foraging in natural or semi-natural circumstances.

The current study is composed of two different experiments. The first experiment was designed to mimic a foraging situation in which a trichromat marmoset might have an advantage in locating an orange fruit, flower, or coloured insect against foliage, tree branches, or detritus from a distance of 6 m or less. Experiment 2 was designed to mimic a foraging situation in which a trichromat may have an advantage in noticing an orange food source (e.g. a berry or insect) against a foliage background at close range (less than 0.5 m). Marmosets, members of the New World family Callitrichidae, are small, arboreal, diurnal primates native to the coastal and interior forests of Brazil. They live in rather small groups (usually from four to 12 individuals) and their diets are composed of fruits, insects and gums. Although there is little data on the colour of food items taken by wild *Callithrix geoffroyi* in the Atlantic forest, it is very likely that their diet contains coloured (red/orange/yellow) fruit and insects, as these are known to occur in similar habitats in the Atlantic

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forest where they form part of the diet of related lion tamarins (*Leontopithecus* spp.) (J. Dietz, personal communication). Trichromatic individuals may have an advantage in locating ripe fruits or coloured insects against the background of greens and browns in which marmosets forage. Our experiments represent the first behavioural tests of the proposed advantages of trichromacy to non-human primates.

2. MATERIAL AND METHODS

(a) *Subjects*

Subjects were 14 subadult and adult marmosets, *C. geoffroyi*, including nine females and five males. Five of the marmosets live in one family group (group 1), and the remaining nine live in another (group 2). The monkeys are housed outdoors, all year round, at the Center for Reproduction of Endangered Species (CRES) at the San Diego Wild Animal Park, CA, USA. The large enclosures (each one 6 m × 6 m × 2.5 m) are described elsewhere (Caine 1996); for this study it is particularly relevant to know that the floors of the enclosures are covered with dirt, weeds, grasses and potted plants. The monkeys forage freely and regularly among these substrates for naturally occurring and provisioned insects and vertebrate prey, and for pieces of fruit that have fallen from provisioning stations into the surrounding foliage and substrates.

(b) *Stimuli*

Both behavioural experiments involved the use of Kix® (Kix, General Mills, Minneapolis, MN, USA) cereal, dyed with either orange or green food colouring. Kix® are small (about 1 cm diameter), spherical pieces of lightly sweetened corn cereal that the marmosets find highly palatable. In experiment 2, pine shavings were dyed green (producing a mottled appearance very similar to the green Kix®) and put in metal pans (23 cm × 33 cm) that were then placed in the enclosures on days of data collection. Because our goal was to mimic a natural situation, there was no attempt to make each piece of cereal 'match' the others. Thus, some were darker, or more uniformly shaded, than others, just as individual pieces of fruit would vary in colour. Likewise, the green pine shavings were sprayed with food colouring to generate a variable appearance. Experiments were conducted from mid- to late morning, under variable natural lighting conditions.

A colour-blind human male who was tested as having deuteranopia–strong deuteranomalia using Ishihara plates was asked to look at the dyed Kix®. He reported that the orange and green Kix® were generally indistinguishable and that they looked similar to the backgrounds of dirt or grass on which they were placed. Additionally, he found that the orange and green Kix® were equally camouflaged by the pine shavings, whereas people of normal trichromatic colour vision found the orange Kix® much easier to see than the green Kix® against the green shavings.

(c) *Procedure*

Both experiments were performed without knowledge of the genotypes of the individuals.

(i) *Experiment 1*

This experiment was designed to mimic a foraging situation in which a trichromat might have an advantage in locating an orange fruit, flower, or coloured insect against foliage, tree branches, or detritus from a distance of 6 m or less. On each of 45 days over the course of six months, orange Kix® alone were broadcast across the enclosure floors. On alternate 45 days, green Kix® alone were used. After the cereal was broadcast, the monkeys were observed for 10 min. Pilot testing had shown that in the smaller group (group 1) rarely were more than four Kix® found by the monkeys in 10 min; six Kix® was the maximum for the larger group (group 2). Therefore, five and seven Kix® were broadcast to groups 1 and 2, respectively, on each of the 45 trials of each colour. No attempt was made to distribute the Kix® to particular areas of the cage, but we did try to disperse the Kix® fairly widely. Because of the predominance of grass and weeds on the floor of the cage compared with bare earth, a majority of the Kix® fell onto a predominantly green substrate. Each time a Kix® was found, the observer recorded elapsed time and the identity of the marmoset that made the discovery.

(ii) *Experiment 2*

This experiment was designed to mimic a foraging situation in which the marmosets might visually inspect a substrate at close range (less than 0.5 m) and where a trichromat may have an advantage in noticing a food source (e.g. a berry or insect) that has orange on it. On each of 45 days over the course of four months (the four months subsequent to the six months in experiment 1), orange Kix® were hidden in pans and those pans were placed in various areas around the floor of the enclosures where the marmosets typically forage. On alternate 45 days, green Kix® were used. Four and six pans were used for groups 1 and 2, respectively, and three Kix® were hidden in each pan. (Pilot testing had shown that group 1 rarely found more than 11 Kix® in 10 min under these conditions, and group 2 usually found no more than 17 Kix®.) The marmosets were free to sift though the shavings in any of the various pans for up to 10 min, and the number of Kix® found by each marmoset was recorded. Each time a Kix® was found, the observer recorded elapsed time and the identity of the marmoset that made the discovery.

(d) *Statistical methods*

Wilcoxon tests (test statistic, T) for correlated samples were used for within-groups comparisons and Mann–Whitney tests (test statistic, U) were used for between-groups comparisons.

(e) *Colour measurement*

To evaluate the absolute colour and colour difference between the background and the coloured dyed cereal balls, a Minolta CM-508d spectrophotometer (Minolta, Instrument Systems Division, Ramsey, NJ, USA) was used. The instrument is a spherical instrument using $d/8$ geometry that was calibrated against absolute black and then against a known white ceramic tile. Spectral reflectance was determined every 20 nm over the visible range of 400–700 nm using 11 mm illumination and 8 mm measurement areas. All measurements were taken through the bottom of a 100 mm × 15 mm polystyrene Petri dish (Fisherbrand, Fisher Scientific, Pittsburgh, PA, USA, Cat. 08–787–12) using illuminant D65 and the CIE 2° standard observer. CIELab values (L^*, a^*, b^*), hue angle (arc tan b^*/a), chroma ($(a^2 + b^2)^{1/2}$) and total difference (CIELab $\Delta E^*ab = ((\Delta L^*)^2 + (\Delta a^*)^2 + (\Delta b^*)^2)^{1/2}$) were calculated using Minolta SpectraMagic® software. An average of at least eight measurements were taken for each sample measurement and the average of at least three sample measurements were used for the average colour measurement. CIELab values provide a convenient method for quantifying colour differences, but it should be noted that they are based on normal human trichromatic vision and may not

accurately reflect colour perception in trichromatic marmosets. In addition, CIELab values are not readily applicable to dichromats.

(f) *Genotyping*

Sixteen individuals of *C. geoffroyi* were genotyped in the study—the 14 subjects in the behavioural study, one individual ('CR') who died before the behavioural study began, and one unrelated male from the Rio de Janeiro Primate Centre (CPRJ). DNA was extracted from plucked hairs either using a Chelex^{TM} method (Garza & Woodruff 1992) or a commercial DNA extraction kit (Qiagen tissue extraction kit, Crawley, UK), according to manufacturers' instructions.

Polymerase chain reactions (PCRs) were performed in a 25 µl total volume containing 0.5 units *Taq* polymerase (PE Applied Biosystems, Foster City, CA, USA), 1×PCR buffer, 50 µM each dNTP, 1.5 mM $MgCl_2$ and 0.4 µM each primer. For subsequent single-stranded conformational polymorphism (SSCP) analysis, the forward primer was end-labelled with [γ-^{32}P]ATP (Sambrook *et al.* 1989). Cycling parameters were: 1×94 °C, 2 min; 35×94 °C, 30 s; 50–58 °C, 45 s; 72 °C, 60 s; 1×72 °C, 5 min.

SSCP gels consisted of 0.5×MDE^{TM} solution (FMC Rockland, ME, USA), and were run in 0.6×Tris-Borate-EDTA at approximately 15 W for 5–7 h at room temperature. Gels were dried and exposed to X-OMAT film (Kodak, Rochester, NY, USA) overnight. For direct double-stranded sequencing, PCR products were cleaned using QiaQuick columns (Qiagen). Sequencing reactions were performed on both strands using dRhodamine or BigDye (PE Applied Biosystems) dye-termination reactions, and run on an ABI 377 sequencer. Sequence data were edited using Sequence Navigator^{TM} (PE Applied Biosystems), and sequences have been deposited in GenBank under accession numbers AF227241–AF227249.

Primers and their annealing temperatures for the polymorphic X-linked opsin locus were as follows: exon 3: OPS3F (5′-GGATCACGGGTCTCTGGT-3′) and OPS3R (5′- CTGCT CCAACCAAAGATG-3′), 50–53 °C; exon 4: OPS4F (5′- CCAT GGCCTGAAGACTTCCT-3′) and OPS4R (5′-GATTTGGGG GCAGAGAAGC-3′), 55–58 °C; exon 5: OPS5F (5′-GTGGCAA AGCAGCAGAAA-3′) and OPS5R (5′-CTGCCGGTTCATAAA GACA-3′), 53–55 °C. Using these primer pairs, 134 bp of exon 3, 137 bp of exon 4 with 45 bp of adjacent intron 4, and 203 bp of exon 5 were obtained.

3. RESULTS

(a) *Genotyping*

When the PCR product from exon 3 of the polymorphic X-linked opsin locus was separated by SSCP, three banding patterns, each consisting of one or two bands, were present among the males, and one or two of these banding patterns were present in each female (data not shown). Sequencing of exons 3, 4 and 5 from females with a single SSCP banding pattern and all males revealed the presence of a total of three alleles at the nucleotide level (haplotypes), with each haplotype correlating with the presence of a particular SSCP banding pattern with exon 3. Sequences of exons 3–5 from females with two SSCP banding patterns demonstrated that they were heterozygous for two out of the same three haplotypes, the haplotypes again correlating with the SSCP bands. The genotypes thus obtained are consistent with the known pedigree of the animals (figure 1).

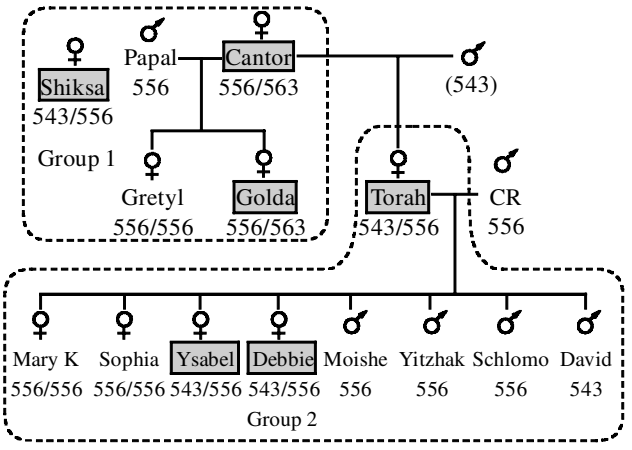

Figure 1. Behavioural subjects, genotypes and relations. Below each individual are the predicted maximum spectral sensitivities in nanometres of their X-linked opsin alleles. Trichromats are shaded, dichromats unshaded. 'CR' was genotyped but died before the behavioural study began. The genotype of Torah's father is inferred. The male from the CPRJ had the 563 nm allele.

The deduced protein sequences of the three haplotypes are identical to the three previously described alleles in the closely related common marmoset (*C. jacchus*), which have maximum spectral sensitivities at 543, 556 and 563 nm (Hunt *et al.* 1993; Shyue *et al.* 1998). As all of the sites thought to be important for determining spectral sensitivity were sequenced from the individuals in the present study (Shyue *et al.* 1998), we conclude that the three alleles identified in *C. geoffroyi* have spectral sensitivities identical to those in *C. jacchus*. At the nucleotide level, each *C. geoffroyi* haplotype shows one or two synonymous substitutions (all transitions) from the haplotypes in *C. jacchus* described by Shyue *et al.* (1998). These are as follows, with the *C. geoffroyi* allele first: 543 nm allele: 516 (T versus C, exon 3), 618 (C versus T, exon 4); 556 nm allele: 555 (T versus C, exon 3); 563 nm allele: 525 (T versus C, exon 3) and 618 (C versus T, exon 5).

(b) *Colour data*

The reflectance spectra for the targets (orange- and green-dyed Kix®) and backgrounds (natural grass and green-dyed wood shavings) are shown in figure 2. As expected, there are large differences in the spectra for the target background of grass and orange-dyed Kix®, which are reflected in the mean CIELab values (grass: CIE L^* 40.8, a^* −2.8, b^* 6.6; orange-dyed Kix®: CIE L^* 47.0, a^* 21.1, b^* 14.7; total difference between grass and orange-dyed Kix® = 26.0ΔE^*ab). There were smaller differences between grass and green-dyed Kix® (green-dyed Kix®: CIE L^* 51.8, a^* −11.6, b^* 14.0; total difference between grass and green-dyed Kix® = 15.9ΔE^*ab). Green-dyed wood shavings provided a better match to green-dyed Kix® than grass (green-dyed wood shavings: L^* 59.2, a^* −15.6, b^* 17.1; total difference between green-dyed wood shavings and green-dyed Kix® = 8.9 ΔE^*ab).

(c) *Behavioural experiments*

(i) *Experiment 1*

Table 1 presents the results of experiment 1. Between-groups tests revealed that trichromats (mean 24.5,

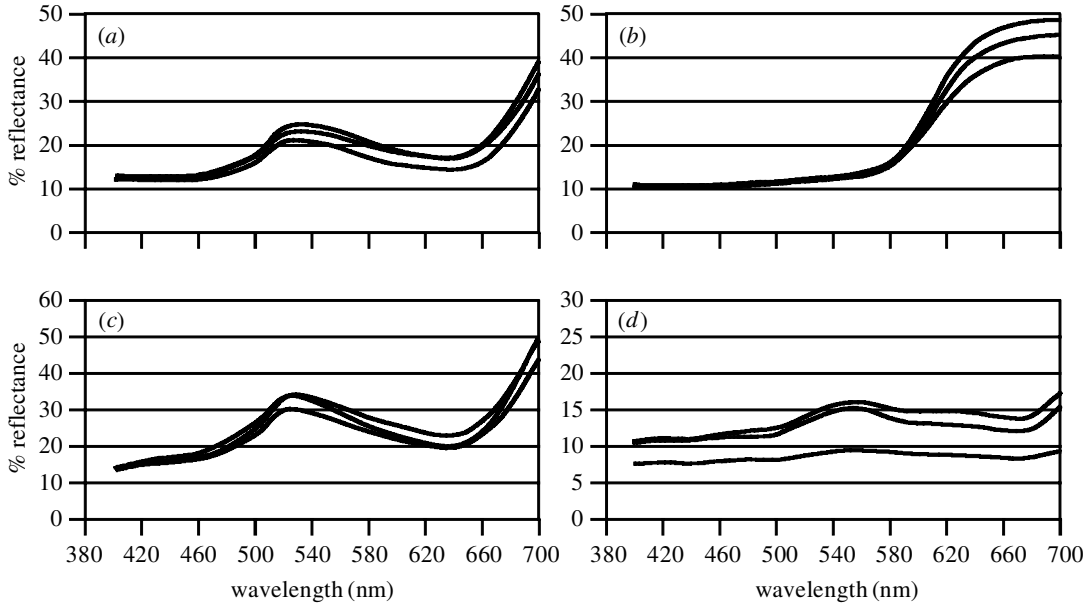

Figure 2. Reflectance spectra of Kix® and background. Each panel shows data for three separate targets, each of which is the average of 8–15 measurements. (*a*) Green Kix®; (*b*) orange Kix®; (*c*) green-dyed wood shavings; and (*d*) grass.

Table 1. *Numbers of Kix® found by dichromats and trichromats in experiments 1 and 2*

	experiment 1 (Kix® broadcast across cage)			experiment 2 (Kix® hidden in green wood shavings)		
	no. of orange found (per cent of total)	no. of green found (per cent of total)	percentage more orange	no. of orange found (per cent of total)	no. of green found (per cent of total)	percentage more orange
trichromats						
Cantor	27 (63%)	16 (37%)	26	39 (54%)	33 (46%)	8
Shiksa	77 (61%)	50 (39%)	21	84 (58%)	60 (42%)	17
Golda	37 (54%)	31 (46%)	9	123 (50%)	121 (50%)	1
Torah	18 (56%)	14 (44%)	13	54 (48%)	58 (52%)	−4
Ysabel	31 (69%)	14 (31%)	38	36 (48%)	39 (52%)	−4
Debbie	32 (59%)	22 (41%)	19	69 (58%)	49 (42%)	17
dichromats						
Papal	16 (44%)	20 (56%)	−11	76 (46%)	88 (54%)	−7
Gretyl	24 (40%)	36 (60%)	−20	116 (51%)	113 (49%)	1
Moishe	26 (49%)	27 (51%)	−2	26 (53%)	23 (47%)	6
MaryKate	12 (50%)	12 (50%)	0	14 (61%)	9 (39%)	22
Yitzhak	28 (48%)	30 (52%)	−3	67 (49%)	71 (51%)	−3
Schlomo	27 (49%)	28 (51%)	−2	167 (52%)	149 (47%)	6
Sophia	11 (37%)	19 (63%)	−27	—[a]	—[a]	—[a]
David	15 (54%)	13 (46%)	7	77 (49%)	80 (51%)	−2

[a] Insufficient total number ($n = 6$) found.

s.e. = 5.7) and dichromats (mean 23.1, s.e. = 3.0) found similar numbers of green Kix® ($U = 23$, $p > 0.05$), but trichromats found significantly more orange Kix® (mean 37.0, s.e. = 8.4) than did the dichromats (mean 19.8, s.e. = 2.5) ($U = 5.5$, $p < 0.05$). Trichromats found significantly more orange than green Kix® ($T = 0$, $p < 0.05$), but dichromats found neither of the two colours more often than the other ($T = 3.5$, $p > 0.05$). On average, trichromats found 20.3% more orange than green Kix® and all of the trichromats found at least 9% more orange than green. Although the sample sizes are small, there was no suggestion that the performance of trichromats with different combinations of alleles (563 nm/553 nm versus 543 nm/556 nm) differed. Most of the dichromats found very similar numbers of orange and green Kix®, and there were no sex differences.

In experiment 1, most of the Kix® discovered by the marmosets (> 90%) were found in the first 5 min of each trial, creating a floor effect for the elapsed times comparisons. Thus there was no significant difference in how quickly the dichromats (mean elapsed seconds = 64.3 and 79.7 for orange and green, respectively; $T = 5$, $p > 0.05$) or

Table 2. *Relative number of Kix® found in the last half (last 5 min) of the trials in experiment 1*

	percentage of orange Kix® found in last 5 min	percentage of green Kix® found in last 5 min	percentage more orange than green Kix® found in last 5 min
trichromats			
Cantor	7.4	6.3	1.2
Shiksa	6.5	4.0	2.5
Golda	8.1	6.5	1.6
Torah	5.6	0.0	5.6
Ysabel	12.9	7.1	5.8
Debbie	0.0	0.0	0.0
dichromats			
Papal	0.0	0.0	0.0
Gretyl	13.0	22.0	−9.0
Moishe	0.0	0.0	0.0
Mary Kate	8.3	0.0	8.3
Yitzhak	10.7	0.0	10.7
Schlomo	3.7	3.6	0.1
Sophia	0.0	0.0	0.0
David	0.0	7.7	−7.7

the trichromats (mean elapsed seconds = 78.4 and 76.6 for orange and green, respectively; $T = 9$, $p > 0.05$) found orange or green Kix® when averaged over all Kix® found throughout the duration of the trials. However, when expressed as the per cent of the total number of that colour found (see table 2), the trichromats found significantly more orange (6.8%) than green (4.1%) Kix® in the last 5 min of the trials ($T = 0$, $p < 0.05$). No such difference emerged for the dichromats (5.0 and 5.4% for orange and green, respectively) ($T = 6$, $p > 0.05$). A between-groups comparison of these times did not yield significance for either green or orange, but the trichromats' means for orange, but not green, were higher than those of the dichromats. The trichromats' data cannot be explained by the possibility that there were fewer green than orange Kix® left unfound late in the trials; going into the last 5 min of the trials, 41.5% of the green Kix® remained undiscovered, while 33.7% of the orange Kix® remained undiscovered.

(ii) *Experiment 2*

Table 1 also presents the results of experiment 2. Neither of the two colours was found in greater numbers by trichromats or dichromats ($T = 5, 12$, $p > 0.05$ for trichromats and dichromats, respectively). The between-groups comparisons also failed to reveal any advantage for the trichromats under the conditions of experiment 2 ($U = 16$, $p > 0.05$ for green Kix®; $U = 20$, $p > 0.05$ for orange Kix®). Similarly, the comparisons of elapsed times (how quickly the Kix® were found) did not reveal differences between trichromats and dichromats or differences within groups according to colour. Marmosets were found to use a differing foraging strategy in experiments 1 and 2: in experiment 1 individuals visually scanned for Kix® from low branches or whilst on the ground, while in experiment 2 individuals immediately stood on the trays and carefully sifted through the wood shavings with their hands.

4. DISCUSSION

A number of investigations have supported the assumption that trichromatic colour vision in primates is an adaptation related to foraging. However, these investigations have been limited to measurements of absorption properties of photopigments and/or spectral reflectance of natural objects such as plant materials (e.g. Nagle & Osorio 1993; Osorio & Vorobyev 1996; Regan *et al*. 1996, 1998; Lucas *et al*. 1998). Here we report the first data, to our knowledge, to show that marmosets foraging under semi-natural conditions differ in their ability to locate a food source depending on the colour of that food and the photopigment genotype of the individual. Trichromats found significantly more orange Kix® than did the dichromats when the cereal was broadcast among the naturally occurring foliage and dirt of the marmosets' large, outdoor enclosure, but green Kix® were found with equal frequency by the trichromats and dichromats. The fact that trichromats and dichromats did not differ in the number of green Kix® discovered suggests that there were no differences between them in overall foraging motivation or skill. Rather, the results are as predicted by theory: trichromats found the orange Kix® easier to see against a predominantly green background than did the dichromats, whereas neither had an advantage in detecting green Kix® against the green background.

In confirmation of this interpretation, in experiment 1, in which marmosets foraged for Kix® cereal on the floor of the cage, trichromats found significantly more orange than green pieces of Kix® while dichromats showed no such advantage in finding orange over green cereal pieces. In addition, the foraging advantage held by trichromats is further supported by an examination of the data from the second 5 min period of the trials in experiment 1. Both di- and trichromat marmosets were very successful at finding Kix® of both colours, and they found them at the highest rates early in the trials. Relatively few Kix® of either colour were found in the last 5 min of a trial, and presumably those particular Kix® were harder to see than the Kix® found in the first few minutes, because they were better obscured by vegetation and/or dappled lighting. One would predict that the trichromats would be particularly successful at finding orange Kix®, compared with green Kix®, when the Kix® were relatively difficult to see. When expressed as the per cent of the total number of that colour found, the trichromats found significantly more orange than green Kix® in the last 5 min of the trials. There was no such difference for the dichromats. It is interesting to note that these effects were found in trichromatic marmosets with 543/556 nm and 556/563 nm phenotypes, which are expected to have less discriminatory ability than those with the 543/563 nm phenotype. Experiments to determine the importance of the background colour (green versus brown) in these effects are underway.

In contrast to the results of experiment 1, in experiment 2 in which the Kix® were placed on trays with wood shavings, the trichromats were not more successful than dichromats at finding orange rather than green Kix®, nor were the trichromats better at finding orange Kix® than the dichromats. This was in spite of the fact that the overall difference in colour contrast between orange

target and background (at least as measured by the CIELab method which is appropriate to human colour vision) was greater for experiment 2 than experiment 1, while the difference in colour contrast between green target and background was lower in experiment 2 than experiment 1. As the marmosets searched for the Kix® at very close range in experiment 2 using a markedly different technique from that used in experiment 1, other cues might have reduced the relative salience of colour for the trichromats. In particular, olfactory or tactile cues might have alerted the monkeys to the location of the Kix® in the pans, or attention to the shape of the round pieces of cereal against the more angular shavings of wood might have mitigated the advantages of colour contrast. In any case, these results suggest that the advantages of trichromacy in locating food in the red/orange part of the spectrum may not generalize to all conditions under which primates forage.

In conclusion, we have shown that trichromats are better able than dichromats to find orange food in at least some conditions. If this difference translates as expected into improved detection of orange/red fruit or insects by trichromats in the wild, it would provide the necessary selective pressure for maintenance of the opsin polymorphism in nature (Shyue *et al*. 1995). As marmosets are not folivorous, an advantage for trichromats in detecting young leaves (Lucas *et al*. 1998) can be discounted in these species. Whether the persistence of dichromats in wild populations is due to the lack of opsin gene duplication on the X-chromosome, or to a specific advantage for dichromats over trichromats in certain situations, is a much discussed issue (e.g. Jacobs 1995). Experiments designed to test the possibility that dichromats might enjoy an advantage in detection of colour-camouflaged food and/or predators (Morgan *et al*. 1992) are currently being pursued.

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