A foraging advantage for dichromatic marmosets (*Callithrix geoffroyi*) at low light intensity

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Most New World monkey species have both dichromatic and trichromatic individuals present in the same population. The selective forces acting to maintain the variation are hotly debated and are relevant to the evolution of the ‘routine’ trichromatic colour vision found in catarhine primates. While trichromats have a foraging advantage for red food compared with dichromats, visual tasks which dichromats perform better have received less attention. Here we examine the effects of light intensity on foraging success among marmosets. We find that dichromats outperform trichromats when foraging in shade, but not in sun. The simplest explanation is that dichromats pay more attention to achromatic cues than trichromats. However, dichromats did not show a preference for foraging in shade compared with trichromats. Our results reveal several interesting parallels with a recent study in capuchin monkeys (*Cebus capucinus*), and suggest that dichromats should perform better for certain tasks, contributing to the maintenance of the colour vision polymorphism.

**Keywords:** colour vision; trichromacy; opsin; callitrichid

1. **INTRODUCTION**

Most New World monkeys have a polymorphic system of colour vision, whereby individuals of the same species may be either dichromatic (roughly equivalent to red–green colour-blind) or trichromatic (*Mollon et al. 1984*). The variation in colour vision is controlled by a single polymorphic opsin locus on the X chromosome, such that males and homozgyous females are dichromats, whereas heterozygous females are trichromats. The polymorphism is maintained by balancing selection, but the mechanisms acting are the subject of considerable debate (e.g. *Mollon et al. 1984; Surridge & Mundy 2002; Surridge et al. 2003; Hiramatsu et al. 2008*). Trichromats have improved discrimination in the red–green part of the spectrum and, although the spectral separation of the three pigments in callitrichids (i.e. marmosets and tamarins) is small (maximum sensitivities approx. 543, 556 and 563 nm), modelling shows that they should be sufficient in assisting foraging tasks, such as finding ripe fruit among leaves (Osorio *et al.* 2004; Wachtler *et al.* 2007). Captive studies support these predictions: trichromatic callitrichids forage more efficiently than dichromats when they can use red/orange colour cues (Caine & Mundy 2000), including colours based on actual fruit eaten by monkeys in the wild (Smith *et al.* 2003). However, recent studies on wild capuchins (*Cebus capucinus*) and spider monkeys (*Ateles geoffroyi frontatus*) failed to find the expected foraging advantage for trichromats (Melin *et al.* 2007; Hiramatsu *et al.* 2008).

There are theoretical grounds for expecting costs for achromatic (i.e. luminance) vision associated with trichromacy (Osorio & Vorobyev 2005), but ecologically relevant tasks where dichromatic monkeys outperform trichromats are little studied. A prominent idea is that dichromats are better at camouflage breaking when there is a colour match between the target and the background (Morgan *et al.* 1992). A test in captive marmosets was equivocal: a red–green camouflage effect was demonstrable when trichromats foraged under different conditions, but dichromats did not significantly outperform trichromats on this task (Caine *et al.* 2003).

Light intensity and spectral composition vary with location in the rainforest and may well influence primate foraging. Theoretical calculations suggest that the advantage of trichromacy over dichromacy should increase at low light levels, because of low photon catch by the S-cone mechanism (Osorio *et al.* 2004). However, there is little empirical work on differential effects of light intensity on foraging ability in dichromats and trichromats. Verhulst & Maes (1998) gave evidence that in spatial tasks at low light levels human dichromats do better than trichromats, but this effect was not repeated (Simunovic *et al.* 2001). Interestingly, light intensity was recently reported to affect foraging of capuchin monkeys for insects (Melin *et al.* 2007): dichromats made more capture attempts under shaded conditions, but not sunny conditions, than trichromats. If trichromats and dichromats differ in performance in ecologically relevant visual tasks this leads to the prediction that they may spend more time on some tasks than others, leading to niche specialization. In a potential example of this, Yamashita and co-workers (2005) found that in certain polymorphic species females spend more time foraging at high light levels than males.

This study compares visual foraging by dichromats and trichromats at a range of photopic intensities; we recorded both performance (i.e. foraging efficiency) and the time spent foraging.

2. **MATERIAL AND METHODS**

Subjects were nine female and six male adult marmosets, *Callithrix geoffroyi*. Four of the marmosets lived in one family group and the remaining 11 lived in another. The monkeys lived out-of-doors at the San Diego Zoo’s Institute for Conservation Research. The large enclosures are described elsewhere (Caine 1996); here it is particularly relevant that the enclosure floors are covered with dirt, weeds, grass and potted plants. The monkeys forage freely and regularly among these substrates. The X-linked opsin locus genotypes of the individuals were reported previously (Caine *et al.* 2003).
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3. RESULTS

The capture rates of individuals are shown in table 1. Within-group comparisons were made with Wilcoxon tests and between-group comparisons were made with Mann–Whitney tests. Capture rates of dichromats did not differ significantly among the three light conditions (average rates of 1/35 s in shade, 1/36.8 s in partial shade, 1/32.9 s in the sun). Trichromats, however, had a significantly slower rate of captures in the shade (average 1/31.8 s) and in partial shade (1/54.1 s) than in the sun (1/32.1 s; $z = 2.02$; $p = 0.04$, for both comparisons). Notably, all five trichromats had slower capture rates in shade than in sun. Between-group comparisons showed no difference between the dichromats and trichromats for capture rates in the sun ($z = 0.61$, $p = 0.54$) or partial shade ($z = 0.98$, $p = 0.32$) but a significantly slower rate for trichromats than dichromats in the shade ($z = 2.2$; $p = 0.03$). Sex and trichromacy are confounded, but unlike trichromatic females, foraging of dichromatic females did not differ between shade and sun (shade $= 1/41.3$ s; sun $= 1/34.4$ s; $z = 1$, $p = 0.28$), and neither did dichromatic females differ from males in either shade (1/41.3 s, 1/30.8 s, respectively; $z = 1.2$, $p = 0.20$) or sun (1/34.4 s, 1/32 s; $z = 0.64$; $p = 0.52$). Even though trichromats were significantly less successful at finding the cereal pieces in shade than in sun, the per cent of total foraging time spent in the shade was virtually identical to that of dichromats (33.6 versus 32.9%, respectively). There were no sex differences in how many total cereal pieces were found during the course of the study, suggesting that there was no systematic bias in foraging effort across sex.

4. DISCUSSION

We demonstrate a foraging advantage for dichromatic marmosets under conditions of low light intensity. An interaction between the effects of light intensity and colour vision phenotype has not been previously shown for callitrichid primates. As discussed now, although the mechanism behind this effect is unclear, it has important consequences for the foraging strategies of wild callitrichids and the mechanism of maintenance of the colour vision polymorphism. There are intriguing parallels with a recent study demonstrating that wild dichromatic capuchin monkeys had higher insect-foraging efficiency than trichromats in shade but not in sunlight (Melin et al. 2007).

What is the mechanism behind the effect seen? Modelling suggests that the advantage of trichromacy over dichromacy for detecting fruit among leaves is greatest at low intensities when performance is limited by photon noise (Olsorio et al. 2004). As both the target and background contain green and yellow hues, it is conceivable that trichromats’ foraging may have been affected by a ‘red–green camouflage effect’, whereby the red–green signal inhibited detection of the targets, but, if so, it is difficult to explain why this was not also found in the sun condition. A simpler explanation is that the dichromats make better use of achromatic cues, and so are less impaired by the reduced utility of colour vision at low intensities. This is consistent with the advantage of dichromat over trichromat capuchins in finding cryptic insects (Melin et al. 2007; see also Morgan et al. 1992). If this explanation is correct, then it might be expected that dichromats and trichromats would spend different amounts of time foraging in the different light conditions (cf. Yamashita et al. 2005), but this was not the case for the marmosets and it is interesting that Melin et al. (2008) did not find evidence of such niche specialization in capuchins either.

The dichromatic advantage uncovered here could be important for the detection of dull-coloured fruits and cryptically coloured insect prey. Purple, black, brown and green fruits are important in the diet of wild tamarins (Smith et al. 2003), and these fruits are not suited to detection using the red–green colour opponent system. Unfortunately, little is known about the colour of foods eaten in the wild by C. geoffroyi.

In terms of the evolutionary forces acting on the opsin polymorphism, the present results are important since they suggest that there are ecologically relevant
Table 1. Rate of capture (time in seconds) of cereal pieces under different light conditions.

<table>
<thead>
<tr>
<th>capture rate</th>
<th>sex</th>
<th>group</th>
<th>genotype</th>
<th>sun</th>
<th>shade</th>
<th>partial shade</th>
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<tr>
<td>trichromats</td>
<td></td>
<td>Cantor F 1</td>
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<td>57</td>
<td>62.1</td>
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<td></td>
<td></td>
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<td>37.7</td>
<td>52</td>
<td>64.4</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Torah F 2</td>
<td>543/556</td>
<td>68</td>
<td>69</td>
<td>86</td>
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<td></td>
<td></td>
<td>Ysabel F 2</td>
<td>543/556</td>
<td>12</td>
<td>27.4</td>
<td>27</td>
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<tr>
<td></td>
<td></td>
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<td>543/556</td>
<td>17.9</td>
<td>54</td>
<td>31.4</td>
</tr>
<tr>
<td>dichromats</td>
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<td>37</td>
<td>37</td>
<td>39</td>
</tr>
<tr>
<td></td>
<td></td>
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<td>556/556</td>
<td>40</td>
<td>52.4</td>
<td>40</td>
</tr>
<tr>
<td></td>
<td></td>
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<td>36.2</td>
<td>35.6</td>
<td>29.3</td>
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<td>556/556</td>
<td>24.6</td>
<td>40.3</td>
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<td>17.7</td>
<td>45.1</td>
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<tr>
<td></td>
<td></td>
<td>Moishe M 2</td>
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<td>28.3</td>
<td>20.6</td>
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</tr>
<tr>
<td></td>
<td></td>
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<tr>
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</table>

visual tasks for which dichromats are better suited. This implies that frequency-dependent selection involving dichromats versus trichromats is an important component of selection at this locus, as suggested by other authors (Osorio et al. 2004; Hiramatsu et al. 2008).

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