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

Nancy G. Caine¹, Daniel Osorio²
and Nicholas I. Mundy^{3,*}

¹Department of Psychology, California State University, San Marcos, CA 92096, USA

²School of Life Sciences, University of Sussex, Brighton BN1 9QG, UK

³Department of Zoology, University of Cambridge, Downing Street, Cambridge CB3 2EJ, UK

*Author for correspondence (nim21@cam.ac.uk).

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 catarrhine 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 dichromat advantage for certain tasks contributes to 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 homozygous 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, grasses 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).

Electronic supplementary material is available at <http://dx.doi.org/10.1098/rsbl.2009.0591> or via <http://rsbl.royalsocietypublishing.org>.

(a) Stimuli

The stimuli were pieces of toasted rice cereal (1–1.5 cm) that were sprayed with green food colouring to create a mottled green/tan appearance. Consequently, they blended in with the substrates of the enclosure, making the foraging task challenging (figure S1 in the electronic supplementary material). The cereal pieces were picked up and eaten by the marmosets one at a time, making it easy to record each occasion when a piece was found and consumed. Representative reflectance spectra from the stimuli combined with modelling of photoreceptor responses showed that there was a substantial red–green signal among their green/tan coloration (figure S2 in the electronic supplementary material).

(b) Procedure

The cereal pieces were broadcast across the floors of the enclosures at the beginning of each trial (two-thirds cup for larger group, one-third cup for smaller group). Data were only collected on sunny days. Because of the angle of the sun, the presence of plants in the cages, and shade cloth over some parts of the mesh walls, there were always multiple areas of sun, partial shade and shade. No attempt was made to ensure that there were equal numbers of cereal pieces in the shade, partial shade or sunny areas. Indeed, it would be impossible to do so, given that the amount of light in any particular spot could change over the course of a trial because of passing clouds.

Light conditions for specific areas were defined as follows. Full sun: no detectable shadows. Shade: sunlight blocked by one or more sources such that the area was in full shadow. Partial shade: sunlight filtered by one or more sources. All data were collected by one observer, but the reliability of identifying areas as sun, partial shade or shade was assessed by comparing independent scores of the observer and another research assistant (not working on this project) on 20 randomly selected areas of the marmosets' enclosures. Of the 20, 18 judgments were the same (=90% agreement). Representative illuminance readings were as follows (mean $\pm$ s.e.m., all $n = 3$): shade: 578.3 ± 31.9 lx; partial shade: 5140 ± 1212 lx; sun: $38\,560 \pm 3460$ lx.

Behavioural data collection consisted of two, 5 min focal animal trials per group on each of 75 days. Every marmoset was observed five times (five, 5 min trials) during the first 5 min after the cereal was presented, and five times during the second 5 min after cereal was presented. During the focal trials, continuous recordings were made of time spent foraging and the number of captures in each of the three conditions (sun, partial shade, shade). All animals in a group foraged together, but low competition and cage size ensured that interference with the focal animal by other group members during recordings was negligible. All data are in terms of rates of foraging success ('captures'): average number of seconds required to capture a piece of cereal.

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 1/51.8 s) and in partial shade (1/54.1 s) than in the sun (1/32 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 ($z = 2$; $p = 0.03$). 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 (Osorio *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.

				capture rate		
	sex	group	genotype	sun	shade	partial shade
<i>trichromats</i>						
Cantor	F	1	556/563	24.5	57	62.1
Golda	F	1	556/563	37.7	52	64.4
Torah	F	2	543/556	68	69	86
Ysabel	F	2	543/556	12	27.4	27
Debbie	F	2	543/556	17.9	54	31.4
<i>dichromats</i>						
Gretyl	F	1	556/556	37	37	39
MaryKate	F	2	556/556	40	52.4	40
Sophia	F	2	556/556	36.2	35.6	29.3
Esther	F	2	556/556	24.6	40.3	36.5
Papal	M	1	556	17.7	45.1	65.3
Moishe	M	2	556	28.3	20.6	34.7
Yitzhak	M	2	556	35	27.2	36.3
Schlomo	M	2	556	39.1	40.7	26.9
Emmett	M	2	556	21.7	22.5	30.5
David	M	2	543	50	28.8	29.5

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).

We thank the marmoset husbandry staff for their cooperation. This work was funded by the Leverhulme Trust and BBSRC.

- Caine, N. G. 1996 Foraging for animal prey by outdoor groups of Geoffroy's marmosets (*Callithrix geoffroyi*). *Int. J. Primatol.* **17**, 933–945. (doi:10.1007/BF02735295)
- Caine, N. G. & Mundy, N. I. 2000 Demonstration of a foraging advantage for trichromatic marmosets (*Callithrix geoffroyi*) dependent on food colour. *Proc. R. Soc. Lond. B* **267**, 439–444. (doi:10.1098/rspb.2000.1019)
- Caine, N. G., Surridge, A. K. & Mundy, N. I. 2003 Dichromatic and trichromatic *Callithrix geoffroyi* differ in relative foraging ability for red–green color camouflaged and non-camouflaged food. *Int. J. Primatol.* **24**, 1163–1175. (doi:10.1023/B:IJOP.0000005985.18112.25)
- Hiramatsu, C., Melin, A. D., Aureli, F., Schaffner, C. M., Vorobyev, M., Matsumoto, Y. & Kawamura, S. 2008 Importance of achromatic contrast in short-range fruit

- foraging of primates. *PLoS ONE* **3**, e3356. (doi:10.1371/journal.pone.0003356)
- Melin, A. D., Fedigan, L., Hiramatsu, C., Sendall, C. & Kawamura, S. 2007 Effects of colour vision phenotype on insect capture by a free-ranging population of white-faced capuchins (*Cebus capucinus*). *Anim. Behav.* **73**, 205–214. (doi:10.1016/j.anbehav.2006.07.003)
- Melin, A. D., Fedigan, L., Hiramatsu, C. & Kawamura, S. 2008 Polymorphic color vision in white-faced capuchins (*Cebus capucinus*): is there foraging niche divergence among phenotypes? *Behav. Ecol. Sociobiol.* **62**, 659–670. (doi:10.1007/s00265-007-0490-3)
- Mollon, J. D., Bowmaker, J. K. & Jacobs, G. H. 1984 Variations in colour vision in a New World primate can be explained by polymorphism of retinal photopigments. *Proc. R. Soc. Lond. B* **222**, 373–399. (doi:10.1098/rspb.1984.0071)
- Morgan, M. J., Adam, A. & Mollon, J. D. 1992 Dichromats detect colour-camouflaged objects that are not detected by trichromats. *Proc. R. Soc. Lond. B* **248**, 291–295. (doi:10.1098/rspb.1992.0074)
- Osorio, D. & Vorobyev, M. 2005 Photoreceptor spectral sensitivities in terrestrial animals: adaptations for luminance and colour vision. *Proc. R. Soc. B* **272**, 1745–1752. (doi:10.1098/rspb.2005.3156)
- Osorio, D., Smith, A. C., Vorobyev, M. & Buchanan-Smith, H. M. 2004 Detection of fruit and the selection of primate visual pigments for color vision. *Am. Nat.* **164**, 696–708. (doi:10.1086/425332)
- Simunovic, M. P., Regan, B. C. & Mollon, J. D. 2001 Is color vision deficiency an advantage under scotopic conditions? *Invest. Ophthalmol. Vis. Sci.* **42**, 3357–3364.
- Smith, A. C., Buchanan-Smith, H., Surridge, A. K., Osorio, D. & Mundy, N. I. 2003 The effect of colour vision status on the detection and selection of fruits by tamarins (*Saguinus* spp.). *J. Exp. Biol.* **206**, 3159–3165. (doi:10.1242/jeb.00536)
- Surridge, A. K. & Mundy, N. I. 2002 Trans-specific evolution of opsin alleles and the maintenance of trichromatic vision in callitrichine primates. *Mol. Ecol.* **11**, 2157–2169. (doi:10.1046/j.1365-294X.2002.01597.x)
- Surridge, A. K., Osorio, D. & Mundy, N. I. 2003 Evolution and selection of trichromatic vision in primates. *Trends Ecol. Evol.* **18**, 198–205. (doi:10.1016/S0169-5347(03)00012-0)
- Verhulst, S. & Maes, F. W. 1998 Scotopic vision in colour-blinds. *Vis. Res.* **38**, 3387–3390. (doi:10.1016/S0042-6989(97)00339-8)
- Wachtler, T., Doi, E., Lee, T.-W. & Sejnowski, T. J. 2007 Cone selectivity derived from the responses of the retinal cone mosaic to natural scenes. *J. Vision* **7**, 1–14.
- Yamashita, N., Stoner, K. E., Riba-Hernandez, P., Dominy, N. J. & Lucas, P. W. 2005 Light levels used during feeding by primate species with different color vision phenotypes. *Behav. Ecol. Sociobiol.* **58**, 618–629. (doi:10.1007/s00265-005-0936-4)