

1       **The effect of colour vision status on insect prey capture efficiency by**  
2                               **captive and wild tamarins (*Saguinus* spp.)**

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4  
5       **Abstract**

6       The colour vision polymorphism of most New World primates is a model system  
7       to study the function of colour vision. Theories for the evolution of primate  
8       trichromacy focus on the efficient detection and selection of ripe fruits and  
9       young leaves amongst mature leaves, when trichromats are likely to be better  
10      than dichromats. We provide data on whether colour vision status affects insect  
11      capture in primates. Trichromatic tamarins (*Saguinus* spp.) catch more prey  
12      than dichromats, but dichromats catch a greater proportion of camouflaged prey  
13      than trichromats. The prey caught does not differ in size between the two visual  
14      phenotypes. Thus two factors may contribute to the maintenance of genetic  
15      polymorphism of middle- to long-wavelength photopigments in Platyrrhines: the  
16      advantage in finding fruit and leaves, which supports the maintenance of the  
17      polymorphism through a heterozygote advantage, and the dichromats'  
18      exploitation of different (e.g., camouflaged) food, which results in frequency-  
19      dependent selection on the different colour vision phenotypes.

20  
21      Key words: polymorphic colour vision; trichromacy; dichromacy; sex differences;  
22      primate

## Introduction

Colour vision is highly variable within the primate order (e.g., Jacobs 1995). All catarrhines (Old World primates) have the same type of colour vision, based on three classes of cone-pigments (trichromacy). In contrast, the platyrrhines (New World primates) and strepsirrhines (lemurs; Tan & Li 1999) show inter- and intra-species variation in their colour vision. Like catarrhines, most platyrrhines have an autosomal short-wavelength (S) pigment gene, but whereas catarrhines have separate middle-wavelength (M) and long-wavelength (L) loci on their X chromosome, platyrrhines have only a single locus, which is represented by several alleles that code for M to L pigments. The only known exceptions are howler monkeys (*Alouatta* spp.), which resemble catarrhines and are uniformly trichromatic (Jacobs 1998). The number of different alleles at this M/L locus varies from one to five in night (*Aotus* spp.) and titi monkeys (*Callicebus* spp.) respectively (see Surridge et al., 2003). Tamarins (*Saguinus* spp.) have three alleles, each coding for a cone pigment (opsin) with a different peak spectral absorbance (Mollon *et al.* 1984). Behavioural experiments on squirrel monkeys (*Saimiri sciureus*) and other platyrrhines (Jacobs 1984, 1998) confirm that heterozygous females are trichromatic, while males and homozygous females are dichromatic.

Potentially, a major advantage of trichromacy is for detection and identification of food, particularly ripe fruits or young leaves in the dappled light of the forest canopy (Dominy & Lucas 2001; Regan *et al.* 2001). Although field studies by Vogel et al. (2007), Hiramatsu et al. (2008) and Melin et al. (2008) failed to demonstrate a trichromat advantage in fruit foraging, there is theoretical (Osorio

& Vorobyev 1996; Parraga et al. 2001; Regan et al. 2001; Osorio et al. 2004) and empirical (Caine & Mundy 2000; Smith et al. 2003) support for this. Thus the polymorphism of the M/L visual pigment gene could be maintained by balancing selection involving a heterozygote advantage (see Surridge et al. 2003). If trichromacy has such an advantage, one must ask why most diurnal platyrrhines have not developed routine trichromacy like the catarrhines. Their nervous systems can support trichromacy, as many female platyrrhines have trichromacy. The opsin-gene duplication step required to take them to routine trichromacy may be mechanically difficult (Jacobs 1995), although the duplication has occurred at least twice: in both howlers and catarrhines. Alternatively, it may be that the colour vision polymorphism is itself adaptive.

Recent evidence of balancing selection (where alleles are maintained within a population through natural selection) has been found by Hiwatashi *et al.* (2010) who suggest a mechanism based on mutual benefit between phenotypes rather than one of frequency-dependent selection for the least common phenotypes. The alternative theories underlying the maintenance of visual polymorphism are reviewed by Kawamura et al. (2010).

Dichromacy has several possible advantages. First, there is evidence that dichromatic humans see better in dim light than trichromats (Verhulst & Maes 1998; but see Simunovic et al. 2001), and Caine et al. (2010) recently reported a foraging advantage for dichromatic Geoffroy's marmosets (*Callithrix geoffroyi*) at low light intensities. Second, dichromats may have improved spatial vision (e.g. Osorio *et al.* 1998). Finally, it may be that dichromats are superior at visually breaking camouflage. Colour is a powerful organising cue to

visual figure-ground discrimination, so that the contours of a cryptic target may be less easily detected against irregular patches of colour that compete as cues for image segregation. This effect is exploited by Ishihara tests for colour deficiency (Birch 1997). Experiments confirm that human and non-human primate dichromats are better able to detect a perceptual organisation based on texture while the target is masked for normal trichromats by a rival organisation based on hue (Morgan *et al.* 1992; Saito *et al.* 2005). Applying the same principle to dichromatic monkeys in their natural habitat would present them with an advantage in the detection of camouflaged prey and predators(e.g., Mollon *et al.* 1984). This hypothesis predicts that dichromats would be more efficient at prey detection, and as a result would capture more camouflaged prey in particular than their trichromatic counterparts.

Recently Melin *et al.* (2007; 2010) compared the prey foraging efficiency of dichromatic and trichromatic white-faced capuchins (*Cebus capucinus*). This indicated a trade-off between efficiency and time spent foraging for different prey categories. Whilst as predicted from a greater ability to break camouflage, dichromats were more efficient at capturing exposed prey, they spent more time foraging for embedded prey. Conversely, trichromats were most efficient in foraging for embedded prey and spent more time searching for exposed prey. Perhaps because of this apparent balance between time and efficiency, dichromats captured no more prey than their trichromatic counterparts overall. The observed difference in foraging efficiency for embedded prey is contrary to expectations, as colour vision is irrelevant. However without data on prey size the results of such studies of foraging efficiency may be confounded, as

99 consuming a single large item can be more efficient than consuming several  
100 smaller ones. Moreover, such studies should ideally take into account the  
101 camouflage or anti-predation strategies of the prey in addition to their physical  
102 location.

103  
104 The present study addresses several of these issues and **investigates the**  
105 **hypothesis for a dichromat advantage in the detection of camouflaged objects**  
106 **by dichromats and whether this translates into a potential fitness advantage**  
107 through the examination of prey capture rates by dichromatic and trichromatic  
108 tamarins. Tamarins are small, diurnal, arboreal callitrichid primates; they spend  
109 much of their time foraging for insects (e.g., Smith, 2000), which are an  
110 important source of protein and lipids. Katydids (Tettigoniidae), in particular  
111 sylvan (Pseudophyllinae) and bush katydids (Phaneropterinae), account for most  
112 prey consumed by tamarins (Smith, 2000). Nocturnal katydids have elaborate  
113 cryptic morphology and behavioural strategies to evade predation during the  
114 day (Nickle & Heymann, 1996). Their diurnal roosting strategies are classified  
115 into four principal categories: concealed, green generalist, bark mimic, and leaf  
116 mimic (Nickle & Castner, 1995). All species using strategies other than  
117 concealment pass the day exposed to view. Bark and leaf mimics closely  
118 resemble bark and leaves respectively, whereas green generalists are less  
119 specialised than leaf mimics. An advantage of tamarins over larger primates for  
120 dietary field studies is their habit of discarding the tegmina of katydid prey, thus  
121 allowing its identification and hence determination of the anti-predation strategy.  
122 The colour vision polymorphism of tamarins is also well understood from  
123 laboratory studies both of opsin spectral sensitivities and of molecular genetics

(e.g., Surridge et al. 2002). By combining controlled experimentation in captivity with field observations, this study examines insect capture rates and investigates whether dichromatic tamarins are better able to catch camouflaged insects than their trichromatic conspecifics.

## **Genotyping Methods**

Visual status was determined (by AKS) by direct sequencing of exons 3, 4 and 5 of the X-linked visual pigment gene. DNA was extracted from faecal material collected from the forest floor without disturbing the wild tamarins or plucked hair from captive tamarins. To pluck hair, no restraint was necessary. The captive tamarins were enticed to the enclosure mesh with a piece of favoured food and a small quantity of hairs (~4 at a time) was plucked through the mesh from the tamarin's tail with sterilised tweezers. In most cases the tamarins did not move during hair plucking but continued to eat the food. Those that moved returned quickly to the food suggesting the plucking caused transient discomfort; a Home Office Inspector confirmed this method of hair plucking does not require formal regulation. The DNA was amplified and sequenced as described previously (Surridge et al. 2002). The amino acids at sites involved in spectral tuning of the photopigment molecule were determined directly from DNA sequences. These were then used to infer the colour vision phenotype (full details are given in Surridge et al. 2002).

## **Captive Study**

*Study animals and housing*

Four groups of saddleback (*Saguinus fuscicollis*) (C1 N=3; C2 N=4; C3 N=2; C4 N=2) and one group of red-bellied tamarins (*Saguinus labiatus*) (C5 N=2) housed at Belfast Zoological Gardens were studied on dry, non-sunny days between June and August 1998. Study animals and their colour vision phenotype are listed in Table 1. All were adults and none of the females was pregnant. The monkeys lived in indoor/outdoor enclosures off exhibit to the public, and with the exception of routine husbandry and testing, had free access between the two enclosures using a hatch. Indoor enclosures measured approximately 1.65 m x 1.55 m x 1.5 m, and had a concrete floor covered with wood shavings, branches, a deep shelf, a nest box, a heat lamp and fluorescent lighting. Testing took place in the outside enclosures (1.95 m x 1.55 m x 3.50 m) that were well furnished with branches and live shrubs, and the floor was covered with bark chips in which grass grew in some places. Fresh water was given daily and was available *ad libitum* from a bowl. The tamarins were fed once daily, usually before 12.30 h with freshly prepared fruit and vegetables and primate pellets together with a selection of marmoset jelly, eggs, vegetables, chicken and insects to maintain variety. Vitamin supplements were also given regularly. The observer (MJP) did not know the visual status of the tamarins at the time of testing.

### Procedure

Study animals were shut indoors whilst the outdoor enclosure was baited with a single adult locust, 5th instar *Locusta* or *Schistocerca* (these brown and yellow diurnal acridids rely flight to evade predation, as such species do not fit the diurnal roosting anti-predation categories of Nickle & Castner, 1995, used to

173 **classify nocturnal tettigoniids).** The locust was placed upon one of three  
174 substrates - a branch, green grass or bare earth - and fixed to the substrate with  
175 garden wire. After baiting, the study animals were allowed access outdoors.  
176 Monkeys in adjacent cages were locked indoors during testing to minimise  
177 disturbance.

#### 178 179 *Recording methods*

180 Data were recorded using continuous behavioural sampling with OBSERVER  
181 software. Twelve 15-minute sessions were performed on each group, four upon  
182 each of the three substrate types. Groups received one session per day,  
183 conducted opportunistically throughout the day. Data were collected on latency  
184 to exit the indoor enclosure, and **the identity of the first animal to** touch the  
185 insect.

#### 186 187 *Analyses*

188 **As priority of access to the outdoor enclosure may have influenced detection of the**  
189 **locust the latency to exit the indoor enclosure was compared between dichromats**  
190 **and trichromats using a Mann-Whitney test. The frequencies with which**  
191 **dichromats and trichromats were the first to touch the locust were examined using**  
192 **an exact test. To remove the potential confound of sex, capture rates were then**  
193 **compared between dichromatic and trichromatic females, with the expected**  
194 **number of captures calculated as a function of the total number of captures and**  
195 **individuals within each group.**

#### 196 197 *Results*



There was no difference in the latency to exit the indoor enclosure between dichromats and trichromats (Mann-Whitney  $U=19$ , 13 D.F.,  $P=0.48$ ). Trichromats were significantly more likely than dichromats to be the first to touch the locust (Exact test  $\chi^2=5.6$ , 1 D.F.,  $P=0.02$ ). Background substrate had no effect on the number touched. When the analyses were limited to females from groups with both di- and trichromatic females and trials where the locust was found (Groups C1 N=12 captures; C2 N=8 captures; C5 N=9 captures), on average trichromat females (N=5) captured 1.6 times as many prey as expected and dichromat females (N=3) caught 0.4 what was expected. This equates to trichromat females making 2.0 more captures than expected, and dichromats making 2.2 fewer captures than expected. Although this is a small sample, it suggests that better insect detection and capture is not related to being female per se, but that trichromacy plays a critical role.

## Field Study

### *Study animals and field site*

Two mixed-species groups of saddleback and moustached tamarins (*Saguinus mystax*) (Troop 1 saddleback N=4, moustached N=7; Troop 1 saddleback N=8, moustached N=8) were observed (by ACS) at the Estación Biológica Quebrada Blanco (for study site details, see Heymann & Hartmann 1991). Study animals and their colour vision phenotypes are listed in Table 1. Both mixed-species troops were well habituated to observers.

### *Recording methods*

The tamarins were observed for approximately 14 days each month, with each species being the focus of observations for seven days. Troop 1 was followed exclusively from January - June 2000. From September until December 2000, observations were divided between Troops 1 and 2. Troop 1 was observed for a total of 126 full days (1234 hrs), and Troop 2 for 25 full days (249 hrs).

Data on insect capture and feeding were collected **whenever observed**. The time at which each tamarin was observed to capture or feed on a prey item was recorded, along with the identity of the prey item to the most precise taxonomic level possible. Where possible, the wings (tegmina and hind wings) and other parts of the prey discarded by the feeding tamarins were collected and labelled for subsequent identification using the collections of the Department of Entomology of the British Museum of Natural History, London and the Systematic Entomology Laboratory of the Smithsonian Institution, Washington. The diurnal roosting strategies of the prey were classified following Nickle and Castner (1995): bark mimic, leaf mimic, green generalist and concealed. Tegmina area, as a proxy for insect size, was derived from on a simple length by width calculation (as most katydid tegmina are approximately rectangular). Leaf mimics (Pseudophyllinae, tribe Pterochrozini) were excluded from analysis of size as they have disproportionately large tegmina in relation to their body mass. Feeding data from infants or those tamarins whose identity was unknown were excluded from all analyses.

### *Colour measurement*

Reflectance spectra were taken (by ACS) using a portable S2000 spectrometer, HL2000 halogen light source, 400  $\mu\text{m}$  fibre-optic cables and 74-UV collimating lenses (200-2000 nm) (all Ocean Optics, Dunedin, Florida, USA), and Satellite 4030CDT lap-top computer (Toshiba) running SpectraWin 4.1 software (Top Sensor systems, Eerbeek, Netherlands) measured against a barium sulphate standard. The spectra of the target insects were taken from the collected tegmina, and those of the possible backgrounds were taken from a series of fresh leaf (upper and lower sides) and bark. The fresh leaf and bark samples were taken from fruit trees known to be fed on by the tamarins at the site (as the exact resting sites of the insects were unknown).

### *Analysis*

Exact tests were used to compare the number of prey caught. The data are potentially confounded by effects of species, season, sex, and reproductive state were dealt with in the following ways. Species differences in visibility to the observer (moustached tamarins occupy a higher vertical niche than saddleback tamarins) combined with differences in insect prey and capture strategies (Smith, 2000) prevent the collapsing of data across species to examine sex or colour vision differences. As such each species was analysed separately. As Troop 1 was observed for a complete year and Troop 2 from September to December where inter-troop comparisons are made data are restricted to Sept – Dec to exclude potential the effect of seasonal variation. Although one of Troop 2's trichromatic females was lactating during data collection her rate of

insect capture was the lowest of the three females in the troop (0.20 items per day), and was less than the mean rate for the dichromatic animals. Therefore the potentially confounding factor of reproduction is unlikely to have biased the data towards higher insect capture. When comparing the defence strategies of the invertebrate prey captured by saddlebacks the data were restricted to those arthropods for which remains were collected. Differences in tegmina area (a proxy for insect size) were analysed using Mann-Whitney and Kruskal-Wallis  $t$ -tests.

## *Results*

During 151 days (1483 hrs), the tamarins were observed to feed on 360 prey items. Of these, 297 were identified to at least tribe, most to species, and their defence strategy determined (Appendix 1). Within Troop 1, saddlebacks ate 164 prey items and moustached tamarins, 106 items. For Troop 2, figures were 56 for saddlebacks and 9 for moustached tamarins. The difference between the troops is accounted for by the numbers of observation days; 126 days for Troop 1 ( $X=0.24$  insects/day/tamarin) and 25 days for Troop 2 ( $X=0.19$  insects/day/tamarin).

Across the whole year within Troop 1, the dichromatic female saddlebacks caught a similar number of insects as the males ( $0.29 \pm 0.03$  prey/day/individual,  $N=2$  females vs.  $0.36 \pm 0.01$  prey/day/individual,  $N=2$  males). However, the trichromatic female moustached tamarins caught three times as many insects as their male group mates ( $0.30 \pm 0.06$  prey/day/individual,  $N=2$  trichromatic females vs.  $0.10 \pm 0.03$  prey/day/individual,  $N=3$  dichromatic males). There was a effect of season on the rate of prey capture, with saddleback tamarins capturing prey at a higher rate

between January and August than September and December ( $0.34 \pm 0.04$  prey/day/individual,  $N=4$  Jan - Aug vs.  $0.26 \pm 0.06$  prey/day/individual,  $N=4$  Sept - Dec). To examine the effect of colour vision status without the potential confounds of seasonal variation, sex and species differences, the mean number of prey captured per day by the dichromatic female saddleback tamarins of Troop 1 was compared to that of the trichromatic females from Troop 2 (Sept – Dec only). Trichromatic females (Troop 2) captured prey at a higher rate ( $0.45 \pm 0.24$  prey/day/individual,  $N=3$  tamarins) than their dichromatic female counterparts (Troop 1:  $0.23 \pm 0.03$  prey/day/individual,  $N=2$  tamarins). This resulted in trichromatic females capturing significantly more prey than their dichromatic counterparts (Exact test  $X^2=4.4$ , 1 *D.F.*,  $P=0.039$ ). To control for habitat quality, prey density etc. without the confound of colour vision status or sex, prey capture rates for male tamarins were compared between groups. The rates for males in Troops 1 and 2 were the same,  $0.29 \pm 0.10$  and  $0.29 \pm 0.12$  prey/day/individual ( $N=2$  &  $3$  tamarins respectively), and similar to that of the dichromatic females in Troop 1. This indicates the difference between the females was unlikely to be attributable to between troop factors. A similar pattern was observed for Troop 1's moustached tamarins with trichromatic females capturing prey at a higher rate (Troop 1:  $0.30 \pm 0.05$  prey/day/individual,  $N=2$  tamarins) than their dichromatic male counterparts (Troop 1:  $0.1 \pm 0.02$  prey/day/individual,  $N=3$  tamarins). This resulted in trichromatic females capturing significantly more prey than their dichromatic male counterparts (Exact test  $X^2=31.9$ , 1 *D.F.*,  $P=0.001$ ).

The distribution of prey between the four defence strategy classes was significantly different between saddleback female dichromats and trichromats

(Sept – Dec) (Exact test  $X^2=9.0$ , 3 *D.F.*,  $P=0.02$ ), but not between males of the two troops (Exact test  $X^2=2.5$ , 3 *D.F.*,  $P=0.59$ ). The effect of visual status was that dichromats captured more leaf and bark mimics, and trichromats more green generalists and concealers. The pattern was similar, though non significant when Troop 1's trichromatic female moustached tamarins were compared with their dichromatic male counterparts (Exact test  $X^2=6.8$ , 3 *D.F.*,  $P=0.086$ ). When the analysis was repeated for the saddleback tamarins with concealed prey removed there was no significant difference in prey distribution between dichromat and trichromat females (Exact test  $X^2=5.1$ , 2 *D.F.*,  $P=0.078$ ).

The tegmina area of katydids captured by dichromatic female saddlebacks (Troop 1) was not significantly different from those captured by their trichromatic counterparts in Troop 2 (Sept – Dec) ( $706\pm186\text{mm}^2$ ,  $N=4$  vs.  $647\pm196\text{mm}^2$ ,  $N=27$ ; Mann-Whitney  $U=43.5$ , 30 *D.F.*,  $P=0.54$ ). Similarly, there was no difference in prey size between the males of Troop 1 and 2 ( $476\pm238\text{mm}^2$ ,  $N=9$  vs.  $667\pm283\text{mm}^2$ ,  $N=19$ ; Mann-Whitney  $U=41.0$ , 24 *D.F.*,  $P=0.08$ ). Utilising the whole dataset there was a significant difference in tegmina area between prey defence strategy classes (bark mimic  $744\pm221\text{mm}^2$ ,  $N=49$ ; concealer  $582\pm208\text{mm}^2$ ,  $N=97$ ; green generalist  $700\pm248\text{mm}^2$ ,  $N=123$ ; leaf mimic  $1837\pm502\text{mm}^2$ ,  $N=19$ ) (Kruskal-Wallis  $X^2=56.7$ , 3 *D.F.*,  $P=0.001$ ). This difference remained when leaf mimics were excluded on the basis of their disproportionately large tegmina in relation to body mass (Kruskal-Wallis  $X^2=16.4$ , 2 *D.F.*,  $P=0.001$ ).

Spectra were recorded from the tegmina of 171 insects from the four main defence strategy classes. Colour loci of the insect and background colours are plotted in a Macleod-Boynton (1979) chromaticity diagram (Figure 1; Regan et al. 2001). Loci are based on modelled cone photoreceptor responses for a tamarin eye with visual pigment sensitivity maxima at 425nm (S), 543nm (M) and, 562nm (L) (Smith et al., 2003). The ordinate (S/L+M) represents the chromatic signals available to dichromatic and trichromatic animals, and the abscissa (L/L+M) correspond to the signals available only to trichromats. As dichromats are unable to distinguish along the red-green axes (L/L+M), they will confuse the colours of leaves and barks, which may be discriminated by trichromats. Examples of reflectance spectra of the green generalist, bark and leaf mimic prey and backgrounds are given in Figure 2. Both green generalists and leaf mimics are well matched to leaves.

The bark-mimic insect spectra are not typical of melanin pigments, whose spectra increase more or less linearly with wavelength (Osorio & Bossmaier 1992), and may instead be chemically related to the green pigments of leaf mimics. Figure 1 shows the variation in bark-mimic prey and background colours. This variation, combined with the fact that the spectra plotted in Figures 2B and 2C are not from insects and the matched backgrounds upon which they preferentially roost, may explain the lack of similarity expected if prey were camouflaged.

## Discussion

370 These data are the first to examine individual differences in insect capture rate  
371 in tamarins. Both the captive and field studies show that trichromats catch more  
372 insect prey than dichromats. The behavioural data from wild tamarins along with  
373 the spectral data suggest that trichromats are superior at detecting green  
374 generalist and concealed insects. However, dichromats appear to be better than  
375 trichromats at catching camouflaged insects (i.e. the bark and leaf mimics), as  
376 predicted. Similar findings have been reported for Geoffroy's marmosets  
377 (*Callithrix geoffroyi*), where trichromats found fewer coloured cereal balls in a  
378 camouflage condition versus a non-camouflage condition, with no such  
379 difference for dichromats (Caine et al. 2003). Although there was no significant  
380 difference between di- and trichromats performance overall in these  
381 experiments, the authors acknowledge that high individual variation lowered the  
382 power of the statistical analyses. As the present investigation incorporates both  
383 naturalistic observations and assesses detection of real prey items, these  
384 studies possess a greater ecological validity than this previous research, and  
385 present the first data for an overall trichromatic advantage for insect capture,  
386 with an advantage for camouflaged insects for dichromats.

387  
388 The reflectance spectra recorded from the tegmina of the tamarins' prey closely  
389 match those of the substrates that they spend the day roosting on. In particular  
390 leaf spectra are closely paralleled by those from both green generalists and leaf  
391 mimics at all wavelengths. The match of cryptic green coloration to chlorophyll  
392 pigmented leaves is also found in frogs (Schwalm et al. 1977), and remarkably  
393 extends to the near infrared (above 700nm). It should be noted that it was not  
394 possible in the field study to determine what background the majority of insects



395 were caught from. Although the ground accounted for the majority of known  
396 capture locations, it is likely that the majority of prey were captured above the  
397 ground as ground capture involved highly conspicuous behaviour, rapid descent  
398 and scanning the forest floor, and yet the location of capture was not seen in  
399 the majority of cases. Of those that were flushed, mimics are only camouflaged  
400 when on appropriate backgrounds. If these insects are flushed they may land  
401 on backgrounds against which they are not camouflaged, a situation where  
402 trichromats might have an advantage. Furthermore trichromats would have an  
403 advantage over dichromats in detecting green generalists on bark backgrounds,  
404 and the flushing of concealed insects may explain the superiority of trichromats  
405 over dichromats for this prey defence class.

406  
407 Although the visual environment may differentially influence the detection  
408 capabilities of the various phenotypes (Yamashita et al. 2005; Caine et al. 2010)  
409 data on the light intensity at the point of capture was not collected due to  
410 obvious practical constraints. Since saddleback tamarins capture the majority of  
411 their prey from the shady understory as opposed exposed canopy (Smith 2000),  
412 they are generally foraging in illumination that should offer a relative advantage  
413 to dichromats. Despite this, trichromats were able to capture more prey overall,  
414 although dichromats did catch more camouflaged prey.

415  
416 The only other comparable studies of the influence of colour vision status on  
417 prey capture in wild primates are by Melin et al. (2007; 2010) for white-faced  
418 capuchins. Their finding of a greater trichromat efficiency when foraging for  
419 embedded prey parallels the greater numbers of concealed prey found by the

present study. This is of interest as colour vision phenotype should be irrelevant when foraging for hidden prey. If visual cues are available or whether it represents a learnt specialisation is unknown. Melin et al. (2007; 2010) also

found that dichromatic monkeys foraged more efficiently for exposed than concealed prey. This dichromat efficiency may be explained by a greater ability to break camouflage (Saito et al. 2005), if the exposed prey were camouflaged. Whilst this is a reasonable assumption, the present study is the first to look at the defence strategy of the prey concerned and show that dichromats do indeed take more highly camouflaged insects. However, trichromats captured a greater number of prey items overall. This almost certainly translates into a fitness advantage as their prey items did not differ significantly in size to those of their dichromatic counterparts.

The maintenance of genetic and phenotypic polymorphism in a sensory system has broad evolutionary relevance. It is clear that the M/L opsin polymorphism for platyrrhines is favoured by balancing selection, rather than being a neutral effect (Surridge et al. 2003; Hiwatashi et al. 2010), and two main hypotheses have been advanced (Mollon et al. 1984). The first is that trichromacy is generally beneficial and the polymorphism is maintained by heterozygote advantage. This hypothesis is plausible but faces the objection that duplication to give separate M and L genes has taken place in only two lineages. An interesting alternative is that the genetic polymorphism is maintained by frequency dependent selection on the colour vision phenotypes. This could be due either to the benefits of foraging opportunities and predator detection conferred to members of groups consisting of different phenotypes or through

multi-niche polymorphism where individuals exploit niches best suited to their phenotype (Levene 1953; Mollon et al. 1984; Melin et al. 2008). The forest environment is composed of visually distinct niches (Endler 1993) and different animals with different colour vision phenotypes may make advantageous use of these local variations (Regan *et al.* 2001). Indeed an advantage for dichromatic marmosets foraging in shade not sun over their trichromatic counterparts has been found (Melin 2007; Caine et al. 2010) demonstrated. There is also theoretical support that different dichromat phenotypes will detect different species of fruit (Osorio et al. 2004). The data we present here for tamarins lend support to heterozygote advantage, as it is known that not only are trichromats better able to detect and select fruit (e.g. Smith *et al.* 2003), but they also catch more insects than their dichromatic counterparts. However, that dichromats catch a greater proportion of camouflaged prey suggests that selection for niche divergence may also be playing a part in maintaining colour vision polymorphism in tamarins. The relative abundance of different classes of insects is therefore important in the relative success of insect foraging in di- and trichromatic tamarins.

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**Table 1** Species, group composition, sex and visual status of tamarins studied.

Species	Group	Sex	Age <sup>*</sup>	Visual status (opsins)
Captive animals: Belfast zoo				
Saddleback	C1	F	A	Trichromat (425+543+563)
		F	A	Trichromat (425+556+563)
		F	A	Dichromat (425+563)
	C2	M	A	Dichromat (425+563)
		F	A	Dichromat (425+543)
		F	A	Trichromat (425+543+563)
		F	A	Trichromat (425+543+563)
	C3	M	A	Dichromat (425+563)
		F	A	Trichromat (425+543+563)
	C4	M	A	Dichromat (425+556)
		F	A	Trichromat (425+556+563)
Red-bellied	C5	M	A	Dichromat (425+563)
		F	A	Trichromat (425+543+563)
		F	A	Dichromat (425+563)

Wild animals: EBQB Peru					
Saddleback					1
	2	F	S	Dichromat (425+556 nm)	
		M	A	Dichromat (425+556 nm)	
		M	A	Dichromat (425+556 nm)	
		F	A	Trichromat (425+543 + 556 nm)	
		F	S	Trichromat (425+543 + 556 nm)	
		F	J	Trichromat (425+543 + 556 nm)	
		F	I	Unknown	
		M	A	Dichromat (425+563 nm)	
		M	A	Dichromat (425+563 nm)	
		M	J	Dichromat (425+543 nm)	
		M	I	Dichromat (425+556 nm)	
Moustache d	1	F	A	Trichromat (425+543 + 563)	

		F	A	Trichromat (425+543 + 563)
		M	A	Dichromat (425+563)
		M	A	Dichromat (425+563)
		M	S	Unknown
		M	I	Dichromat (425+563 nm)
		M	I	Dichromat (425+563 nm)
	2	M	A	Dichromat (425+543 nm)
		M	A	Dichromat (425+543 nm)
		M	S	Dichromat (425+543 nm)
		M	J	Dichromat (425+543 nm)
		F	A	Dichromat (425+543 nm)
		F	A	Unknown
		F	S	Unknown
		F	J	Unknown

\* A = adult, S = subadult, J = juvenile, I = infant

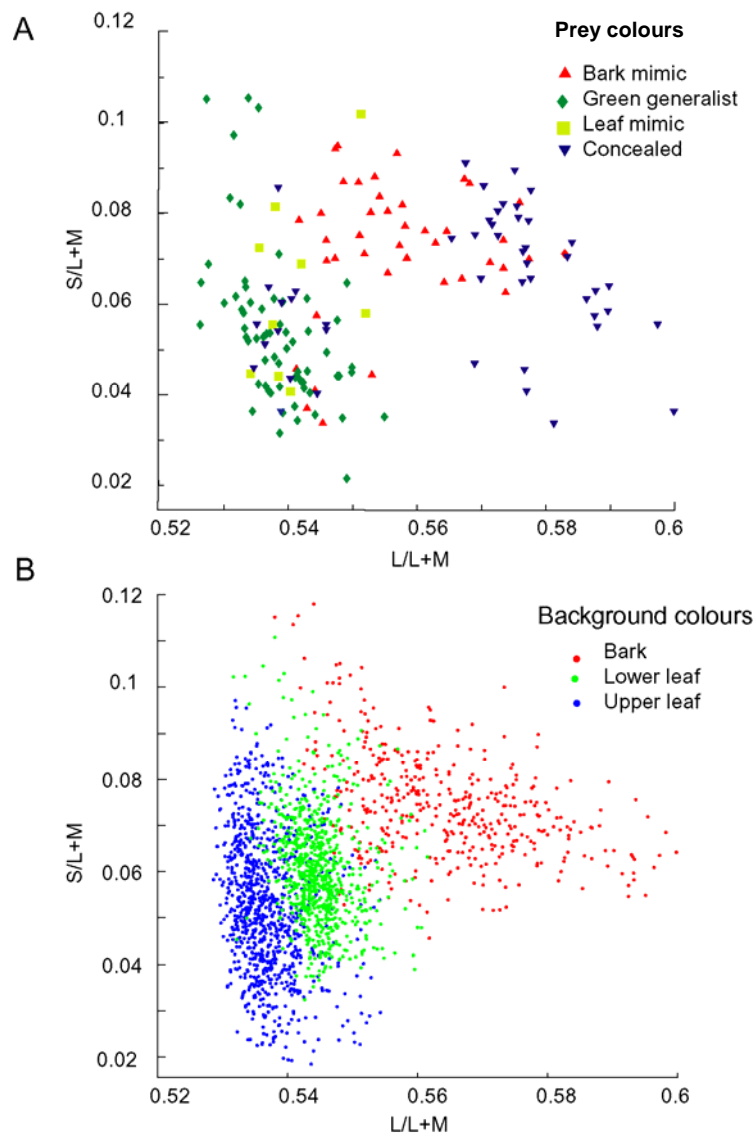


Figure 1. Colour loci of A) prey defence class strategy and B) background colours recorded in a Macleod Boynton (1979) chromaticity diagram.

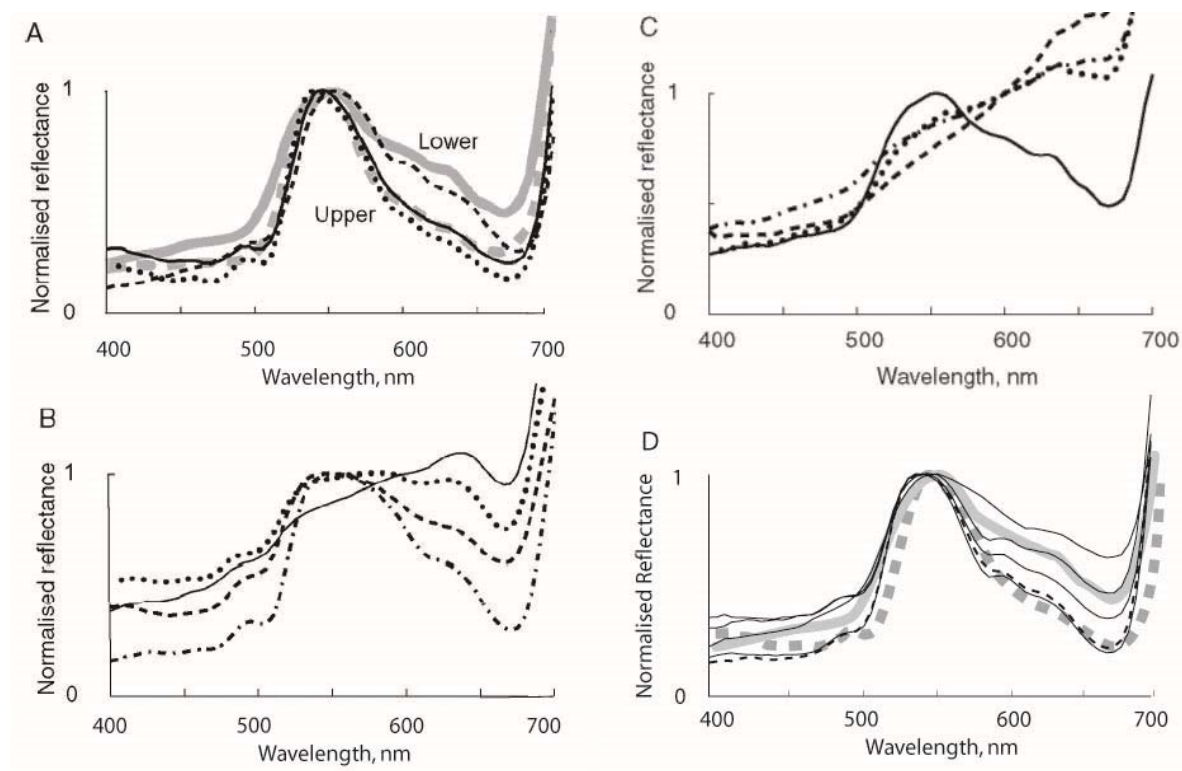


Figure 2. Examples of reflectance spectra of insects and backgrounds normalised to the maximum between 500 and 600nm. A) Spectra of three green generalist insects (black lines), and the means of all lower and upper leaf surfaces (grey lines). B) Spectra of four bark mimic insects, and C) of four tree barks. D) Spectra of five leaf mimics (black lines: solid, *Cycloptera speculata*; dashed *Typophyllum* sp.), and the means of all lower and upper leaf surfaces (grey lines).

**Appendix 1** Insect species and their defence strategies caught by dichromatic and trichromatic saddleback and moustached tamarins

Order	Family	Subfamily	Tribe	Species	Defence strategy	S. fuscicollis				S. mystax				Grand total	
						Grp 1		Grp 2	Total	Grp 1		Grp 2			Total
						Di	Di	Tri		Di	Tri	Di	??		
Blattaria	Blaberidae	Blaberinae		<i>Phortioeca maximiliani</i>	Concealed	1			1						1
		Zetoborinae		<i>Schizopilia fissicollis</i>	Unknown	1			1						1
Mantodea	Mantidae	Choeradodinae	Choeradodini	<i>Choeradodis rhomboidea</i>	Green generalist	1			1		1			1	2
		Photinainae	Photinaini	<i>Macromantis ovalifolia</i>	Green generalist					2	5			7	7
		Stagmomantinae	Stagmomantini	<i>Stagmomantis</i> sp.	Unknown	1			1						1
Orthoptera	Romaleidae	Romaleidae	Romaleini	<i>Titanacris humboltii</i>	Unknown			1	1						1
	Tettigoniidae	Conocephalinae	Agaeciini	<i>Eschatoceras</i> sp.	Concealed	1			1						1
			Copiphorini	<i>Copiphora gracilis</i>	Green generalist	1	1	1	3						3
				<i>C. cf. gracilis</i>	Green generalist	1			1	1	2			3	4
				<i>Eurymetopa obesa</i>	Concealed	10		1	11	2	2			4	15
				<i>Lamniceps</i> sp.	Green generalist	1			1		1			1	2
				<i>Liostethus gladius</i>	Green generalist		1		1						1
			<i>Lirometopum</i> sp.	Concealed	10		1	11		9			9	20	
		Listroscelidinae		<i>Monocerophora spinosa</i>	Green generalist	6			6		1			1	7
		Phaneropterinae	Dysoniini	<i>Paraphidnia verrucosa</i>	Unknown							1		1	1
			Steirodontini	<i>Cnemidophyllum cf eximium / lineatum</i>	Green generalist	1			1						1
				<i>Steirodon (Frontium)</i> sp.	Green generalist	1			1		1			1	2
			<i>Anaulacomera</i> sp.	Green generalist						1			1	1	

		<i>Hyperphrona</i> sp. 1	Green generalist	1			1						1
		<i>Hyperphrona</i> sp. 2	Green generalist					2				2	2
		<i>Lobophyllum</i> sp.	Green generalist	1			1						1
Pseudophyllinae	Cocconotini	<i>Cocconotus cf aethiops</i>	Concealed	1			1						1
		<i>Eubliastes aethiops</i>	Concealed	5	3		8						8
		<i>Eubliastes</i> sp. 1	Concealed	1			1						1
		<i>Eubliastes</i> sp. 2	Concealed						1			1	1
		<i>Schedocentrus basalis</i>	Concealed	6		2	8						8
		<i>S. cf basalis</i>	Concealed	6	1		7						7
		<i>S. cf tessellatus</i>	Concealed	5			5						5
		<i>Schedocentrus</i> sp.	Concealed	3		3	6						6
		Unknown sp. 1	Concealed	3			3		1			1	4
		Unknown sp. 2	Concealed			2	2						2
	Phyllomimini	<i>Choeroparnops</i> sp. 1	Concealed	8			8		2			2	10
		<i>Choeroparnops</i> sp. 2	Concealed	1			1						1
		<i>Triencentrus</i> sp. 1	Concealed	1		1	2						2
		<i>Triencentrus</i> sp. 2	Concealed	2			2						2
	Pleminiini	<i>Acanthodis longicauda</i>	Bark mimic	3			3						3
		<i>Ancistrocercus excelsior</i>	Bark mimic		1		1						1
		<i>Championica</i> sp.	Bark mimic		1		1						1
		<i>Leurophyllidium maculipenne</i>	Bark mimic	7		1	8	1			1	2	10
		<i>L. luridum</i>	Bark mimic	12	1	1	14	2	7			9	23
		<i>Leurophyllum cf luridum</i>	Bark mimic	2			2						2
		<i>L. cf. vulturinum</i>	Bark mimic	1	1		2						2



				<i>L. cf vulturinum</i> sp. 2	Bark mimic	2			2					2	
				<i>Leurophyllum</i> sp. 2	Bark mimic	3	2	1	6					6	
				<i>Leurophyllum</i> sp. 3	Bark mimic					1			1	1	
				<i>Rhinischia</i> sp. 1	Bark mimic	1			1					1	
				<i>Rhinischia</i> sp. 2	Bark mimic	1			1					1	
			Pterochrozini	<i>C. cf falcifolia</i>	Leaf mimic	1			1		1			1	2
				<i>Cycloptera speculata</i>	Leaf mimic	3	1		4	4	4		1	9	13
				<i>Pterochroza nimia</i>	Leaf mimic					1				1	1
				<i>Typophyllum mortuifolium</i>	Leaf mimic	2			2						2
				<i>T. cf mortuifolium</i>	Leaf mimic	1			1						1
				<i>Typophyllum</i> sp. 1	Leaf mimic			1	1						1
			Pterophyllini	<i>Pseudopterophylla</i> sp.	Green generalist	8	1	2	11	4	2	1		7	18
				<i>Caloxiphus</i> sp. 1	Green generalist			1	1						1
				<i>Diophanes salvifolius</i>	Green generalist	12	7	11	30	13	19		2	34	64
				<i>Lophaspis</i> sp. 1	Unknown	2			2		1			1	3
				<i>Scorpioricus</i> sp. 1	Green generalist	1	1	1	3						3
			Phasmatodea	Pseudophasmatidae	Pseudophasmatinae	Stratocleini	<i>Olcypoides cf. tithonus</i>	Unknown	1			1			
Xerosomatinae	Prexaspini	<i>Metriophasma myrsilus</i>			Unknown	1			1					1	
Grand Total						144	22	31	197	31	63	2	4	100	297