



Effects of colour vision phenotype on insect capture by a free-ranging population of white-faced capuchins, *Cebus capucinus*

AMANDA D. MELIN*, LINDA M. FEDIGAN*, CHIHIRO HIRAMATSU†,
COURTNEY L. SENDALL* & SHOJI KAWAMURA†

*Department of Anthropology, University of Calgary

†Department of Integrated Biosciences, Graduate School of Frontier Sciences, University of Tokyo

(Received 19 April 2006; initial acceptance 30 May 2006;
final acceptance 10 July 2006; published online 29 November 2006; MS. number: A10426)

Unlike most eutherian mammals, which have dichromatic (two-colour) vision, most platyrrhine primate species have polymorphic colour vision. This unique characteristic is enabled via multiple alleles for a mid- to long-wavelength-sensitive (M/LWS), single-locus opsin gene on the X chromosome. In combination with the autosomal opsin common to most vertebrates, this arrangement provides heterozygous females with trichromatic (three-colour) vision, whereas homozygous females and males are dichromats. Trichromatic vision enables visual differentiation among longer-wavelength colours, such as red, orange, yellow and green. Currently, many researchers attribute the evolution and maintenance of polymorphic colour vision to trichromat (= heterozygote) advantage. However, dichromacy may be more suited for achromatic tasks, such as penetrating colour camouflage, especially under low-light conditions. We evaluated whether dichromatic capuchin monkeys (*Cebus capucinus*) were more efficient than trichromatic monkeys at capturing camouflaged and noncamouflaged insects. Through faecal DNA analysis, we determined the genotypes of the M/LWS opsins for 34 capuchins in two groups inhabiting Santa Rosa National Park, Costa Rica. Dichromatic monkeys were more efficient at detecting camouflaged, surface-dwelling insects, especially under conditions of low ambient light. However, unexpectedly, trichromats were more efficient in extracting embedded, noncamouflaged insects from substrates. To our knowledge, this is the first study to document a foraging advantage to dichromatic monkeys in the wild. Our findings show that there is a lack of heterozygote advantage in foraging for surface-dwelling insects and therefore indicate that this mechanism may not be the sole driving force maintaining polymorphic colour vision in this population.

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Keywords: *Cebus capucinus*; detection and capture of camouflaged prey; foraging skills; polymorphic colour vision; visual communication; white-faced capuchin

Many vertebrates, including fish, reptiles and birds, have tetrachromatic (four-colour) vision, and correspondingly they possess four families of cone opsin genes. However, during the nocturnal stage of mammalian evolution, two of these gene families were lost (Heesy & Ross 2001).

Correspondingly, almost all eutherian mammals are dichromatic; in this regard, primates are unique in their capacity for trichromatic vision.

Animals with trichromatic vision can distinguish among mid- to long wavelengths of light (greenish to reddish colours) that are indistinguishable to dichromats. Selection for trichromatic vision in primates may have been driven by various foraging challenges, such as finding fruit (Mollon 1991; Osorio & Vorobyev 1996; Caine & Mundy 2000; Regan et al. 2001; Smith et al. 2003; Osorio et al. 2004; Riba-Hernandez et al. 2005) or young leaves (Lucas et al. 1998; Sumner & Mollon 2000; Dominy & Lucas 2001, 2004) in variably illuminated

Correspondence: A. D. Melin, Department of Anthropology, University of Calgary, 2500 University Drive, N.W., Calgary, AB T2N 1N4, Canada (email: amelin@ucalgary.ca). S. Kawamura, Department of Integrated Biosciences, Graduate School of Frontier Sciences, University of Tokyo, Seimeiou 502, 5-1-5 Kashiwanoha, Kashiwa, Chiba 277-8562, Japan (email: kawamura@k.u-tokyo.ac.jp).

environments, like tropical forests. However, trichromatic colour vision may also be important for detecting conspecific social signals (Changizi et al. 2006). Interestingly, catarrhine primates (Old World monkeys, apes and humans) differ from platyrrhine primates (New World monkeys) in the mechanism enabling trichromatic vision, and selection for the evolution of colour vision may well differ between the two lineages (Dominy et al. 2003).

Like most vertebrates, primates in both lineages have an autosomal, short-wavelength-sensitive (SWS) opsin, which is most sensitive to light wavelengths around 420 nm. However, after the divergence of the two infraorders, a duplication of the X-linked, mid- to long-wavelength-sensitive (M/LWS) opsin occurred in the catarrhine ancestor, resulting in routine trichromacy in Old World primates. The M/LWS opsins are most sensitive to light wavelengths around 530 nm and 560 nm, respectively. Unlike catarrhines, most platyrrhine primates, with the exception of howler monkeys, *Alouatta* spp., possess a single locus on the X chromosome for a polymorphic M/LWS opsin gene (Hunt et al. 1998). This arrangement enables heterozygous females to be trichromatic, whereas homozygous females and males are dichromatic. In most platyrrhines there are three M/LWS opsin alleles, with peak sensitivities around 530 nm, 545 nm and 560 nm, and correspondingly six possible phenotypes, three trichromatic and three dichromatic (SurrIDGE & MUNDY 2002).

Colour vision polymorphism has persisted in primate populations for up to 14 million years (SurrIDGE & MUNDY 2002) and increasing attention is being devoted towards understanding the mechanism of balancing selection by which it evolved and is maintained (Jacobs 1998; Buchanan-Smith 2005). To date, the most prevalent explanation is that colour vision polymorphism confers a heterozygote advantage to trichromatic individuals (overdominance selection). This hypothesis asserts that trichromacy is more advantageous overall than dichromacy, and that the presence of multiple alleles functions to increase the number of trichromats in the population. This model also posits that routine trichromacy does not exist in platyrrhines as it does in catarrhines simply because an M/LWS opsin gene duplication event has not yet occurred. However, there are other hypotheses, which are not necessarily mutually exclusive, predicting that trichromacy is not better overall but that individuals of different phenotypes are suited for different tasks. These hypotheses are: frequency-dependent selection, mutual benefit of association and multiple-niche polymorphism (Mollon et al. 1984).

To evaluate the various hypotheses of balancing selection, it is necessary to evaluate the relative abilities of individuals of each phenotype to perform tasks that affect their fitness, such as foraging, avoiding predators and interacting with conspecifics. If trichromats always outperform dichromats, then a heterozygote advantage probably explains the polymorphism. However, if dichromats outperform trichromats for certain tasks, then the selective pressure for routine trichromacy would be less than that predicted by the heterozygote advantage, or such selection might be absent altogether. Additionally, if dichromats and trichromats are suited to different

foraging tasks, they may differentially devote their time to different foraging behaviours (Mollon et al. 1984).

Studies on both human (Morgan et al. 1992) and nonhuman primates (Caine et al. 2003; Saito et al. 2005b) have found that dichromacy is beneficial for breaking colour camouflage. Morgan et al. (1992) suggested that colour interferes with texture detection and chromatic signals mask luminance (brightness) signals. Additionally, since the nervous system of trichromatic primates combines the signals from two M/LWS receptors into a single luminance signal, these different inputs could interfere with the perception of brightness (Osorio & Vorobyev 1996; Osorio et al. 2004). Since texture and luminance gradients are used for colour-blind tasks such as motion detection and shape identification (Mollon 1989), dichromacy is more advantageous for penetrating camouflage and other achromatic tasks. However, no study to date has identified an advantage to dichromatic monkeys in the wild.

Breaking camouflage may help wild primates to detect potential predators or prey. However, few cases of primates being attacked by predators are witnessed, making the former difficult to evaluate. Since omnivorous monkeys capture many insects over the course of a day and most surface-dwelling insects are well camouflaged against their background as a defence mechanism (Campbell 1996; Lev-Yadun et al. 2004), studying insect predation is an ideal way to evaluate a monkey's ability to penetrate camouflage.

Environmental conditions may also affect the potential advantages or disadvantages of one type of colour vision over the other. In the natural world, the amount of ambient light is affected by weather, time of day, location in the canopy and amount of surrounding foliage (Endler 1993). Achromatic vision becomes relatively more important as the amount of ambient light decreases, which is evident in the nocturnal adaptations of many animals. Within the order Primates, for example, several nocturnal loriform prosimians, infraorder Lorisiformes (Kawamura & Kubotera 2004) and the only nocturnal anthropoid, the owl monkey, genus *Aotus* (Jacobs 1997), have lost the SWS opsin and are truly colour-blind, being monochromatic. Therefore, in polymorphic species, dichromatic vision may be especially advantageous over trichromatic vision for achromatic tasks, such as breaking insect camouflage, in darker conditions.

Other insects avoid predation by dwelling in places that are difficult to access, such as holes, crevices, under bark, rolled in leaves or within braches or thorns. Detection of these insects does not require breaking camouflage, but instead requires increased use of auditory and olfactory cues (Phillips et al. 2003). Therefore, the colour vision type of the predator should not be important for extracting embedded insects. This task can be seen as a control for evaluating the relative abilities of dichromatic and trichromatic monkeys to capture noncamouflaged insects.

Research Questions

(1) Are dichromats better than trichromats at capturing surface-dwelling insects?

(2) Does the amount of ambient light differentially affect the ability of dichromats and trichromats to capture surface-dwelling insects?

(3) Are dichromats and trichromats equally able to capture embedded insects?

(4) Do dichromats and trichromats spend equal amounts of time in different foraging behaviours?

METHODS

Study Site

We conducted behavioural observations in Santa Rosa National Park of the Area de Conservacion Guanacaste (ACG), northwestern Costa Rica (10°45′–11°00′N, 85°30′–85° 45′W). The park is composed of tropical dry forest in various successional stages. Rainfall in Guanacaste Province is highly seasonal; mean annual rainfall is approximately 2 m, almost all of which is accumulated between mid-May and mid-December.

Study Species

White-faced capuchins, *Cebus capucinus*, are small (2–4 kg), omnivorous monkeys found throughout Central and South America from Honduras to Ecuador (Rowe 1996). They live in polygamous groups of approximately 15 individuals, are moderately sexually dimorphic (Fedigan & Jack 2001), and are known for their diverse diet and complex foraging techniques. A large portion of their diet comprises insects. A recent study in Santa Rosa National Park found insects to constitute 27% of the capuchin diet; of all insects eaten, roughly half (45%) were surface-dwelling insects that were gleaned from leaves and bark (Young 2005).

We collected behavioural data on two groups of capuchins, Cerco de Piedro (CP) and Los Valles (LV), giving a combined total of 34 individuals of various ages (Table 1). Age classes were categorized as follows: small immatures = 1–2 years of age; large immatures = 3–5 years of age; subadult males = 6–9 years of age (no subadult female stage); adult females > 6 years or age; adult males > 10 years of age. Data were not collected on individuals less than a year in age.

All monkeys were individually identified based on a combination of their age, sex, facial markings and, where present, scars. The genotypes of the M/LWS opsin gene in the individuals were determined through faecal DNA analysis and the population was verified to be polymorphic for colour vision type (Hiramatsu et al. 2005). To minimize observer bias, the researchers collecting behavioural data did not learn the specific colour vision genotypes of the study subjects, or the frequency of different genotypes within the groups, until after data collection.

Collection of Behavioural Data

We conducted 10-min (wet season) and 15-min (dry season) focal animal samples (Altmann 1974). Focal subjects were chosen randomly, within an age–sex class,

and we rotated sequentially through the different age–sex categories. We attempted to sample all individuals equally over the study period, at different times of day and under different environmental conditions. Each group was followed twice per week on two consecutive days from dawn until dusk, with observers switching half-way through the day. We collected data during May–August 2004 and January–May 2005 for a total of 246 h of focal animal samples.

When the focal monkey was foraging, we recorded the surrounding foliage cover as well as other environmental variables, such as relative height in the canopy, weather and time of day. We categorized the surrounding foliage cover into three categories: ‘open’: no overhead leaves or other vegetation; ‘shaded’: some overhead vegetation, but not enough to completely block passage of sunlight; ‘closed’: overhead vegetation dense enough to create dark shadows and not permit direct passage of sunlight.

Each attempt by the focal animal to capture an insect was recorded as an event, either capture or miss, within the ongoing behavioural state. We defined an ‘insect attempt’ as a pounce or lunge made by the focal monkey towards an invertebrate. If the attempt led to a successful grab by the monkey, we considered it a capture. If the insect eluded the attempt, this was recorded as a miss. Once an insect was captured, we recorded whether the monkey subsequently ate or rejected it. The substrate that the insect was gleaned or extracted from, as well as the type and colour of insect, was recorded whenever possible. If the insect was not seen well enough to be identified, it was classified as ‘unknown’.

‘Surface-dwelling’ insects were those gleaned from the exterior surface of any substrate, most often from the surfaces of live leaves, branches and vines. The surface-dwelling insects that we saw the monkeys eat most often were caterpillars, cicadas, grasshoppers, katydids, stick insects and beetles. This is in accordance with Young’s (2005) study on capuchin insect foraging. All of these insects are well camouflaged against their surroundings. Captures of noncamouflaged, surface-dwelling insects (those with aposematic coloration, or cryptic insects against a background of a different colour) were very few and not included in our analyses. Since the vast majority of surface-dwelling insects are camouflaged, ‘unknown’ insects were included in the camouflage analysis.

All insects that were actively extracted from substrates and large enough to be individually captured and eaten were included in the ‘embedded’ category. Most often these were in the families Orthoptera or Blattellidae. The monkeys also fed on ants, termites and other small, colonial insects by licking them out of branches, seed pods or acacia thorns. The latter (mostly Hymenoptera) were not included in our analysis since many were eaten simultaneously and they were not captured in the same manner as the relatively larger insects.

Ambient Light Data Collection

We measured ambient light under the three foliage cover conditions by taking irradiance readings with a USB2000

Table 1. Pertinent life-history, social and colour vision details for each individual monkey (*Cebus capucinus*) in the present study

Name	Study group	Sex	Age class	Colour vision type*
Monkey 1	CP	Female	Adult	Dichromat (560/560)
Monkey 2	CP	Female	Adult	Dichromat (560/560)
Monkey 3	CP	Female	Adult	Dichromat (560/560)
Monkey 4	CP	Female	Large immature	Dichromat (560/560)
Monkey 5	CP	Female	Large immature	Dichromat (560/560)
Monkey 6	CP	Female	Large immature	Dichromat (560/560)
Monkey 7	CP	Female	Small immature	Dichromat (560/560)
Monkey 8	CP	Female	Small immature	Dichromat (560/560)
Monkey 9	CP	Female	Large immature	Dichromat (560/560)
Monkey 10	CP	Female	Adult	Dichromat (560/560)
Monkey 11	CP	Female	Adult	Dichromat (560/560)
Monkey 12	CP	Female	Adult	Dichromat (560/560)
Monkey 13	CP	Male	Subadult	Dichromat (560)
Monkey 14	CP	Male	Large immature	Dichromat (560)
Monkey 15	CP	Male	Small immature	Dichromat (560)
Monkey 16	CP	Male	Adult	Dichromat (560)
Monkey 17	CP	Male	Adult	Dichromat (530)
Monkey 18	LV	Female	Small immature	Dichromat (545/545)
Monkey 19	LV	Female	Adult	Trichromat (545/560)
Monkey 20	LV	Female	Adult	Trichromat (545/560)
Monkey 21	LV	Female	Adult	Trichromat (530/560)
Monkey 22	LV	Female	Adult	Trichromat (530/545)
Monkey 23	LV	Female	Adult	Trichromat (530/545)
Monkey 24	LV	Female	Adult	Trichromat (545/560)
Monkey 25	LV	Female	Large immature	Trichromat (530/545)
Monkey 26	LV	Male	Adult	Dichromat (560)
Monkey 27	LV	Male	Adult	Dichromat (560)
Monkey 28	LV	Male	Adult	Dichromat (560)
Monkey 29	LV	Male	Subadult	Dichromat (560)
Monkey 30	LV	Male	Subadult	Dichromat (560)
Monkey 31	LV	Male	Subadult	Dichromat (560)
Monkey 32	LV	Male	Large immature	Dichromat (530)
Monkey 33	LV	Male	Small immature	Dichromat (545)
Monkey 34	LV	Male	Small immature	Dichromat (?)

*Values in parentheses indicate the peak sensitivity of each M/LWS opsin in the genotype.

miniature plug-and-play spectrometer, P200-UV/VIS fibre cable and CC-3 opaline glass cosine corrector (Ocean Optics, Dunedin, Florida, U.S.A.) connected to a notebook computer. Readings were taken 2 days per week over the period of the study.

Data Analysis

There are at least three distinct stages in the capture of a surface-dwelling insect: (1) detection of the prey by the predator; (2) successful capture of prey by the predator; and (3) selection of only palatable prey by the predator. We measured the efficiency of each monkey at every stage to evaluate which, if any, are influenced by the monkey's colour vision type. While there are also several stages to the capture of embedded insects, owing to space constraints, we only assess one efficiency measure in this paper, capture rate.

An observer cannot definitively know when a monkey has detected an insect (stage 1). Therefore, to evaluate this measure indirectly, we calculated the rate of 'insect attempts', either capture or miss, per hour of visual foraging. We include failed insect captures (misses) in this analysis because, arguably, the monkeys indeed

detected the insect. We defined visual foraging behaviour as 'scanning of forest substrates while moving or stationary'. We excluded the duration of foraging time in fruiting trees because, arguably, the monkeys were more likely to be searching for fruits than insects under these circumstances. Of the 246 h of focal animal samples, we collected just over 82 h of data when focal animals were visually foraging outside of fruit trees, and for which we recorded 1534 captures of surface-dwelling insects. To evaluate the effect of light condition on capture rates, we also conducted an analysis of attempt rate by foliage cover.

To evaluate the ability of an individual to successfully capture an insect once it was detected (stage 2), we calculated the proportion of successful (prey captured) to unsuccessful (prey missed) attempts. We calculated the proportion of insects rejected (not eaten) to accepted (eaten) after capture to evaluate an individual's ability to select only palatable prey (stage 3).

To measure the efficiency of each individual for a capture task that did not involve breaking insect camouflage, we calculated capture rate for embedded insects. This was accomplished by taking the number of embedded insects captured per hour of extractive foraging behaviour (peeling, picking at, digging in or unfurling forest substrates) for each individual. For this analysis, we used 18 h of focal data.

Statistical Analyses

We used Mann–Whitney U tests to compare overall rates of attempted captures, proportion of rejected captures, proportion of successful attempts and proportion of time spent in different foraging behaviours by colour vision type (dichromat versus trichromat), sex (male versus female) and study group (CP versus LV). We chose nonparametric statistics because of our relatively small sample size. For capture attempt rates of surface-dwelling insects under different environmental conditions, we used a mixed design, repeated measures ANOVA. This test is designed to compare a dependent variable, in this case capture attempt rate, for the same subjects under a variety of illumination conditions, and is beneficial because it accounts for interindividual variation and detects interactions between variables. The between-subjects factor for our tests was colour vision type and the within-subjects factors were the different foliage cover conditions. To our knowledge, there is no nonparametric equivalent of this test.

One of our study groups, CP, consisted entirely of dichromatic monkeys (Table 1), probably as a result of an unusually long tenure of the alpha male and resultant inbreeding (Jack & Fedigan 2006). This, in conjunction with the X-linked component of colour vision, whereby only females can be trichromatic, created the possibility for sex or group differences to confound the colour vision analysis. To account for this, we tested for group differences by comparing the males (dichromats) in each group to each other. To account for sex differences, we compared males and females of the same group and same phenotype (dichromat) to each other.

We predicted dichromats to have an advantage in breaking camouflage a priori based on previous studies that have found a significant advantage to dichromats in penetrating colour camouflage in human and nonhuman primates (see Introduction); hence we used one-tailed tests to compare dichromats to trichromats. However, tests between study groups, sexes and ages were all two tailed. We also used two-tailed tests for analysing differences between dichromats and trichromats for the capture rate of embedded insects and for time spent in different foraging behaviours.

RESULTS

Rate of Attempted Captures of Surface-dwelling Insects

The median rate for all individuals in this analyses ($N = 34$) was 19.87 attempts per hour and this ranged from 10.01 to 51.81. No significant difference was found between the two study groups (Mann–Whitney U test: $U = 20.00$, $N_1 = 5$, $N_2 = 9$, $P = 0.739$) or between the sexes ($U = 28.00$, $N_1 = 12$, $N_2 = 5$, $P = 0.833$). When we tested the rate of attempted captures between individuals with different colour vision types (Fig. 1), the median capture rate was 19.96 for dichromats and 16.34 for trichromats. In other words, dichromats made approximately four more capture attempts per hour than trichromats did ($U = 57.00$, $N_1 = 27$, $N_2 = 7$, $P = 0.055$).

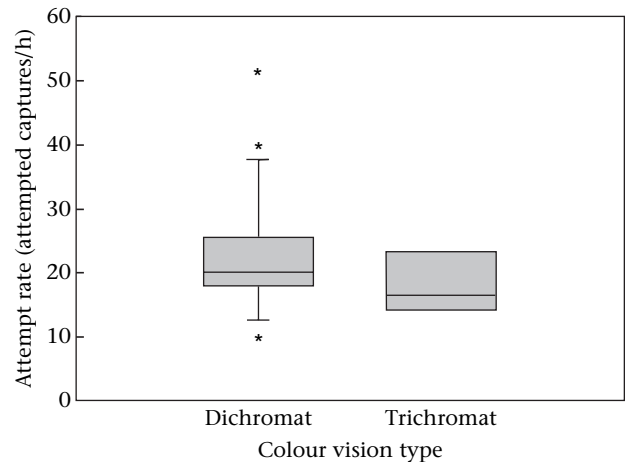


Figure 1. Median, upper and lower quartiles, with fifth and 95th percentiles and outliers when present, for rate of attempted captures of surface-dwelling insects by dichromatic and trichromatic capuchin monkeys.

To test the effect of the visual environment on each monkey's insect detection efficiency, we evaluated the rate of attempted captures under three conditions of overhead foliage cover: 'open', 'shaded' and 'closed'. Irradiance readings of the relative strength of different light wavelengths across the visual spectrum were taken under each of the three conditions. There was a 10-fold decrease in irradiance from the lightest (open) condition to the moderate (shaded) condition and another 10-fold decrease from the moderate to the darkest (closed) condition. The predominant colour of light also differed between conditions, with a shift from predominantly blue light (around 450 nm) in the 'open' condition to a stronger peak in the green area of the spectrum (around 550 nm) in the 'closed' condition.

Figure 2 shows the mean capture attempt rates by dichromats ($N = 26$) and trichromats ($N = 7$) under each of the three foliage cover conditions. One dichromat (Table 1, Monkey 3) was excluded from this analysis because

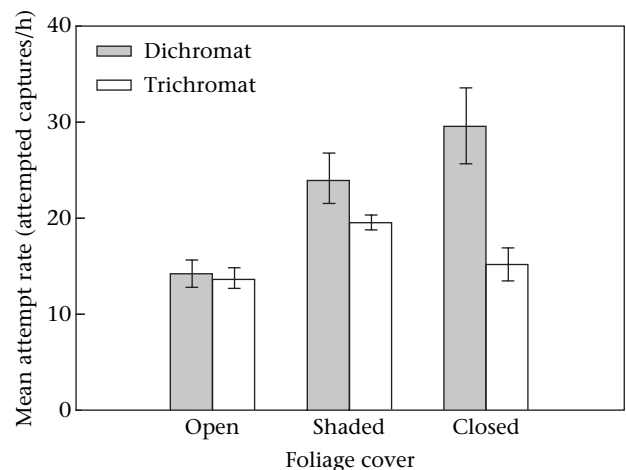


Figure 2. Mean \pm SD rate of attempted captures of surface-dwelling insects by dichromatic and trichromatic capuchin monkeys in different foliage cover.

we did not have observation time for her in the closed canopy condition. The mean attempt rates by dichromats and trichromats under the 'open' condition (the lightest condition with few to no leaves overhead) were very similar. However, in the 'shaded' condition (moderate leaf coverage) and especially in the 'closed' condition (densest leaf coverage), dichromats attempted to capture more insects per hour than did trichromats. Overall, dichromats made more capture attempts per hour as foliage cover increased. Trichromats showed an increase in capture rate from the 'open' to the 'shaded' condition, but then showed a lower attempt rate under the 'closed' condition.

We found a significant main effect of both colour vision type (ANOVA: $F_{1,31} = 3.535$, $P = 0.035$) and foliage cover ($F_{2,30} = 8.701$, $P = 0.001$); dichromats made more capture attempts per hour than did trichromats and this increased with increasing foliage cover. Dichromats and trichromats were differentially affected by the foliage cover condition. However, the interaction effect between colour vision type and the foliage cover was not significant ($F_{1,31} = 2.741$, $P = 0.108$).

We then looked for directional differences between attempted capture rates of dichromats and trichromats based on foliage cover, since we predicted that dichromats would perform better than trichromats in denser foliage as a result of the lower ambient light. For each individual in the study, we calculated three values corresponding to the difference in attempt rates between two foliage conditions: (1) shaded–open, (2) closed–shaded, (3) closed–open. We then ran a t test comparing dichromats to trichromats for each measure. The results are presented in Table 2. The mean rate of attempted captures for dichromats increased significantly more (equal variance not assumed, Table 2) from open to closed canopy than the mean trichromat attempt rate did. The change in attempt rates between other foliage categories was not significantly different between dichromats and trichromats.

Proportion of Successful Insect Capture Attempts

The median proportion of successful insect captures ($N = 34$) was very high, 0.89 (range 0.74–1.0). There was no difference in the proportion of successful capture

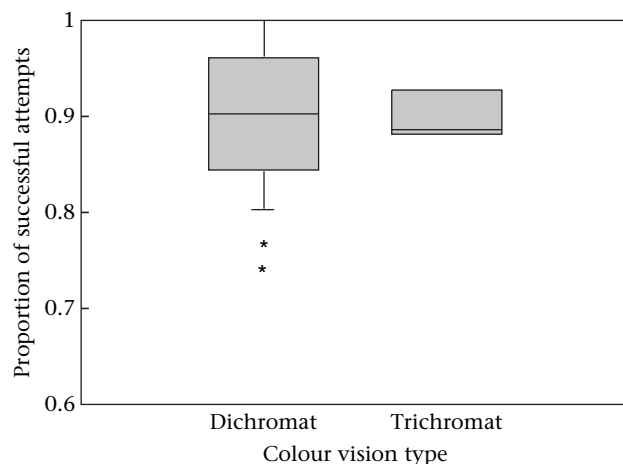


Figure 3. Median, upper and lower quartiles, with fifth and 95th percentiles and outliers when present, for proportion of successful insect capture attempts by dichromatic and trichromatic capuchin monkeys.

attempts between dichromats and trichromats (Mann–Whitney U test: $U = 94.50$, $N_1 = 27$, $N_2 = 7$, $P = 1.000$; Fig. 3). There were also no differences between males and females ($U = 24.00$, $N_1 = 12$, $N_2 = 5$, $P = 0.527$) nor between the two study groups, CP and LV ($U = 19.50$, $N_1 = 5$, $N_2 = 9$, $P = 0.689$).

Proportion of Insects Rejected After Capture

The median proportion of insects that were rejected after being captured over all individuals ($N = 34$) was very low, 0.00 (range 0.00–0.111) and did not differ between dichromats and trichromats (Mann–Whitney U test: $U = 86.50$, $N_1 = 27$, $N_2 = 7$, $P = 0.647$; Fig. 4). We also did not detect a difference between males and females ($U = 22.00$, $N_1 = 12$, $N_2 = 5$, $P = 0.324$) nor between the two study groups, CP and LV ($U = 21.00$, $N_1 = 5$, $N_2 = 9$, $P = 0.743$), for proportion of insects rejected after capture.

Capture Rate of Embedded Insects

In addition to gleaning insects from forest surfaces, capuchins also extracted them from under or within

Table 2. Results of the t test comparing the change in rate of attempted insect captures between different foliage cover conditions for dichromatic and trichromatic capuchin monkeys (SPSS 14.0)

Foliage cover	Equal variances	Levene's test for equality of variances		t test for equality of means		
		F	P	t	df	P (two-tailed)
Shaded–Open	Assumed	2.281916	0.141017	0.85833	31	0.40
	Not assumed			1.399453	28.05473	0.17
Closed–Shaded	Assumed	3.90958	0.056963	0.996246	31	0.33
	Not assumed			1.709662	30.56027	0.097
Closed–Open	Assumed	4.700334	0.037952	1.655461	31	0.11
	Not assumed			2.616556	26.01011	0.015*

*Indicates statistical significance.

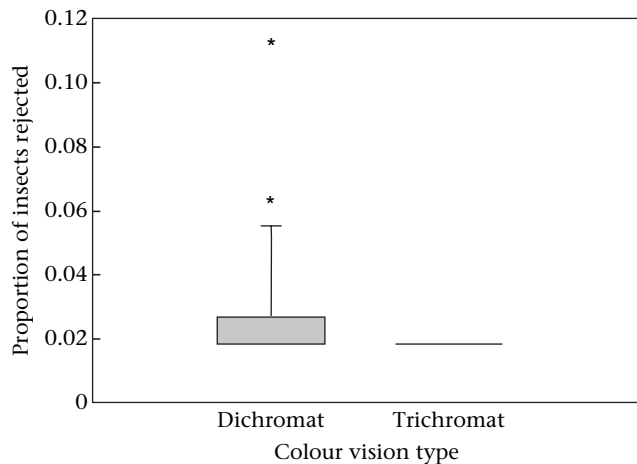


Figure 4. Median, upper and lower quartiles, with fifth and 95th percentiles and outliers when present, for proportion of insects rejected after being caught by dichromatic and trichromatic capuchin monkeys.

substrates. The median capture rate ($N = 32$) was 16.00 insects/h (range 2.66–101.08). Two monkeys (Table 1, Monkeys 3 and 24) were excluded from this analysis since we had less than 5 min of extractive foraging data for each of them. The capture rates of embedded insects by dichromats and trichromats are displayed in Fig. 5a. Unexpectedly, trichromats extracted significantly more insects per hour than did dichromats (Mann–Whitney U test: $U = 33.00$, $N_1 = 6$, $N_2 = 26$, $P = 0.030$).

We found no significant difference in the capture rate of embedded insects when group CP was compared to group LV (Mann–Whitney U test: $U = 20.00$, $N_1 = 5$, $N_2 = 9$, $P = 0.739$), or when males were compared to females ($U = 17.00$, $N_1 = 5$, $N_2 = 11$, $P = 0.234$). In an attempt to rule out any other factor, we also ran a test of capture efficiency for embedded insects by age and found a marginally significant difference among age classes (Kruskal–Wallace test: $\chi_3^2 = 7.607$, $P = 0.055$). The capture rate increased steadily from individuals in the youngest age class, ‘small immature’, to ‘adult’, the oldest age class (Fig. 5b).

To evaluate age as a possible confounding variable, we ran the colour vision analysis again and included only adults. The patterns were the same; trichromats had a higher mean capture rate than dichromats, but the tendency was then marginally nonsignificant (Mann–Whitney U test: $U = 11.00$, $N_1 = 5$, $N_2 = 10$, $P = 0.086$). To test whether age effects were confounded by colour vision type, we removed trichromats from the age analysis. The same age pattern, with older individuals being more efficient than younger individuals, was seen although it was now also nonsignificant (Kruskal–Wallace test: $\chi_3^2 = 3.939$, $P = 0.268$). Age patterns within the trichromat phenotype were difficult to assess because of the six trichromats in the study population, five were adult and one was a large immature, giving a low sample size of younger animals. The adults were not significantly different from the one large immature (Mann–Whitney U test: $U = 0.00$, $N_1 = 5$, $N_2 = 1$, $P = 0.143$). However, the capture rate for the large immature monkey was lower than each adult’s capture rate.

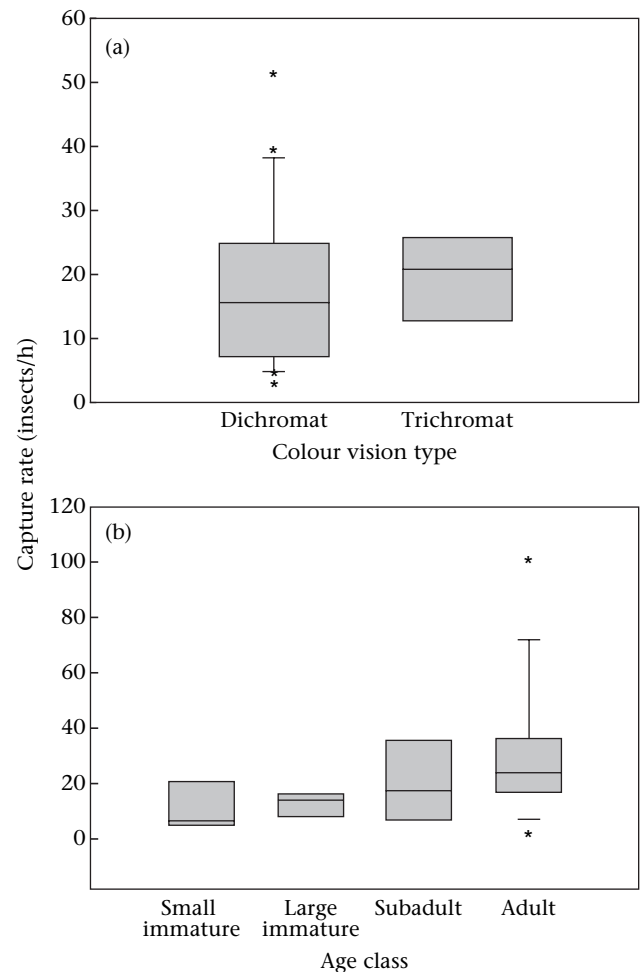


Figure 5. Median, upper and lower quartiles, with fifth and 95th percentiles and outliers when present, for capture rate of embedded insects by (a) dichromatic and trichromatic capuchin monkeys and (b) small immature, large immature, subadult and adult capuchin monkeys.

Time Spent in Different Foraging Behaviours

Dichromatic and trichromatic capuchins may differentially devote foraging time to visual and extractive behaviours; to test this we divided total foraging time into the proportion of time spent in visual foraging, extractive foraging or other (food processing, feeding) foraging behaviours. We used individuals in the analysis for which we had both visual and extractive foraging data (same data set as for the extractive capture rate analysis; $N = 32$). Overall, the capuchins devoted more time to visual foraging (median proportion 0.68, range 0.44–0.86) than to extractive foraging (median proportion 0.14, range 0.05–0.27). There were no differences between phenotypes, sexes or study groups in the proportion of time devoted to visual foraging (Mann–Whitney U test: dichromats versus trichromats: $U = 73.00$, $N_1 = 26$, $N_2 = 6$, $P = 0.809$; males versus females: $U = 20.00$, $N_1 = 5$, $N_2 = 11$, $P = 0.396$; group CP versus group LV: $U = 19.00$, $N_1 = 5$, $N_2 = 9$, $P = 0.641$) or extractive foraging (dichromats versus trichromats: $U = 50.00$, $N_1 = 26$, $N_2 = 6$, $P = 0.176$;

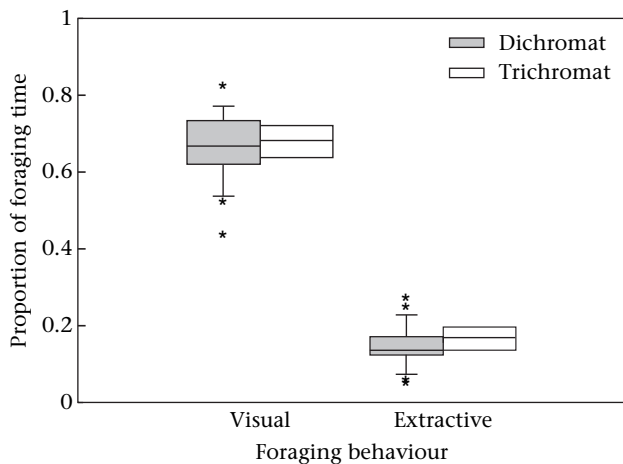


Figure 6. Median, upper and lower quartiles, with fifth and 95th percentiles and outliers when present, for proportion of total foraging time spent in visual and extractive foraging behaviours for dichromatic and trichromatic capuchin monkeys.

males versus females: $U = 12.00$, $N_1 = 5$, $N_2 = 11$, $P = 0.079$; group CP versus group LV: $U = 10.00$, $N_1 = 5$, $N_2 = 9$, $P = 0.096$; Fig. 6).

DISCUSSION

To date, most of the work on primate colour vision has been conducted on Old World primates, although the volume of research on New World primates is growing rapidly. Research initiatives on captive populations have already substantiated significant behavioural differences between individuals of different colour vision type (Caine & Mundy 2000; Smith et al. 2003; Saito et al. 2005a). Only recently have studies on wild populations begun. An advantage of dichromatic over trichromatic individuals has yet to be documented for any wild group of monkeys. Our study contributes to research on primate colour vision by investigating the foraging behaviour of individuals with different colour vision types in free-ranging white-faced capuchins living in a tropical dry forest.

We found that dichromat monkeys made more capture attempts for surface-dwelling insects per hour of visual foraging than trichromats did. While the difference in overall capture rates was only marginally significant, and thus should be interpreted with caution, we suggest that colour vision phenotype may be an important determinant of an individual's ability to efficiently detect these insects. This view is further supported by our results because we found a significant main effect of colour vision type in our repeated measures analysis, which is a more powerful test.

Our results also suggest an interesting relationship between foliage cover and colour vision type on an individual's ability to detect insects. Under the 'closed' canopy condition, dichromats performed much better than trichromats, whereas under the 'open' condition, which was the lightest, there was no apparent difference between colour vision types. Osorio et al. (2004) discuss how the yellow–blue mechanism of colour vision (the

only colour channel available to dichromats) fails at relatively low light intensities. Thus, it is possible that in bright light the improved chromatic vision of dichromatic monkeys impairs their ability to find cryptic insects, while in darker lighting the dichromats are effectively colour-blind and have the greatest advantage. Alternatively, that dichromats made more insect capture attempts per hour as foliage density increased is not necessarily due to an absolute advantage for dichromatic vision in dark over light conditions. Rather, the higher capture rate may reflect a higher insect abundance in areas with dense foliage than in areas without leaves overhead. Capuchins in our study spent the most time foraging in closed canopy conditions during the wet season, probably because caterpillars, which reside on the undersides of leaves and are a dominant component of the capuchin food repertoire (Young 2005), are more abundant during this time.

The capture rates of trichromats under different foliage conditions can be explained by this possibility of higher insect abundance in dense foliage as well. Trichromats made more insect capture attempts per hour in the shaded canopy than in the open, perhaps because a higher insect abundance in moderate foliage (shaded canopy) outweighed the disadvantage of being in moderately darker conditions. However, their capture performance was lowest in the darkest condition, 'closed' canopy, where they may be sufficiently disadvantaged by the lack of light so that capture rate decreased. Detailed studies on insect availability in different foliage conditions are, however, required to support these suggestions.

Proportion of Successful Attempts and Subsequent Rejection of Surface-dwelling Insects

Overall, capuchins were very successful at gleaning insects from various forest surfaces and in capturing insects that they subsequently consumed. The mean proportion of successful 'insect attempts', 0.89, was quite similar to the percentage of successful attempted insect captures (90%) reported by Harrison-Levine et al. (2003) for Venezuelan sakis, *Pithecia pithecia*, suggesting high success: attempt ratios may be common among insectivorous primates. The proportion of insects rejected after being caught was low. This indicates that in general capuchins are (1) able to recognize and capture only those insects that they find palatable or (2) that capuchins will eat almost everything they capture, or both.

While an individual's colour vision type influenced the detection rate of surface-dwelling insects, it did not appear to affect the monkey's ability to successfully complete a capture attempt, nor did it affect whether the prey was rejected subsequent to capture. This result suggests that, of the three stages of the insect-capture process, colour vision is important solely at the detection stage (stage 1), and is not important for completing a capture once an insect is detected (stage 2) or capturing only palatable insects (stage 3).

In our analyses we have not separated the captures of insects with red–green mosaic camouflage from insects

with a monotone camouflage strategy. Dichromatic vision is thought to be advantageous for detecting differences in shape and brightness, which would aid in breaking both monotone and mosaic camouflage. However, dichromats may be especially advantaged over trichromats in locating insects with mosaic camouflage, as the multiple chromatic signals may directly interfere with the trichromat's perception of brightness, or trichromats may be more heavily reliant on chromatic signals (see Introduction). Division of insects captured by type of camouflage may provide further insight and is an exciting possibility for future studies.

Capture Rate of Embedded Insects

Trichromatic monkeys captured significantly more embedded insects per hour of extractive behaviour than dichromats did. This result was not anticipated; we predicted that dichromats and trichromats would perform equally well at extracting insects, as vision seems to be less important for obtaining embedded insects than for capturing exposed prey.

We also found that insect-extracting ability, like many complex or challenging tasks, may improve with age. Each subsequent age class had a higher capture rate than the younger groups before. The pattern seemed to increase in a gradual fashion, without a clear line separating one or more of the age class(es) from the others. This result suggests that individuals steadily improve in their proficiency at extracting insects throughout their adolescence until they reach maturity. If this is the case, the following explanation may account for the observation that trichromats are more efficient in capturing embedded insects: since insects are composed of a much higher proportion of protein than any other capuchin food and they are also an important fall-back food when fruit is less available (McCabe 2005), if all capuchins need a certain proportion of insects in their diet, and if trichromats are not as adept at catching camouflaged surface-dwelling insects, perhaps the trichromats turn to embedded insects instead. Tasks involved in successfully and efficiently capturing embedded insects include recognizing ideal places to find them, listening for exact locations under bark, using hand-eye coordinated techniques to extract them, and removing them from the substrate in a timely manner. The age results from our analysis, while only marginally significant, suggest that extracting prey is a learned skill, which is improved with practise. If trichromatic capuchins rely on embedded insects more so than dichromats do, then this may explain why they extracted more insects per unit time. Conversely for dichromats, capturing surface-dwelling insects may be an easier or less time-consuming task than extracting them, and thus dichromatic monkeys may rely more heavily on capturing surface-dwelling insects as a result.

We also predicted that if individuals of different colour vision type are better suited for different foraging tasks, they may differentially divert their foraging time to these tasks. However, when we analysed the proportion of time that dichromats and trichromats spent in different

foraging behaviours we found no difference between dichromats and trichromats in the time they spent in visual or extractive foraging behaviours. Furthermore, another recent analysis found that dichromats and trichromats did not differ in time spent feeding on insects caught during visual and extractive foraging nor in the proportion of foraging time spent under different foliage cover conditions (A. D. Melin, L. M. Fedigan, C. Hiramatsu & S. Kawamura, unpublished data). Thus, it remains to be seen how the differing foraging efficiencies we observed fit into the puzzle of polymorphic colour vision. Perhaps more answers will be revealed through detailed nutritional studies comparing the diets of dichromatic and trichromatic monkeys and studies examining finer levels of niche divergence.

In conclusion, the results of this study suggest that there is no heterozygote advantage to capuchin monkeys foraging for surface-dwelling insects. Instead, we find dichromacy to be advantageous over trichromacy for this task. Our findings do not discount the idea that there are many foraging tasks, and environmental conditions, for which trichromacy is undoubtedly favourable. We suggest that individuals of different phenotype are more or less adept at different foraging tasks and that understanding the manifestations of this, possibly in combination with multiple-niche polymorphism or mutual benefit of association with individuals of different phenotypes, may better explain the presence and persistence of polymorphic colour vision, at least in this particular study population.

Acknowledgments

We would like to acknowledge Drs Filippo Aureli and John Addicott for helpful advice. We are grateful to the following organizations for funding: Alberta Ingenuity Fund, Natural Sciences and Engineering Research Council of Canada (NSERC), American Society of Primatologists and the University of Calgary (A.D.M.); NSERC and the Canada Research Chairs Program (L.M.F.); Grant-in-Aid for Japan Society of the Promotion of Science Fellow (15-11926) (C.H.); Grant-in-Aid for Scientific Research (B) (1640515) of the Japan Society for the Promotion of Science (S.K.). We thank Roger Blanco and the Costa Rican Park Service for permission to work in ACG and all the members of the capuchin and spider monkey research teams for their contributions to the long-term database and companionship in the field. We also thank two anonymous referees, who suggested many helpful changes and thereby improved our manuscript.

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