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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

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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.

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, Seimeitou 502, 5-1-5 Kashiwanoha, Kashiwa, Chiba 277-8562, Japan (email: kawamura@k.u-tokyo.ac.jp).

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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 lorisiform prosimians, infraorder Lorisifomes (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?