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Highly polymorphic colour vision in a New World monkey with red facial skin, the bald uakari (*Cacajao calvus*)

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Colour vision is highly variable in New World monkeys (NWMs). Evidence for the adaptive basis of colour vision in this group has largely centred on environmental features such as foraging benefits for differently coloured foods or predator detection, whereas selection on colour vision for sociosexual communication is an alternative hypothesis that has received little attention. The colour vision of uakaris (*Cacajao*) is of particular interest because these monkeys have the most dramatic red facial skin of any primate, as well as a unique fission/fusion social system and a specialist diet of seeds. Here, we investigate colour vision in a wild population of the bald uakari, *C. calvus*, by genotyping the X-linked opsin locus. We document the presence of a polymorphic colour vision system with an unprecedented number of functional alleles (six), including a novel allele with a predicted maximum spectral sensitivity of 555 nm. This supports the presence of strong balancing selection on different alleles at this locus. We consider different hypotheses to explain this selection. One possibility is that trichromacy functions in sexual selection, enabling females to choose high-quality males on the basis of red facial coloration. In support of this, there is some evidence that health affects facial coloration in uakaris, as well as a high prevalence of blood-borne parasitism in wild uakari populations. Alternatively, the low proportion of heterozygous female trichromats in the population may indicate selection on different dichromatic phenotypes, which might be related to cryptic food coloration. We have uncovered unexpected diversity in the last major lineage of NWMs to be assayed for colour vision, which will provide an interesting system to dissect adaptation of polymorphic trichromacy.

1. Introduction

Colour vision is a key trait that has been fertile ground for demonstrating adaptations in animal sensory systems. Most work has focused on adaptations of colour vision to environmental conditions, such as ambient light or food. Several recent studies in invertebrates and vertebrates have shown a link between colour vision and intraspecific signalling (e.g. [1–4]), but there has been relatively little work on mammals. In New World monkeys (NWMs), colour vision is highly variable, and a substantial body of research has investigated the ecological and evolutionary basis of this variation [5], which has implications for the acquisition of trichromacy in humans, apes and Old World monkeys (Catarrhini) [6]. The most frequent colour vision system in NWMs is polymorphic trichromacy, in which individuals of the same species may be either dichromats or trichromats. In these species, there are multiple alleles at the single X-linked opsin locus encoding middle- to long-wave-sensitive (MWS/LWS) visual pigments. This leads to

heterozygous females being trichromats, whereas homozygous females and hemizygous males are dichromats [5,7]. Almost all NWM genera studied to date have a polymorphic system, including callithrichids such as marmosets (*Callithrix*), cebids such as capuchin monkeys (*Cebus*, *Sapajus*), atelids such as spider (*Ateles*) and woolly (*Lagothrix*) monkeys, and pitheciids such as titi (*Callicebus*), saki (*Pithecia*) and bearded saki (*Chiropotes*) monkeys [8,9]. The two exceptions are the nocturnal owl monkeys (*Aotus*), which are monochromatic, and the howler monkeys (*Alouatta*), in which all males and females are trichromatic (routine trichromacy) [10–12].

The selective advantages of trichromacy for primates and the evolutionary forces maintaining colour vision polymorphism have been the subject of considerable discussion. Among environmental targets for selection, there is substantial support for a foraging advantage for trichromats for yellow/red fruit and/or young leaves compared with dichromats [13–17]. The high degree of folivory of howler monkeys has been suggested to account for the evolution of routine trichromacy in this lineage [18]. Predation by snakes and carnivores has also been implicated in the evolution of trichromacy [19,20]. An alternative hypothesis is that trichromacy functions in intraspecific signalling, enabling individuals to discriminate levels of oxygen saturation in red, blood-engorged areas of bare skin [21]. To date, this hypothesis has primarily been applied to catarrhines, with examples including the facial skin in mandrills and macaques, and sexual swellings of chimpanzees and macaques [21]. By contrast, the possibility that trichromacy functions in intraspecific signalling in NWMs has rarely been considered.

A consistent advantage for trichromatic females (such as foraging) would be sufficient to maintain colour vision polymorphism in polymorphic species via overdominance. However, there is evidence for visual tasks in which dichromats outperform trichromats in both captivity and the wild, such as detection of camouflaged food [22–24] and improved foraging at low (mesopic) light levels [25]. In addition, an absence of fitness differences between female dichromats and trichromats in a long-term field study of capuchin monkeys [26] suggests that trichromat advantage alone is not operating. Together, these suggest that frequency-dependent selection may be a more likely explanation for the persistence of colour vision polymorphism in so many NWM species.

The uakaris, *Cacajao*, comprise a genus of pitheciid NWMs endemic to Amazonia that is unusual in several respects. Uakaris have a specialized diet with a high proportion of seeds from fruits with relatively cryptic coloration [27,28]. They have a unique social system for NWMs, forming very large groups of up to 200 individuals, with a high degree of fission–fusion behaviour [29,30]. Most notably, the bald uakari, *C. calvus*, has bright red facial skin, in common with several catarrhine primates [31] and two other NWMs (the red-faced black spider monkey, *Ateles paniscus*, and the red-nosed bearded saki, *Chiropotes albinus*) [32,33]). The bald uakari provides the most extreme example of red facial skin of all primates. In this species, the red coloration extends over the entire head, which is sparsely haired, unmelanized and an intense scarlet, due to the underlying blood supply [34,35]. The red coloration is subjectively more intense in adult males in comparison with females [36], and the enlarged temporal muscles of the adult males further exaggerate the trait in this sex [37,38]. In addition, the overall pelage colour is reddish orange or reddish golden [32]. Together, these unique features mean that the colour vision of uakaris is of great interest.

Foraging on cryptic food might diminish the importance of trichromatic colour vision, whereas sexual selection on male red coloration might enhance selection on trichromacy. However, there is currently no information on colour vision in uakaris, and indeed they are now the only major lineage of NWMs in which colour vision remains unexplored.

There is an excellent understanding of the structure–function relationship of primate MW/LW opsin photopigments [9,39–41], showing that the majority of variation in the maximal spectral sensitivity (λ_{max}) of opsins can be attributed to three amino acid sites encoded in exons 3 and 5. In this study, we investigate colour vision in a wild population of the bald uakari in Peru by genotyping the X-linked opsin locus at these key sites affecting spectral sensitivity. We find that a polymorphic system of colour vision is present in this species, and uncover an unprecedented number of functional alleles for a single NWM population.

2. Material and methods

(a) Sampling

We followed a single group of Peruvian red uakaris (*Cacajao calvus ucayalii*) in November and December 2010 within an area of 600 ha in the Lago Preto Conservation Concession, on the Yavari River, Peru (4°28' S, 71°46' W). Group size was unconfirmed, owing to wide group spread and a high degree of fission–fusion behaviour, but a minimum of 80 animals used the study area during the period. Sixty faecal samples were collected from leaf litter as soon as possible after defaecation, but individual animals were not identified. To ensure rapid desiccation, we preserved one small piece of each sample (0.2–0.5 g) on filter paper in 30 ml container 80% full of dry silica gel. A further two samples were available from the Yanayacu-Pucate River population (4°56' S, 74°08' W), which is separated from the Yavari population by a wide river barrier [42].

(b) DNA extraction, sex determination and mtDNA genotyping

For DNA extraction from faecal samples, we used the QIAGEN QIAamp Stool Mini Kit (Qiagen) following the standard protocol as recommended by the supplier with only minor changes [43]. Afterwards, DNA concentration was measured on a NanoDrop ND-1000 spectrophotometer and samples were stored at –20°C until further processing. To determine the sex of individuals, we used a PCR-based gonosomal sexing system (C. Roos 2010, unpublished data). The complete mitochondrial cytochrome *b* gene (1140 bp) was sequenced in all individuals, resulting in seven haplotypes that were used here to aid identification of individuals from faecal samples. Full details of mitochondrial DNA (mtDNA) sequencing will be published elsewhere (C. Roos *et al.* 2011, unpublished data). Sequences are available from the authors upon request.

(c) Genotyping of the X-linked opsin locus

We designed oligonucleotide primers to amplify exons 3 and 5 of the LWS/MWS opsin gene from an alignment of existing NWM data from Genbank: Exon 3, Primer3CCF2 5'-CTCTGGTCCCTGGCCATCATT-3' and Primer3CCR2 5'-CCCCTTACCTGCTCAACCAA-3'; Exon 5, Primer5CCF2 5'-AGAGTCCGAATCCA CCCAGA-3' and Primer5CCR3 5'-TGCCGGTTCATGAAGACAT-3'. PCR reactions contained approximately 50 ng DNA template, 2.5 mM each dNTP, 1× PCR buffer, 1.5 mM MgCl₂, 0.1U Taq DNA polymerase (Bioline), 0.25 μM each primer and ddH₂O to a final volume of 20 μl. After an initial denaturation

Table 1. X-linked opsin amino acid variants at key functional sites, inferred functional alleles and inferred colour vision in wild uakaris.

sample size	exon 3	exon 5		inferred alleles (λ_{\max} nm)	inferred vision
	180	277	285		
2 M, 3 F	A	F	A	535	dichromatic
1 F	A	Y	A	543	dichromatic
4 M, 5 F	A	F	T	550	dichromatic
2 M, 1 F	A	Y	T	556	dichromatic
3 M, 3 F	S	Y	T	562	dichromatic
3 F	A	F	T/A	535/550	trichromatic
1 F	A	F/Y	T	550/556	trichromatic
2 F	A/S	F	T	550/555	trichromatic
1 F	A/S	Y	T	556/562	trichromatic

at 94°C for 5 min, the thermocycling profile consisted of 43 cycles at 94°C for 30 s, 57°C for 20 s and 72°C for 30 s, and a final extension at 72°C for 5 min. Each PCR was performed with a negative control consisting of ddH₂O instead of template DNA. Each exon was amplified and sequenced one to five times on sense and antisense strands per individual (electronic supplementary material, table S1) to avoid genotyping errors (i.e. to ensure correct scoring of heterozygous sites). Since no repeat genotypes gave conflicting results, allelic dropout in heterozygotes could be excluded.

PCR products were purified by adding 0.05U Exonuclease I, 0.25U Shrimp Alkaline Phosphatase (Affymetrix) and 0.7 μ l of ddH₂O add to each 6 μ l PCR product. They were then heated at 37°C for 30 min followed by 15 min at 80°C. Sequencing on both strands was performed at the DNA Sequencing Facility (Department of Biochemistry, University of Cambridge, UK) with an Applied Biosystems 3730 DNA Analyser. Sequences were edited using SeqMan in Lasergene 10 (DNASTar, Madison, WI, USA) and aligned/translated in MEGA 5 [44].

(d) Data analysis

Colour vision phenotypes for each individual were inferred by combining data from exons 3 and 5 of the LWS/MWS opsin gene, with predicted maximum spectral sensitivity (λ_{\max}) from critical positions at exon 3 (position 180) and exon 5 (277 and 285) [45]; we also checked site 294 [46]. Chi-square tests were used to test for heterogeneity in allele frequencies. Simulations of the colour vision of selected uakari opsin genotypes were carried out with the method of [44] with the λ_{\max} for the shortwave opsin set to 420 nm.

3. Results

We determined the sex, mtDNA haplotype and X-linked opsin genotypes for 34 faecal samples (electronic supplementary material, table S1). Three pairs of faecal samples (from two males and one female) yielded identical mtDNA and opsin sequences, and we conservatively consider that these are samples from the same individuals in the following analyses. All other samples yielded unique genotypes. We therefore analysed genotypes from 31 total individuals, comprising 11 males and 20 females.

We identified multiple functional alleles at the X-linked opsin locus defined by variation at the three key amino

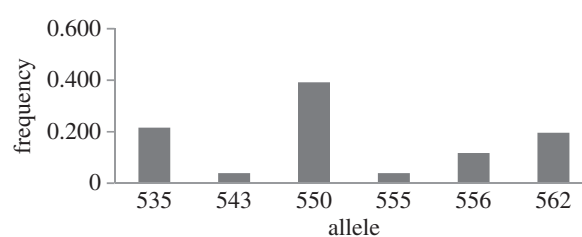


Figure 1. Allele frequencies of inferred LWS/MWS visual pigments in the bald uakari monkey (*Cacajao calvus*). $n = 51$ X chromosomes.

sites determining spectral sensitivity (180, 277, 285; table 1). Two further variable sites occurred (276, 309), which have not been implicated in functional effects. All alleles were verified by the two exons being independently amplified and sequenced in multiple samples (five alleles), or, where only present in a single individual, from amplification and sequencing both exons independently at least twice (one allele; electronic supplementary material, table S1). In addition, all exons with heterozygous sites were sequenced at least twice. No individual presented more than one heterozygous site across the three sites in the two exons, so haplotype inference was straightforward.

The results demonstrate a polymorphic system of colour vision in the bald uakari. First, some females were heterozygous for one or more key amino acid sites (35%, 7/20), whereas no heterozygotes were found among males (0/11), following the pattern expected for an X-linked polymorphic system. Second, in total we found six alleles defined by variation across the three key sites, an unprecedented number in a single primate species. Five of these alleles have been described previously in other species. The sixth allele, with the three-site pattern serine–phenylalanine–threonine (SFT), is novel and was found in two heterozygous females. Following the additive rule for the phenotypic effects of substitutions at these sites [40], the alanine (A) to serine (S) transition at site 180 should add approximately 5 nm to the λ_{\max} of the alanine–phenylalanine–threonine (AFT) allele (550 nm), giving a predicted λ_{\max} of the novel allele of approximately 555 nm; we hereafter refer to this as the 555 nm allele. This is slightly less than the λ_{\max} of the previously described allele alanine–tyrosine–threonine (AYT) (556 nm), and functional studies will be needed to determine whether these two

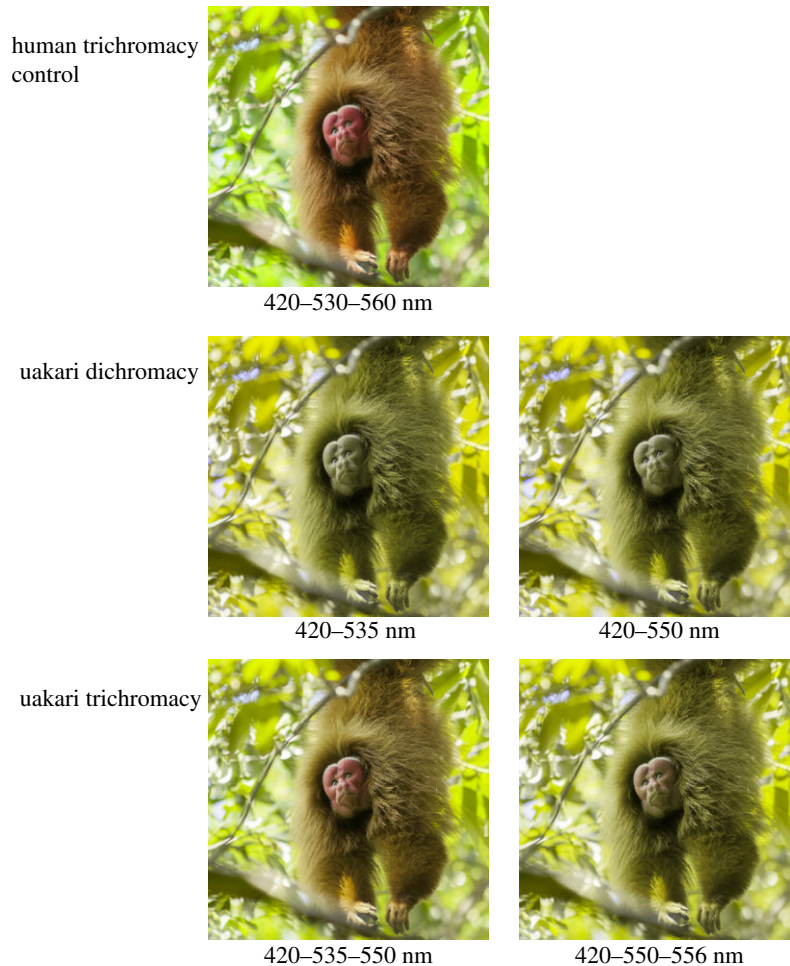


Figure 2. Simulated appearance of a male bald uakari for a trichromatic human observer compared among predicted colour vision phenotypes of bald uakari [47].

opsins have sufficient λ_{\max} separation to provide useful red–green colour vision in a trichromat. Across all alleles, there was no variation at site 294 (all alleles with Asparagine (N)), a site which can affect tuning in other primates [46].

The frequencies of the six alleles among the 51 X chromosomes sampled are shown in figure 1. Allele frequencies varied from 0.039 to 0.392, and showed significant heterogeneity ($\chi^2 = 27.23$, $P < 0.05$). The three most common alleles had λ_{\max} of 535, 550 and 562 nm (figure 1), whereas the 543 nm allele was the rarest allele, sampled in a single individual. Four types of heterozygote were found: 535/550 nm, 550/556 nm, 550/555 nm and 556/562 nm (table 1). Simulated colour vision for representative genotypes is shown in figure 2.

4. Discussion

The system of X-linked colour vision polymorphism we have uncovered in the uakari is similar to that of a large majority of other NWMs, occurring in all families and at least 14 genera. With all major lineages now sampled, there are just two NWM genera with other types of colour vision—routine trichromacy in *Alouatta* and monochromacy in *Aotus*. However, the presence of six functional allelic types in a wild primate population is unprecedented. Most species of NWM, including all callitrichids, cebids and polymorphic atelids, have two to three, or occasionally four, alleles. Among wild populations of the three other pitheciid genera (a saki, *Pithecia irrorata* [9,48]; a bearded saki, *Chiropotes utahicki* [8]; a titi

monkey, *Callicebus brunneus* [45]), the three alleles found (535, 550 and 562 nm) were the same as the three most common alleles in the uakari. Another species of titi monkey (*C. moloch*) is the only other species of NWM in which more than four alleles have been reported [49]. However, the five alleles (530, 535, 542, 550 and 562 nm) were found in a captive population, and it is unknown whether all of these alleles co-occur in the same wild population. In addition to the novel 555 nm allele found in the uakari, the 556 nm allele has not been previously described in pitheciids.

We now consider the selective forces that are responsible for such a high degree of colour vision polymorphism in uakaris. High allelic diversity may reflect trichromat advantage, since the greater the number of alleles, the higher the potential proportion of female heterozygotes. Discussions of the adaptive advantage of trichromats in NWMs have largely centred on foraging ability. Studies modelling the chromatic signal of food items eaten in the wild and experimental studies in captivity have confirmed that trichromacy is well suited to many foraging tasks involving yellow/red food against a green foliage background [13–16,50]. However, trichromacy may be a disadvantage for cryptic food [22–24], which probably includes the sclerocarpic fruits whose unripe and mature seeds represent a major proportion of the uakaris' diet [28,51,52], although we emphasize that further evidence (such as colour vision modelling of food items of uakaris) is required. Trichromatic NWMs may also be better at detecting predators such as carnivores and snakes [19,20]. So far only raptor predation on uakaris has been documented, where

colour vision is probably less relevant [53]. However, the fact that snakes and jaguars may prey on monkeys larger than uakaris within trees suggests that the threat represented by them should not be discounted [54,55].

Another possibility is that the large number of photopigment alleles in the bald uakari could be related to intraspecific signalling involving red coloration, and in particular the uniformly red facial skin of males. The red facial skin of uakaris bears the hallmarks of a sexually selected trait, being more prominent in males than females (with males also having more prominent heads because of enlarged temporal muscles) [56,57]. Although the mating system of uakaris is poorly understood, there is strong circumstantial evidence for a polygynous system related to male coloration. Uakaris have large group sizes and fission–fusion behaviour [30], which are associated with greater male ornamentation in primates [38]; sexual dimorphism in visual traits is stronger in polygynous primates [58], and there is some evidence that subgroups of uakaris are composed of affiliative male units that are outnumbered by females [59]. In addition, large group sizes in NWMs are associated with simple facial patterns, as found in uakaris [60].

In routinely trichromatic Old World monkeys, the intensity of red coloration of male facial skin has been shown to be a sexually selected signal, such as in mandrills and rhesus macaques [61,62]. These results accord with the finding that primate trichromacy is well suited for discriminating the degree of oxygen saturation in the blood in bare skin [21]. There has been good progress in recent years in identifying the proximate factors that lead to variation in sexually selected skin coloration in non-human primates [63,64]. In uakaris, this could be related to testosterone or to specific genotypes, as it is in mandrills [65,66], and/or to parasitism and immune status, following some of the main theoretical explanations for the evolution of sexually selected ornaments [53,67–69]. There is anecdotal evidence that the red face of the bald uakari varies with health, becoming pale in sick uakaris [33,34,70], and the structure of the uakari facial skin allows a direct external assessment of haematological status [34], suggesting that the colour of the face would be an honest indicator of health. Intriguingly, uakaris appear particularly susceptible to infection by two blood-borne parasites: they showed the highest rates of infection by the malaria parasite *Plasmodium brasiliensis* of any NWM [71] and had an infection rate of 100% for trypanosomatids (*Trypanosoma cruzi* and *T. rangeli*) compared with 64% for other primates on the Yavari River in Peru [72]. Hence, the physiological effects of plasmodial and trypanosomal infections might be two aspects of male quality that are signalled by facial coloration in uakaris.

These considerations support the possibility that high levels of colour vision polymorphism in the bald uakari

might be an adaptation for sexual selection on male (facial) coloration. Colour vision simulations provide evidence for the conspicuousness of the red male head to female uakari trichromats (figure 2). Trichromacy in female uakaris could serve an important function in discriminating male quality via facial coloration, and give trichromatic females an advantage over dichromats.

If trichromatic advantage alone were operating, we would expect to find a high proportion of heterozygous females, but only 35% of females in our study are heterozygous. This might be simply attributable to inbreeding in this single sampled population. An alternative explanation is that selection is more complex, and involves frequency-dependent selection in which there are some situations in which dichromats outperform trichromats or other dichromats. For example, dichromats may have a foraging advantage for cryptic food, or dichromats with longer wavelength alleles may have a foraging advantage over other dichromats [24,25,50]. However, it is difficult to envisage a scenario in which frequency-dependent selection alone could lead to the low heterozygosity, and a contribution of inbreeding remains likely.

In conclusion, uakaris have surprisingly diverse colour vision, and it is plausible that sexual selection is a contributory factor, although other adaptive advantages may well be involved. Further clarification of the selective forces acting on uakari colour vision will require behavioural studies. It will be of great interest to elucidate these mechanisms further, since uakaris may be a model for the evolution of colour vision in catarrhines, in which ancestrally evolved trichromatic colour vision for foraging then became co-opted for use in sociosexual signalling [73] (but see [74]).

Ethics. Data were collected with a permit from INRENA (Instituto Nacional de Recursos Naturales) of the Peruvian government, and the methodology complied with their regulations.

Data accessibility. Nucleotide sequences have been deposited in Genbank (accession nos. KP867064–KP867097).

Authors' contributions. M.B. and N.I.M. conceived the study; M.B. collected field samples; J.C., C.R. and M.B. generated the data; J.C. and N.I.M. analysed the data; J.C., M.B., C.R., E.W.H. and N.I.M. wrote the manuscript. All authors gave final approval for publication.

Competing interests. We declare we have no competing interests.

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