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Effect of polymorphic colour vision for fruit detection in the spider monkey *Ateles geoffroyi*, and its implications for the maintenance of polymorphic colour vision in platyrrhine monkeys

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Summary

Most platyrrhine monkeys have an X-linked tri-allelic polymorphism for medium and long wavelength (M/L) sensitive cone photopigments. These pigments' sensitivity maxima (λ_{max}) range from 535 to 562 nm. All animals also have an autosomally coded short-wavelength-sensitive (S) cone pigment. In populations with three M/L alleles there are six different colour vision phenotypes. Heterozygous females have trichromatic colour vision, while males and homozygous females are dichromats. The selective basis for this polymorphism is not understood, but is probably affected by the costs and benefits of trichromatic compared to dichromatic colour vision. For example, it has been suggested that trichromats are better equipped than dichromats to detect fruit against a leaf background. To investigate this possibility, we modeled fruit detection by various colour vision phenotypes present in the frugivorous spider monkey, *Ateles geoffroyi*. Our study population is thought to have three M/L alleles with cone pigment λ_{max} values close to 535, 550 and 562 nm. The model predicted that all trichromat phenotypes had an advantage over dichromats, and the 535/562 nm phenotype was best; however, the model predicted that dichromats could detect all of the fruit species consumed by spider monkeys. We conclude that the heterozygote advantage experienced by females may be the most plausible explanation for the maintenance of this polymorphism in *A. geoffroyi*. Nevertheless, more studies need to evaluate social foraging behaviour and the performance of different phenotypes of other New World monkeys to determine if this is a global explanation for this phenomena or more specific to *A. geofforyi*.

Key words: Costa Rica, platyrrhines, spider monkey, *Ateles geoffroyi*, fruit detection, colour vision, genetic polymorphism.

Introduction

Most species of platyrrhine (New World) primates have one cone photopigment (opsin) gene located on the X chromosome (Jacobs and Neitz, 1985, 1987), but frequently this locus is polymorphic. There are up to three alleles, which encode opsins with spectral sensitivities in the middle-to-long (M/L) wavelength range, having sensitivity maxima (λ_{max}) from 535 nm to 562 nm (Jacobs et al., 1996). All diurnal primates have an autosomally coded short wavelength (λ_{max} 425 nm) cone pigment. As a result of the M/L polymorphism, there is intraspecific variation in colour vision. The presence of three alleles gives six possible colour vision phenotypes. Heterozygous females with two M/L opsins are trichromatic, while males and homozygous females are dichromats (Jacobs, 1998).

An animal with trichromatic colour vision requires a mixture of three primaries to match any colour, but it is probably of more practical relevance that having two receptors with the greatest sensitivity to wavelengths above 500 nm allows animals to discriminate colours that we recognize as red, yellow and green, and may otherwise be confused by dichromats. As fruit eaten by primates are often yellow or red it has long been suggested that trichromacy evolved for frugivory (Allen, 1879; Polyak, 1957; Regan et al., 2001). Only fairly recently has this suggestion been tested, in part prompted by the discovery of M/L opsin polymorphism in New World monkeys. Modeling studies that estimate receptor responses to fruit and leaf spectra, either for market fruits (Osorio and Vorobyev, 1996) or for food eaten by wild trichromatic primates (Regan et al., 1998; Sumner and Mollon 2000a,b) lend support to Allen's proposal, as do two recent experimental studies on captive animals. These experiments, with omnivorous platyrrhines, showed that trichromatic individuals of marmosets (*Callithrix geoffroyi*) and tamarins (*Saguinus* spp.) were better than dichromatic individuals at finding food objects with orange hues at >5m distance (Caine and Mundy, 2000), where the colour had been chosen to match natural food colours (Smith et al., 2003).

If trichromatic colour vision is advantageous for finding fruit, how can we explain why most New World monkeys are polymorphic? Mollon et al. (1984) put forward four potential explanations: (1) group selection; (2) frequency dependent selection; (3) spatial heterogeneity of environment; and (4) heterozygote advantage. Owing to its occurrence in many species with long independent evolutionary histories, it is virtually certain that the M/L polymorphism is stable (Surridge and Mundy, 2002; Surridge et al., 2003) and therefore the fitness of the various alleles must be frequency-dependent (i.e. alleles are selectively favoured when rare). This means that of the four original hypotheses, the most plausible explanation is either (hypothesis 2) frequency dependent selection for the *phenotypes*, or (hypothesis 4) heterozygote advantage (Surridge et al., 2003). Frequency dependent selection of the various colour vision phenotypes might arise because different phenotypes can exploit different types of food, thereby reducing competition. However, the actual variation in foraging abilities of the different colour vision phenotypes is unknown. Alternatively, polymorphism might be maintained simply by the advantage of trichromacy over dichromacy (heterosis or overdominance; Surridge and Mundy, 2002). The main difficulty with this explanation is to account for why most New World primates have not benefited from the M/L gene duplication that has occurred independently in both howling monkeys (*Alouatta* sp.) and Old World primates (Catarrhines). Amongst these routinely trichromatic groups there is very little polymorphism, with all individuals having a 535 nm M-pigment and a 562 nm L-pigment.

To understand the maintenance of M/L polymorphism in platyrrhines, it is necessary not only to determine the advantage of trichromacy over dichromacy in fruit detection, but also the performance of different phenotypes in detecting different kinds of fruit. This question is especially pertinent to spider monkeys, *Ateles* sp., which are highly frugivorous, with different species spending between 57% and 77% of their total feeding time on fruit (Cant, 1977; Chapman, 1987; Symington, 1988). They prefer ripe to unripe fruit, or to any other food (Symington, 1988). Laboratory tests on two individuals of *Ateles geoffroyi* suggest that this species has more acute colour discrimination than most platyrrhines (Blakeslee and Jacobs, 1982).

This study evaluates different types of spider monkey colour vision by modelling their performance in detecting fruit against a background of leaves. The only published study (Jacobs and Deegan, 2001) of spider monkey opsin genetics reported only 562 nm and 550 nm alleles, but we believe that our study population had three M/L alleles, giving pigments with sensitivity maxima at 535, 550 and 562 nm (W.-H. Li, personal communication). The model here is similar to that used previously by Osorio and Vorobyev (1996). It assumes that the contrast sensitivity of the animals is independent of stimulus intensity (i.e. Weber's law holds), as is likely to be the case in bright viewing conditions (Rovamo et al., 2001). We consider that a fruit is detectable if its difference from the leaf background exceeds a specific threshold (1 just noticeable difference; 1 jnd). This threshold is based on data from human laboratory studies (Wyszecki and Stiles, 1982; Vorobyev and Osorio, 1998).

Materials and methods

Study site and species

The study site was Punta Rio Claro Wildlife Refuge (8°39′N, 83°44′E) on the Osa Peninsula in Southwestern Costa Rica. This area is classified as tropical humid forest (Holdridge et al., 1971). Mean annual rainfall is 3000 mm, but with a marked dry season from December–April (Hartshorn, 1983). *Ateles geoffroyi* Kuhl 1820, one of four species in its genus, is distributed from Tamaulipas and Jalisco, Mexico on both coasts, to Oaxaca and southeastern Panama (Reid, 1997). As already mentioned, sequencing of opsin genes from our study population indicates the presence of 535 nm, 550 nm and 562 nm M/L alleles (W.-H. Li, personal communication).

Foraging data collection

Foraging by one troop of *Ateles geoffroyi* containing 30 individuals was studied from May 1999 to May 2000. Data were collected 2 days per week from 6:00 h to 18:00 h using 2 min continual focal animal observations to obtain information on fruit consumption (Altmann, 1974). All individuals were identified to sex and age-class; focal animals were randomly changed after each 2 min observation. Only data from adults were included in the analysis because juveniles were infrequently observed.

Fruits were considered consumed when monkeys bit into the fruit more than twice, swallowing either the pulp or the entire fruit. Samples of food fruits were mostly collected when monkeys accidentally dropped fragments. However, when the entire fruit was consumed, samples were collected from fresh fruits that fell off the branch while the monkey foraged. When fruit samples could not be obtained while collecting foraging data, we returned the following day and used a telescopic tree pruner to collect samples from the same part of the same tree. To describe the background colours against which fruits were seen, we collected two mature leaves surrounding the fruits where monkeys were feeding. Only the upper surfaces of these leaves, those which we presumed the monkeys to be observing, were recorded.

Colour measurement

We recorded the reflectance spectra of consumed fruits and background leaves in the field using a portable field kit (Lucas et al., 2001) that incorporates a fibre optic spectrometer (S2000, Ocean Optics, Dunedin, FL, USA) connected to a laptop portable computer *via* a PCMCIA card (DAQCard1200, National Instruments, Austin, TX, USA). Samples were placed in a purpose-built chamber connected to the spectrometer with illumination provided by a 12 V 3100k tungsten halogen lamp (LS-1, Ocean Optics, Palo Alto, CA, USA). Spectra were referenced to a standard flat surface of barium sulphate powder.

Estimating performance of phenotypes

To compare different visual phenotypes we use a model that accurately describes colour thresholds of humans and other animals. The model assumes that these thresholds are set by photoreceptor noise in chromatic (i.e. colour opponent) mechanisms, and that the achromatic (brightness) signal is not used (Vorobyev and Osorio, 1998; Kelber et al., 2003).

For an eye viewing a stimulus, the quantum catch of a photoreceptor *i*, Q_i, is given by:

$$Q_i = \int_{\lambda_{min}}^{\lambda_{max}} R_i(\lambda)S(\lambda)I(\lambda)d\lambda , \quad (1)$$

where λ is the wavelength, and λ_{min} and λ_{max} are the lower and upper limits of the visible spectrum respectively. Here, we assume λ_{min}=390 nm and λ_{max}=700 nm. The spectral sensitivity of the *i*th photoreceptor is $R_i(\lambda)$; the reflectance spectrum is $S(\lambda)$, and $I(\lambda)$ is the illumination spectrum.

When Q_i is high, the contrast threshold can be assumed to be independent of intensity. Then noise levels are given by:

$$\delta Q_i = \omega_i Q_i , \quad (2)$$

where ω_i is the Weber fraction (Wyszecki and Stiles, 1982). If the receptor signal is given by:

$$f_i = \ln(Q_i) , \quad (3)$$

then for dichromatic and trichromatic eyes, respectively, the chromatic distances between the target (fruit) and background (leaf) stimuli are:

$$(\Delta S)^2 = \frac{(\Delta f_L - \Delta f_S)^2}{(\omega_S)^2 + (\omega_L)^2} \quad (4)$$

and

$$(\Delta S)^2 = \frac{\omega_S^2(\Delta f_L - \Delta f_M)^2 + \omega_M^2(\Delta f_L - \Delta f_S)^2 + \omega_L^2(\Delta f_S - \Delta f_M)^2}{(\omega_S\omega_M)^2 + (\omega_S\omega_L)^2 + (\omega_M\omega_L)^2} , \quad (5)$$

where Δf_i denotes the difference in f_i values between target and background stimuli and the subscripts *L*, *M* and *S* indicate long, medium and short wavelength photoreceptors, as appropriate.

Evaluation of chromaticity differences

The discriminability of any two spectra is predicted by the above model in terms of 'just noticeable difference' units (or jnds), where 1 jnd is the minimum threshold at which the performance of an observer can detect a target against a background. When the difference between these two stimuli exceeds 1 jnd the target is detectable, while one falling below this threshold is not. This model offers a clear criterion for the performance of colour vision close to threshold. As thresholds in field conditions may not match those in the laboratory, for example due to variations in stimulus size (Rovamo et al., 2001; Parraga et al., 2001), we take account of suprathreshold performance by noting when *differences* in estimated detectability between two phenotypes exceed 1 jnd (Table 1).

We assumed the following Weber fractions: ω_L=0.02; ω_M=0.02 and ω_S=0.08, which are close to measured psychophysical thresholds for humans (Wyszecki and Stiles, 1982; Osorio and Vorobyev, 1996). We assume that the total number of M/L cones is fixed in dichromats and trichromats, so that for the dichromat M/L mechanism $\omega_L=0.02/(2)^{0.5}$. Fruit and leaf spectra of a given species of plant obviously vary, in part due to variation in solar exposure of mature leaves (Dominy et al., 2003). Given that fruit are relatively rare amongst leaves, a reasonable estimate of visibility is the *minimum* difference between a fruit spectrum and all leaf spectra. For this reason, whenever possible, we measured the spectra for more than one fruit sample and the performance for a given species was then calculated as the median of these minima. A standard illuminant of sunlight spectrum recorded from a large forest gap was used; this illuminant closely approximates D65 (figured in Lucas et al., 2003). Although illumination spectra vary substantially in the forest we do not take account of the effects of such variation, as these are likely to be negligible for the task modelled here (Osorio and Vorobyev, 1996).

Table 1. *A comparison of the predicted performance of six phenotypes of model spider monkey fruit detection*

(A) Trichromatic *vs.* Dichromatic*

Wavelength	535	550	562
535/562	74	72	62
535/550	50	41	44
550/562	41	38	35

(B) Trichromatic phenotypes

Wavelength	535/562	535/550	550/562
535/562	–	61	64
535/550	0	–	15
550/562	0	0	–

(C) Dichromatic phenotypes

Wavelength	535	550	562
535	–	10	17
550	25	–	7
562	33	25	–

*In no cases did dichromats perform better than trichromats.

Numbers represent the percentage of fruit species in which the mean signal (jnd values) for one phenotype (row) exceeded another phenotype (column) by a value greater than 1 jnd.

Calculation of yellow-blue and red-green colour signals

Where a description of colour of an object is needed and not just a colour difference, it is convenient to assume that colour is coded by blue–yellow (*BY*) and red–green (*RG*) opponent mechanisms (Regan et al., 1998). The responses of the L (562 nm), M (535 nm) and S (430 nm) cones, relative to an achromatic standard, are respectively given by the quantum catches of the receptor Q_L, Q_M and Q_S:

$$BY = Q_S/(Q_L+Q_M) ; RG = Q_L/(Q_L+Q_M) . \quad (6)$$

Using these parameters the colour of a fruit can be defined as either bluer or yellower, and either redder or greener than the leaf background (Regan et al., 1998; Lucas et al., 2004). We used Mann–Whitney tests to: (a) determine if the difference between the colour of the fruit species and the background was significantly different between the yellow–blue or red–green channels, (b) to determine if consumed fruits signal more at the yellow or blue section of the yellow–blue channel, and (c) to determine if consumed fruits signal more at the red or green section of the red–green channel.

Results

Chromaticities of fruits consumed by spider monkeys

Foraging data were collected over 66 days for a total of 460 contact hours, averaging 7 h observation per day. A total of 821 focal animal observations were collected, and of these only 75 corresponded to male observations. *Ateles geoffroyi* were observed eating a total of 65 species of fruit during the study period. A total of 369 reflectance spectra were measured from outer fruit coverings of 39 species, which comprised 77.5% of the fruit diet during the observation period. Of these, the model predicted that all three trichromatic phenotypes (with M/L pigments at 535/562, 535/550, 550/562 nm) were able to detect all of the species analyzed. In contrast, the dichromatic phenotype with a 562 nm pigment detected 38 species and the dichromatic phenotypes with 535 nm and 550 nm alleles, 37 species. The dichromatic phenotypes (i.e. males and homozygous females) not only detected most of the fruit species, but also were able to detect the most important species in the fruit diet of this primate (Fig. 1).

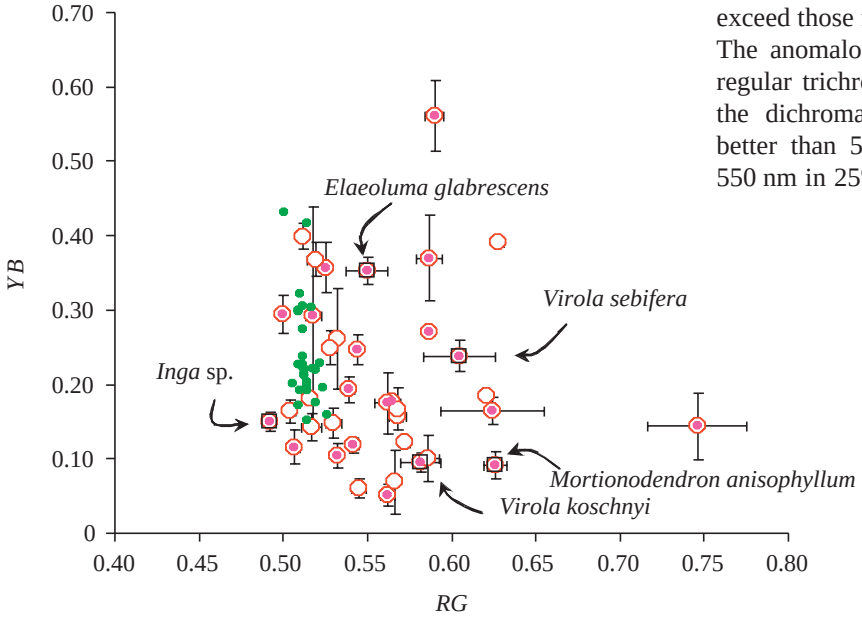

Fig. 1. Distribution of fruit chromaticities from the diet of *Ateles geoffroyi* for red–green (*RG*) and yellow–blue (*YB*) colour vision signals, as defined in the text. Values are calculated for cone sensitivities of the standard catarrhine type of trichromatic colour vision with 535 and 562 nm pigments. Green circles represent the background (i.e. mature leaves), red circles represent fruits consumed by spider monkeys (N=39 species, representing more than 77.5% of feeding time in fruits). Red circles with pink dots represent the fruit species also eaten by males. The five most important species in the diet of *A. geoffroyi* are marked with squares and have the species names beside them. Whiskers represent standard errors of fruit chromaticities.

The difference between fruit colour and background was significantly different for blue–yellow and red–green signals (Mann–Whitney test, U=418.5, P=0.04, d.f.=1), with greater differences between fruit and background being observed for the blue–yellow signal (Fig. 1). Differences in blue–yellowness were distributed approximately equally on both sides of the mean background chromaticity with no tendency for a blue or yellow bias (Mann–Whitney test, U=189, P=0.38, d.f.=1). For the red–green signal, all but two species were redder than the background (U=0, P=0.02, d.f.=1).

Fruit detection performance by phenotype

We have predicted that nearly all the fruit species could be detected by all six phenotypes, in that the fruit differed from leaves by at least 1 jnd. It is also interesting to ask if performance *differed* between phenotypes by at least 1 jnd (Table 1). The performance of the regular trichromat was better than the three dichromatic phenotypes (Table 1A) as well as the two anomalous trichromats (Table 1B). The two anomalous trichromats were very similar in performance; for only 15% of the species did colour signals for the 535/550 phenotype exceed those for the 550/562 phenotype by >1 jnd (Table 1B). The anomalous trichromats did not perform better than the regular trichromat for any of the species (Table 1B). Within the dichromatic phenotypes, the 562 nm allele performed better than 535 nm in 33% of the species and better than 550 nm in 25% of species.

Discussion

Several studies have suggested that trichromacy is beneficial for frugivory, particularly for detecting ripe fruit at long distances (Caine and Mundy, 2002). Since edible fruit is often scarce (Jordano, 2000), trichromatic colour vision may increase foraging efficiency. In species with a single M/L locus it has been suggested that the heterozygote advantage of trichromacy may be sufficient to maintain the X-polymorphism (Mollon et al., 1984; Surridge et al., 2003). This argument makes no assumptions about the social interactions in primates. However Lucas and others (2004) propose that the advantage will be greatest for primate species that forage in social groups because trichromats will be able to lead conspecifics to fruit-bearing trees, thus all individuals in a group would benefit

regardless of their actual phenotype. Frequency-dependent selection on phenotypes, originally proposed by Mollon and others (Mollon et al., 1984), is the alternative explanation. This latter proposal is also quite likely to depend on social interactions, because it requires either that the visual polymorphism reduces competition or promotes group efficiency by allowing specialization (see also Regan et al., 2001).

Our results support the hypothesis that trichromacy is advantageous for frugivory in platyrrhine monkeys. Phenotypes with the 535 nm and 562 nm alleles are best, and these are the genes found in routinely trichromatic Old World and howling monkeys. Furthermore, our observations of spider monkey behaviour provide some support for the notion that social interactions are important in foraging for this species. Foraging subgroups of the study population in our study site most frequently consisted of 2–3 adult females with their associated offspring. Although all male subgroups were common, as has been described by other studies (Symington, 1988; Chapman, 1990), these subgroups frequently met with subgroups containing females throughout the day. Although agonistic interactions occurred more often in feeding trees than under other circumstances and usually resulted in low-ranking females being pushed out of feedings trees, the entire subgroup benefited from the *discovery* of the feeding tree, as all individuals eventually fed in the tree. In such cases, fruit foraging in spider monkeys does not appear to be an individual task but rather more of a group task. Under these conditions, the heterozygote advantage of trichromacy may be the most plausible explanation for maintaining the X-polymorphism in *A. geoffroyi*. Nevertheless, more studies need to evaluate social foraging behaviour and the performance of different phenotypes of other New World monkeys to determine if this is a global explanation for this phenomena or more specific to *A. geoffroyi*.

According to our model, dichromacy appears to be adequate for the detection of most of the fruit species in the diet of *A. geoffroyi* (37–38 species of the 39 consumed) including the five most important species in the fruit diet of this primate. Interestingly, Snodderly (1979) put forward an opposite suggestion (prior to the discovery of M/L polymorphism) that trichromacy would be of little benefit to platyrrhine monkeys because most of the fruits they consume are cryptically coloured – and hence could not be located by any type of colour vision. In practice, whilst there are a number of cryptic (i.e. green) fruit, Snodderly's suggestion does not seem to hold for many species eaten by primates, and overall our results agree with previous studies that have shown dichromacy to be useful in fruit detection in studies with Old World monkeys (Dominy and Lucas, 2001; Sumner and Mollon, 2000a).

Several conclusions can be made from our study. First, when fruit colour is considered separate from other fruit traits, it can play an important role in fruit selection by platyrrhine monkeys. Since dichromatic phenotypes were able to detect 94–97% of all the fruit species that were detected by trichromatic phenotypes, including the five most important species in their diet, the performance of dichromats in detecting fruit is not as poor as previously suggested by Jacobs (1998). Second, although trichromacy always has an advantage for fruit detection at long distances for the individuals with this trait, factors such as social interactions and sub-group composition while foraging may also provide an advantage for other individuals in the group that are not trichromatic. Thus in the population of *A. geoffroyi* studied, the polymorphic alleles for colour vision may be maintained due to a heterozygote advantage. However, our conclusions should be taken with caution, since we lack information on the genotype of the population studied, and our model does not include the effect of illumination intensity on performance.

Three issues need to be clarified to better understand the advantage of trichromatic colour vision for frugivory, and hence the evolution of colour vision in platyrrhine primates. First, the actual frequencies of alleles in natural populations need to be determined. Second, the antiquity of opsin alleles in Atelid monkeys (Surridge and Mundy, 2002) must be defined. And third, experimental evidence that primates actually use colour as a cue to select fruits needs to be demonstrated. Finally future studies should incorporate these elements, along with social relationships among individuals and the actual fitness increase of trichromats (Surridge et al., 2003), in order to understand the evolution of trichromacy in primates.

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