CHAPTER 3

DID PRIMATE TRICHROMACY EVOLVE FOR FRUGIVORY OR FOLIVORY?

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Introduction

Primate colour vision

Most mammals have two types of cone photopigment, short-wave-sensitive (S) and long-wave-sensitive (L); and a dichromatic colour sense is provided by a comparison of the signals from the different cones in which these two pigments reside (Jacobs 1993). Most platyrrhine primates (New World monkeys), and probably some lemuriformes of Madagascar, exhibit sex-linked polymorphic colour vision: some females are trichromatic, having two different L photopigments with peak sensitivity (λ_{max}) in the range 536–564 nm (in addition to their S pigment, λ_{max} 430 nm), whereas other females and all males possess only one L photopigment, and are therefore dichromatic (Bowmaker *et al.* 1987; Jacobs and Blakeslee 1984; Jacobs *et al.* 1981; Mollon *et al.* 1984; Tan and Li 1999; Jacobs and Deegan, Chapter 2). All catarrhines (Old World monkeys and apes) and one genus of platyrrhines, *Alouatta*, have developed uniform trichromacy, such that all individuals possess two L pigments with λ_{max} values at about 530 and 560 nm, the former of which is normally referred to as a middle-wave (M) pigment (Bowmaker *et al.* 1991; Dulai *et al.* 1994; Dulai *et al.* 1999; Hunt *et al.* 1998; Jacobs and Deegan 1999; Jacobs *et al.* 1996; Kainz *et al.* 1998).

Whether the primates possess one or two types of L pigment, a comparison of the signal from L cones and S cones is mediated by a small population of bistratified ganglion cells, which project to the koniocellular layers of the Lateral Geniculate Nucleus and constitute a neural channel that is thought to remain largely separate from other visual pathways (Dacey and Lee 1994; Hendry and Reid 2000; Martin *et al.* 1997). In primates with two types of L cone (often called M and L), a separate comparison of the signals from these two types is mediated by the parvocellular system (which is present in all primates and is thought to subserve the resolution of spatial detail). Together these S/L and L/M subsystems create trichromacy.

The uniform trichromacy of *Alouatta* is known to have arisen separately from that of catarrhines, perhaps from a polymorphic arrangement similar to that seen in other platyrrhines. The polymorphic state may be ancestral to all primates,

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anteceding the catarrhine uniform trichromacy also. Alternatively, the polymorphism of platyrrhines, the polymorphism of Malagasy strepsirhines, and the uniform trichromacy of catarrhines, may all have arisen separately from a dichromatic ancestor. Regan *et al.* (2001) review this debate.

The advantage of trichromacy?

What was the selective advantage of the extra, L/M, subsystem of colour vision? The main hypothesis has been that the advantage lay in finding fruit amongst foliage (Allen 1879; Mollon 1989; Osorio and Vorobyev 1996; Polyak 1957). Primary evidence in support of this frugivory hypothesis has come from Regan *et al.* (1998, 2001), who measured (1) the spectral properties of the fruit in the diets of three platyrrhine species in French Guiana, (2) the spectral properties of the leaves that form the natural background against which these fruit must be found, and (3) the various illumination conditions of the forest environment. By modelling the signal-to-noise ratios for detecting fruit against foliage for all possible pairs of L pigment sensitivities, they found that the photopigments of *Alouatta seniculus* and of the trichromatic individuals of *Ateles paniscus* and *Cebus apella* are well optimized for detecting the fruit in the monkeys' diets against the natural background of forest leaves.

It has further been proposed that fruit signals and primate colour vision have co-evolved (Polyak 1957). For a recent discussion, see Regan *et al.* (2001). However, the relative advantages of different fruit colours to the plants, and the question of whether or not the plants' evolution has been affected by primate colour vision, do not directly impinge on our primary concern here—the selective advantage of trichromacy to the primates.

Lucas *et al.* (1998) have suggested an alternative hypothesis: that the advantage of trichromatic vision lay in the detection of red or reddish/brown colouration in the edible young leaves of some tropical plants. This folivory hypotheses has been compared to the frugivory theory by Sumner and Mollon (2000*a*). We used methods similar to those of Regan *et al.* (1998, 2001), but applied them to six catarrhine species in an African forest (Kibale, Uganda). We found that the L/M subsystem provides an advantage for detecting both fruits and young leaves amongst mature foliage, and furthermore, that the spectral positions of the primates' pigments are optimized for both tasks. We concluded that finding any of these food items may have been an important selective advantage in the original development, and in the subsequent maintenance and tuning, of primate trichromacy.

However, Dominy and Lucas (2001) have concluded, from similar spectral data also collected in Kibale, that "leaf consumption [has] unique value in maintaining trichromacy in catarrhines," that "the fruit-feeding hypothesis for trichromacy in higher primates is unconvincing," and that "full trichromatic vision evolved originally for leaf foraging in higher primates." Note that they make conclusions about both the original selective advantage and the advantage that maintains trichromacy today, factors which need not be the same. In addition, there are at least three "original" events to consider: the establishment of the polymorphic situation, perhaps more than once, the establishment of uniform trichromacy in *Alouatta*, and the establishment of uniform trichromacy in catarrhines. The most important selective advantage may have been different for each of these cases, just as the relative importance of folivory and frugivory in maintaining polymorphism or uniform trichromacy may differ between different species today.

We examine below how Dominy and Lucas, using data similar to ours, reached different conclusions and why we believe that the evidence cannot support their claims.

Evidence and arguments for the folivory and frugivory hypotheses

The spectroradiometric evidence

Dominy and Lucas' derived their conclusions both from their primary evidence, and from secondary arguments. We consider first their primary arguments, which may be summarized as follows:

(1) Leaves that primates select have higher than average ratios of protein to toughness (their Fig. 2).

(2) This ratio is correlated with the leaves' signal in the L/M colour subsystem (calculated as $L/(L + M)$, where L and M are the quantum catches of the L and M cones).

(3) $L/(L+M)$ is better than luminance at discriminating consumed from mature leaves.

(4) The pre-existing colour signal (calculated as $S/(L + M)$) cannot discriminate between consumed leaves and mature leaves, but can discriminate between fruit and mature leaves because the average of the fruit's $S/(L + M)$ values is lower than that of mature leaves (their Fig. 3), and thus the L/M channel is unnecessary for finding fruit, but necessary for finding edible leaves.

(5) While the fruit diets of different primates differ in their chromaticity distributions, the leaf diets of the different primates do not, possibly explaining why all primates with uniform trichromacy have very similar $\lambda_{\max}$ values for their M and L cones (close to 530 and 560 nm, see Introduction, this chapter).

Dominy and Lucas supported points (1) and (2) with important new data. These arguments, however, while consistent with the folivory hypothesis, do not elevate it above the frugivory hypothesis because similar points can be made for fruit: Dominy and Lucas do not report the physicochemical characteristics of the fruit they measured, but primates tend to select ripe fruit, which have higher than average nutrient content (e.g. Simmen and Sabatier 1996; Wrangham *et al.* 1993) and lower than average hardness or toughness. For example, we found that for most species of consumed fruit in Kibale, the force required to puncture the skin of samples of different maturity (our measure of ripeness) was inversely related to their $L/(L + M)$ chromaticity values (Sumner and Mollon 2000*b*).

Likewise, point (3), that edible and mature leaves can better be discriminated by their $L/(L+M)$ chromaticity values than by luminance, is indeed consistent with the folivory hypothesis (and replicates our findings, e.g. figure 11A of Sumner and Mollon 2000*a*), but it is not inconsistent with the frugivory hypothesis, because fruits too can be better detected amongst mature leaves by their $L/(L+M)$ chromaticity values than by luminance (e.g. Sumner and Mollon 2000*a*, pp. 1973–4). Dominy and Lucas do not report how they calculated that "the red–green colour channel was a far better discriminant," and do not give the equivalent results for the fruits they measured. We suggest that a comparison of the mean signal-to-noise ratios may be appropriate. For our data collected in Kibale, the signal-to-noise ratio for detecting edible leaves against mature leaves (measured in the canopy in cloudy conditions) was about seven times higher using $L/(L+M)$ than luminance ($L+M$ or simply L for a dichromat), and for detecting ripe fruits against mature leaves it was about 14 times higher (the exact values depend on the relative sampling of different species and of different stages of maturity, on the type of illumination (sunlight, blue sky or cloudy) and on the exact λ_{max} of the dichromat's L cone)[1].

The main pillar of Dominy and Lucas' proposal that trichromacy evolved for folivory was argument (4), that frugivores do not need the additional "red–green" ($L/(L+M)$) colour channel, because the fruit was discriminable from mature leaves by the dichromat's existing "blue–yellow" ($S/(L+M)$) channel. However, they showed only that the distributions of the $S/(L+M)$ signal for fruit and foliage have statistically distinguishable means (their Fig. 3). This is to confound (a) the discriminability of two overlapping statistical distributions and (b) the discriminability of individual elements drawn from those distributions. To be camouflaged, a class of objects does not have to display the whole range of visual appearances found in their surroundings, they need only appear like a subsection of their surroundings. To be detected, therefore, a target must lie outside

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[1] Although the chromaticity and luminance distributions in figure 1 of Dominy and Lucas (2001) are similar to our data, the exact values on each axis are different. Dominy and Lucas do not give the details of how they calculated S, M, and L, or luminance, and nor do they tell us how they defined the boundary of their "domain of mature foliage (outlined in green)" in their figure 1. The differences in $L/(L+M)$ and $S/(L+M)$ probably arose from different normalization of the S, M, and L sensitivity curves (i.e. different assumptions about relative sensitivity of the cone classes) (D. Osorio, personal communication; P. Lucas, personal communication). This would affect the values, but not the form of the results, because, for example, a change in the relative sensitivity of L and M must affect equally all samples with equal $L/(L+M)$ values. Since no arguments are made from the absolute values of the results, all conclusions will be unaffected. The luminance axis may not be so easily dismissed: although labelled "luminance," the legend states that it is "a proportion of reflectance from a compacted barium-sulphate powder standard" (i.e. mean reflectance), but does not say what sensitivity function (e.g. $V\lambda$ or $L+M$) this has been weighted by, or even whether one was used at all. It seems unlikely that a weighting factor for the primates' sensitivity was omitted, but some of the reflectance values plotted by Dominy and Lucas in their figure 1b are curiously low (values below 2 per cent would normally appear black to a human observer).

the distractor distribution, not simply away from the mean. The important thing to a primate observer is whether a *particular* chromaticity is more likely to be a fruit or a leaf, regardless of what chromaticities other leaves and other fruits may have. If targets are much rarer than distractors (as in the case of fruit in the forest), when any particular chromaticity that might be a target or distractor is observed from a distance, it will most likely be a distractor. This argument is effectively taking a Bayesian approach of prior probability. The "frequency" axis of Dominy and Lucas' figure 3 gives, we assume, simply the number of samples they collected of each category. If the plots were scaled to reflect the total number of fruit and leaves that might be in a primate's visual field as it scans the canopy, then at nearly every $S/(L+M)$ chromaticity value the number of fruits would be dwarfed by the number of leaves (see Fig. 3.1). Even if some fruit were detectable by a dichromat using S/L, as long as the L/M channel provided an added advantage, it would still be selected for (this is the same argument as put forward above for luminance—that although some edible leaves and fruit have higher luminance than mature leaves, the L/M channel is a "better discriminant").

Where diets of primates are concerned, any argument that relies crucially on the exact statistics of samples will be insecure, because samples from different studies will vary. For example, although the mean $S/(L+M)$ values for the edible leaves and fruit differed in Dominy and Lucas' study, in our data they do not. Dominy and Lucas' samples of

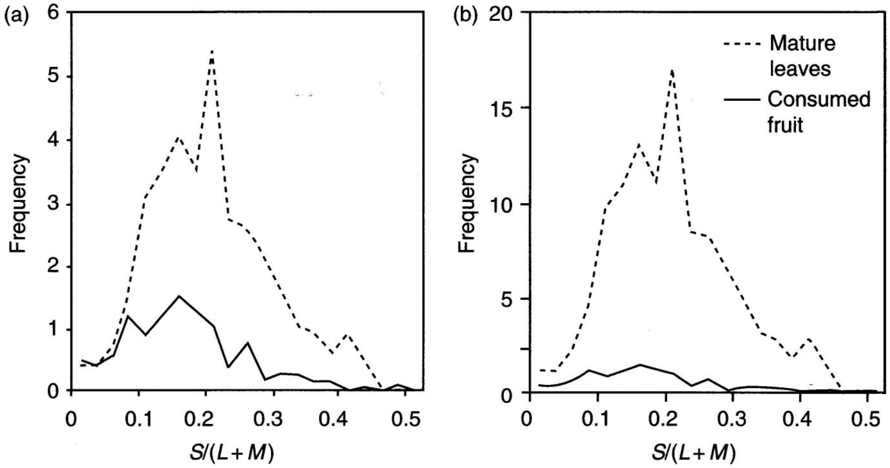

Figure 3.1 (a) Distribution of $S/(L+M)$ chromaticity values for the consumed fruits and mature leaves in figure 3.3A of Dominy and Lucas (2001). The "frequency" axis corresponds to the total number of samples measured, and thus the relative scaling of fruit and leaves is somewhat arbitrary. The ratio of leaves to fruit in the field of view of a primate searching for fruit, while difficult to estimate exactly, would probably range from 100 : 1 to much higher ratios. (b) Replots of the data of (a) with a very conservative ratio of 10 : 1 for the total number of mature leaves and fruit. At every value of $S/(L+M)$ chromaticity, the mature leaves outnumber the fruits, and thus any given chromaticity in the $S/(L+M)$ colour system is more likely to represent a distractor than a target.

these eaten items may be more representative because their fieldwork extended over a longer period (8 months vs 4 months). However, in the case of the mature foliage, we do claim to have made measurements that are more representative of the distribution viewed by a primate in the canopy. Dominy and Lucas measured the chromaticities only of collected samples, and these do not fully represent the distribution of signals in the forest. We additionally made measurements of leaves *in situ* in the canopy, and these display an extended range of S/L chromaticity values compared to our measurements of collected samples (especially when viewed from below), owing to light transmitted though the blade in the canopy as well as reflected light (see Sumner and Mollon 2000*a*, pp. 1971–3 and Regan *et al.* 2001, pp. 249–51). *In situ* the range of luminances is also extended, owing to differing angles of leaf blade and local shadows. When measurements of collected samples are compared, it appears that some fruits and edible leaves lie outside the mature leaf distribution on the luminance and S/L axes, and thus would be detectable by dichromats. But when the distribution of foliage *in situ* is considered, the food items do not lie outside the foliage distribution in S/L, and very few do in luminance, and thus the dichromatic primate could not reliably spot the fruit or young leaves on the basis of their colour, and would find it very difficult on the basis of luminance (especially for fruit, which tend to grow more in the shadows of the mature leaves than do the young leaves). On the other hand, in the phylogenetically newer, L/M channel of the trichromat, even the *in situ* foliage produces only a very limited distribution of signals, and most targets lie outside this distribution. Therefore, in the natural forest environment, the advantage of trichromacy for finding both fruit and leaves is larger than estimated from collected samples alone.[2]

It is clear that the L/M ("red–green") channel offers an advantage for finding both fruits and young leaves. There are other useful cues too, such as shape, position, smell, touch, or sound (e.g. alerting from birds) (Dominy *et al.* 2001), but their existence would not stop trichromacy being selected for if it gave a primate a competitive edge. Since all the arguments raised above apply to both frugivory and folivory, how might we distinguish between the theories? In the absence of other constraints, we might expect the L/M channel to be optimized for the task that most influenced its evolution. Following the modelling procedure developed by Regan and Mollon (Regan *et al.* 1998, 2001), we have calculated signal-to-noise ratios for detecting target food items amongst foliage for all possible combinations of M and L cone spectral sensitivities (Sumner and Mollon 2001). We did this separately for the fruit and leaf diets of the six studied primates in Kibale and we found that in all cases the maximum signal-to-noise ratios were yielded by a pair of pigments very close to those that the primates actually possess: about 530

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[2] Dominy and Lucas cite Sumner and Mollon (2000*b*) to support their claim that "although the red–green colour channel can help a group to identify such fruits at long range, the yellow–blue channel can often do this too." However in that paper we discussed the separate task of discriminating ripe fruit from unripe fruit (at short range), not the task of detecting fruit amongst foliage.

and 560 nm. The two sets of targets, edible leaves and fruit, produce virtually identical results because it is not the exact spectral properties of the targets themselves, but rather the properties of the mature foliage background that determine which spectral positions are optimal: the pair of λ_{max} values that yield maximum signal-to-noise is determined chiefly by minimising the variance of the chromaticities of mature leaves (Sumner and Mollon 2000*a*). This may explain why all extant trichromatic primates have similar photopigment tuning despite varied diets (cf point (5) of Dominy and Lucas' argument above). It also means that spectroradiometric data cannot tell us whether the most important things to detect amongst foliage were fruit, young leaves, or something else altogether, such as conspecifics or other animals.

Secondary arguments

Since spectroradiometric data cannot decide the folivory–frugivory debate, we might turn to other evidence. The primate species that are polymorphic for colour vision (most platyrrhines and at least some lemuroids; see Introduction of this chapter) offer the opportunity for directly testing whether trichromatic individuals are more successful than dichromatic conspecifics in foraging for fruit or for young leaves in the forest. However, since a study of this kind has not yet been published, let us briefly assess some of the secondary arguments.

Dominy and Lucas point out ecological differences between the diets and habitats of those primates exhibiting uniform trichromacy (Old World monkeys and apes, plus *Alouatta*) and those exhibiting polymorphic vision. The folivory hypothesis is supported by the fact that young leaves tend to be a more important food resource (in terms of both overall quantity consumed and reliance on it in times of fruit shortage) to catarrhines and *Alouatta* than to many platyrrhines, and that there seem to be more reddish young leaves in Africa and Asia than in South America (see Dominy and Lucas 2001; Dominy 2002). In the case of the folivorous colobines, which eat very little ripe fruit, leaf-finding is probably more important than fruit-finding in maintaining their trichromacy today, but this need not be true of when it originally evolved. It is believed that the specialized leaf-eating of colobines is a derived characteristic and that the ancestral catarrhine, being small, ate much more fruit than leaves (Martin 1990). Dominy and Lucas mention also that fruit may be found using other pre-ingestive cues, such as smell and texture. It could equally be argued that young edible leaves are a much less sporadic resource in the forest than fruit and can be found by their likely position at the ends of twigs.

Dominy and Lucas further argue that because 'basically dichromatic' platyrrhine species eat similar fruit to catarrhine primates and find it with 'no apparent difficulty', the idea that catarrhine trichromacy evolved for fruit-finding is implausible. However, firstly, no known diurnal platyrrhine is uniformly dichromatic. Secondly, no-one has reported that platyrrhines have difficulty finding young leaves: there are no published data on individual differences in fruit-finding or leaf-finding between trichromatic and dichromatic individuals. Thirdly, the use of a trait for a particular need in one population might easily occur without the invention or use of that trait in another population with a similar need: in the latter population there may be other means of solving the problem, there may be reasons for not wanting the trait, or the necessary step of invention may simply not have occurred.

If the initial genetic event needed to create uniform trichromacy from the polymorphic state has simply never occurred in the lineages of extant polymorphic primates, then comparisons of the diets and habitats of uniformly trichromatic and polymophic species are in fact not relevant. In order for a polymorphic species to become uniformly trichromatic, there needs to be an unequal cross-over at mieosis, so creating an X chromosome with two different viable middle/long-wave photopigment genes. This X chromosome then needs to be spread and maintained in the population. Why has this happened only in catarrhines and separately in *Alouatta*, but not in any other primate lineages despite the advantages in finding fruit and young leaves that should benefit all species? There are three possible types of reason: (1) As mentioned above, the required genetic event, followed by fertilization of the egg and survival of the embryo, may have occurred only in catarrhines and *Alouatta* and the polymorphism in other species may have been maintained by 'pure heterozygous advantage' (Mollon *et al.* 1984). (2) The advantage of trichromacy to catarrhines and *Alouatta* may have been more than to other platyrrhines and lemuroids (e.g. because the latter eat fewer leaves, as Dominy and Lucas argue, or because their social behaviour enables dichromatic individuals to find food via trichromatic individuals, or because South American fruits can more easily be spotted by their lightness or found using other pre-ingestive cues). (3) There may be advantages in being dichromatic, or in having a polymorphic group with dichromacy and different types of trichromacy all present. The latter possibility is discussed in detail by Mollon *et al.* (1984) and Regan *et al.* (2001).

Conclusions

The spectroradiometric evidence is consistent with both the folivory and frugivory hypotheses, and tests of intraspecific differences in foraging success between dichromatic and trichromatic individuals are yet to be reported. Therefore, there is at present no primary evidence that distinguishes between the theories. Secondary arguments can be made in favour of each theory, but our tentative conclusions would be that leaf-finding was probably important (as well as fruit-finding) in the spread of uniform trichromacy in *Alouatta*, and may now be the most important factor maintaining trichromacy in highly folivorous catarrhine species. In other species there is probably a range in the relative importance of frugivory and folivory in maintaining trichromacy, depending on diet, on fruiting and leafing cycles of the habitat, and on other uses of trichromacy such as discriminating the colours of pelage. Since ancestral primates are believed to have relied much more on fruit than leaves, fruit-finding was probably the most important factor in the original emergence of uniform trichromacy in Old World primates, and probably also in the emergence of the polymorphic states in South American monkeys and in lemurs.

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References

Allen, G. (1879). The Colour-Sense: Its Origin and Development. London: Trubner & Co.

Bowmaker, J. K., Astell, S., Hunt, D. M., & **Mollon, J. D.** (1991). Photosensitive and photostable pigments in the retinae of Old World monkeys. *Journal of Experimental Biology* **156**, 1–19.

Bowmaker, J. K., Jacobs, G. H., & **Mollon, J. D.** (1987). Polymorphism of photopigments in the squirrel monkey: a sixth phenotype. *Proceedings of the Royal Society of London B* **231**, 383–90.

Dacey, D. M. & **Lee, B. B.** (1994). The 'blue on' opponent pathway in primate retina originates from a distinct bistratified ganglion cell type. *Nature* **367**, 731–5.

Dominy, N. J. (2002). Incidence of red leaves in the rain forest of Kibale National Park, Uganda: shade-tolerators and light-demanders compared. *African Journal of Ecology* **40**, 94–6.

Dominy, N. J., & **Lucas, P. W.** (2001). Ecological importance of trichromatic vision to primates. *Nature* **410**, 363–6.

Dominy, N. J., Lucas, P. W., Osorio, D., & **Yamashita, N.** (2001). The sensory ecology of primate food perception. *Evolutionary Anthropology* **10**, 171–86.

Dulai, K. S., Bowmaker, J. K., Mollon, J. D., & **Hunt, D. M.** (1994). Sequence divergence, polymorphism and evolution of middle-wave and long-wave visual pigment genes of great apes and Old World monkeys. *Vision Research* **34**, 2483–91.

Dulai, K. S., von Dornum, M., Mollon, J. D., & **Hunt, D. M.** (1999). The evolution of trichromatic color vision by opsin gene duplication in New World and Old World primates. *Genome Research* **9**, 629–38.

Hendry, S. H. C. & **Reid, R. C.** (2000). The koniocellular pathway in primate vision. *Annual Reviews in Neuroscience* **23**, 127–53.

Hunt, D. M., Dulai, K. S., Cowing, J. A., Julliot, C., Mollon, J. D., Bowmaker, J. K., Li, W.-H., & **Hewett-Emmett, D.** (1998). Molecular evolution of trichromacy in primates. *Vision Research* **38**, 3299–306.

Jacobs, G. H. (1993). The distribution and nature of colour vision among the mammals. *Biological Reviews* **68**, 413–71.

Jacobs, G. H. & **Blakeslee, B.** (1984). Individual variations in color vision among squirrel monkeys (*Saimiri sciureus*) of different geographical origins. *Journal of Comparative Psychology* **98**, 347–57.

Jacobs, G. H., Bowmaker, J. K., & **Mollon, J. D.** (1981). Behavioural and microspectrophotometric measurements of colour vision in monkeys. *Nature* **292**, 541–3.

Jacobs, G. H. & **Deegan, J. F.** (1999). Uniformity of colour vision in Old World monkeys. *Proceedings of the Royal Society of London B* **266**, 2023–8.

Jacobs, G. H., Neitz, M., Deegan, J. F., & **Neitz, J.** (1996). Trichromatic colour vision in New World monkeys. *Nature* **382**, 156–8.

Kainz, P. M., Neitz, J., & **Neitz, M.** (1998). Recent evolution of uniform trichromacy in a New World monkey. *Vision Research* **38**, 3315–20.

Lucas, P. W., Darvell, B. W., Lee, P. K. D., Yuen, T. D. B., & Choong, M. F. (1998). Colour cues for leaf food selection by long-tailed macaques (*Macaca fascicularis*) with a new suggestion for the evolution of trichromatic colour vision. *Folia Primatologica* **69**, 139–52.

Martin, P. R., White, A. J. R., Goodchild, A. K., Wilder, H. D., & Sefton, A. E. (1997). Evidence that blue-on cells are part of the third geniculocortical pathway in primates. *European Journal of Neuroscience* **9**, 1536–41.

Martin, R. D. (1990). Primate Origins and Evolution. Princeton: Princeton University Press.

Mollon, J. D. (1989). "Tho she kneel'd in that Place where they grew. . . ." *Journal of Experimental Biology* **146**, 21–38.

Mollon, J. D., Bowmaker, J. K., & Jacobs, G. H. (1984). Variations of colour vision in a New World primate can be explained by polymorphism of retinal photopigments. *Proceedings of the Royal Society of London B* **222**, 373–99.

Osorio, D. & Vorobyev, M. (1996). Colour vision as an adaptation to frugivory in primates. *Proceedings of the Royal Society of London B* **263**, 593–99.

Polyak, S. (1957). The Vertebrate Visual System. Chicago: University of Chicago Press.

Regan, B. C., Julliot, C., Simmen, B., Viénot, F., Charles-Dominique, P., & Mollon, J. D. (1998). Frugivory and colour vision in *Alouatta seniculus*, a trichromatic platyrrhine monkey. *Vision Research* **38**, 3321–7.

Regan, B. C., Julliot, C., Simmen, B., Viénot, F., Charles-Dominique, P., & Mollon, J. D. (2001). Fruits, foliage and the evolution of the primate colour-sense. *Philosophical Transactions of the Royal Society of London B* **356**, 229–83.

Simmen, B. & Sabatier, D. (1996). Diets of some French Guianan primates: food composition and food choices. *International Journal of Primatology* **17**, 661–93.

Sumner, P. & Mollon, J. D. (2000*a*). Catarrhine photopigments are optimised for detecting targets against a foliage background. *Journal of Experimental Biology* **203**, 1963–86.

Sumner, P. & Mollon, J. D. (2000*b*). Chromaticity as a signal of ripeness in fruits taken by primates. *Journal of Experimental Biology* **203**, 1987–2000.

Tan, Y. & Li, W.-H. (1999). Trichromatic vision in prosimians. *Nature* **402**, 36.

Wrangham, R. W., Conklin, N. L., Etot, G., Obua, J., Hunt, K. D., Hauser, M. D., & Clark, A. P. (1993). The value of figs to chimpanzees. *International Journal of Primatology* **14**, 243–56.