

# Fruits, foliage and the evolution of primate colour vision

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Primates are apparently unique amongst the mammals in possessing trichromatic colour vision. However, not all primates are trichromatic. Amongst the haplorhine (higher) primates, the catarrhines possess uniformly trichromatic colour vision, whereas most of the platyrhine species exhibit polymorphic colour vision, with a variety of dichromatic and trichromatic phenotypes within the population.

It has been suggested that trichromacy in primates and the reflectance functions of certain tropical fruits are aspects of a coevolved seed-dispersal system: primate colour vision has been shaped by the need to find coloured fruits amongst foliage, and the fruits themselves have evolved to be salient to primates and so secure dissemination of their seeds. We review the evidence for and against this hypothesis and we report an empirical test: we show that the spectral positioning of the cone pigments found in trichromatic South American primates is well matched to the task of detecting fruits against a background of leaves. We further report that particular trichromatic platyrhine phenotypes may be better suited than others to foraging for particular fruits under particular conditions of illumination; and we discuss possible explanations for the maintenance of polymorphic colour vision amongst the platyrhines.

**Keywords:** coevolution; frugivory; seed dispersal; trichromacy; platyrhine; colour vision polymorphism

## 1. REVIEW

Many primates have trichromatic colour vision, and possess three distinct types of retinal cone photoreceptor. These different types contain different photopigments: the short-wave (S) sensitive cones contain a pigment with a peak sensitivity between 420 and 430 nm, and the middle-wave (M) and long-wave (L) sensitive cones contain pigments with peak sensitivities between 530 and

565 nm. Amongst the mammals, trichromatic colour vision is apparently unique to the primates (Jacobs 1993), for most mammals are dichromats, possessing just two classes of cone photoreceptor.

### (a) *The two subsystems of primate colour vision*

In order to make discriminations on the basis of colour, the outputs of the different classes of cone must be compared. In the primate visual system, there exist two classes of ganglion cell that are generally thought to carry information about colour. One class, the midget ganglion

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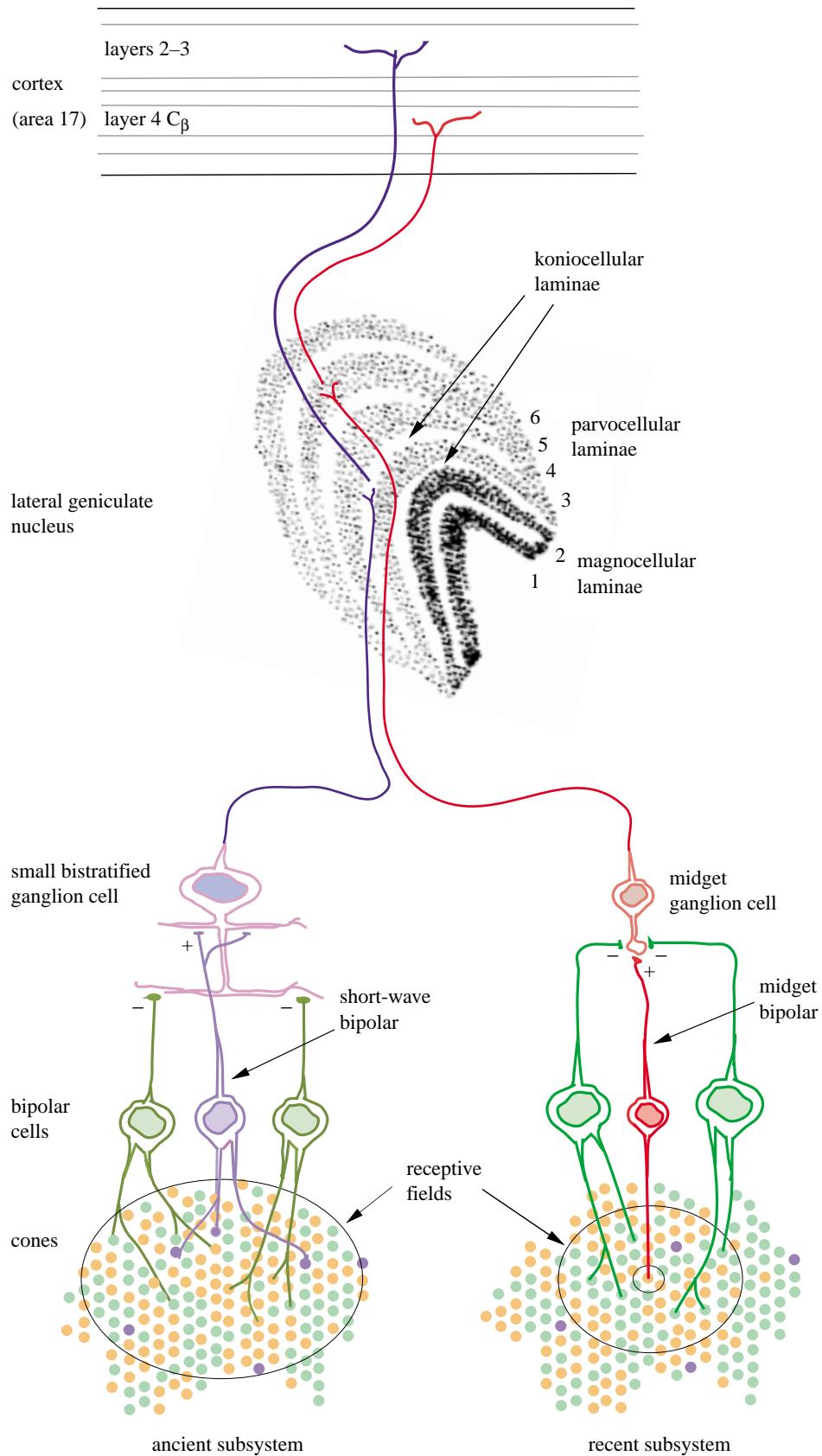


Figure 1. The two subsystems of primate colour vision. A schematic of the photoreceptor matrix shows the S, M and L cones in blue, green and orange, respectively. The phylogenetically ancient subsystem (left) draws opposed inputs from the S cones, on the one hand, and from the L and M cones on the other. Its signals are carried by the small bistratified ganglion cells and then the koniocellular laminae of the LGN. The recent subsystem (right) compares the signals of the L and M cones. Its signals are thought to be carried by midget ganglion cells and the parvocellular layers of the LGN. Note that the small bistratified cell does not show centre-surround opponency in its receptive field, whereas the midget ganglion cell does.

cells, have small receptive fields with centre-surround opponency, accepting input of one sign from a central region of their receptive field, and opposing it with input drawn from the surrounding region. They respond when the inputs to the centre and the surround regions are not uniformly illuminated: for example, when a spot or bar of light falls on the receptive field. However, midget ganglion cells may also draw inputs to the centre and the surround from different cone classes. In the foveal region, the input to the centre may be drawn exclusively from a single L or M cone (Goodchild *et al.* 1996), while the surround draws input either exclusively from the other cone class, or from both L and M cones. Whichever of the latter possibilities is correct (it is currently a matter of debate), the effect is that such ganglion cells exhibit chromatic opponency: they will respond not only when a spot or bar falls on the receptive field, but also when they are uniformly illuminated by a light with a spectral composition that stimulates the centre and the surround regions to different extents.

A separate set of ganglion cells seems to be specialized for carrying the information signalled by S cones. These are the small bistratified ganglion cells: they have larger receptive fields than midget cells at similar retinal eccentricities, and they lack centre-surround opponency, instead taking 'ON' inputs exclusively from S cones and opposing them with 'OFF' inputs from M and L cones in a coextensive retinal region (Dacey & Lee 1994).

Thus, there seem to be two separate channels encoding chromatic information in the primate retina, one carried by the midget ganglion cells, and the other by the small bistratified ganglion cells (figure 1). Because they draw inputs from different sets of cone receptors, these cells carry different information: specifically, the midget cells signal the ratio of excitation of L cones to M cones, and the small bistratified cells signal the relative excitation of the S cones. These two channels are maximally polarized by chromatic modulations between red and blue, or violet and yellow, respectively (Derrington *et al.* 1984). At higher levels in the visual pathway, the two channels remain separate: the midget ganglion cells project to the parvocellular layers of the lateral geniculate nucleus (LGN), while the small bistratified cells project to the koniocellular cells in the interlaminar layers of the LGN (Martin *et al.* 1997; Reid *et al.* 1997).

Perceptions mediated solely by the channel originating in the bistratified cells are often curiously indistinct. The most striking example occurs when an edge can be detected only by the S cones. Such an edge is ill-defined, and the areas on either side of the border melt into each other (Liebmann 1927). This effect demonstrates the poor spatial resolution of our vision when it depends on the S cones alone.

It has been argued that these two neural channels represent distinct subsystems of colour vision that evolved at different times and for different purposes (Mollon 1989). It is thought that early mammals were equipped with just two cone types: the majority of cones had a peak spectral sensitivity in the middle- to long-wavelength range, with a minority of S cones sparsely scattered throughout the cone matrix. The difference in their excitations gave a basic, dichromatic colour signal, and this arrangement is found in most modern mammals (Jacobs

1993). The channel that originates in the small bistratified ganglion cells mediates this primordial subsystem of colour vision. More recently, some primates evolved distinct L and M cone classes. In retinas with both L and M cones, the midget cells can carry information about colour by drawing centre and surround inputs from different classes of cone. However, midget cells are also found in the retina of dichromatic primates that do not possess distinct L and M cone classes (Ghosh *et al.* 1996), suggesting that the second, phylogenetically recent subsystem of colour vision is parasitic upon a channel that is primarily used for carrying information about fine spatial detail (Mollon & Jordan 1988).

This view of the midget cells carrying information about both colour and spatial detail is not universally accepted. An alternative hypothesis (Rodieck 1991; Calkins & Sterling 1999) is that the midget cells are used only to carry information about spatial detail, and that their accidental property of signalling chromatic information is not exploited. Instead, according to this hypothesis, there exists a separate class of ganglion cells making up *ca.* 5% of the total population, which lack centre-surround opponency and are used specifically to compare the L and M cone outputs (possibly with some small S cone input also). Such cells have yet to be identified morphologically in the primate retina, if they exist. To some extent, it does not matter to our discussion which hypothesis is correct: in either case, chromatic information is carried separately in two distinct neural channels originating in different classes of retinal ganglion cell.

#### **(b) Variations in primate colour vision**

In the Old World (catarrhine) monkeys and apes, so far as is known, there is a uniform trichromatic colour vision, based on photopigments with peak sensitivities in the range 424–434, 531–539 and 562–568 nm (e.g. Bowmaker *et al.* 1991; Jacobs *et al.* 1991; Dulai *et al.* 1994). However, not all primate species exhibit uniform trichromacy. In many New World (platyrhine) monkeys, colour vision is polymorphic, different animals of the same species showing wide variations on measures of colour vision. For example, in the squirrel monkey (*Saimiri sciureus*), behavioural tests suggest that all male monkeys are dichromats but that approximately two-thirds of females are trichromats (Jacobs 1984; Jacobs & Blakeslee 1984). Microspectrophotometry (MSP) studies have measured the sensitivity curves of the cone pigments in squirrel monkeys whose phenotype has been determined by independent, behavioural methods. These studies (Jacobs *et al.* 1981; Mollon *et al.* 1984; Bowmaker *et al.* 1987) found an S cone pigment in the population with a peak sensitivity at around 433 nm, and three different M or L cone pigments with peak sensitivities at 536, 550 and 564 nm. Monkeys diagnosed behaviourally as dichromats possessed the S cone pigment and one of the three L or M pigments, whereas those diagnosed as trichromats possessed the 433 nm pigment and two of the other three. Thus there are six colour vision phenotypes in the squirrel monkey population. An explanation for the polymorphic colour vision of the squirrel monkey was given by Mollon *et al.* (1984), who suggested that there is a single X-chromosome locus for an M or L cone pigment

gene in these animals, with three alleles of this gene in the population. Owing to X-chromosome inactivation (Lyon 1962), heterozygous females will express their alternative alleles in separate cones and so may achieve trichromacy.

Examination of other platyrhine species has shown that polymorphic colour vision is the rule, rather than the exception (Jacobs 1998a). However, there is a great deal of interspecific variation in the number of X-linked photopigment alleles in the population, and in the peak sensitivities of the photopigments they encode. Thus, in the spider monkey *Ateles geoffroyi*, there appear to be just two L- or M-type pigment alleles in the population (Jacobs 1998b): electroretinogram (ERG) flicker photometry (Jacobs & Deegan 1993b) and DNA sequencing (Hagstrom *et al.* 1993) show that their peak sensitivities are around 550 and 562 nm. Other platyrhine monkeys have three X-linked photopigment alleles in the population. For example, colour vision in *Cebus apella* resembles that of *Saimiri sciureus*: ERG flicker photometry (Jacobs & Neitz 1987) and MSP (Bowmaker & Mollon 1980) show that these have peak sensitivities at *ca.* 536, 550 and 562 nm. In the callitrichid lineage (marmosets and tamarins) there are at least three X-linked alleles in the population, but the pigments encoded have peak sensitivities different from those of *Cebus* and *Saimiri*: MSP and ERG flicker photometric measurements on *Callithrix jacchus*, *Saguinus fuscicollis* and *Saguinus oedipus* reveal peak sensitivities at *ca.* 543, 556 and 562 nm (Tovée *et al.* 1992; Jacobs *et al.* 1987; Jacobs 1994). And in some platyrhines, there may be as many as five X-linked photopigment alleles: in the dusky titi monkey *Callicebus moloch*, Jacobs & Deegan (1999) have reported cone pigments with peak sensitivities at 530, 536, 542, 549 and 561 nm, in different dichromatic males.

There are two known exceptions to the polymorphism typical of most platyrhines. The first is the uniform monochromacy of the owl monkey, *Aotus trivirgatus*, which possesses a single 543 nm cone type (Wikler & Rakic 1990; Jacobs *et al.* 1993). The second is the uniform trichromacy of the howler monkeys (genus *Alouatta*). Genetic analysis has revealed distinct L and M opsin gene sequences in individual male *Alouatta caraya* and *Alouatta seniculus* monkeys; and ERG flicker photometry has provided additional evidence for trichromacy in the case of individual males of *A. caraya* (Jacobs *et al.* 1996a). The peak sensitivities of the L and M cone pigments of *Alouatta* have not been established empirically, but the sequences of their L and M genes are very similar to the sequences encoding the 536 and 562 nm alleles found in *Cebus apella* (Hunt *et al.* 1998), suggesting that the L and M cone pigments in *Alouatta* have peak sensitivities at similar wavelengths.

Until very recently it was thought that the remaining primates, the prosimians, either exhibited a typical mammalian dichromacy or were monochromatic: Jacobs & Deegan (1993a) report only two cone pigments in *Lemur catta* and *Eulemur fulvus*, while the S cone pigment appears to have been lost in nocturnal species such as the bush-baby *Otolemur crassicaudatus* (Deegan & Jacobs 1996; Jacobs *et al.* 1996b). However, Tan & Li (1999) have recently reported a polymorphism of the X-linked opsin gene in three diurnal Malagasy lemuroid species,

suggesting that at least some female prosimians may enjoy trichromatic colour vision.

The two types of ganglion cell that subserve the two channels of colour vision were originally identified in Old World primates. However, the physiological basis of colour vision appears to be very similar in New World primates. Midget cells have been identified morphologically in the retinas of both dichromatic and trichromatic individuals from platyrhine species with polymorphic colour vision: *Callithrix jacchus* (Ghosh *et al.* 1996), and *Cebus apella* (Yamada *et al.* 1996). Midget cells apparently never receive input from S cones, and so they exhibit colour opponency only in trichromatic primates, which possess distinct L and M cone classes. Small bistratified ganglion cells have been described in both dichromatic and trichromatic individuals of *Callithrix jacchus* (Ghosh *et al.* 1997) and *Cebus apella* (Silveira *et al.* 1998), and as in Old World primates, these cells take inputs of one sign from S cones and of the opposite sign from L and M cones.

### (c) *The evolution of trichromacy in primates*

Primates are the only mammalian order where trichromatic colour vision has been found (Jacobs 1993). Two unanswered questions are: when did trichromacy first arise in primates; and how has colour vision subsequently evolved in the different primate lineages? These questions have usually been discussed specifically with reference to the differences between platyrhine and catarrhine primates (Mollon 1991; Hunt *et al.* 1998). However, any new account of the evolution of the primate colour sense should take into account the polymorphism of the L or M opsin gene found in some prosimians (Tan & Li 1999), as well as the differences between platyrhine and catarrhine colour vision. We highlight three issues of contention.

- (i) *The nature of colour vision in ancestral primates.* We can safely infer that the ancestor to the strepsirrhine-haplorhine radiation was at least potentially dichromatic, for all living primate species that have been studied possess a functional X-linked opsin gene and an autosomal short-wave opsin gene (although in some nocturnal species the latter is non-functional (Jacobs *et al.* 1996b)). However, the ancestor might equally have possessed polymorphic colour vision, or even uniform trichromacy. If the ancestral primate was dichromatic, the evolution of the L or M opsin gene polymorphism found in some strepsirrhine lineages has been a separate event from the evolution of trichromacy in the catarrhines and of polymorphic colour vision in the platyrhines, and convergent evolution must account for the similarities in the spectral tuning of the L or M group of pigments in different branches of the primate order. On the other hand, if the ancestral primate possessed polymorphic or uniformly trichromatic colour vision, this has subsequently degraded into dichromacy and monochromacy in some branches of the primate order, but the similarities in spectral tuning of the L or M group of pigments now seen in different branches may reflect common origins.
- (ii) *The antiquity of uniform trichromacy.* At some point in primate evolution, an unequal crossing over placed

two X-linked opsin genes on to a single X-chromosome, to give the potential for uniform trichromacy in both males and females. This may have happened very early in the evolution of primates, and subsequently been lost by strepsirrhines and platyrhines, or it may have happened later on, in the haplorhine branch. It may have occurred only once, before the split between catarrhines and platyrhines, and have been retained by all catarrhines but lost by platyrhines except *Alouatta*; or it may have occurred twice, once early on in the catarrhine ancestry and a second time in the evolution of *Alouatta*. It may even occur frequently but seldom be retained in the gene pool, if it confers little advantage as an adaptation (Hunt *et al.* 1998).

- (iii) *Polymorphic colour vision as an intermediate step in the evolution of uniform trichromacy.* The initial crossing over placing two opsin genes on a single X-chromosome may have occurred in a dichromatic species, giving identical copies of an L or M gene which subsequently diverged, leading to uniform trichromacy. Alternatively, polymorphic colour vision may have been an intermediate step in the evolution of trichromacy, and the initial crossing over may have placed two different alleles of a polymorphic L or M opsin gene on to a single X-chromosome, giving an almost immediate potential for uniform trichromacy. It may even be the case that the uniform trichromacy in catarrhines evolved in a dichromatic ancestor, whereas that found in *Alouatta* evolved in a polymorphic ancestor.

Unfortunately, much of the available evidence from molecular genetics can be interpreted in different ways to reach different conclusions. Some investigators (Hunt *et al.* 1993; Dulai *et al.* 1994) have sequenced the coding regions of the L and M genes of Old World primates and various New World primate L- or M-type alleles, and others have sequenced the non-coding introns (Shyue *et al.* 1995). The general finding is that there are fewer substitutions per site in comparisons between Old World L and M genes than in comparisons between Old World and New World genes, and the inference that is generally drawn is that the Old World L and M genes diverged after the split between catarrhine and platyrhine lineages. The weakness in this deduction is that it implicitly assumes that every gene is entirely independent of every other gene. But different genes in a single species have the opportunity to interchange material by gene conversion (Balding *et al.* 1992), resulting in genetic homogenization. Thus, the L and M genes may have diverged before the catarrhine-platyrhine radiation, and the finding that the L and M genes of catarrhines are now more similar to each other than to any platyrhine allele may simply be a result of gene conversion between the catarrhine L and M genes. This view is reinforced by the curious fact that several of the introns of the human L and M genes are more similar in their nucleotide sequence than are the exons, even though the introns ought to be under little selection pressure to stop them diverging. Thus, in the human L and M genes, intron 2 differs at only six nucleotides out of 1987, the 1552 nucleotides of intron 4 are identical (Shyue *et al.* 1994; Zhou & Li 1996) and intron 5 shows

only two differences in 2282 nucleotides (Zhao *et al.* 1998). A high homology is also reported for intron 4 of L and M genes in chimpanzee and in baboon (Zhou & Li 1996). It is remarkable that the exons of the two genes have retained their separate identities when the much longer introns that surround them have been homogenized. The implication is that all the amino acid differences between the long- and middle-wave opsins are under selection pressure, if not because they affect spectral tuning, then because they affect the stability and function of the molecule.

Hunt *et al.* (1998) have also argued that uniform trichromacy in catarrhines and polymorphic colour vision in platyrhines evolved independently, subsequent to the divergence of these two lineages. Unlike earlier studies that reached this conclusion, their argument is based on the observation that within each set of genes (the Old World L and M genes, and the various New World L- or M-type alleles) there exist particular differences that are not shared between the two sets of genes. They sequenced coding regions of the L and M genes of several Old World primates and of *Alouatta seniculus*, and the three L/M alleles of *Cebus apella* and *Callithrix jacchus*. Apart from the three sites (180, 277, 285) known to be critical for the spectral tuning of cone pigments (Neitz *et al.* 1991) they found 17 sites at which the L and M genes encoded different amino acids, and at 16 of these 17 sites, the substitution was either different in New World and Old World primates, or the substitution was found in one group and not another. For example, at site 229, all Old World genes and some New World genes encode isoleucine, but the 563 nm allele of *Cebus*, the 556 and 563 nm alleles of *Callithrix*, and the L gene of *Alouatta* encode phenylalanine. Hunt *et al.* (1998) argue that the most parsimonious explanation of these data is that the trichromatic systems of Old and New World primates evolved separately (and, by inference, from a dichromatic ancestor). However, all these data really tell us is that the platyrhines and catarrhines have been evolving on separate paths for some time. For example, at some point in platyrhine evolution, a substitution must have occurred at site 229 in a long-wave allele. The data say nothing about whether the common ancestor of the platyrhines and the catarrhines possessed one or several L or M alleles.

One case where the molecular genetic evidence does seem convincing regards the origin of trichromacy in howler monkeys (*Alouatta*). Dulai *et al.* (1999) have shown that the sequences upstream of the L and M genes in catarrhine primates diverge after 236 bp, whereas the sequences upstream of the L and M genes in *Alouatta seniculus* are homologous for over 600 bp. Furthermore, in *Alouatta* there are two, rather than one, locus-control regions in the X-linked opsin gene array. This suggests that the unequal crossing over that placed two opsin genes on the X-chromosome of Old World primates was a separate event from that which placed two opsin genes on the X-chromosome of *Alouatta*. Howler monkeys also appear to have two slightly different sequences in the promoter regions immediately upstream of the L and the M opsin genes (Kainz *et al.* 1998).

As for the origin of trichromacy in primates, Tan & Li (1999) suggest that polymorphic colour vision arose early in primate evolution. As well as finding a polymorphism

in the L or M opsin genes of three lemuroid species, they found a wider distribution of L-like and M-like opsin genes amongst different prosimian species. For example, they found one species of tarsier (*Tarsius syrichta*) with an L opsin gene and a different species (*Tarsius bancanus*) with an M opsin gene. Amongst the 15 lemuroid species that they examined, drawn from five families, they found M opsin genes in 12 species and L opsin genes in six. These prosimian M and L opsin genes are thought to encode pigments with spectral sensitivities similar to the platyrhine 543 nm and 558 nm alleles. Tan & Li (1999) argue that the most likely explanation for this scattered distribution of L and M opsin genes amongst various prosimian species is that a common ancestor had polymorphic colour vision. Their hypothesis is appealing, but we should bear in mind that opsins can apparently evolve with startling rapidity in response to changes in environmental circumstances (e.g. Bridges & Yoshikami 1970). Thus, the common spectral tuning of opsins observed in many different branches of the primate order may be a common response to a common evolutionary pressure.

Whatever the origins of polymorphic and trichromatic colour vision in primates, a further question remains: why is the trichromatic trait apparently unique to primates? One proposal is that trichromatic colour vision arose in primates for the purpose of finding strongly coloured fruits amongst leaves.

#### (d) *Frugivory and seed dispersal by primates*

Most primates eat fruit, and many eat it in large quantities. For example, amongst the catarrhines, fruit constitutes ca. 80% of the diet of *Cercopithecus cebus* (Soud & Gautier-Hion 1986), 95% of the diet of *Macaca sinica*, 60% of the diet of *Presbytis obscura*, and 68% of the diet of *Pan troglodytes* (Richard 1985). McConkey (1999) found that gibbons (*Hylobates mülleri* × *agilis*) spent 62% of their feeding time on fruit. Amongst the platyrhines, fruit constitutes ca. 90% of the diet of *Ateles paniscus* (Van Roosmalen 1985; Guillotin *et al.* 1994), 47% of the diet of *Saguinus midas* (Pack *et al.* 1999), and 60% of the diet of *Saguinus geoffroyi* (Hladik & Hladik 1967). In Peru, Terborgh (1983) found that five primate species (*Cebus apella*, *Cebus albifrons*, *Saimiri sciureus*, *Saguinus fuscicollis*, *Saguinus imperator*) all spent over 96% of their feeding time concentrating on fruit in the wet season when it is most abundant. Terborgh remarks that other categories of plant material may be available year-round, but are eaten mainly or exclusively when fruit is scarce, which suggests that fruit is the preferred resource whenever it is available.

At the same time, the plants whose fruits the primates eat are competing for seed dispersal. Effective dispersal of seeds is critical to reproductive success in plants, for several reasons: seeds that fall close to their parent plant must compete with it for resources; clustered, poorly dispersed seeds make an attractive prize for consumers; and seed dispersal in space and time allows a parent to produce offspring capable of taking advantage of suitable environments when they arise (Howe & Smallwood 1982). One of the most common adaptations in flowering plants to secure seed dispersal is to produce edible fruits, for zochory, or dispersal by animals (Allen 1879; Ridley 1930; Van der Pijl 1972). Both the animals that consume

fruits and the plants that produce them benefit from this mutual interaction: the plants provide nutritious tissues closely associated with the seeds, and the animals that eat the fruits may then drop, spit, regurgitate or defecate the seeds at a distance from the parent plant. This deposition at a distance may be important in seed dispersal, but it is only half the story. Seeds deposited a distance from the parent plant may subsequently be destroyed by seed predators or pathogens, or be secondarily dispersed by dung-beetles and other animals (Chapman 1995). Whether the battle for survival is won or lost may depend on secondary dispersal: for example, Chapman (1989) placed seeds in artificial dung-piles in Santa Rosa National Park, Costa Rica, and found that 98% of seeds had disappeared or had been destroyed within 70 days of placement; and Shepherd & Chapman (1998) have shown that seeds placed at depths of 1–3 cm, where dung-beetles are likely to bury them, are less likely to be found by predators and are more likely to germinate than seeds that remain at the surface.

Ecological studies have identified a certain subset of tropical plants whose fruits are disproportionately consumed by primates, and which may therefore depend on primates for seed dispersal. These fruits tend to share certain physical characteristics. Thus, in Gabon, Gautier-Hion *et al.* (1985) found that fruits taken by primates typically weigh 5–50 g, contain seeds weighing 0.5–2.5 g, have a succulent pulp or a seed with a firmly attached, edible aril, and are usually yellow, orange or red. In contrast, fruits taken by birds were generally small (less than 5 g), red or purple, without seed protection, and often dehiscent with arillate seeds; and fruits eaten by rodents were generally dull in colour (brown or green), with dry, fibrous flesh, and well-protected seeds. McConkey (1999) found that gibbons in Borneo predominantly ate fruits that were large, yellow or orange, with a juicy, soft pulp, containing a small number of well-protected seeds. Knight & Siegfried (1983) in South Africa did not distinguish between primate and other mammalian consumers, but found that mammal-dispersed fruits tend to be large (over 14 mm in diameter), and green, brown, yellow, or orange in colour. In Peru, Janson (1983) also did not distinguish between fruits dispersed by primates and those dispersed by other mammals, but he found that mammal-dispersed fruits tended to be large (over 14 mm in diameter) and green, brown, yellow or orange, with a hard external coat. At the same site, Terborgh (1983) found that yellow, orange and red fruits were by far the commonest in the diets of five species of monkey. Finally, in French Guiana, those fruits that are taken almost exclusively by monkeys tend to have a few oblong seeds of medium-to-large size (2–3 cm) embedded in a juicy pulp that is closely attached to the seeds. The seeds are protected by a tough, indehiscent pericarp, which is typically yellow, orange or red in colour (Charles-Dominique 1993; Julliot 1994).

The set of traits shared by fruits dispersed by a particular class of consumer can be interpreted as adaptation to that dispersal agent (Ridley 1930; Van der Pijl 1972), and is known as a dispersal syndrome. Characteristics of the primate seed-dispersal syndrome are a yellow, orange or red colour, which makes the fruits conspicuous (at least, to a trichromatic consumer); a hard indehiscent

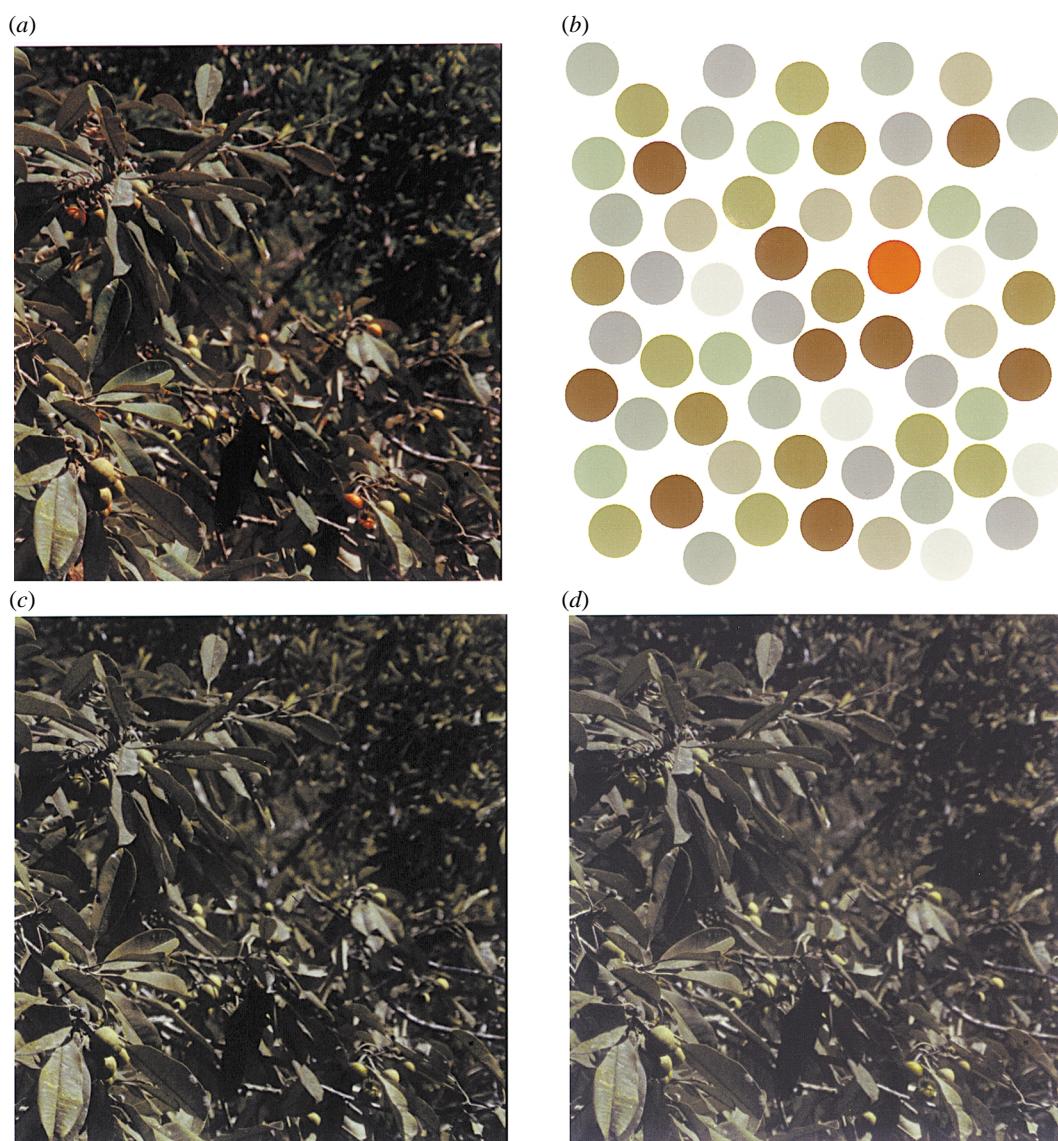


Figure 2. The formal similarity between the natural task facing monkeys foraging for fruit, and laboratory visual search tasks. (a) Fruits of *Manilkara bidentata* (Sapotaceae) photographed in the forest canopy at Les Nouragues. *Alouatta seniculus*, *Ateles paniscus* and *Cebus apella* all eat these fruits. (b) Typical stimulus array from a laboratory visual search task: the task might be to press one button if the orange circle is present, and a different button if the orange circle is absent. The chromaticity of the orange target circle is the same as the chromaticity of a fruit in (a), and the chromaticities of the distractors were drawn from the chromaticities of leaves in (a). (c,d) The same photograph as it would appear to a protanope (c) and a deuteranope (d), illustrating the importance of trichromatic colour vision for locating the fruit.

pericarp, to protect the seeds from predation by granivorous birds and rodents; and edible, nutritious pulp, as an incentive for primates to consume the fruits and swallow the seeds.

Despite forming a large part of the diets of many primate species, fruit may be a scarce resource. The mature fruit of any particular tree may be available for only one or two months of the year, and some trees do not bear fruits annually. In French Guiana, the biomass of fruit production varies between 10 g and 5000 g dry mass per hectare per day (Sabatier 1985), depending on the time of year. However, many of the fruits in this total are inedible for primates: over one year, Julliot (1996) found the fruits of 185 different species on a transect in French Guiana, but only 28% of these were ever

consumed by the howler monkey *Alouatta seniculus*. Clearly, edible fruit can be hard to find.

How might colour vision assist primates in finding fruits? Objects that differ in colour from their background attract attention to themselves. Laboratory visual search experiments show that search is rapid and independent of the number of items in the visual array, when the target item is of a unique colour among distractors of a different colour, provided that the difference is of moderate size (Treisman & Gelade 1980; Nagy & Sanchez 1990; D'Zmura 1991; Bauer *et al.* 1996). Colour-defective human observers experience real difficulty in the natural visual search task of detecting fruit amongst foliage on trees and shrubs (Steward & Cole 1989), suggesting that normal trichromatic colour vision conveys an advantage in this

task. If trichromatic colour vision reveals the presence of fruit at a distance, it should have considerable survival value for primates.

Figure 2 shows the similarity between laboratory visual search tasks and the natural visual search task facing primates, and also illustrates the difficulties faced by dichromatic individuals in detecting fruits against foliage. The photograph in figure 2a was taken in the canopy at Les Nouragues in French Guiana, and it shows fruits of a species known to be consumed by primates. Figure 2b shows the sort of stimulus array that might be used in a laboratory visual search experiment, the task being to find an orange circle. In both figure 2a and 2b the orange targets 'pop out' against the variegated green distractors.

We have used the method developed by Meyer & Greenberg (1988) and Viénot *et al.* (1995) to render the photograph in figure 2a as it would appear to the two common dichromatic human phenotypes, protanopes (figure 2c) and deutanopes (figure 2d). In these dichromatic renderings, the fruits do not 'pop out' of the background foliage in the way that they do in the normal photograph. Trichromatic colour vision is clearly important in finding fruits against a background of foliage.

#### (e) *The hypothesis of coevolution between fruits and primates*

Certain tropical plants produce vividly coloured fruits, apparently in order to attract primates, and trichromatic colour vision helps primates to detect these fruits. The 19th-century naturalist Grant Allen put forward the hypothesis that: 'what flowers are to the colour-sense in insects, fruits are to the colour-sense in birds and mammals'. Of course, there are differences between pollination and dissemination: in particular, insect pollinators have an incentive to go to locations suitable for pollen to be deposited (other flowers), whereas vertebrate seed dispersers do not have any incentive to deposit their seeds at a suitable location. But there are strong similarities: in both cases, plants attract animals with a conspicuous stimulus that signals an edible reward, and in both cases plants use these animals to disseminate genetic material. Only 20 years after the publication of *The origin of species*, Grant Allen was able to spell out how the colour vision of birds and mammals might have mutually evolved with brightly hued, fleshy fruits in plants. A 'sport' in the forest, by chance more conspicuously coloured than other fruits of the species, is more likely to achieve successful dispersal:

'How fruit began to acquire these brilliant tints is not difficult to see. We found already, in the case of flowers, that all external portions of a plant, except such green parts as are actually engaged in assimilating carbon under the influence of solar energies, show a tendency to assume tints other than green. This tendency would...be increased by natural selection in those seeds which, like fruits-proper, derive benefit from the observation of animals.'

(Allen 1879, p. 110.)

And those animal dispersers that are more able to detect coloured fruits are more likely to survive and pass on this capacity:

'If in any species the need for distinguishing different colours ever arose, and if by its side there also arose a

nascent structure for so distinguishing them, then those individuals in which that structure was most fully developed would survive from generation to generation, in virtue of their superior adaptation to the needs of their environment above their less highly endowed compeers'.

(Allen 1879, p. 132.)

Polyak (1957, pp. 973–974) summarized this process: 'The evolution of colored fruits, of course, was a process parallel to the evolution of the color sense in the animals to be attracted.... This relationship became beneficial to both partners, which profited from it: the animals in getting food, the plants in perpetuating themselves and spreading into new regions.' Such a process would now be described by ecologists as coevolution.

Allen's hypothesis, then, is that primate colour vision and the reflectance functions of the fruits they eat have coevolved. According to Janzen (1980), coevolution requires that 'a trait of one species has evolved in response to a trait in another species, which trait itself has evolved in response to the trait in the first. This definition requires specificity—the evolution of each trait is due to the other—and reciprocity—both traits must evolve.' In the case of primates and fruits there are, however, difficulties in demonstrating that these criteria have been fulfilled.

First, the interaction between plants and primates is seldom a tightly limited one between two species, as may occur between plants and their insect pollinators (e.g. between bee-orchids and bees): both plants and primates may have been influenced by other selective pressures. Although many primate species consume large quantities of fruits, they may fall back on alternative resources, such as leaves, flowers or insects, when fruits are scarce. As for the plants, there are usually other potential seed dispersers besides primates: for example, in the study of Gautier-Hion *et al.* (1985) in Gabon, 72 types of fruit were eaten by primates, but 68 of these were taken by at least one other major group of consumers (birds, rodents, ruminants or elephants). The entire guild of consumers may potentially influence the traits of the fruits. Some plants adopt a 'generalized' seed-dispersal strategy, producing many fruits of low nutritional value available to many consumers (McKey 1975; Howe 1980); but even those fruits that might be regarded as 'specialized' for particular dispersers may be taken by many consumers (Howe 1993). However, we do know of two exceptional cases where a plant species appears to depend upon a single primate species for seed dispersal. In Gabon, *Cola lizae* (Sterculiaceae) is apparently disseminated exclusively by gorillas: few animals other than primates eat the fruits, only gorillas swallow the seeds and disperse them by endozoochory, and the seedling survival rate is far higher for seeds deposited in faeces at gorilla nest sites than for seeds deposited elsewhere, whether in faeces or not (Tutin *et al.* 1991). In Borneo, gibbons appear to be the only dispersers of *Parkia javanica* (Fabaceae). Although other animals consume the fruits, they all consume them for the seeds; and seeds that fall under the crown of the tree are rapidly consumed by seed predators (McConkey 1999).

Second, the coevolution hypothesis assumes that there is a selective advantage for the plant that is specialized for dispersal by primates. Direct evidence of such an advantage would be a higher recruitment rate of

Table 1. Fruits eaten by monkeys at Les Nouragues

(The columns for the three monkey species show whether each species has been observed to consume each fruit. If seeds are definitely dispersed by endozoochory (according to Van Roosmalen (1985), Julliot (1992) or Zhang (1994)), then this is indicated in the dispersal column. If these sources report that seeds are destroyed by monkeys, this is indicated in the predation column. In cases where it seems likely that seeds were dispersed or destroyed, but direct evidence is lacking, this is indicated by 'probable' in the appropriate column.)

plant species	monkey			seed dispersal	seed predation
	<i>Alouatta seniculus</i>	<i>Ateles paniscus</i>	<i>Cebus apella</i>		
Anacardiaceae					
<i>Tapirira cf. obtusa</i> <sup>a</sup>	yes	yes	yes	probable	no
Annonaceae					
<i>Duguetia cf. surinamensis</i> <sup>b</sup>	no	yes	yes	no	no
Apocynaceae					
<i>Ambelanias acida</i>	no	yes	yes	yes	no
<i>Lacistema aculeata</i>	yes	no	yes	yes <sup>c</sup>	no
<i>Parahancornia fasciculata</i>	yes	yes	yes	yes <sup>c</sup>	no
Araceae					
<i>Philodendron insigne</i> <sup>b,d</sup>	no	no	yes	no	yes
Arecaceae					
<i>Astrocaryum paramaca</i>	no	no	yes	no	yes
<i>Bactris acanthocarpoides</i>	no	no	yes	no	yes
<i>Maximiliana maripa</i>	no	no	yes	yes <sup>e</sup>	no
Bignoniaceae					
<i>Arrabidea mollis</i>	no	yes	no	no	yes
unidentified sp.	no	no	yes	no	yes
<i>Ananas cf. nanus</i>	no	no	yes	no	no
Burseraceae					
<i>Tetragastris panamensis</i> <sup>d</sup>	yes	yes	yes	yes	no
cf. <i>Tetragastris</i> <sup>d</sup>	yes	no	no	probable	no
unidentified spp. <sup>d</sup>	yes	yes	yes	probable	no
Caesalpiniaceae					
<i>Eperua falcata</i> <sup>b</sup>	yes	no	yes	no	yes
<i>Eperua rubiginosa</i> <sup>b</sup>	yes	no	yes	no	yes
<i>Vouacapoua americana</i> <sup>b</sup>	yes	yes	no	no	yes
Cecropiaceae					
<i>Pourouma</i> sp. <sup>a</sup>	no	no	yes	probable	no
<i>Pourouma tomentosa</i> <sup>a</sup>	yes	no	yes	yes	no
Chrysobalanaceae					
<i>Licania alba</i>	no	no	yes	no	yes
<i>Licania cf. heteromorpha</i>	no	no	yes	no	yes
<i>Licania cf. latifolia</i>	no	no	yes	no	yes
Cucurbitaceae					
unidentified sp.	no	no	yes	probable	no
Cyclanthaceae					
<i>Ludovia lancifolia</i>	yes	yes	yes	yes	no
<i>Stelestylis surinamensis</i>	no	yes	yes	no	no
Euphorbiaceae					
<i>Drypetes variabilis</i>	yes	no	no	yes	no
<i>Glycydendron amazonicum</i>	no	yes	no	yes <sup>e</sup>	no
Fabaceae					
<i>Dussia discolor</i>	no	yes	yes	probable	no
Hippocrateaceae					
cf. <i>Salacia</i> sp.	no	yes	no	probable	no
cf. <i>Salacia/Cheiloclinium</i> sp.	no	yes	no	probable	no
unidentified sp.	no	no	yes	probable	no
Icacinaceae					
<i>Dendrobangia boliviensis</i>	yes	no	yes	yes	no
<i>Poraequiba guianensis</i>	no	no	yes	no	no
Lecythidaceae					
<i>Eschweilera apiculata</i>	no	no	yes	no	yes
<i>Eschweilera cf. micrantha</i>	no	no	yes	no	yes
<i>Eschweilera coriacea</i>	no	no	yes	no	yes
<i>Gustavia hexapetala</i>	no	no	yes	yes <sup>c</sup>	no

continued

Table 1 *continued*

plant species	monkey			seed dispersal	seed predation
	<i>Alouatta seniculus</i>	<i>Ateles paniscus</i>	<i>Cebus apella</i>		
<i>Lecythis persistens</i> subsp. <i>aurantiaca</i>	no	no	yes	no	yes
<i>Lecythis persistens</i> subsp. <i>persistens</i>	no	no	yes	no	yes
Loganiaceae					
<i>Strychnos</i> sp.	no	no	yes	probable	no
Melastomataceae					
<i>Mouriri crassifolia</i>	yes	no	no	yes	no
Mimosaceae					
<i>Inga</i> cf. <i>capitata</i>	no	yes	no	probable	no
<i>Inga gracilifolia</i>	yes	no	yes	yes <sup>c</sup>	no
<i>Inga huberi</i>	no	no	yes	yes <sup>c</sup>	no
<i>Inga leiocalycina</i>	no	no	yes	yes <sup>c</sup>	no
<i>Inga pezzizifera</i>	no	no	yes	yes <sup>c</sup>	no
<i>Inga rubiginosa</i>	no	no	yes	yes <sup>c</sup>	no
<i>Inga thibaudiana</i>	no	no	yes	yes <sup>c</sup>	no
<i>Inga</i> sp.	no	no	yes	probable	no
Moraceae					
<i>Bagassa guianensis</i>	yes	yes	yes	yes	no
<i>Brosimum guianensis</i>	yes	yes	yes	yes	no
<i>Ficus nymphaefolia</i>	yes	yes	no	yes	no
<i>Helicostylis pedunculata</i>	yes	yes	no	yes	no
Myristicaceae					
<i>Iryanthera sagotiana</i> <sup>d</sup>	yes	yes	no	yes	no
<i>Virola michelii</i> <sup>d</sup>	yes	yes	no	yes	no
<i>Virola</i> sp. nov. <sup>d</sup>	yes	yes	no	yes	no
Passifloraceae					
cf. <i>Passiflora crenata</i>	no	no	yes	probable	no
Polygalaceae					
<i>Moutabea guianensis</i>	yes	yes	yes	yes <sup>c</sup>	no
<i>Moutabea</i> sp.	no	yes	no	probable	no
Rubiaceae					
<i>Duroia eriopila</i>	no	no	yes	yes <sup>c</sup>	no
<i>Posoqueria latifolia</i>	no	no	yes	yes <sup>c</sup>	no
Sapindaceae					
<i>Paullinia</i> sp.	no	yes	no	no	probable
<i>Talisia</i> sp.	no	no	yes	probable	no
Sapotaceae					
<i>Chrysophyllum lucentifolium</i>	yes	yes	yes	yes <sup>c</sup>	no
<i>Chrysophyllum prieurii</i>	yes	yes	no	yes <sup>c</sup>	yes <sup>f</sup>
cf. <i>Chrysophyllum sanguinolentum</i>	no	no	yes	probable	no
<i>Diplōon cuspidata</i> <sup>a</sup>	yes	yes	no	probable	no
<i>Ecclinusa lanceolata</i>	yes	yes	yes	probable	no
<i>Ecclinusa</i> cf. <i>ramiflora</i>	no	no	yes	yes <sup>c</sup>	no
<i>Manilkara bidentata</i>	yes	yes	yes	yes <sup>c</sup>	no
<i>Micropholis cayennensis</i>	yes	no	yes	yes <sup>c</sup>	no
<i>Micropholis</i> cf. <i>egensis</i>	no	yes	yes	probable	no
<i>Micropholis obscura</i>	yes	yes	yes	yes <sup>c</sup>	no
<i>Pouteria ambelaniifolia</i>	yes	yes	yes	yes <sup>c</sup>	no
<i>Pouteria egregia</i>	yes	yes	no	yes <sup>c</sup>	no
<i>Pouteria guianensis</i>	yes	yes	yes	yes <sup>c</sup>	no
<i>Pouteria gonggrijpii</i>	no	no	yes	probable	no
<i>Pouteria laevigata</i>	yes	yes	no	yes <sup>c</sup>	no
<i>Pouteria torta</i> subsp. <i>glabra</i>	yes	no	yes	yes <sup>c</sup>	no
<i>Pouteria</i> cf. <i>venezuelense</i> <sup>a</sup>	no	no	yes	probable	no
<i>Pouteria</i> sp.	no	yes	no	probable	no
<i>Pradosia ptychandra</i>	no	no	yes	probable	no
unidentified spp.	no	yes	no	probable	no
Solanaceae					
<i>Solanum</i> sp.	yes	no	no	yes	no

*continued*

Table 1 *continued*

<b>Sterculiaceae</b>					
<i>Sterculia frondosa</i>	no	yes	yes	no	yes
<i>Sterculia pruriens</i>	no	yes	no	no	yes
<i>Theobroma subincanum</i>	yes	yes	yes	yes <sup>g</sup>	yes
<b>Violaceae</b>					
<i>Leonia glycycarpa</i>	no	yes	yes	yes <sup>c</sup>	no
<b>Unidentified</b>					
three unidentified spp.	no	no	yes	no	yes
unidentified sp.	yes	no	no	no	yes

<sup>a</sup>These fruits were black (less than 2% lightness) and were excluded from the analyses, because the reflectance spectra recorded for them presumably represented dirt and/or specular reflections. An analysis based on chromaticity seems rather meaningless for these fruits.

<sup>b</sup>The immature fruits of these species were eaten. In the case of *Duguetia cf. surinamensis* it was not possible to be certain whether or not the fruits consumed by monkeys were mature.

<sup>c</sup>These fruits fall within the 'primate dispersal syndrome' defined by Julliot (1994), on all grounds except colour: they have a hard, indehiscent outer coat and contain a few large seeds embedded in nutritious pulp.

<sup>d</sup>These fruits exhibited two different colours. Reflectance measurements of both coloured parts were made and included in the analyses.

<sup>e</sup>Seeds dropped beneath parent plant.

<sup>f</sup>Immature fruits of this species were consumed for seeds by *Ateles paniscus*.

<sup>g</sup>Seeds destroyed by *Cebus apella* but probably dispersed by *Ateles paniscus*.



Figure 3. The three primate species studied, photographed at Les Nouragues. (a) The red howler monkey, *Alouatta seniculus*. (b) The tufted capuchin, *Cebus apella*. (c) The black spider monkey, *Ateles paniscus*. (Photographs (a,b), B. Regan; (c), R. Leguen.)

seedlings from seeds that had been processed by primates, compared with those that had not. In the case of some plants, such as *Cola lizae* and *Parkia javanica* described above, this seems to be the case; but other studies have found that processing by primates reduces the survival rate of seeds: for example, Overdorff & Strait (1998) found that most of the seeds processed by three lemur species in Madagascar failed to germinate, even when the seeds were passed apparently undamaged in faeces. Thus, the efficiency of seed dispersal by primates is still a matter of debate (Chapman 1995; Lambert 1998). Indirect evidence for the hypothesis—and evidence that

primate dispersal has a powerful impact on the recruitment of seedlings—is provided by Julliot (1994), who found in French Guiana that the seedlings of *Chrysophyllum lucentifolium* were more densely distributed in plots around sleeping trees used by howler monkeys (*Alouatta seniculus*) than in control plots, and that beneath the dormitory trees, seedlings were clustered around individual defecation points. However, clustering may reduce the later viability of seedlings. Moreover, Julliot (1994) did record some seedlings of *Chrysophyllum lucentifolium* in control plots. So it remains unknown what proportion of the total seedling population lies outside the vicinity of dormitory

trees, what proportion of these seedlings arises from seeds disseminated by primates—and whether trees that themselves bear fruit are more likely to have arisen from seeds dispersed by primates.

Third, from the primates' point of view, colour vision helps to detect not only fruits, but any object coloured differently from the background, such as flowers, young leaves (which are often yellowish or reddish) and other animals. Lucas *et al.* (1998) have argued that the need to detect reddish young leaves, in times when fruits are scarce, has exerted a stronger selection pressure on primates for trichromacy than has the need to detect brightly coloured fruits. Primate colour vision also plays a role in visual communication: colour is important to some primates in socio-sexual signals (Wickler 1967) and threat displays (Hingston 1933). So the evolution of primate trichromacy may have been influenced by factors other than the advantage conferred at detecting fruits.

Thus, the mere existence of brightly coloured fruits that are apparently specialized for dispersal by primates cannot be taken as evidence for coevolution. However, we can further test the hypothesis by examining how well matched are the properties of the primate visual system to the specific task of detecting fruits in their natural environment. That is what our experimental study set out to do.

#### (f) Testing hypotheses in visual ecology

Most ecological studies of natural colour signals have measured colour in human terms. This usually takes the form of arbitrary colour categorization applied by one particular observer, with labels such as 'red', 'yellow', etc. However, it has been stressed that experiments relating natural colour signals to their receivers must take into account the nature of the receiver's colour perception (Cuthill & Bennett 1993; Bennett *et al.* 1994). Some previous studies of the matching between the visual systems of particular animals, and the particular tasks required of those visual systems, have taken into account the nature of the animal's colour perception by using spectral measurements of natural stimuli to calculate the physiological signals that would be initiated in the animal's visual system by those stimuli.

There have been two broad approaches to testing whether colour vision is optimized for a particular task. One is to test whether colour vision maximizes the variance of the chromatic distribution of a class of stimuli, or the number of discriminable stimuli. The other is to test whether colour vision maximizes the number of stimuli discriminable from a background, or the number of stimuli in one class that are distinct from a second class.

The first approach was taken by Chittka and his colleagues (Chittka & Menzel 1992; Chittka *et al.* 1993), studying the matching between the colour vision of Hymenoptera such as honeybees, and the flowers that they pollinate. They measured the reflectance spectra of a large number of flower blossoms known to be visited by Hymenoptera, and expressed the colours of these flowers in a perceptual colour space developed for Hymenoptera. In their model they allowed the spectral sensitivity functions of the hymenopteran photoreceptors to vary, and found that the largest variance in flower colours is

obtained with photoreceptor spectral sensitivities very similar to those actually present in Hymenoptera. These spectral sensitivities also maximize the number of flower colours that are just discriminable from one another. Lythgoe & Partridge (1989) took a similar approach to natural signals in a forest environment. They measured reflectance spectra for green leaves, brown leaves and forest litter, and modelled the colour signals that would be presented to mammalian dichromats with different cone pigment pairings, allowing  $\lambda_{\max}$  to vary from 350 to 600 nm. The maximum standard deviation in the colour signals offered to a mammalian dichromat from green leaves occurs with pigments having peak sensitivities at 420–450 nm and 510–520 nm, whereas for brown leaves the maximum standard deviation is achieved with pigment  $\lambda_{\max}$ -values of 430–460 nm and 570 nm or longer. Many dichromatic mammals have cone pigment pairings similar to those that maximize the standard deviation in the chromaticities of green leaves, suggesting that their visual systems are well adapted to discriminating between leaf colours.

In a different study, Lythgoe & Partridge (1991) took the second approach, and determined the optimal photopigment pairings for dichromatic teleost fish to discriminate various signals (grey surfaces or seaweed) from the background scattered light in green coastal water. They found that the largest number of seaweed or grey surface reflectance spectra were discriminable from the background when the  $\lambda_{\max}$ -values of the photopigments were 440–460 nm and 530–600 nm. Pigment pairings in this range are indeed often found in teleost fish living in coastal waters. Osorio & Vorobyev (1996) also took this approach to determine the optimal photopigments for dichromatic and trichromatic primates to distinguish between fruits and leaves. They used the reflectance spectra of supermarket fruits, and of unspecified leaves. The spectral tuning of one cone pigment was varied at a time, and they used Weber fractions to calculate the just-noticeable difference (JND) in colour between two stimuli. For dichromatic primates, with a short-wave pigment  $\lambda_{\max}$  fixed at 430 nm, the largest number of fruits lying one or more JNDs from the leaves was obtained with a long-wave pigment  $\lambda_{\max}$  between 520 and 580 nm. For trichromatic primates, with two pigments fixed at 430 and 565 nm, a third pigment in the range 490–530 nm gave the largest number of fruits that were just discriminable from the leaves.

We have tested how well matched is primate colour vision to the task of finding specific fruits against rainforest foliage. We have published a short report of this work elsewhere (Regan *et al.* 1998). Our method differs from that of Osorio & Vorobyev (1996) in some important respects. The importance of colour vision in frugivory is not in discriminating between fruits and foliage, but in drawing attention to fruits. Visual search experiments show that the larger the colour difference between targets and distractors, and the smaller the colour difference between distractors, the faster the target can be identified (Duncan & Humphreys 1989; Barbur *et al.* 1991; Bauer *et al.* 1996). We therefore consider the optimal photopigments to be those that maximize the signal-to-noise ratio for detecting fruit targets against the visual noise of the leaf distractors, rather than those that

maximize the number of fruits that lie one or more JNDs from the leaves. Second, the phylogenetically ancient subsystem of primate colour vision, which signals the relative excitation of the S cones, is unlikely to be useful in the task of searching for fruits amongst foliage, because it has poor spatial resolution, and the fruits eaten by primates, when seen at a distance, are usually too small to be resolved by this subsystem. For this reason, when determining the spectral positioning of the cone pigments that maximizes the signal-to-noise ratio for detecting fruits against leaves, we consider only the phylogenetically more recent channel of colour vision, which signals the relative excitation of the L and M cones. Third, to test the matching between primate colour vision and the task of detecting fruits against leaves, it is obviously important to use natural colour signals rather than colour signals from supermarket fruits, for these latter have been subject to the attentions of plant breeders who may have striven to achieve highly saturated colours; and only those fruits that exhibit a desired colour may be displayed on supermarket shelves, for marketing reasons.

## 2. EXPERIMENTAL STUDY

### (a) Overview

The three most common primate species in French Guiana, *Alouatta seniculus*, *Ateles paniscus* and *Cebus apella*, are all frugivorous to a greater or lesser extent. Colour vision in *Alouatta* is uniformly trichromatic, whereas colour vision in the last two species is polymorphic, with both dichromatic and trichromatic individuals. Our aims were: (i) to test whether trichromatic colour vision conveys an advantage over dichromatic vision for these primates when foraging for fruit; (ii) to determine whether the particular forms of trichromacy possessed by some platyrhine monkeys are optimized for that task; and (iii) to ask whether, in polymorphic species, different phenotypes have the advantage for detecting particular fruits in particular illuminants.

We collected a large number of fruits eaten by these three species, along with leaves from many species of tree, and measured their spectral reflectance functions. We quantified the colour signals presented to primates by fruits and leaves by expressing them in chromaticity diagrams calculated for dichromatic and trichromatic monkeys (rather than in chromaticity diagrams for humans), taking into account the different absorption spectra of the cones present in each individual phenotype.

For the three primate species studied, our computer modelling demonstrates that trichromatic phenotypes are always at an advantage in finding fruit amongst foliage and that the spectral positioning of the cone pigments of trichromatic individuals is well matched to this detection task. We show that those fruits whose morphology suggests adaptation for primate dispersal occupy a narrowly defined region of colour space. We further show that the different trichromatic platyrhine phenotypes have slight advantages at detecting particular fruits under particular natural illuminants. We discuss the implications of our results both for the hypothesis of coevolution between coloured fruits and primate colour vision, and for the understanding of polymorphic colour vision amongst the platyrhines.

### (b) Data collection and spectral measurements

#### (i) The site

Data were collected between 1993 and 1995 at the Les Nouragues scientific station in French Guiana, a site situated in primary tropical lowland rainforest. The site is located at 40°5'N, 52°40'W, ca. 100 km from Cayenne, the administrative capital, and 60 km from the nearest permanent habitation. The area has been undisturbed by human activity since the disappearance of the Nouragues Indians in the 18th century. The altitude of the forest varies from 80 to 411 m. The mean daily minimum temperature is 21 °C and the mean daily maximum is 31 °C, with very little seasonal variation. Mean annual precipitation is 3200 mm, spread over about 260 days, although this varies from year to year. During the year there are two dry seasons: a regularly occurring long dry season lasting about three months from September to November, and a shorter and less predictable dry season lasting about a month in March.

Vegetation is typical of primary tropical lowland forest. Surrounding the encampment, the forest has a continuous canopy, typically 30–40 m in height, with emergent trees regularly reaching 45 m and occasionally 60 m. However, individual regions of forest vary in canopy height, density of undergrowth and flora, and all five vegetational subtypes identified by Mittermeier & Van Roosmalen (1981) in a similar area in Surinam can be found near the camp.

#### (ii) Primates studied

The primate species that are the focus of this study are the three largest primates in French Guiana: the red howler monkey *Alouatta seniculus*, the black spider monkey *Ateles paniscus* and the tufted capuchin monkey *Cebus apella*. Individuals of the three species are shown in figure 3. The species vary in the extent to which they rely on fruit as a food source. The genus *Ateles* is one of the most frugivorous amongst New World primates, and fruits constitute 85–90% of the diet of *Ateles paniscus* in French Guiana and Surinam (Van Roosmalen 1985; Guillotin *et al.* 1994; Simmen & Sabatier 1996). In contrast, *Alouatta* is the most folivorous New World primate, and there are periods of the year when *Alouatta seniculus* eats only leaves and flowers (Julliot 1992). Nevertheless the diet of *Alouatta seniculus* in French Guiana does include a year-round average of 25–50% fruit (Guillotin *et al.* 1994; Julliot 1994). *Cebus apella* is more omnivorous and eats principally fruits, seeds, and insects, with small quantities of leaves, stems and other animal matter. Fruits probably make up ca. 50% of its diet in French Guiana (Guillotin *et al.* 1994; Zhang 1994).

The three species all disperse most of the seeds that they consume. In French Guiana, Julliot (1992) found intact seeds in faeces of *Alouatta seniculus* from 86 plant species. These species made up ca. 90% of the total fruit diet. The average intestinal transit time for seeds was estimated as 20 h 40 min; so the seeds are generally deposited some distance from the parent plant. Van Roosmalen (1985) found that seeds of 138 species, making up 93.5% of the fruit diet of *Ateles paniscus* in Surinam, were passed intact in faeces. For *Cebus apella* in French Guiana, Zhang (1994) found intact seeds of 113 species in faecal samples,

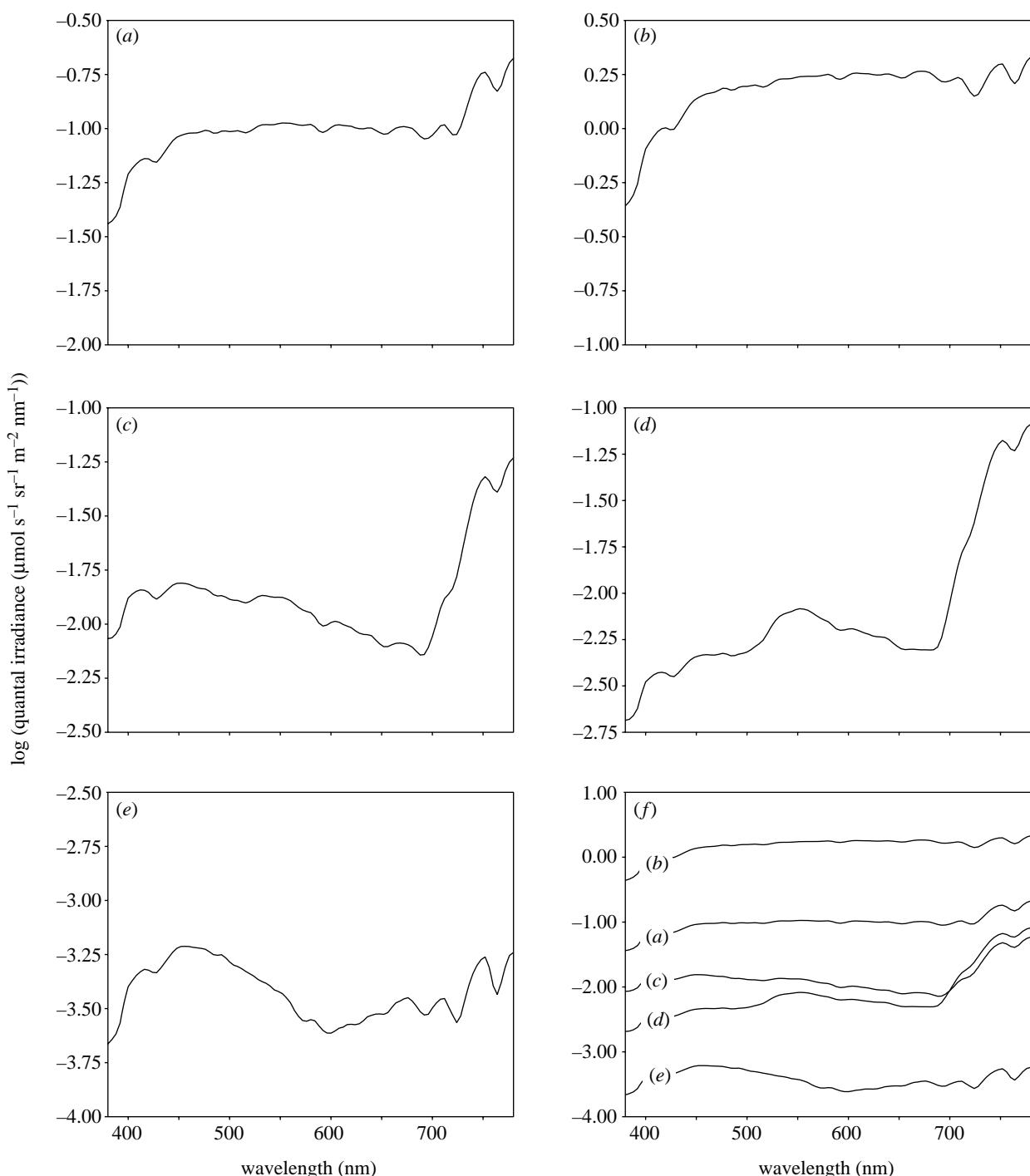


Figure 4. Typical illuminant spectra at Les Nouragues, recorded at different times and under different weather conditions. The data are plotted as irradiance spectra in quantal units on a logarithmic ordinate. (a–c) Daytime measurements made in the canopy: (a) when the sun was behind clouds; (b) with the white plaque in direct sunlight; (c) in shade on a sunny day. (d) A daytime measurement made in shade at the forest floor on a sunny day; (e) a measurement made in the canopy on a clear evening just after sunset. (f) All five spectra on the same graph, to illustrate the four log-unit variation in intensity. Note the similarity between illuminants (a) and (b), and note the varying spectral biases of the illuminants: (a,b) are fairly flat from 400 to 700 nm, (c) is biased to short wavelengths, (d) is biased to middle wavelengths, and (e) is lacking in middle wavelengths. Endler (1993) classifies forest light environments into five categories, of which four are represented here: illuminants (a,b) would fall into his ‘open/cloudy’ category and might be described as whitish; illuminants (c–e) would fall into his ‘woodland shade’, ‘forest shade’ and ‘early/late’ categories and might be described as bluish, greenish and purplish, respectively.

making up 84% of the number of plant species whose fruits were consumed.

However, there may be some difference in the quality of seed dispersal by the three primate species. *Ateles paniscus* is probably the most effective disperser of the three, because it passes a larger number of seeds than

*Cebus apella* (being a bigger animal), and because those seeds passed by *Ateles paniscus* are scattered when defecated, unlike those passed by *Alouatta seniculus*, which fall in dung-piles bound together by digested leaves. It may also be the case that particular plant species are better suited to dispersal by particular primate species.

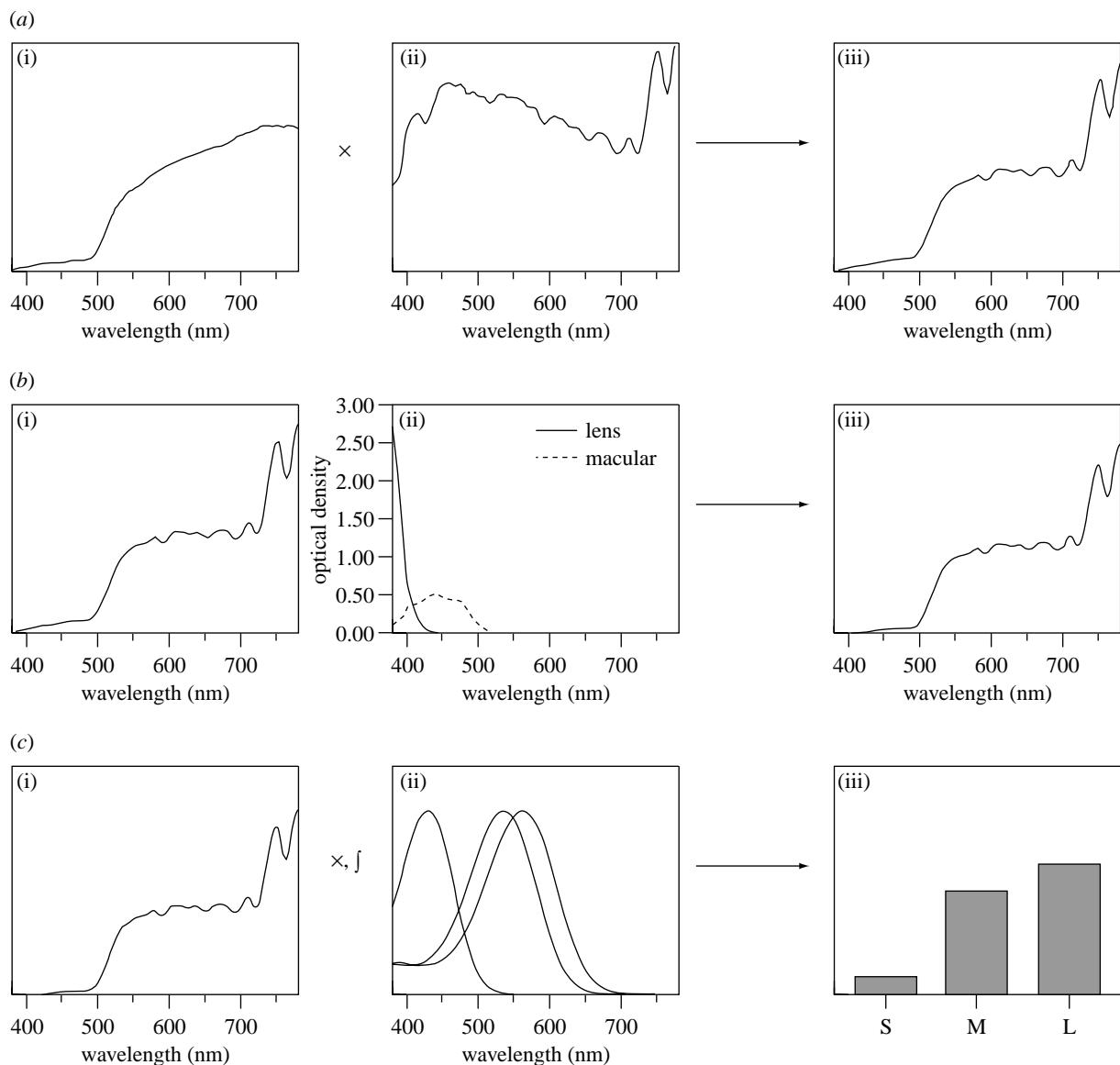


Figure 5. The general method of calculating the colour signal offered by an object in the canopy to a foraging primate. (a) (i) The reflectance spectrum of an object is multiplied by (ii) an illuminant measured in the canopy to yield (iii) the radiance spectrum that the object would present in the forest canopy. (b) (iii) The radiance spectrum of the object is attenuated by the lens and macular pigment of the primate. (ii) Lens and macular pigment curves are shown in optical density units, which are  $\log_{10}$  of the factor by which light is attenuated. (c) (i) The adjusted radiance spectrum is multiplied by (ii) each of the three cone sensitivity curves and integrated over wavelength to give (iii) the quantum catch in each class of cone. These quantum catches are then used to calculate signals in post-receptoral channels, as described in the text (§ 2(c)).

For example, *Ateles paniscus* is very restricted in its habitat, preferring high forest (Mittermeier & Van Roosmalen 1981), and will tend to deposit the seeds it ingests in a similar habitat to that in which they were ingested. On the other hand, *Cebus apella* is more likely to deposit seeds in a variety of habitats: for pioneer plants such as *Pourouma* spp., effective dispersal may depend on seeds being deposited in a habitat different from the one in which they were ingested. In the case of *Pourouma* this may mean being deposited beneath a canopy gap. The question of the quality of seed dispersal by primates is an important one, as it bears considerably on whether or not the characteristics of the fruits consumed have evolved to suit the primates' needs.

### (iii) Sampling of primate diets

Samples of fruit eaten by the three species of primate studied were collected by following groups of monkeys, and observing what they ate. Nearly all the fruits eaten by monkeys came from the crowns of trees, from lianas and from epiphytes in the trees. We were often able to collect the discarded outer rinds or shells of fruits that had actually been harvested and consumed by monkeys. In some cases, additional samples were collected on a later occasion from plants where monkeys had been observed to feed, or from the ground below. If monkeys were known, from previous studies at Les Nouragues (Julliot 1992; Zhang 1994; Simmen & Sabatier 1996), to eat a particular fruit, but monkeys were not observed feeding on that fruit

during the course of the fieldwork, then we gathered samples of that fruit from other locations if it was available. Fruits consumed by monkeys were sampled from 90 different plant species. To characterize the background against which fruits are detected, leaves were sampled from 18 species whose fruit were eaten by monkeys, and from 13 other species.

Table 1 lists the species whose fruits were consumed by monkeys at Les Nouragues, along with the consumers. Where one of three long-term studies of the ecology of these primate species (Van Roosmalen 1985; Julliot 1992; Zhang 1994) has reported that seeds were definitely dispersed or destroyed (predated) by monkeys, we have shown that fact in the column headed 'seed dispersal' or 'seed predation'. In other cases, where we believe that seeds are dispersed or destroyed but do not have direct evidence, we have indicated that with 'probable' in the appropriate column.

#### (iv) Reflectance spectra

The reflectance spectrum of each specimen was measured as soon as possible after collection, using a Photo Research PR650 telespectroradiometer (Photo Research, Chatsworth, CA, USA). Specimens were illuminated by natural light. The radiance spectrum of light reflected from each specimen was measured at 45° to its surface, and divided by the radiance spectrum of light reflected from a nominally perfect diffuser (a Photo Research RS-2 barium sulphate reflectance standard) to obtain a reflectance spectrum, sampled at 4 nm intervals between 380 and 780 nm. Five hundred and seventy-nine measurements of fruits from 88 plant species were made using this method, and 125 measurements of leaves from 18 species. Raw data from our study are available at <http://vision.psychol.cam.ac.uk/spectra/>.

At the beginning of the study, a small number of measurements were made of fruits and leaves flown to Paris in chilled containers. These measurements were made using a Bentham spectroradiometer, and a tungsten filament lamp to illuminate the specimens. The spectral distribution of light reflected from each specimen was measured at 5 nm intervals between 380 and 780 nm, and divided by the spectral distribution of light reflected from a white reference plaque of compressed magnesium oxide, to obtain a reflectance spectrum. Five measurements of fruits from two plant species, and 30 measurements of leaves from 13 species were made in this way. We believe that these measurements are at least as accurate as those made by the Photo Research device. The chromaticities of leaves measured in Paris are compared with those measured at Les Nouragues in figures 7e and 8e.

Previous measurements of the reflectance spectra of fruits eaten by primates and of the leaves that form their background have been made by Snodderly (1979) and by Cooper *et al.* (1986), using samples flown to laboratories abroad.

#### (v) In situ radiance spectra

The aim of the fieldwork was to collect an accurate set of measurements of the visual stimuli encountered by primates foraging for food. We multiplied our spectral reflectance measurements of fruits and leaves with an illuminant spectrum, in order to reconstruct typical stimuli

that might be offered to primates in the wild. But these reconstructions represent only a subset of possible natural stimuli, for they assume purely matte reflections from uniformly illuminated surfaces. In the rainforest canopy, these assumptions do not always hold. The illumination of different surfaces varies, according to the local forest geometry: objects may show highlights of specular reflection, as well as matte reflections; and some leaves may be viewed primarily by transmitted rather than reflected light. In order to capture these complexities of illumination, we made additional measurements of the radiance spectra of objects in their natural environment. We climbed trees using speleological equipment and recorded the radiance spectra of around 550 leaves using the PR650 telespectroradiometer. Unfortunately, *in situ* measurements of the radiance spectra of fruits proved very difficult to obtain: fruiting trees were sometimes over 50 m high, and fruits often clustered at the ends of branches, making it difficult to get close enough to measure them.

#### (vi) Illuminant spectra

The spectral composition of the illumination in the canopy was measured almost every time that *in situ* measurements of leaves or bark were made, by measuring the radiance spectrum of light reflected from the barium sulphate reflectance standard. The irradiance spectrum of the ambient light at any point is a function of the spectral composition of all radiant sources that illuminate that point: in forests these include leaves, bark, blue sky, clouds and sun (Endler 1993). Therefore each time the illuminant was measured, the weather conditions, the presence or absence of direct solar illumination, and the location in the forest (in the canopy, below the canopy, on the ground) were all noted.

These measurements of the illumination were multiplied with spectral reflectance measurements, in order to reconstruct the visual stimuli presented to foraging primates. We made 66 measurements of illuminant spectra at different times and places at Les Nouragues, but as they all fall into a small number of classes (Endler 1993), we have used only the five typical illuminant spectra illustrated in figure 4 in our analyses. The spectra are expressed in figure 4 in molar units:  $\mu\text{mol s}^{-1}\text{sr}^{-1}\text{m}^{-2}\text{nm}^{-1}$ . Spectra were converted from units of  $\text{quanta s}^{-1}\text{sr}^{-1}\text{m}^{-2}\text{nm}^{-1}$  to molar units by dividing by Avogadro's number. This was done to make the data comparable with those of Endler (1993) who also used molar units.

### (c) The general model

To calculate the colour signal offered by a fruit or a leaf to a foraging primate, we begin with its radiance spectrum. If the radiance spectrum was not measured directly, we reconstructed it by multiplying the reflectance spectrum of the object by the illuminant. The process is illustrated in figure 5a.

#### (i) Pre-receptoral filtering

Before light can reach the monkey's photoreceptors, it must first pass through the various structures of the eye including the cornea, aqueous humour, crystalline lens, vitreous humour and the neural layers of the retina. All of these filter the light reaching the photoreceptors, but

the most significant are the lens and the neural retina. Primate lenses are yellow, absorbing in the ultraviolet and the violet regions of the spectrum (Cooper & Robson 1969). The neural retina contains a yellow pigment, known as the macular pigment, which is densest in the macula lutea, the central region of the retina including the fovea. It consists of two carotenoids, lutein and zeaxanthin (Bone *et al.* 1985), and it absorbs predominantly at the short-wave (violet to blue) end of the visible spectrum, with a peak absorption near 460 nm. The density of macular pigment may be related to diet, as primates cannot synthesize carotenoids, and all carotenoid compounds must therefore be obtained from food-stuffs (Rothschild 1975). An increased consumption of carotenoids has been shown to lead to an increased density of macular pigmentation, at least in some individuals (Edwards *et al.* 1996).

We adjusted radiance spectra to allow for the filtering effects of the lens and macular pigments (figure 5b). No data were available for the spectral absorption characteristics of the lenses or macular pigments of the primate species in our study. So we used the lens absorption curve given by Tovée *et al.* (1992) for another platyrhine monkey, the marmoset *Callithrix jacchus*. In the absence of any published macular pigment absorption spectra for platyrhine monkeys, we used the curve for man given by Wyszecki & Stiles (1982), and we have generally assumed that the density of macular pigmentation in these monkeys is the same as the average density found in man (although we do report the effect of systematically changing the macular pigment density, such as might arise from variations in diet).

At any layer between two surfaces with different refractive indices, some light is lost by reflection. We corrected for this by assuming that 5% of incident quanta were reflected at the anterior surfaces of the eye (Hecht *et al.* 1942).

#### (ii) Pigment absorbance and cone absorptance spectra

The absorbance spectra of monkey cone pigments were estimated using the polynomial formula of Baylor *et al.* (1987), at wavelengths from 380 to 780 nm:

$$\log C_\lambda = \sum_{n=0}^6 a_n \left[ \log \left( \frac{\lambda_m}{\lambda \cdot \lambda_r} \right) \right]^n.$$

This formula gives the sensitivity  $C_\lambda$  at any wavelength  $\lambda$  for any cone pigment, where  $\lambda_r = 561$  nm,  $\lambda_m$  is the wavelength of maximum sensitivity expressed in nanometres,  $\lambda$  is expressed in micrometres, and the coefficients  $a_0$  to  $a_6$  are  $-5.2734$ ,  $-87.403$ ,  $1228.4$ ,  $-3346.3$ ,  $-5070.3$ ,  $30881$  and  $-31607$ . In generating absorbance spectra, Baylor *et al.*'s (1987) formula produces a secondary peak, with absorbance rising beyond  $\lambda_{max} + 250$  nm. This is a consequence of the formula being a polynomial and does not reflect the behaviour of real visual pigments; so the absorbances of the cone pigments calculated from this formula were set to zero at wavelengths beyond  $\lambda_{max} + 250$  nm.

This polynomial formula allows us to generate absorbance spectra for cone pigments with any peak sensitivity. We have assumed that the polymorphic L- or M-type cone pigments of *Cebus apella* have peak sensitivities at 536, 550 and 562 nm (Bowmaker & Mollon 1980; Jacobs & Neitz 1987), those of *Ateles paniscus* at 550 and 562 nm

(Hagstrom *et al.* 1993; Jacobs & Deegan 1993b), and the M and L pigments of *Alouatta seniculus* at 536 and 562 nm (Jacobs *et al.* 1996a). Only for *Ateles* has there been a direct measurement of S cone sensitivity (Jacobs & Deegan 1993b), suggesting a peak near 430 nm, although behavioural tests strongly suggest that *Cebus* must also possess S cones (Grether 1939). There is currently no evidence for or against the presence of S cones in *Alouatta*. We have assumed that all three species possess similar S cone pigments with a peak sensitivity at 430 nm.

The spectra generated by Baylor *et al.*'s formula are absorbance spectra, appropriate for an infinitely thin layer of visual pigment. In a real photoreceptor, the light arriving at lower layers of photopigment in the receptor outer segment has already been filtered by earlier layers of pigment, altering its spectral distribution. We corrected for this self-screening, assuming that the average axial optical density of the cones was 0.3 (Bowmaker *et al.* 1987).

#### (iii) Receptor quantum catches and post-receptoral signals

To calculate the rate at which quanta of light arrive from a particular natural object at the photoreceptors, the physical parameters of both the object being viewed, and of the eye of the viewer, must be specified. For all our calculations we have assumed that the stimuli are circular, 30 mm in diameter, and viewed from a distance of 10 m, representing a target of 0.17 degrees of visual angle. Although arbitrary, such parameters are realistic for a monkey in a tree viewing a medium-sized fruit in the same tree or in one nearby. As for the eyes of the viewer, the comparative data of Schultz (1940) show that the eyes of *Cebus*, *Ateles* and *Alouatta* differ in mass by at most 25%. We have therefore used the same values for the eyes of all three species. We took the diameter of the pupil to be 3 mm. The inner segments of primate cones typically have a diameter of ca. 2.8 µm (Polyak 1941) and Geisler (1989) estimated that the sampling aperture of a cone is ca. 80% of the inner segment diameter. We therefore took the sampling aperture of a single cone to be 2.2 µm. We also assumed that 223 µm at the central retina corresponded to 1 degree of external visual angle (this is the ratio given by Perry & Cowey (1985) for *Macaca fascicularis*, an Old World primate of similar size to the ones in our study). We assumed that the cones are arranged in a hexagonal lattice, with equal numbers of L and M cones in trichromatic eyes, and we have ignored the presence of S cones in this lattice. Finally, we have assumed that dichromatic eyes contain the same total number of cones per unit area as trichromatic eyes.

These dimensions provide a scaling coefficient to transform spectra from radiance units ( $\text{quanta s}^{-1} \text{sr}^{-1} \text{m}^{-2} \text{nm}^{-1}$ ), to available quanta from the stimulus per cone class at each wavelength interval ( $\text{quanta nm}^{-1} \text{s}^{-1}$ ). This scaling does not affect the relative quantum catches of the different cone types, but only the absolute quantum catches, and so does not affect calculations of the chromaticities of natural objects. However, the absolute values are important in considering random fluctuations in quantum catches as a source of noise in visual detection tasks. For this purpose, we have calculated quantum catches for an integration time of 100 ms (Hood & Finkelstein 1986).

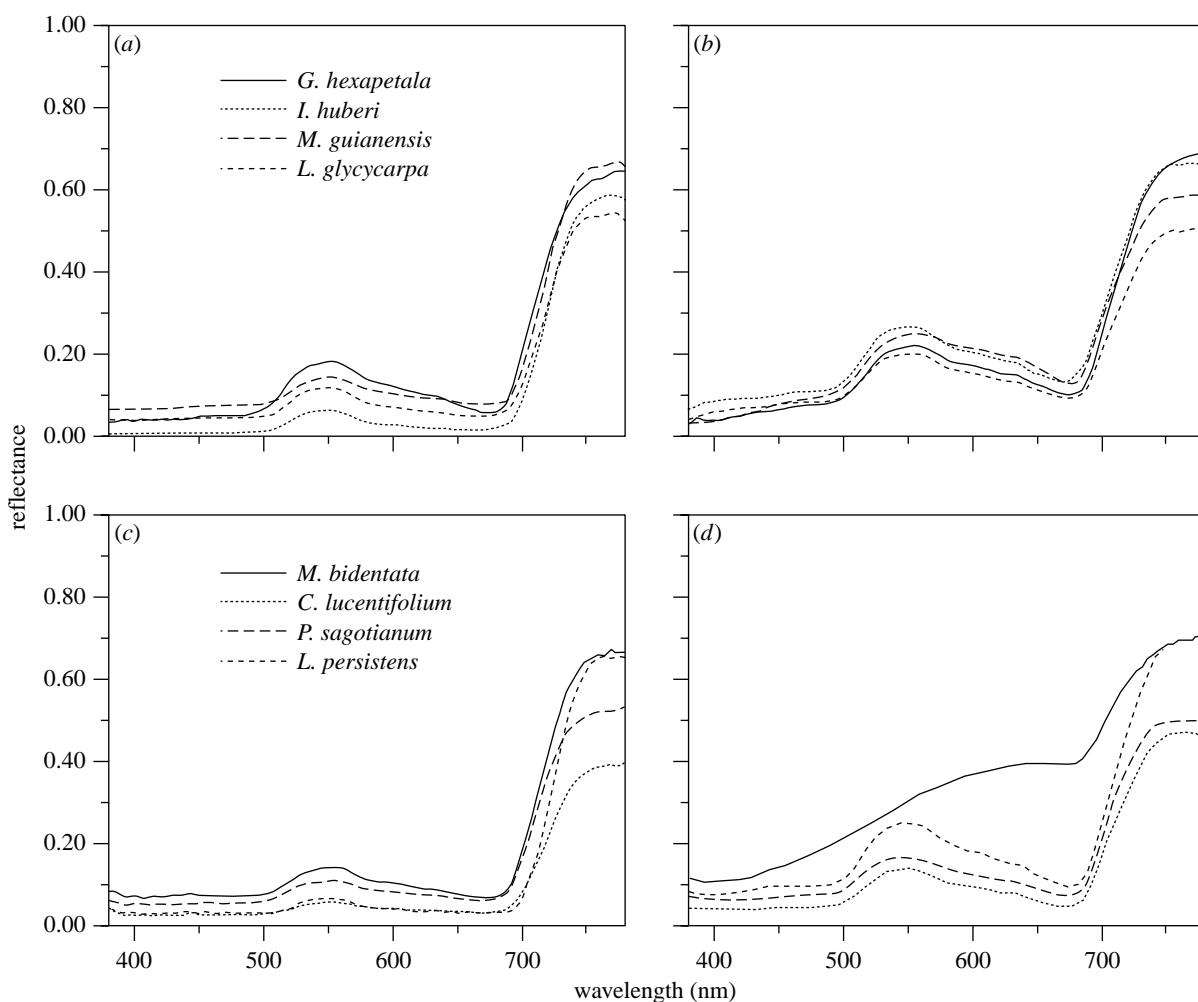


Figure 6. Reflectance spectra of upper and lower surfaces of leaves. (a, b) Reflectance spectra measured at Les Nouragues, from single leaves of *Gustavia hexapetala* (Lecythidaceae), *Inga huberi* (Mimosaceae), *Moutabea guianensis* (Polygalaceae) and *Leonia glycycarpa* (Violaceae); (a) upper surfaces and (b) lower surfaces. (c, d) Reflectance spectra measured in Paris, from single leaves of *Manilkara bidentata* (Sapotaceae), *Chrysophyllum lucentifolium* (Sapotaceae), *Protium sagotianum* (Burseraceae) and *Lecythis persistens* subsp. *aurantiaca* (Lecythidaceae); (c) upper surfaces and (d) lower surfaces. The aberrant spectrum for a leaf lower surface is for *Manilkara bidentata*—this is typical of leaf undersides of this species.

The quantum catches in each class of photoreceptor were calculated by multiplying the cone absorptance spectra with the stimulus spectra, and integrating the resulting spectrum over wavelength. The process is illustrated in figure 5c. As outlined earlier (§1(a)), in the primate visual system the photoreceptor signals are combined in post-receptoral channels. The inputs to the two channels of colour vision in trichromatic monkeys were calculated as  $x = Q_L/(Q_L + Q_M)$  and  $y = Q_S/(Q_L + Q_M)$ , where  $Q_S$ ,  $Q_M$  and  $Q_L$  represent the quantum catches in the S, M and L cones. These values represent the inputs to the channels of colour vision thought to be subserved by the midget ganglion cells and the small bistratified cells, respectively. We have assumed that the luminance signal is drawn equally from M and L cones, and so we have specified luminance as  $Q_L + Q_M$ . Dichromatic monkeys possess just one class of L- or M-type cones, and lack colour-opponent midget ganglion cells. The inputs to their two post-receptoral channels were calculated as  $Q_S/Q_L$  and  $Q_L$ , corresponding to a colour channel, and a luminance channel, respectively. Where we have plotted luminance in our graphs, we have

arbitrarily scaled the total quantum catches  $Q_L + Q_M$  or  $Q_L$  by a factor of  $1.86 \times 10^{-4}$ , which, for the 430, 536 and 562 nm phenotype, converts total quantum catch to approximately the luminance in  $\text{cd m}^{-2}$  that would be experienced by a human observer.

Plotting  $y$  against  $x$  yields a chromaticity diagram that is an analogue of the MacLeod–Boynton diagram for man (MacLeod & Boynton 1979). We have used these diagrams to specify the colour signals offered to trichromatic platyrhine monkeys by fruits and leaves, and we have constructed different versions of the diagrams for monkeys with different complements of cone pigments. Although we have restricted our study to plant materials, chromaticity diagrams such as these would also be the most appropriate means of studying other ecologically significant colour signals—for example, the pelage colours of conspecifics, and the colours of predators and prey.

#### (d) Results

##### (i) Leaves

It has been shown that two factors critical to performance in visual search tasks are the similarity of targets

to non-targets, and the heterogeneity of distractors (Duncan & Humphreys 1989): visual search is hard when the targets are similar to the distractors, and when the distractors differ widely from each other. For a primate, the likelihood of spotting any particular fruit in a tree, or the time taken to find it, therefore depends both on the chromaticity difference between the fruit and its surroundings, and on the variation in chromaticity amongst the surrounding items. To analyse the natural search task facing primates, we therefore begin with the foliage background against which fruits are most often seen.

A total of 155 reflectance spectra were measured for upper and lower surfaces of leaves of 31 plant species. Examples for four leaves measured in Paris, and four leaves measured at Les Nouragues, are shown in figure 6. The spectra of seven out of the eight leaves are typical: they have low reflectance at short wavelengths, a peak between 530 and 560 nm, a gradual decline in reflectance to 680 nm, and a high reflectance at wavelengths longer than this, in the far red. The upper surfaces of leaves are usually darker (having lower overall reflectance) than lower surfaces. There appear to be no systematic differences between the leaf reflectance spectra measured in Paris and those measured at Les Nouragues.

These reflectance spectra are very similar to those that have been measured for a variety of leaves from different environments (e.g. Shull 1929; Nickerson *et al.* 1945; Rabideau *et al.* 1946; Billings & Morris 1951; Gates *et al.* 1965; Snodderly 1979; Cooper *et al.* 1986). What variation there is amongst these leaves is probably due to slight differences in the relative concentrations of chlorophylls and carotenoids in the leaves (Rabideau *et al.* 1946). The sole anomaly among the 31 species that we measured was *Manilkara bidentata*: the reflectance spectra of the upper surfaces of this plant's leaves are unremarkable, but the lower surfaces reflect progressively more light from 420 to 680 nm, without showing a peak between 530 and 560 nm. The spectrum of the underside of one such leaf is shown in figure 6. These undersides appeared orange to human observers. Similar anomalies can be found in earlier studies: for example, one of the foliage curves given by Nickerson *et al.* (1945) looks similar, as does the curve given by Cooper *et al.* (1986) for a *Solanum rugosum* leaf from French Guiana.

#### *Comparison of leaf chromaticities for different platyrhine phenotypes, and for man*

We calculated the chromaticities of the 155 leaves in our sample from the reflectance measurements, using an illuminant spectrum that had been measured in the canopy on a cloudy day (the spectrum of this illuminant is shown in figure 4). These are illustrated in figure 7, in chromaticity diagrams for the three different trichromatic phenotypes thought to be present amongst the primate species studied. For comparison, the data are also plotted in the MacLeod–Boynton diagram for human observers; and in order to compare data from measurements made in Paris with data from measurements at Les Nouragues, figure 7e also shows the Paris and Les Nouragues data with different symbols.

The most striking feature of the diagrams in figure 7 is that the leaf chromaticities are distributed along a

vertical, S cone axis in colour space, running from the illuminant towards a point between 560 and 570 nm on the spectrum locus, with rather little variation in the input to the  $L/(L+M)$  channel. This is the case for all three trichromatic platyrhine chromaticity diagrams, as well as for the MacLeod–Boynton diagram. In terms of human perception, such a distribution would be described as lying on a tritan axis, along which discrimination is mediated by S cone signals alone. Hendley & Hecht (1949), in their pioneering study of chromaticities in natural scenes, found a similar chromatic distribution for foliage samples. As will be seen later, the perpendicular distribution of leaf chromaticities proves to be critical in our analysis.

To compare the data for the different platyrhine phenotypes, we calculated the standard deviations of the chromaticity data along the two axes, as well as the correlations between the two axes. These values are summarized in table 2. The correlation coefficient between chromaticity values on the  $L/(L+M)$  and on the S cone axis gives a rough idea of the tilt of the distribution of leaf chromaticities. The correlation coefficients are all low, as would be expected from the near-vertical distributions of leaf chromaticities.

One notable feature of the data in table 2 is that the standard deviation of the chromaticities along the  $L/(L+M)$  axis is about twice as large for the 430, 536 and 562 nm phenotype as for the other two trichromatic phenotypes (the scales of the  $L/(L+M)$  axes in the diagrams of figure 7 differ accordingly). This does not necessarily mean that the phenotypes with more narrowly separated photopigments experience less saturated colours, for the range of inputs to the  $L/(L+M)$  channel may be scaled to the dynamic range of higher-order neurons. A similar process of contrast adaptation occurs in our own visual system, scaling the apparent saturation of colours according to the range of chromaticities recently experienced (Webster & Mollon 1991, 1994). However, quantum noise will have a more severe effect on those phenotypes that experience a smaller range of absolute input signals, and those phenotypes may exhibit poorer colour discrimination on the  $L/(L+M)$  axis.

A further important feature of figure 7 is that the chromaticity data plotted in the MacLeod–Boynton diagram (figure 7a) appear very similar to those plotted in the chromaticity diagram for a 430, 536 and 562 nm phenotype (figure 7b). This similarity is reassuring, for although the cone sensitivity curves used to construct the two diagrams have been derived by quite different means, the peak sensitivities of human cone pigments (*ca.* 419, 531 and 558 nm (Dartnall *et al.* 1983)) are not dissimilar from those used to construct figure 7b. Two differences between the diagrams do deserve mention. The first is that the gamut of leaf chromaticities, running vertically down the diagram, is centred on the abscissa at a value of about 0.66 for the MacLeod–Boynton diagram and about 0.54 for the platyrhine diagram. The second is that the vertical positioning of the leaf distribution relative to the spectrum locus is lower for the platyrhine diagram than for the MacLeod–Boynton diagram. In other words, the top of the leaf distribution is level with a wavelength shorter than 500 nm for the MacLeod–Boynton diagram, but longer than 500 nm for the platyrhine diagram. The

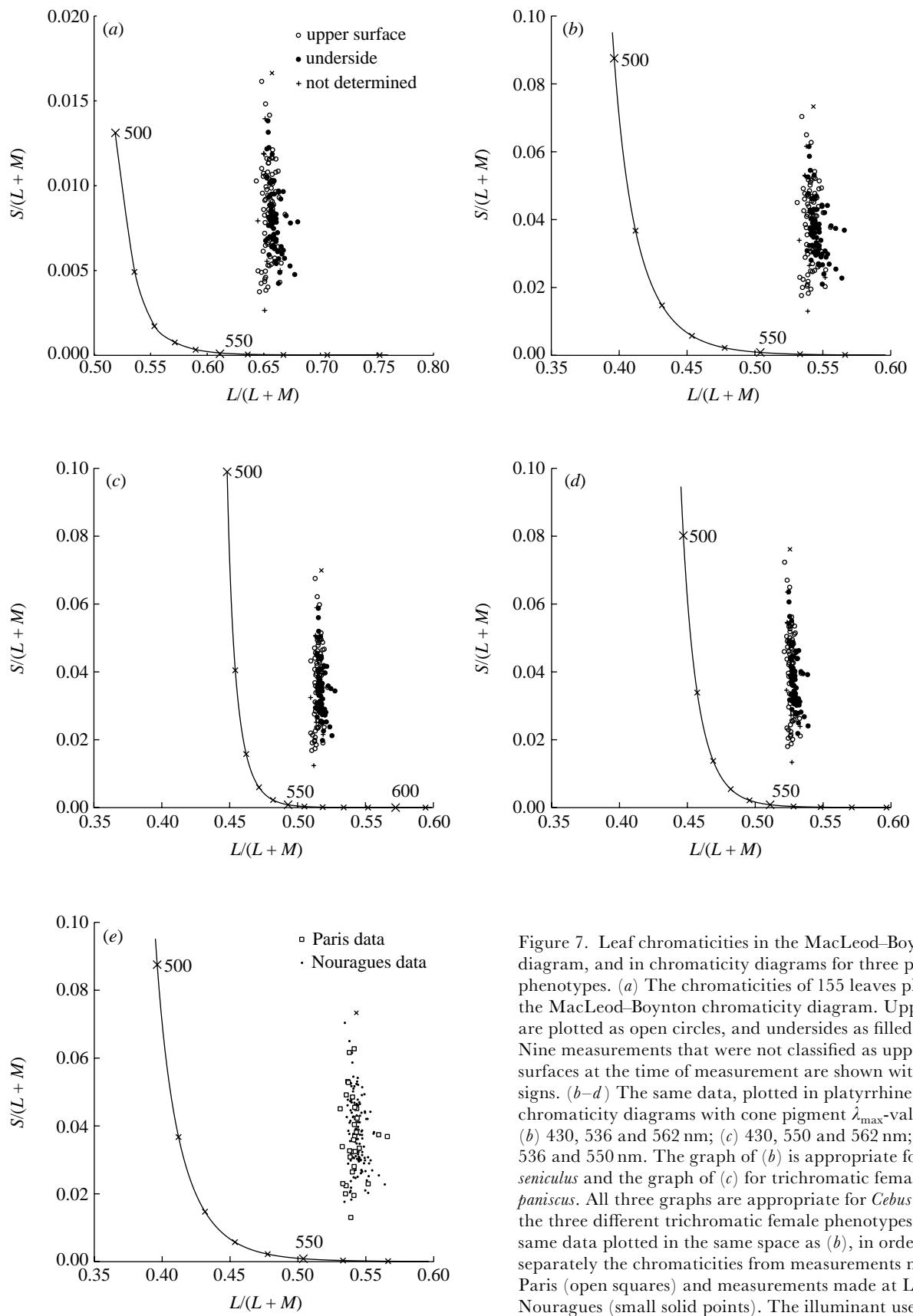


Figure 7. Leaf chromaticities in the MacLeod-Boynton diagram, and in chromaticity diagrams for three platyrhine phenotypes. (a) The chromaticities of 155 leaves plotted in the MacLeod-Boynton chromaticity diagram. Upper surfaces are plotted as open circles, and undersides as filled circles. Nine measurements that were not classified as upper or lower surfaces at the time of measurement are shown with plus signs. (b–d) The same data, plotted in platyrhine monkey chromaticity diagrams with cone pigment  $\lambda_{\max}$ -values of (b) 430, 536 and 562 nm; (c) 430, 550 and 562 nm; (d) 430, 536 and 550 nm. The graph of (b) is appropriate for *Alouatta seniculus* and the graph of (c) for trichromatic female *Atelis paniscus*. All three graphs are appropriate for *Cebus apella*, for the three different trichromatic female phenotypes. (e) The same data plotted in the same space as (b), in order to show separately the chromaticities from measurements made in Paris (open squares) and measurements made at Les Nouragues (small solid points). The illuminant used was measured in the canopy on a cloudy day, and is plotted as a cross on each diagram. The spectrum locus appears as a solid line, with wavelengths marked by a cross every 10 nm.

Table 2. Statistics of the distributions of leaf chromaticities for different trichromatic and dichromatic phenotypes

( $\mu_{L/M}$ ,  $\mu_S$ ,  $\sigma_{L/M}$  and  $\sigma_S$  are means and standard deviations of the leaf distributions along the L/M and S cone axes;  $r_1$  is Pearson's product-moment correlation coefficient between values on S and L/M axes, and  $r_2$  Pearson's product-moment correlation coefficient between values on S and luminance axes.)

data set	$N$	$\mu_{L/M}$	$\sigma_{L/M}$	$\mu_S$	$\sigma_S$	$r_1$	$r_2$
reflectance spectra	155	0.5276	0.0029	0.0389	0.0109	-0.369	-0.046
430, 536, 550 nm phenotype	155	0.5436	0.0056	0.0375	0.0106	-0.210	-0.057
430, 536, 562 nm phenotype	155	0.5161	0.0028	0.0357	0.0101	-0.033	-0.069
430, 550, 562 nm phenotype	155	—	—	0.0822	0.0228	—	-0.032
430, 536 nm phenotype	155	—	—	0.0737	0.0209	—	-0.058
430, 550 nm phenotype	155	—	—	0.0691	0.0196	—	-0.078
430, 536, 562 nm upper surfaces only	73	0.5416	0.0046	0.0383	0.0120	-0.015	-0.134
430, 536, 562 nm undersides only	73	0.5461	0.0055	0.0368	0.0080	-0.414	0.083
<i>in situ</i> spectra							
430, 536, 562 nm daytime, cloudy	245	0.5434	0.0065	0.0319	0.0149	-0.031	0.350
430, 536, 562 nm daytime, sunny	221	0.5434	0.0058	0.0327	0.0168	-0.263	0.076

first difference arises because the L cone sensitivity used to construct the MacLeod–Boynton diagram is roughly double the M cone sensitivity, whereas the two cone sensitivities used for the platyrhine diagram are equal. The second difference arises because the marmoset lens pigment used in constructing the platyrhine diagrams is denser than the human lens pigment at short wavelengths.

In the diagrams of figure 7 upper and lower leaf surfaces are plotted with distinct symbols. Both upper and lower surfaces show a similar variation along the L/M axis, but along the S cone axis, the upper surfaces show greater variation than the lower surfaces. In table 2 data are also given separately for the upper and lower surfaces of leaves.

Finally, figure 7e shows that the chromaticities of the 30 leaves measured in Paris are evenly scattered throughout the distribution of leaf chromaticities.

#### The dichromatic phenotypes

In figure 8 we plot the same leaf data in diagrams showing luminance against relative S cone excitation, for the dichromatic phenotypes of *Cebus apella* and *Ateles paniscus*. These diagrams represent the entire space of potential visual signals for dichromatic animals, as dichromats have only the S cone colour channel and a luminance channel. We have also plotted a luminance versus S cone diagram for a trichromatic monkey with photopigments at 430, 536 and 562 nm (such as *Alouatta seniculus* or some individuals of *Cebus apella*). All of these diagrams show very little correlation between the relative S cone excitation elicited by a leaf, and its luminance. The correlation coefficients are included in table 2. It is interesting that the distribution of leaf data on this diagram for the trichromatic phenotype is very similar to the distributions for dichromatic phenotypes. This suggests that a plot of luminance against relative S cone excitation for a trichromatic phenotype also indicates well the range of visual sensations available to a dichromat. For this reason in certain later diagrams, the data are shown for only one (trichromatic) phenotype, in the form of a standard chromaticity diagram and a luminance versus S cone diagram like the ones here.

From figure 8 it is apparent that upper and lower surfaces of leaves are well separated on the luminance axis: the lower surfaces are almost all lighter than the upper surfaces. This arises because the leaf reflectance spectra all show higher overall reflectance for undersides than for upper surfaces (figure 6).

We have once again compared measurements made in Paris with measurements made at Les Nouragues, in figure 8e: the Paris data are evenly scattered throughout the leaf data. As there are no obvious differences between the two sets of data we do not distinguish them in further analyses.

#### Comparison of *in situ* and reflectance data

Because every individual leaf has its own unique illuminant, *in situ* radiance measurements of leaves give a better representation of the range of chromaticities present in a natural scene than reflectance spectra. Unfortunately, in the field there is seldom sufficient time to make a large number of radiance measurements before the sun comes out or goes behind clouds, changing the illumination. We have therefore grouped together *in situ* measurements of leaf radiance spectra made on different days, according to the prevailing weather conditions at the times when the measurements were made. The chromaticities and luminances calculated from these *in situ* measurements are shown in figure 9, for prevailing sunny and cloudy weather conditions. The statistics of these distributions are included in table 2.

Two features of the data shown in figure 9 require comment. First, the undersides of leaves *in situ* tend to have much lower values on the S cone axis (and are thus more saturated in colour) than the upper surfaces, a difference that is not seen in the diagrams for leaf chromaticities reconstructed from reflectance spectra. Second, leaf upper surfaces measured *in situ* are brighter, on average, than lower surfaces, whereas reflectance measurements show that leaf undersides tend to be lighter (have higher absolute reflectance) than leaf upper surfaces. These differences probably arise from differences in the relative importance of transmitted and reflected light for upper and lower surfaces of leaves. Because the sky is the principal light source, leaf upper surfaces

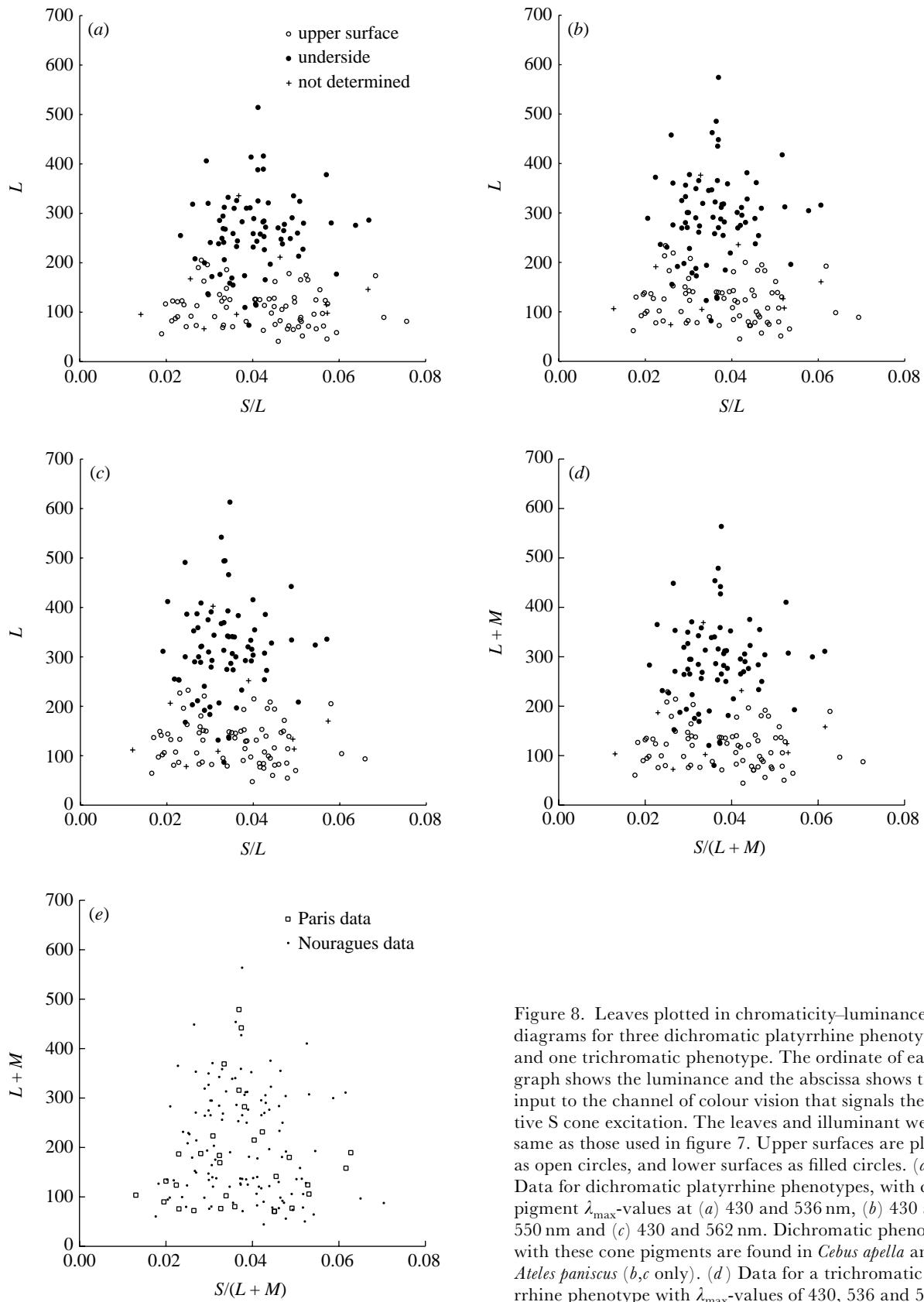


Figure 8. Leaves plotted in chromaticity-luminance diagrams for three dichromatic platyrhine phenotypes, and one trichromatic phenotype. The ordinate of each graph shows the luminance and the abscissa shows the input to the channel of colour vision that signals the relative S cone excitation. The leaves and illuminant were the same as those used in figure 7. Upper surfaces are plotted as open circles, and lower surfaces as filled circles. (a–c) Data for dichromatic platyrhine phenotypes, with cone pigment  $\lambda_{\max}$ -values at (a) 430 and 536 nm, (b) 430 and 550 nm and (c) 430 and 562 nm. Dichromatic phenotypes with these cone pigments are found in *Cebus apella* and *Ateles paniscus* (b,c only). (d) Data for a trichromatic platyrhine phenotype with  $\lambda_{\max}$ -values of 430, 536 and 562 nm, found in *Alouatta seniculus* and some *Cebus apella* individuals. (e) The same data as in (d), with leaf measurements made in Paris (open squares) shown separately from measurements made at Les Nouragues (small solid points).

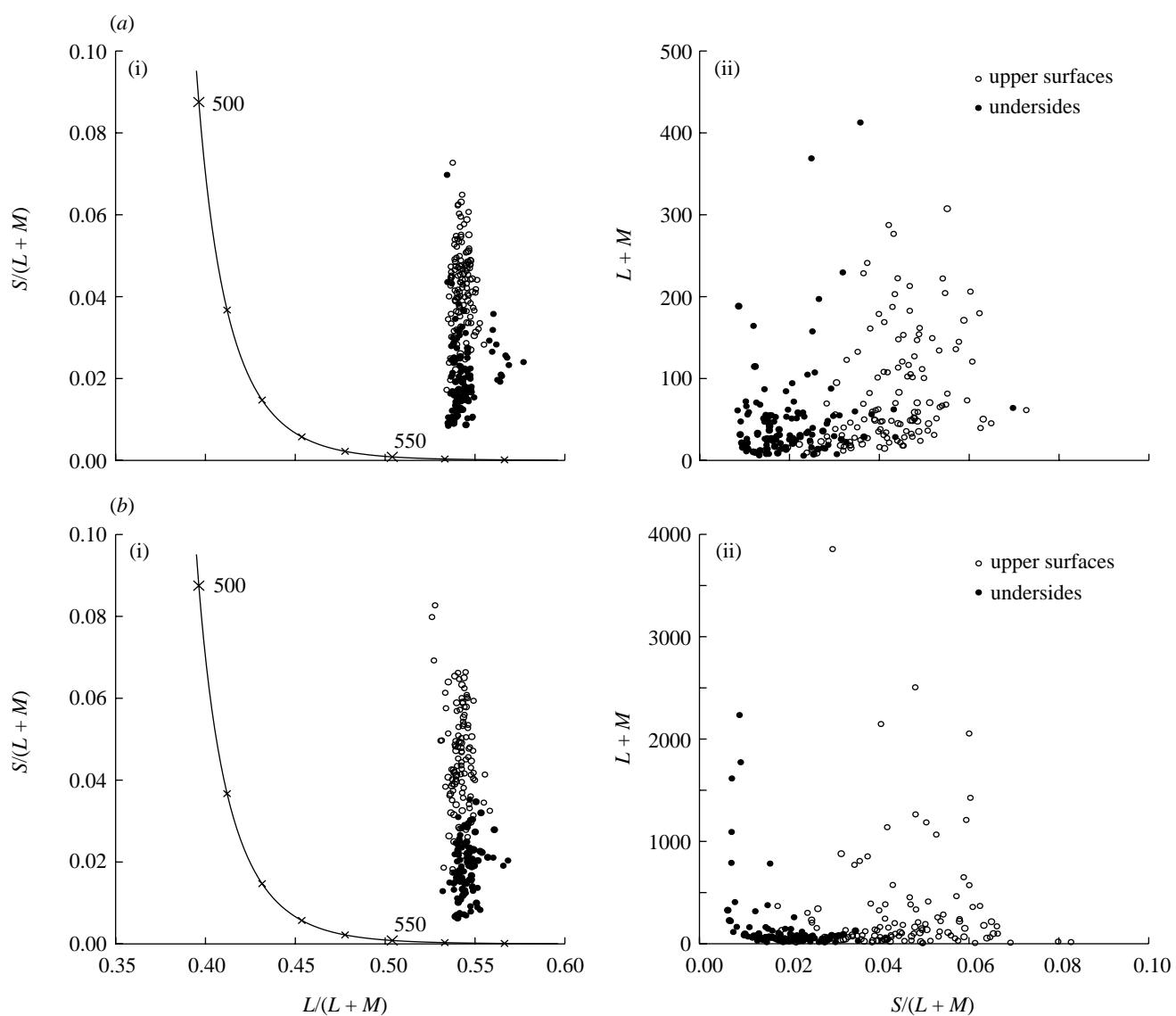


Figure 9. Chromaticities of leaves calculated from *in situ* radiance measurements under different weather conditions. Data are plotted in (i) chromaticity diagrams and (ii) diagrams showing luminance versus S cone excitation. The data were calculated for a platyrhine monkey with cone pigment  $\lambda_{\text{max}}$ -values at 430, 536 and 562 nm, such as *Alouatta seniculus*. All measurements were made in the canopy, but data from each graph come from different days and different locations, and have been grouped according to the weather conditions when the measurements were made. (a) Two hundred and forty-five measurements made in the daytime when the sun was behind clouds; (b) 221 measurements made in the daytime when the sun was shining. Open circles, upper surfaces; closed circles, undersides.

usually receive stronger illumination than lower surfaces, which explains why upper surfaces viewed *in situ* tend to be brighter than lower surfaces. For the same reason, relatively more light radiating from leaf undersides than from leaf upper surfaces has been transmitted through the leaf and subjected to filtering by chlorophyll and carotenoid pigments. Consequently, leaf undersides viewed *in situ* tend to be a more saturated green than upper surfaces.

The most important result, however, is that the overall distribution of leaf chromaticities derived from *in situ* measurements is very similar to that reconstructed from reflectance measurements. There are some small differences in the means of the distributions along the two chromatic axes, and the variance in the distribution along the S cone axis is significantly higher for the *in situ*

measurements, but the two sets of data are otherwise similar. Most importantly, in both cases the distribution of leaf chromaticities is closely aligned with the S cone axis, and there is rather little variation along the L/M axis. In the analyses described later in this article, we have used only the data derived from leaf reflectance spectra to represent the background against which fruits must be detected. We justify this approach by the similarity between the distributions derived from *in situ* and reflectance measurements.

#### (ii) Fruits

Photographs of some fruits eaten by monkeys at Les Nouragues are shown in figure 10, along with their reflectance spectra, and the chromaticities and luminances

reconstructed from those reflectance spectra for a trichromatic monkey with cone pigment  $\lambda_{\max}$ -values at 430, 536 and 562 nm, such as *Alouatta seniculus*. The fruits chosen illustrate some of the variety of fruit morphologies and colours included in the diets of primates at Les Nouragues.

#### *Crypsis and conspicuousness*

Previous studies of the reflectance spectra of fruits consumed by vertebrates in tropical forests (Snodderly 1979; Cooper *et al.* 1986) have distinguished between cryptic and conspicuous (or contrasting) fruits. Cryptic fruits have reflectance spectra similar to the reflectance spectrum of the background, and thus are hard to spot. Conspicuous fruits have reflectance spectra that differ from the background, making a contrast in colour or lightness. Cooper *et al.* (1986) stated that, as a general rule, cryptic fruits are eaten by nocturnal vertebrates, particularly bats, and contrasting ones by diurnal vertebrates, particularly birds and monkeys. Monkeys do, however, eat some cryptic fruits. Snodderly (1979) found that cryptic coloration was exhibited by every fruit whose seeds were destroyed by monkeys, and he argued that crypsis is a defence against seed predation. In fact, these ideas—that fruits whose seeds are destroyed by predators should exhibit cryptic coloration, and that fruits whose seeds are dispersed should be conspicuous—were already clear to Grant Allen in 1879, and on crypsis and conspicuousness it is hard to better his words:

‘A nut is a hard-coated seed, which deliberately lays itself out to escape the notice and baffle the efforts of the monkeys and other frugivorous animals. Instead of bidding for attention by its bright hues, like the flower and fruit, the nut is purposely clad in a quiet coat of uniform green, indistinguishable from the surrounding leaves . . .’  
(Allen 1879, p. 106.)

‘But the greatest need of all, if the plant would succeed in enticing the friendly parrot or the obsequious lemur to disperse its seed, is that of conspicuousness. Let the fruit be ever so luscious and ever so laden with sweet syrups, it can never secure the suffrages of the higher animals if it lies hidden beneath a mass of green foliage, or clothes itself in the quiet garb of the retiring nut. To attract from a distance the eyes of wandering birds or mammals, it must dress itself up in a gorgeous livery of crimson, scarlet and orange.’  
(Allen 1879, pp. 109–110.)

Chromaticity diagrams like those in figure 10 allow us to evaluate crypsis and conspicuousness in terms appropriate for the primates that eat the fruits. If the chromaticity of a fruit lies within the range of leaf chromaticities, then that fruit must be considered cryptic. The more the chromaticity differs from that of the leaf chromaticities, the more conspicuous the fruit should be. (One might argue that conspicuity increases only up to a certain point, since laboratory visual search experiments have established that search for a coloured target does not get faster beyond a certain threshold colour difference (Nagy & Sanchez 1990; D’Zmura 1991; Bauer *et al.* 1996). However, in the real world, this threshold colour difference must depend on the size and distance of the target: when viewing a small target from afar, optical aberrations and veiling light will reduce the effective colour difference between target and background.)

On the other hand, a high lightness is probably not sufficient for conspicuousness. Under natural conditions the forest is dappled by light filtering through different layers of leaves, and the leaves make varying angles to the illumination, displaying highlights of specular reflection (Mollon 1989). Even if an object has a higher reflectance than leaves, some parts of a natural scene, such as a glimpse of sky through leaves, or a specular reflection, may still have higher luminance.

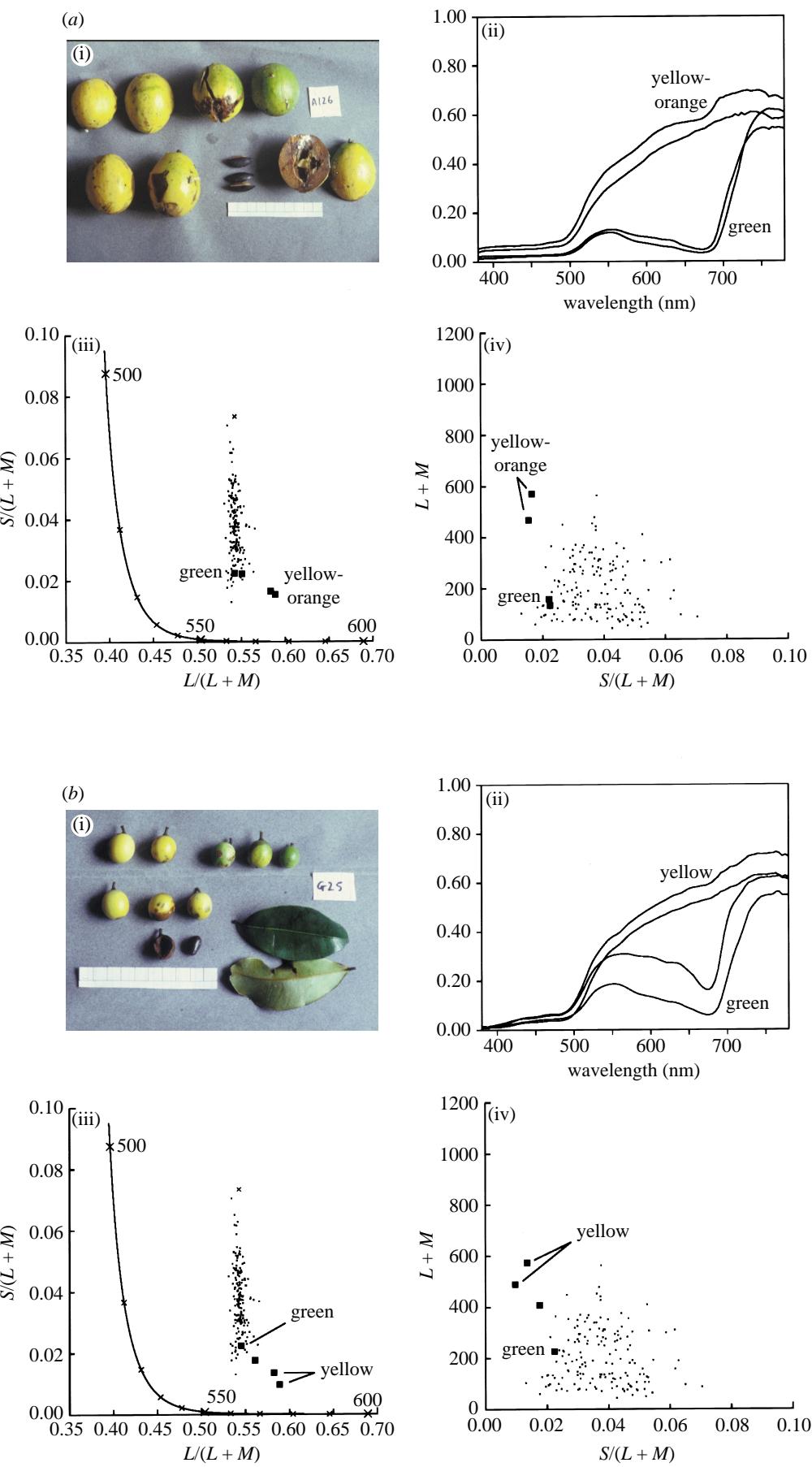
Of the fruits in figure 10, *Chrysophyllum lucentifolium*, *Micropholis* cf. *egensis*, cf. *Tetragastris* sp., *Iryanthera sagotiana*, *Virola michelii* and *Sterculia frondosa* should all be conspicuous to a trichromatic monkey such as *Alouatta seniculus*. *Inga thibaudiana*, *Eschweilera* cf. *micrantha* and *Bactris acanthocarpoides* are all just distinguishable from the leaves by colour, but must be fairly inconspicuous; and *Tapirira* cf. *obtusa* is cryptic. In fact, *Chrysophyllum lucentifolium*, *Micropholis* cf. *egensis*, *Iryanthera sagotiana* and *Virola michelii* become conspicuous only when mature: the green versions of the former two fruits, and the valves of the last two (which are all that is visible before dehiscence) are cryptic. To the dichromatic phenotypes of *Ateles paniscus* and *Cebus apella*, only the fruits of *Chrysophyllum lucentifolium*, *Micropholis* cf. *egensis*, and *Tetragastris* sp. are distinct from the leaf distribution in the luminance versus S cone excitation diagrams. These fruits may be distinguishable from leaves under good viewing conditions, although it is unlikely that they are particularly conspicuous to dichromats. All the other fruits lie within the leaf distribution in these diagrams, and must be cryptic to dichromats.

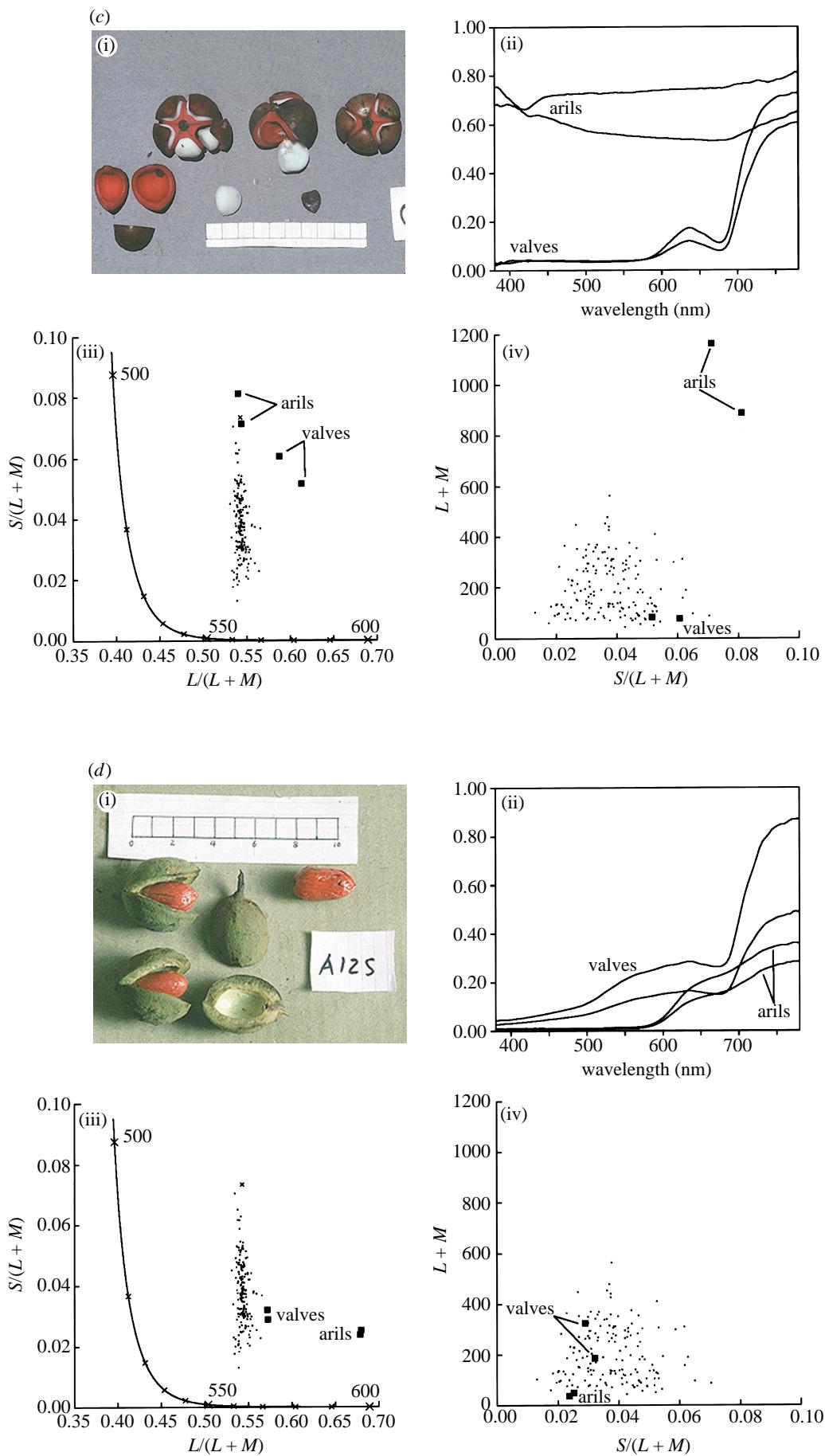
#### *Fruits eaten by the three primate species studied*

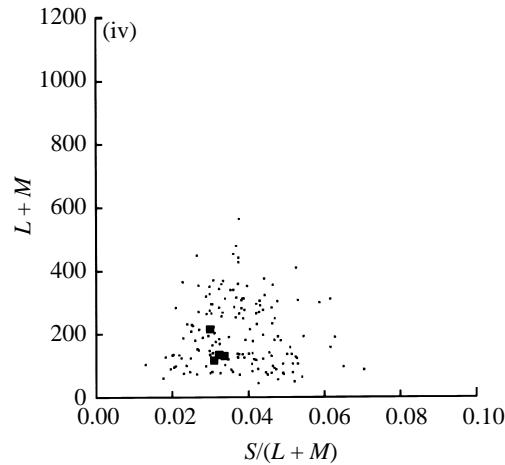
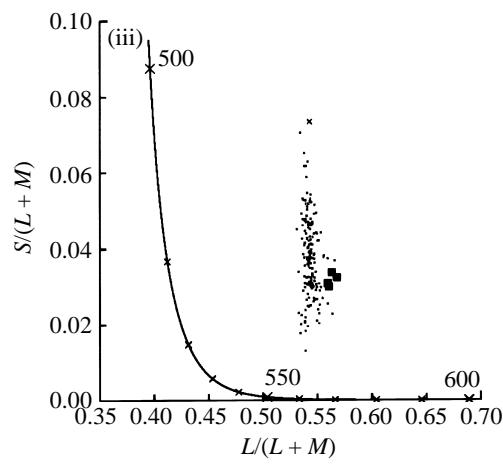
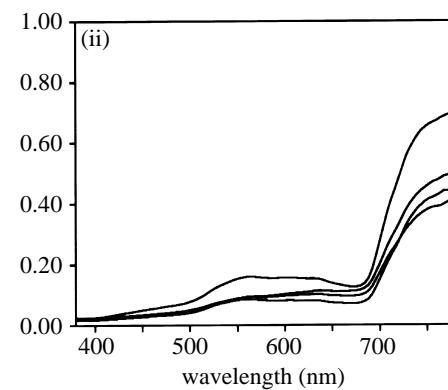
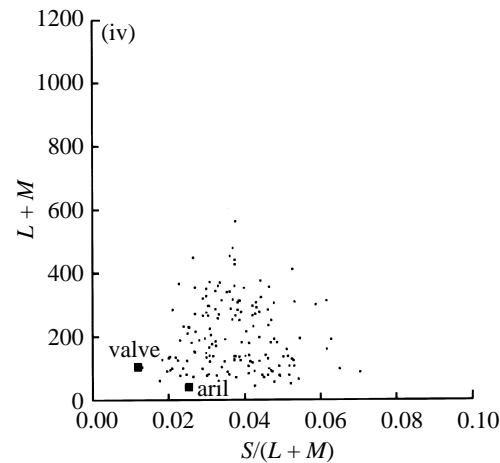
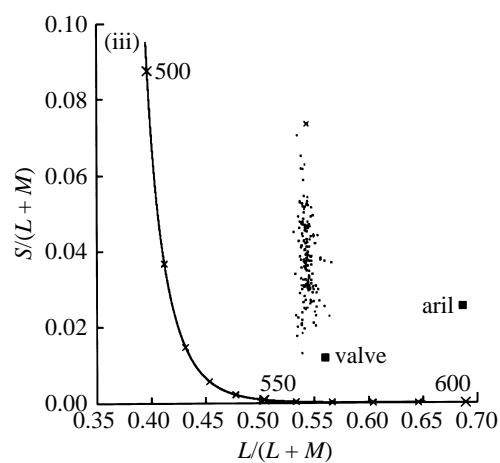
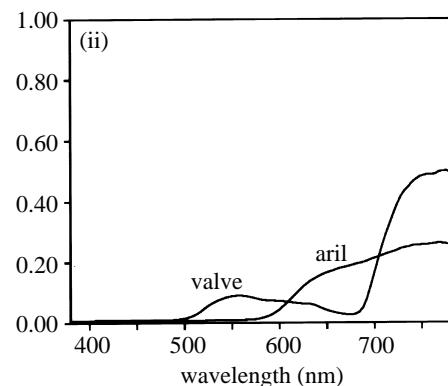
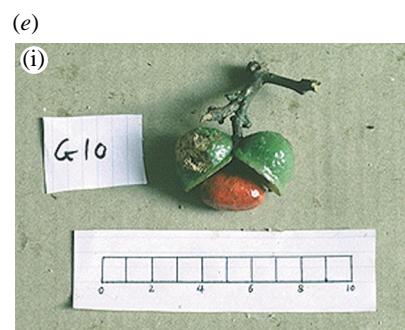
The chromaticities and luminances of fruits eaten by the three primate species studied are shown in figure 11. These diagrams should only be taken as a rough idea of the chromaticity distributions of fruits in the diets of these species, as some fruits must have been over-sampled and others under-sampled, relative to their importance in the diets.

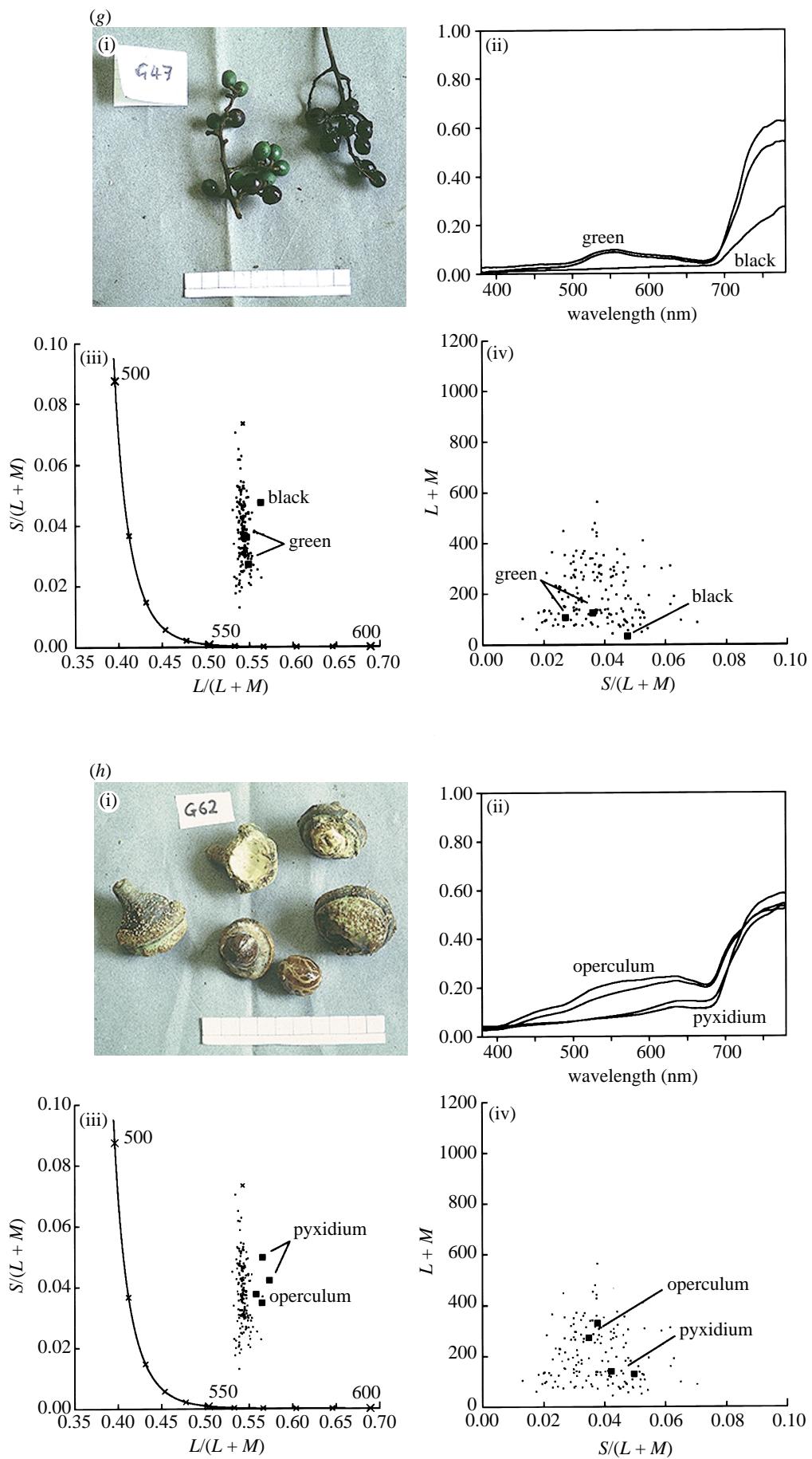
The range of fruit chromaticities is overwhelmingly similar for the three primate species, but some differences are apparent: more measurements lie within the limits of the leaf distribution for *Cebus apella* than for the other two species, and no measurements for *Cebus apella* fall at the extreme right of the diagram. The chromaticities at the extreme right in the diagrams for *Ateles paniscus* and *Alouatta seniculus* belong to the crimson arils of fruits of the Myristicaceae family (*Virola* spp. and *Iryanthera sagotiana*), which are consumed by *Ateles* and *Alouatta* but not by *Cebus apella*.

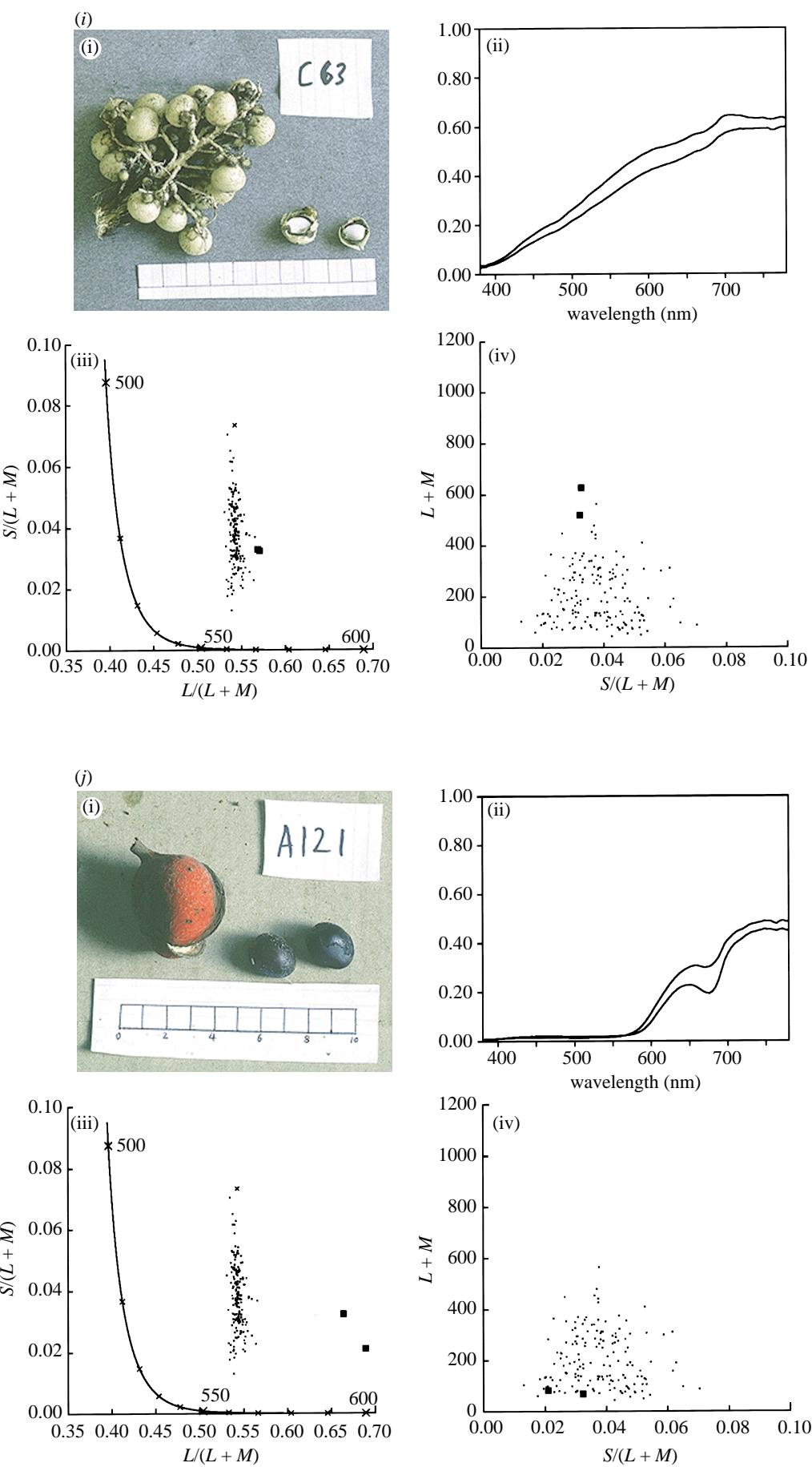
A further salient feature of figure 11 is that no fruits eaten by monkeys have chromaticities lying to the left of the leaf distribution. This region of the chromaticity diagram is where blue and blue-green objects would be plotted. In fact, blue fruits seemed to be rather rare, and the only ones that we observed at Les Nouragues were borne on ground-level herbs of the Melastomataceae and Rubiaceae families. Apart from these, the only blue objects in the Guianan forest seem to be the brilliant metallic blue wings of *Morpho* butterflies, which are highly conspicuous to a human observer. In figure 12 we have plotted the reflectance spectra of blue fruits obtained from the ground-level herb *Psychotria ctenophora* (Rubiaceae) and the reflectance spectrum of the iridescent blue wing of a











*Morpho* butterfly, and the corresponding locations in a chromaticity diagram appropriate for *Alouatta seniculus*. The butterfly wing and the *Psychotria* fruits lie a long way to the left of and above the leaf distribution in the chromaticity diagram. Given the conspicuousness of blue objects in the forest, the absence of blue fruits in the Guianan forest is remarkable, and suggests that blue fruit pigments may be rather hard for plants to manufacture.

To compare how effective the different colour vision phenotypes of the three primate species would be at discriminating between fruits and leaves, we have counted the number of fruit chromaticities that lie outside the distribution of leaf chromaticities, for each of the three distributions shown in figure 11. For trichromatic phenotypes this is the number of measurements that lie to the right of the leaf distribution, and for dichromatic phenotypes this is the number of measurements that have either a higher or a lower S cone excitation than all the leaves. The numbers are shown in table 3.

The values in table 3 illustrate forcefully the advantage of trichromacy for frugivorous primates: between three and ten times more fruits are distinguishable from leaves by trichromatic phenotypes than by dichromatic phenotypes.

Table 3 also shows that relatively more fruits eaten by *Cebus apella* have chromaticities within the leaf distribution than fruits eaten by the other two species, both for trichromatic phenotypes (24% for *Cebus apella* versus 14% for *Ateles paniscus* and 18% for *Alouatta seniculus*) and for dichromatic phenotypes (83–92% for *Cebus*, versus 74–82% for *Ateles*). This difference is significant for

trichromatic phenotypes ( $\chi^2 = 9.26$ , 2 d.f.,  $p < 0.05$ : we took the mean number of fruits inside the leaf distribution for the three trichromatic phenotypes of *Cebus*, and compared this with the numbers of fruits inside the leaf distribution for the single trichromatic phenotypes of *Alouatta* and *Ateles*). The difference is also significant for the 430 and 562 nm dichromatic phenotype of *Cebus* and *Ateles* ( $\chi^2 = 6.26$ , 1 d.f.,  $p < 0.05$ ) but not for the 430 and 550 nm dichromatic phenotype ( $\chi^2 = 3.39$ , 1 d.f.).

These results suggest that *Cebus apella* eats more fruits that are cryptic than the other two primate species. One reason for this may be that *Cebus* eats a much higher proportion of green *Inga* spp. fruits than the other species. But it may also reflect the fact that *Cebus* consumes more fruits for their seeds than do the other species: table 1 shows that *Cebus* was the sole primate consumer of 13 out of the 21 species whose fruits were predated. Such fruits may more often be cryptic than fruits whose seeds are dispersed, although our data suggest that this is strictly true only for dichromatic phenotypes (this is discussed below in the section on seed dispersal and seed predation). In this light it is interesting to contrast the performance of the dichromatic phenotypes of *Ateles paniscus* and those of *Cebus*: dichromatic *Ateles* are able to detect a comparatively larger number of the fruits that they eat. This may be because more fruits eaten by *Ateles* belong to the primate seed-dispersal syndrome, and differ from leaves on the S cone axis as well as the L/M axis of colour vision, making them discriminable (if not conspicuous) to dichromats.

Figure 10. Ten fruits consumed by monkeys at Les Nouragues. (i) A photograph of each fruit is shown, along with (ii) the reflectance spectra of several specimens, and (iii, iv) chromaticities and luminances calculated from these reflectance spectra. Data are plotted in (iii) chromaticity diagrams and (iv) luminance versus S cone excitation diagrams. In this figure and in future figures, unless otherwise stated, chromaticities and luminances have been calculated for a platyrhine monkey with cone pigment  $\lambda_{\text{max}}$ -values at 430, 536 and 562 nm, such as *Alouatta seniculus*, using the same illuminant used to construct figure 7, measured in the canopy on a cloudy day. Leaf data, in this and future figures, are the same as shown in figure 7, and are shown with small solid points. (a) *Chrysophyllum lucentifolium* (Sapotaceae), a fruit consumed by all three species of monkey studied. This is one of the most heavily consumed fruits in the diets of *Alouatta seniculus* and *Ateles paniscus*. The monkeys eat the pulp contained within these fruits, and swallow the seeds. (b) *Micropholis* cf. *egensis* (Sapotaceae), a fruit consumed by *Ateles paniscus* and *Cebus apella* at Les Nouragues. The reflection spectra and chromaticity diagrams show data from two fruits that were yellow and mature, one fruit that was green, and one fruit in an intermediate state of maturity. (c) cf. *Tetragastris* sp. (Burseraceae). Fruits of the Burseraceae family, such as this, are consumed in moderate quantities by all three species of monkey studied. This fruit is dehiscent: when immature, the outer surface is green, but when mature, the outer surface turns purple and the valves open and fall off, each revealing a snow-white aril surrounding a seed. The parts that are exposed to the view of a frugivore in the forest are the valves and the arils; data for these are indicated separately. The monkeys swallow the aril and the seed. (d) *Virola michelii* (Myristicaceae). This fruit is consumed in moderate quantities by *Alouatta seniculus*, very heavily by *Ateles paniscus*, and not at all by *Cebus apella*. It is dehiscent, and when it is mature, the brownish valves separate to reveal a thinnish red-magenta aril surrounding a large seed. The monkeys swallow the aril and the seed. (e) *Iryanthera sagotiana* (Myristicaceae). This fruit is consumed in moderate quantities by *Alouatta seniculus* and *Ateles paniscus*. It is dehiscent, and when the fruit is mature, the green valves separate to reveal a red aril surrounding a large seed. The monkeys swallow the aril and the seed. (f) *Inga thibaudiana* (Mimosaceae). Fruits of the genus *Inga* are consumed very heavily by *Cebus apella*, moderately by *Ateles paniscus* and occasionally by *Alouatta seniculus*. This fruit is typical of *Inga*: it is a green, indehiscent pod, containing seeds surrounded by white, sugary arils. Monkeys open the pods and swallow the seeds and the arils, or sometimes suck the arils and spit out the seeds. (g) *Tapirira* cf. *obtusa* (Anacardiaceae). These fruits are consumed occasionally by all three species of monkey studied. They are green when immature and become black with maturity. Note that the black fruit is darker than all the leaves. These and other black fruits have been excluded from further analyses, for reasons described in the notes to table 1. (h) *Eschweilera* cf. *micrantha* (Lecythidaceae). This woody fruit is typical of the genera *Lecythis* and *Eschweilera*, and contains a few nut-like seeds. The fruits resemble lidded containers: the main part of the container is called the pyxidium, and the lid, the operculum. The fruits dehisce when mature: the lid drops off, and the seeds may drop to the forest floor. *Cebus apella* consumes the seeds of this fruit. (i) *Bactris acanthocarpoides* (Arecaceae). *Cebus apella* cracks open the cream-coloured fruits of this palm, and eats the seeds. (j) *Sterculia frondosa* (Sterculiaceae). These fruits are dehiscent and open to reveal black seeds embedded in a mass of prickly orange hairs. *Cebus apella* occasionally consumes the seeds of this fruit. *Ateles paniscus* has been observed to consume the seeds of a similar fruit (*Sterculia pruriens*).

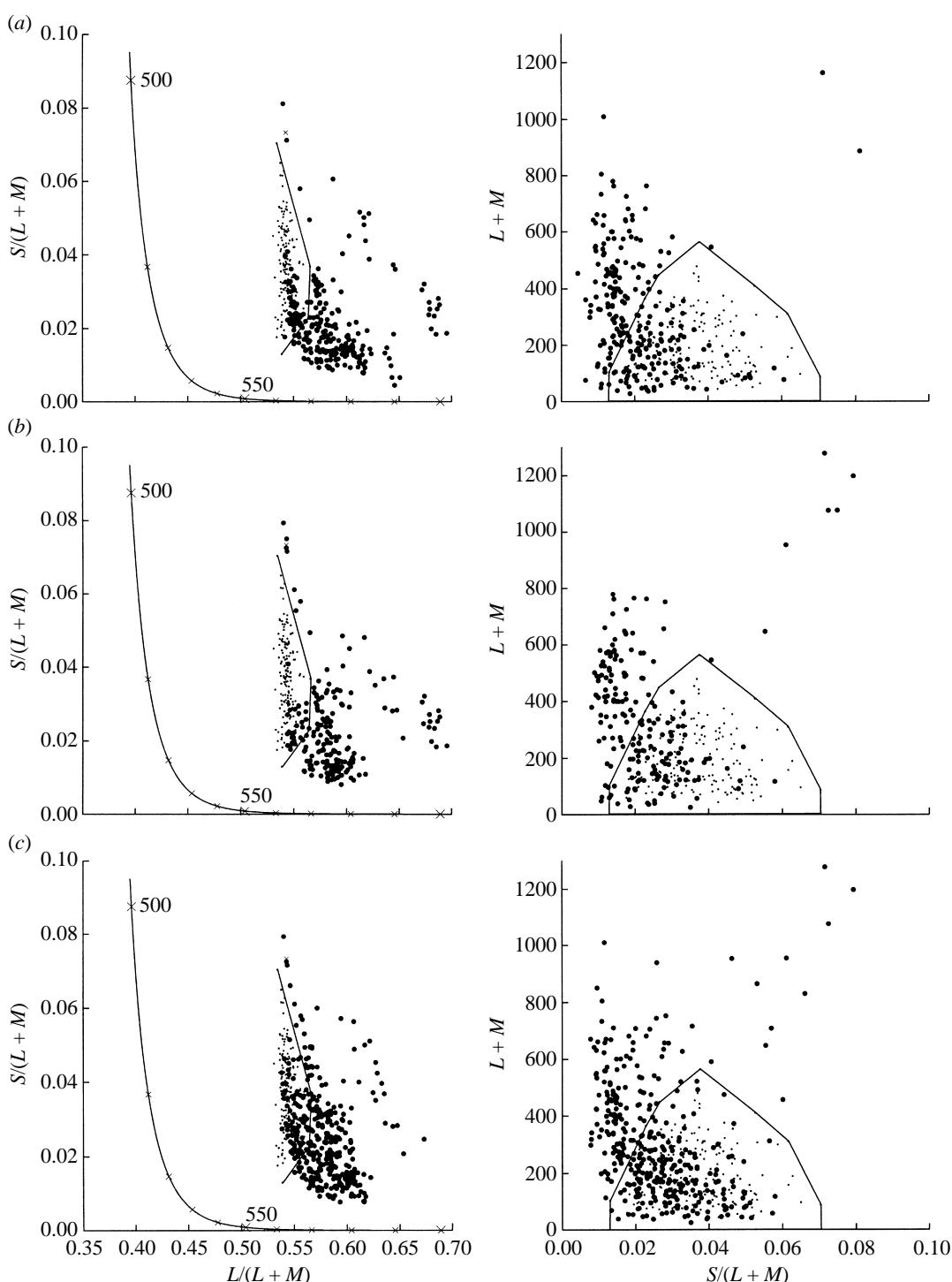


Figure 11. Chromaticities of fruits eaten by the three primate species studied at Les Nouragues (a) *Alouatta seniculus*, 250 measurements; (b) *Ateles paniscus*, 197 measurements; (c) *Cebus apella*, 372 measurements. For ease of comparison, fruit chromaticities are presented in all cases for a phenotype with cone pigment  $\lambda_{\max}$ -values at 430, 536 and 562 nm, although it is not thought that this phenotype exists in *Ateles paniscus*. The chromaticities of 155 leaves reconstructed from reflectance spectra are shown with small points. For extra clarity, the limits of the distribution of leaf chromaticities have been shown with solid lines in the diagrams. The figure shows data for fruit of every species that we measured and that is known to be eaten by monkeys, with the exception of five species which were excluded because they were black (table 1 identifies these species), and *Ananas cf. nanus* (Bromeliaceae) which was excluded because it is a ground-level herb that would not normally be seen against canopy foliage. These six species have also been excluded from all further analyses.

#### *Are the primate photopigments optimal for detecting fruits against leaves?*

Our method allows us to investigate the colour signals that would be offered to monkeys if they possessed cone pigments with different spectral sensitivities. Figure 13 shows the chromaticities of leaves and of the three species

of fruit that Julliot (1992) found were most commonly consumed by *Alouatta seniculus* at Les Nouragues: *Bagassa guianensis*, *Chrysophyllum lucentifolium* and *Vouacapoua americana*. (*Alouatta* destroys the seeds of *Vouacapoua americana* and disseminates the seeds of the other two species.) These chromaticities are plotted in figure 13a, in

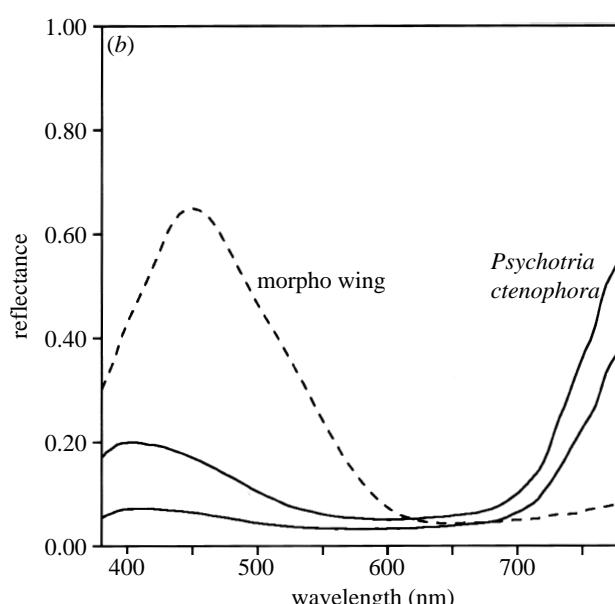
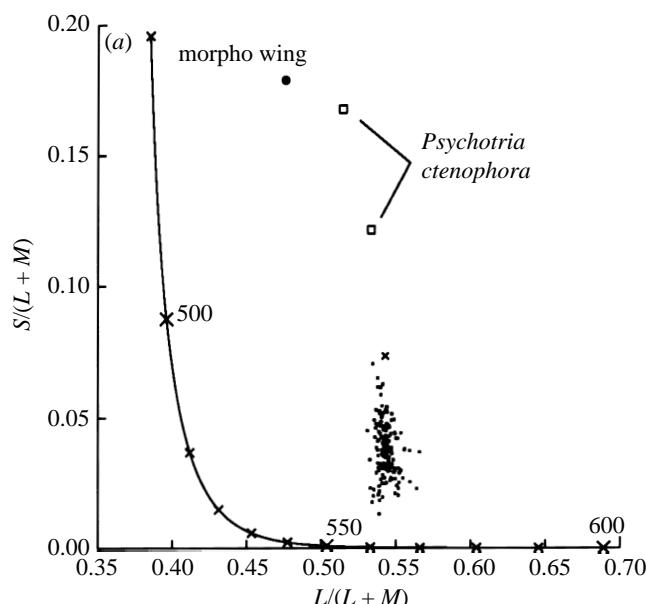


Figure 12. (a,b) Chromaticities and reflectance spectra of two blue objects found in the forest at Les Nouragues: the wing of a *Morpho* butterfly, and the fruits of *Psychotria ctenophora* (Rubiaceae), a herb growing at ground level. (c) Some fruits of *Psychotria ctenophora*. Note that the reflectance spectra of *Morpho* butterfly wings vary with viewing angle, the apparent colour varying from purple-blue to blue-green (Wright 1967). The spectrum presented here is appropriate for just one viewing angle.

a diagram constructed with  $\lambda_{\max}$ -values evenly spaced through the spectrum, at 430, 485 and 540 nm (a triplet never observed in primates) and in figure 13b in a diagram appropriate for *Alouatta seniculus*, with  $\lambda_{\max}$ -values at 430, 536 and 562 nm. The critical difference between the two diagrams is that the distribution of leaf chromaticities is almost vertical in the diagram for the pigments actually possessed by *Alouatta seniculus*, but strongly tilted in the diagram for the evenly spaced pigments. The photopigments possessed by *Alouatta* separate fruits and leaves into two groups along the L/M axis, but the other triplet of photopigments does not. Thus, a primate such as *Alouatta* could distinguish fruits from leaves by L/M signals alone, whereas a primate equipped with pigments at 430, 485 and 540 nm would need to combine L/M signals with S cone signals. But the latter phenotype would be at a severe disadvantage, because the large receptive fields of the small bistratified ganglion cells (see figure 1) and the correspondingly

poor spatial resolution of the S cone channel would mean that such a primate would be unable to spot fruit at a distance.

The optimal photopigments for a primate foraging for fruit amongst leaves should therefore separate the fruit and leaf chromaticities as well as possible along the L/M axis. In figure 13 we have projected the chromaticities of fruits and leaves on to the abscissa. In the case of the hypothetical phenotype with  $\lambda_{\max}$ -values at 430, 485 and 540 nm, the fruit and foliage distributions overlap. In contrast, the foliage distribution is nearly vertical in the chromaticity diagram constructed for the pigments of *Alouatta seniculus*, and when projected on to the abscissa, forms a tight cluster and does not overlap with the fruits. This finding is reminiscent of that of Nagle & Osorio (1993), who calculated the variance in the L/M channel of colour vision from foliage-dominated natural scenes, keeping the separation of the L and M cones constant but varying their peak sensitivities. They found that the

Table 3. Numbers of measurements of fruits that can be distinguished from leaves by chromaticity, for fruits eaten by three species of primate

(The numbers tabulated are the numbers of measurements of fruits eaten by each species that lie outside the distribution of leaves on chromaticity diagrams, calculated separately for (a) the trichromatic phenotypes and (b) the dichromatic phenotypes of each species. The number of measurements in each data set is shown in the  $N$  column. Data for *Alouatta seniculus* appear only in section (a) because all individuals possess trichromatic colour vision.)

(a) trichromatic phenotypes

data set	$N$	430, 536, 562 nm	430, 536, 550 nm	430, 550, 562 nm
<i>Alouatta seniculus</i>	250	205 (82%)	—	—
<i>Ateles paniscus</i>	197	—	—	170 (86%)
<i>Cebus apella</i>	372	282 (76%)	282 (76%)	284 (76%)

(b) dichromatic phenotypes

data set	$N$	430, 536 nm	430, 550 nm	430, 562 nm
<i>Ateles paniscus</i>	197	—	35 (18%)	52 (26%)
<i>Cebus apella</i>	372	29 (8%)	45 (12%)	65 (17%)

variance in the L/M channel was minimized when the L and M pigments had the peak sensitivities found in human cones.

Clearly then, of these two phenotypes, the one with the photopigment complement of *Alouatta seniculus*, at 430, 536 and 562 nm, has the advantage. But if the photopigments were different, could the monkeys do even better at detecting fruits amongst leaves? To answer this question, we treat the visual search task facing monkeys as a signal detection task: monkeys must detect a signal (a fruit) against noise. We believe the S cone channel is of little use for spotting fruits at a distance, owing to its poor spatial resolution, and we therefore consider only the channel of colour vision that compares the quantum catches of the L and M cones. We systematically vary the peak sensitivities of the two photopigments that make inputs to this channel, and observe how the signal-to-noise ratio varies as the photopigments take different  $\lambda_{\max}$ -values.

We refer to the photopigments now as P and P', as they can have any arbitrary  $\lambda_{\max}$ -value. For every pair of photopigments P and P' with  $\lambda_{\max}$  in the range from 400 to 640 nm, in 2 nm steps, we calculated the putative input signal to the midget ganglion cells (the chromaticity) as  $Q_P/(Q_P + Q_{P'})$  for our sample of 155 leaf spectra, and for the spectra of the fruit included in the diets of the three species of monkey (250 spectra for *Alouatta seniculus*, 197 spectra for *Ateles paniscus* and 372 spectra for *Cebus apella*). The method used for calculating these chromaticities was the same as that used for generating chromaticity diagrams.

In our modelling, we assume that the monkey detects fruits against the leaves by their chromaticity, and therefore the bigger the difference between the fruit chromaticity and the average leaf chromaticity, the easier the task. We calculated the signal for each fruit as the difference between the fruit chromaticity and the mean of the leaf chromaticities. The most important source of noise in this visual detection task is the variability amongst the

leaf chromaticities, which we call 'leaf noise'. This is analogous to the width of the leaf histograms in figure 13. The leaf noise was calculated as the standard deviation of the distribution of leaf chromaticities. However, a minor source of noise arises from random fluctuations in the quantum catches of the different cone classes ('quantum noise'). Quantum noise arises from the discrete nature of light: the absorption of photons by photoreceptors is a random process, and the number of photons absorbed per unit time varies, leading to intrinsic uncertainty in the chromaticity and luminance of a stimulus. The quantum catch  $Q$  per unit time strictly follows a Poisson distribution, but if  $Q$  is not small then the distribution approximates a normal distribution with mean and variance both equal to  $Q$ . From this, we can calculate the statistical distribution of a chromaticity: the mean is  $Q_P/(Q_P + Q_{P'})$ , and the variance is  $[Q_P^{-1} + (Q_P + Q_{P'})^{-1}] \cdot [Q_P/(Q_P + Q_{P'})]^2$ . The unit time-interval is equal to the integration time for the cones, which we took to be 100 ms (Hood & Finkelstein 1986).

The overall noise for the signal detection task was calculated by adding together leaf noise and quantum noise: we took the square root of the sum of the variance in leaf chromaticities, the variance in the chromaticity of the fruit due to quantum noise, and the mean variance in the leaf chromaticities due to quantum noise. We calculated the signal-to-noise ratio individually for each fruit spectrum, and the mean of these was taken, for all the fruits in the diet of a particular species of monkey, to obtain a measure of the efficiency of the pigments P and P' at separating fruit and leaf chromaticities.

The diagrams of figure 14 show how the mean signal-to-noise ratio varies with the  $\lambda_{\max}$ -values of P and P', for the fruits eaten by each of the three primate species. The signal-to-noise ratios are expressed as a percentage of the maximum obtained for any P, P' pairing; the lighter a region is, the higher the mean signal-to-noise ratio. The visual pigment pairings found in dichromatic platyrhine monkeys, with  $\lambda_{\max}$  at 430 nm and 535–565 nm, offer

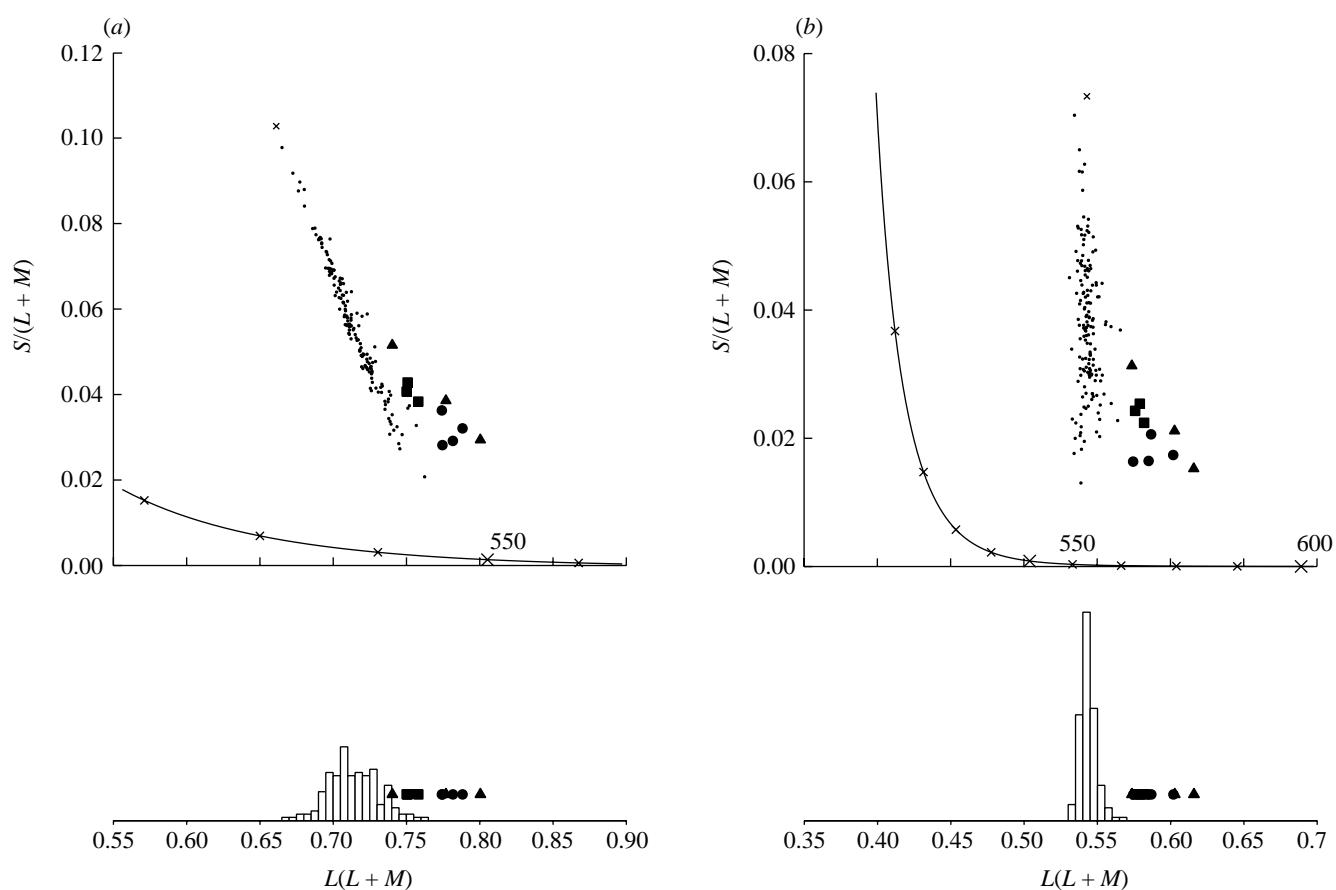


Figure 13. The three fruits most commonly consumed at Les Nouragues by *Alouatta seniculus*, and the foliage background, in chromaticity diagrams for different sets of photopigments. The small solid points show the chromaticities of foliage, and the large symbols show those of the fruits: *Bagassa guianensis* (triangles), *Chrysophyllum lucentifolium* (circles), and *Vouacapoua americana* (squares). (a) A triplet of pigments with  $\lambda_{\text{max}}$ -values evenly spaced through the spectrum: 430, 485 and 540 nm, a set never observed in primates. (b) The set of pigments thought to be present in *Alouatta seniculus*, 430, 536 and 562 nm. Notice that the foliage distribution is tilted to the right in (a), but that in (b) the foliage chromaticities fall on a near-vertical line (as they do for other trichromatic platyrhine phenotypes, as shown in figure 7). The histograms beneath each diagram show the distribution of foliage chromaticities when projected on to the abscissa: note that fruit and foliage are better separated in (b) than in (a).

poor performance, providing a mean signal-to-noise ratio of only 20–30% that of the best pairings. In contrast, the spectral tunings of the L and M photopigments in trichromatic platyrhine monkeys all lie in the region where the signal-to-noise ratio is over 80% of the maximum possible. The highest signal-to-noise ratios are obtained in a small ‘island’, with one pigment in the range 500–550 nm and the other in the range 540–600 nm. In a sense, then, the primate photopigments are optimal for the task of detecting fruits against leaves, in that there are no alternative pairings that do the task much better. However, there is a considerable range of ‘optimal’ values, all of which do the task equally well. We return to this issue in the Discussion (§2(e)ii), where we consider other influences on the spectral positioning of the primate cone photopigments.

### (iii) Effects of lens and macular pigment

The optical density of the human lens pigment increases with age (Pokorny *et al.* 1987) and that of the macular pigment may change with diet (Edwards *et al.* 1996); so it is reasonable to expect that they may vary in

other primates. We have therefore investigated the extent to which the results of our model are affected by the values chosen for the optical densities of the lens and macular pigment.

The chromaticities of the 155 leaves whose reflectance spectra we measured were recalculated using different corrections for lens and macular pigment: we tested the standard macular pigment correction with no lens correction, and we tested the standard lens correction with no macular pigment correction, or corrected for double the standard macular pigment optical density. The calculations were made for a platyrhine monkey with the cone pigments thought to be present in *Alouatta seniculus*, with  $\lambda_{\text{max}}$  at 430, 536 and 562 nm. The results are shown in figure 15, and the statistics of the distributions are shown in table 4.

The main effect of both the lens pigment and the macular pigment is to compress the distribution of leaf chromaticities along the S cone axis: the standard deviation of chromaticities along the S cone axis is almost halved when the lens correction is applied, compared with when it is not applied, and the macular pigment has

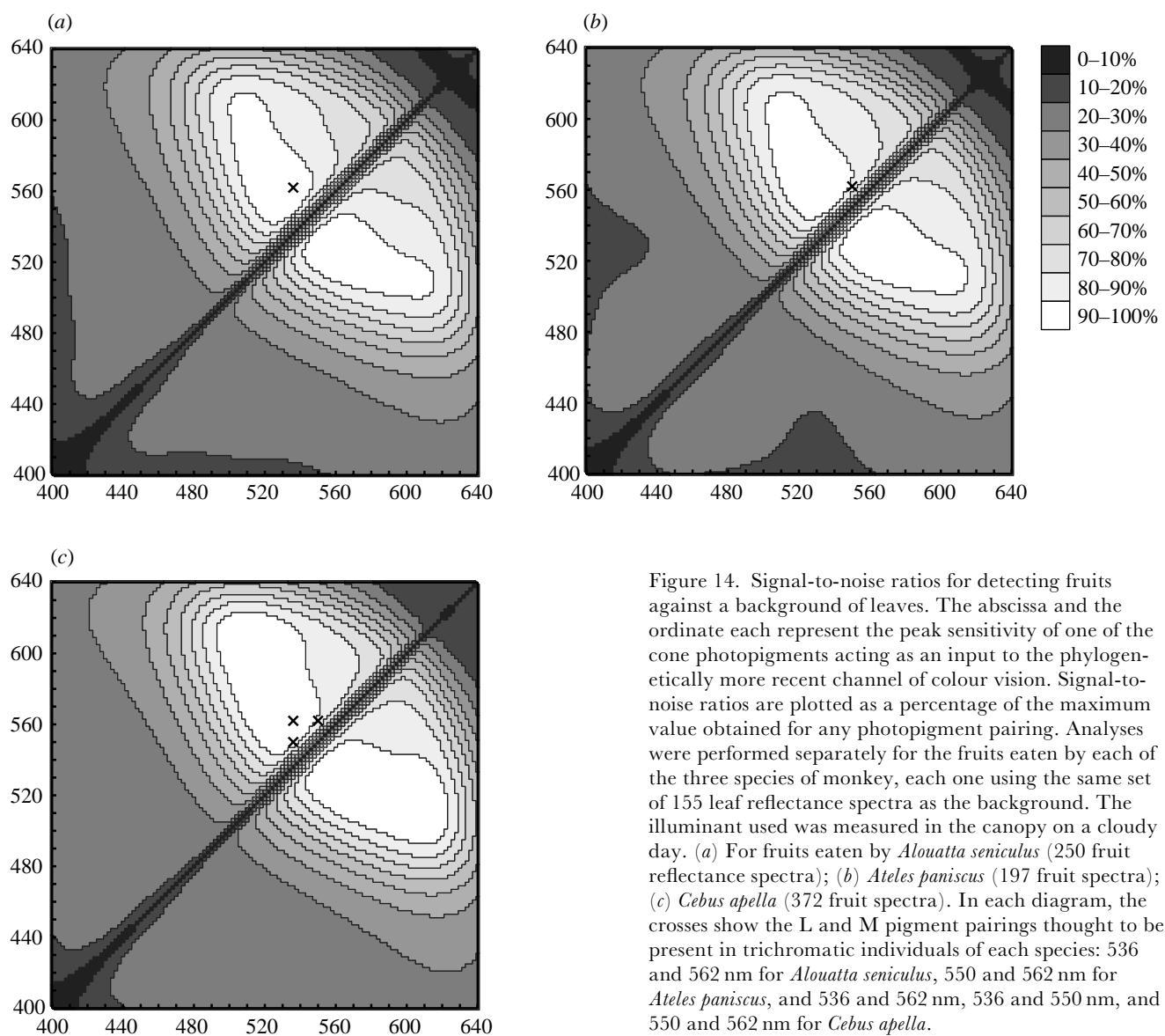


Figure 14. Signal-to-noise ratios for detecting fruits against a background of leaves. The abscissa and the ordinate each represent the peak sensitivity of one of the cone photopigments acting as an input to the phylogenetically more recent channel of colour vision. Signal-to-noise ratios are plotted as a percentage of the maximum value obtained for any photopigment pairing. Analyses were performed separately for the fruits eaten by each of the three species of monkey, each one using the same set of 155 leaf reflectance spectra as the background. The illuminant used was measured in the canopy on a cloudy day. (a) For fruits eaten by *Alouatta seniculus* (250 fruit reflectance spectra); (b) *Ateles paniscus* (197 fruit spectra); (c) *Cebus apella* (372 fruit spectra). In each diagram, the crosses show the L and M pigment pairings thought to be present in trichromatic individuals of each species: 536 and 562 nm for *Alouatta seniculus*, 550 and 562 nm for *Ateles paniscus*, and 536 and 562 nm, 536 and 550 nm, and 550 and 562 nm for *Cebus apella*.

an even greater compressive effect. The reason for this compression is that both lens and macular pigments absorb more light at short wavelengths than long, reducing the quantum catch in the S cones relative to the L and M cones.

Changing the macular pigment correction has the further effect of changing the standard deviation of the L/M chromaticities of the leaf distribution (i.e. the leaf noise). The standard deviation obtained either with double the standard macular pigment optical density, or with no macular correction applied, is higher than that obtained with the normal macular correction (table 4), thus impairing the detection of fruits amongst leaves. In a modification of an earlier analysis (Mollon & Regan 1999), we systematically varied the density of macular pigment, from zero to three times the mean optical density found in humans, and calculated the standard deviation of the L/M chromaticities of the leaf distribution, i.e. the leaf noise, for each macular pigment density. The results are shown in figure 16.

The minimum leaf noise is achieved with a macular pigment optical density of 0.37 at its absorption

maximum of 460 nm. (Mollon & Regan (1999) report minimum leaf noise at an optical density of 0.495; this difference in results arises because we have assumed in this paper that the M cone  $\lambda_{\max}$  of *Alouatta* is 536 nm, rather than 530 nm.) Estimates of the average density of macular pigment at 460 nm in human eyes vary considerably from 0.22 (Hammond & Caruso-Avery 2000) (these authors note that their value is unusually low) to 0.495 (Wyszecki & Stiles 1982). However, macular pigment densities in this range all lie in the trough of the curve relating leaf noise to macular density, giving at most 1% more leaf noise than the minimum. Assuming that a density in this range is typical for primates, it may be that the macular pigment helps to maximize the visibility of signalling fruits against foliage. As primates must sequester their carotenoids from their food, the macular density may, in part, be controlled by these very fruits.

However, we should not expect an exact match between the observed macular pigment density and the optical density that gives theoretically the minimum leaf noise. The observed macular pigment densities between 0.22 and 0.495 are for small central fields (typically 0.5 to

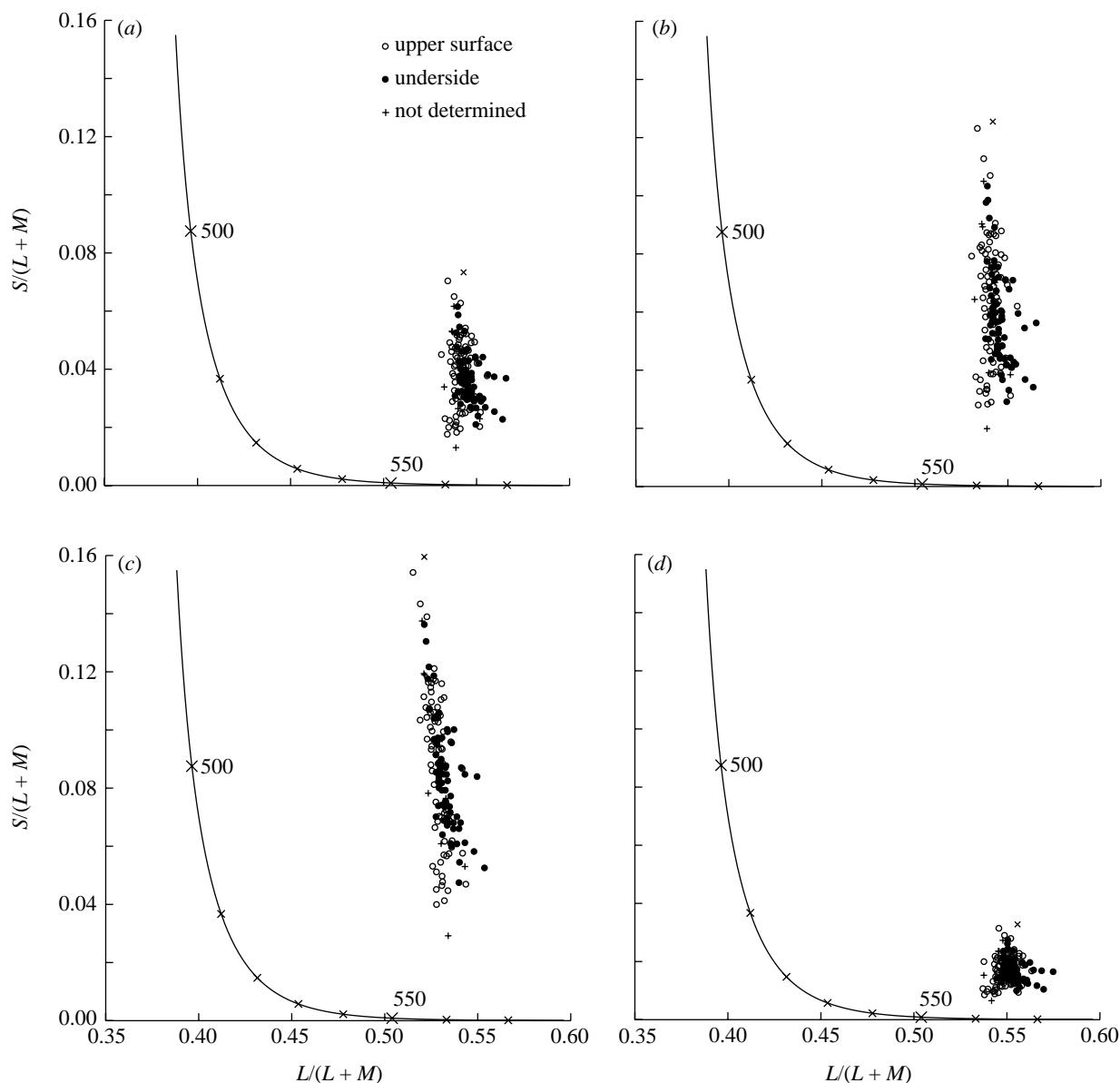


Figure 15. Effect of optic media on leaf chromaticities. The chromaticities of leaves have been calculated for a platyrhine monkey with cone pigment  $\lambda_{\max}$ -values at 430, 536 and 562 nm, such as *Alouatta seniculus*, with different corrections for optic media. The leaves and illuminant were the same as those used in figure 7. (a) Using standard lens pigment and macular pigment. These data are identical to those in figure 7b, but are repeated here for comparison. (b) With the standard macular correction, but no lens correction. (c) With the standard lens correction, but no macular correction. (d) With the standard lens correction, and assuming a macular pigment with twice the normal optical density.

1.3 degrees in diameter), but in fact the density of macular pigment varies with field size and position (Snodderly *et al.* 1984) as well as varying between individuals (Hammond *et al.* 1996). It is in the nature of a visual search task that a target may be spotted in peripheral vision, and therefore the exact amount of 'leaf noise' in the task we have modelled must be understood to vary slightly with the retinal location of the target, as well as from individual to individual.

To what extent do the optic media affect the spectral positioning of the photopigments required to give high signal-to-noise ratios for detecting fruits against leaves? We have repeated the calculations described in the preceding section, using different corrections for pre-receptoral filtering, to determine the signal-to-noise ratios

for detecting the fruits eaten by *Alouatta seniculus* against leaves. The results are shown in figure 17.

If no correction for the lens pigment is applied, the results remain essentially identical. This is perhaps unsurprising, for the marmoset lens pigment used in the analysis has almost all its effect below 420 nm (figure 5b), but both the fruits eaten by primates, and the leaves, reflect little light below 420 nm.

In contrast, changes in macular pigment density do have an effect. Removing the macular pigment shifts the  $\lambda_{\max}$ -values of the pigments giving the largest signal-to-noise ratios to longer wavelengths, and increasing its optical density shifts them to shorter wavelengths. Although the effects are small, the cone pigments possessed by *Alouatta seniculus* no longer give a signal-to-noise ratio within 10%

Table 4. Statistics of the distributions of leaf chromaticities using different corrections for optic media. The distributions were calculated for a trichromatic phenotype with cone pigment  $\lambda_{\max}$ -values at 430, 536 and 562 nm

( $\mu_{L/M}$ ,  $\mu_S$ ,  $\sigma_{L/M}$  and  $\sigma_S$  are means and standard deviations of the leaf distributions along the L/M and S cone axes;  $r_1$  is Pearson's product-moment correlation coefficient between values on S and L/M axes, and  $r_2$  Pearson's product-moment correlation coefficient between values on S and luminance axes.)

data set	$N$	$\mu_{L/M}$	$\sigma_{L/M}$	$\mu_S$	$\sigma_S$	$r_1$	$r_2$
430, 536, 562 nm, standard optic media	155	0.5436	0.0056	0.0375	0.0106	-0.210	-0.057
430, 536, 562 nm, no lens correction	155	0.5432	0.0056	0.0607	0.0194	-0.302	-0.099
430, 536, 562 nm, no macular correction	155	0.5306	0.0060	0.0851	0.0232	-0.625	-0.030
430, 536, 562 nm $\times$ 2 macular correction	155	0.5510	0.0060	0.0170	0.0045	0.041	-0.067

of the maximum possible. It is clear that the macular pigment must be considered in conjunction with the cone pigments in judging how well matched the retina is to tasks of chromatic discrimination.

#### (iv) Effect of the illuminant

One important variable affecting the chromaticity and luminance of natural objects is the illuminant. Figure 18 shows the chromaticities of the 155 leaves whose reflectance spectra we measured, calculated using illuminants measured under different weather conditions, and at different levels of the forest. These illuminants are illustrated in figure 4, and were chosen as exemplars of typical forest illuminants. The chromaticities were calculated for a platyrhine monkey with the cone pigments thought to be present in *Alouatta seniculus*, with  $\lambda_{\max}$ -values at 430, 536 and 562 nm.

The statistics of the distributions given in figure 18 are shown in table 5. In each case, the distribution of leaf chromaticities runs from the chromaticity of the illuminant to a point between 560 and 570 nm on the spectrum locus. Changing the illuminant chiefly affects the distribution of chromaticities along the S cone axis: for example, the standard deviation of chromaticities along this axis is more than doubled if the illuminant is changed from one measured at the forest floor to one measured in the evening. Independent adaptation of each cone class (von Kries 1902/1970) would, however, suffice to ensure that the appearance of the leaf background differed little between different illuminants.

A more important feature of table 5 is that there is very little difference in the standard deviation of chromaticities along the L/M axis under different illuminants. For *Alouatta seniculus* at least, the leaf noise in the visual search task of detecting fruits against leaves would therefore differ rather little between illuminants. However, the results of figure 18 and table 5 were calculated for only one trichromatic phenotype, and it remains possible that the leaf noise is greater under some illuminants than others for the other trichromatic platyrhine phenotypes. If this is the case, particular phenotypes might be better suited to foraging in particular light environments. We have therefore repeated the calculations of signal-to-noise ratios offered by different visual pigment pairings for detecting the fruits eaten by *Cebus apella* against leaves, using three different illuminants. (We have used the diet of *Cebus apella* because it is known that there are several trichromatic phenotypes within the

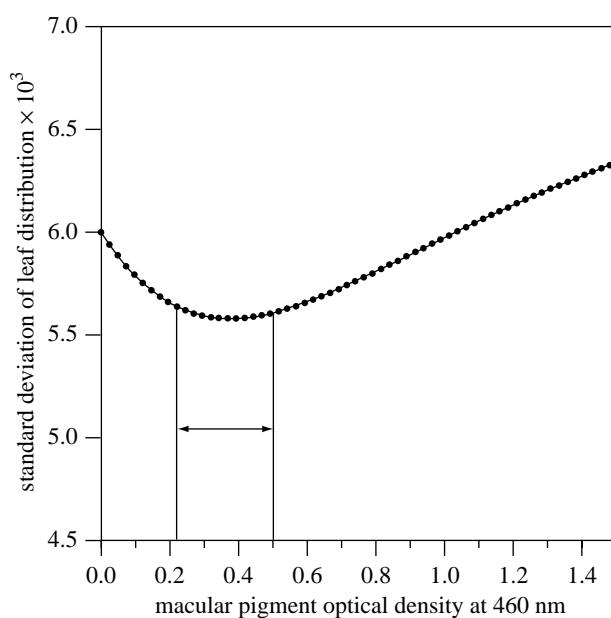


Figure 16. The standard deviation on the L/(L + M) axis of the foliage distribution of figure 15, plotted as a function of the assumed optical density of the macular pigment that screens the photoreceptors. The arrow shows a range of estimates for the average macular density in man (0.22–0.495). Note that any macular density in this range generates a standard deviation of foliage chromaticities close to the minimum. We used M and L cone pigment  $\lambda_{\max}$ -values of 536 and 562 nm, those thought to be present in *Alouatta seniculus*.

population of this primate species.) The results are shown in figure 19.

There are considerable differences between the results for the three illuminants. Most notably, the pigments that give the largest signal-to-noise ratios for the 'forest floor, shade' and the 'canopy shade' illuminants are shifted apart, relative to those that give the largest signal-to-noise ratios for the 'canopy, cloudy' illuminant. The phenotype of *Cebus apella* with the cone pigments most widely separated in  $\lambda_{\max}$  now achieves a signal-to-noise ratio of 75–80% of the maximum possible, but the 430, 536 and 550 nm and 430, 550 and 562 nm phenotypes achieve signal-to-noise ratios of only 50–60% of the maximum possible. This is simply because the two shade illuminants are an order of magnitude less intense than

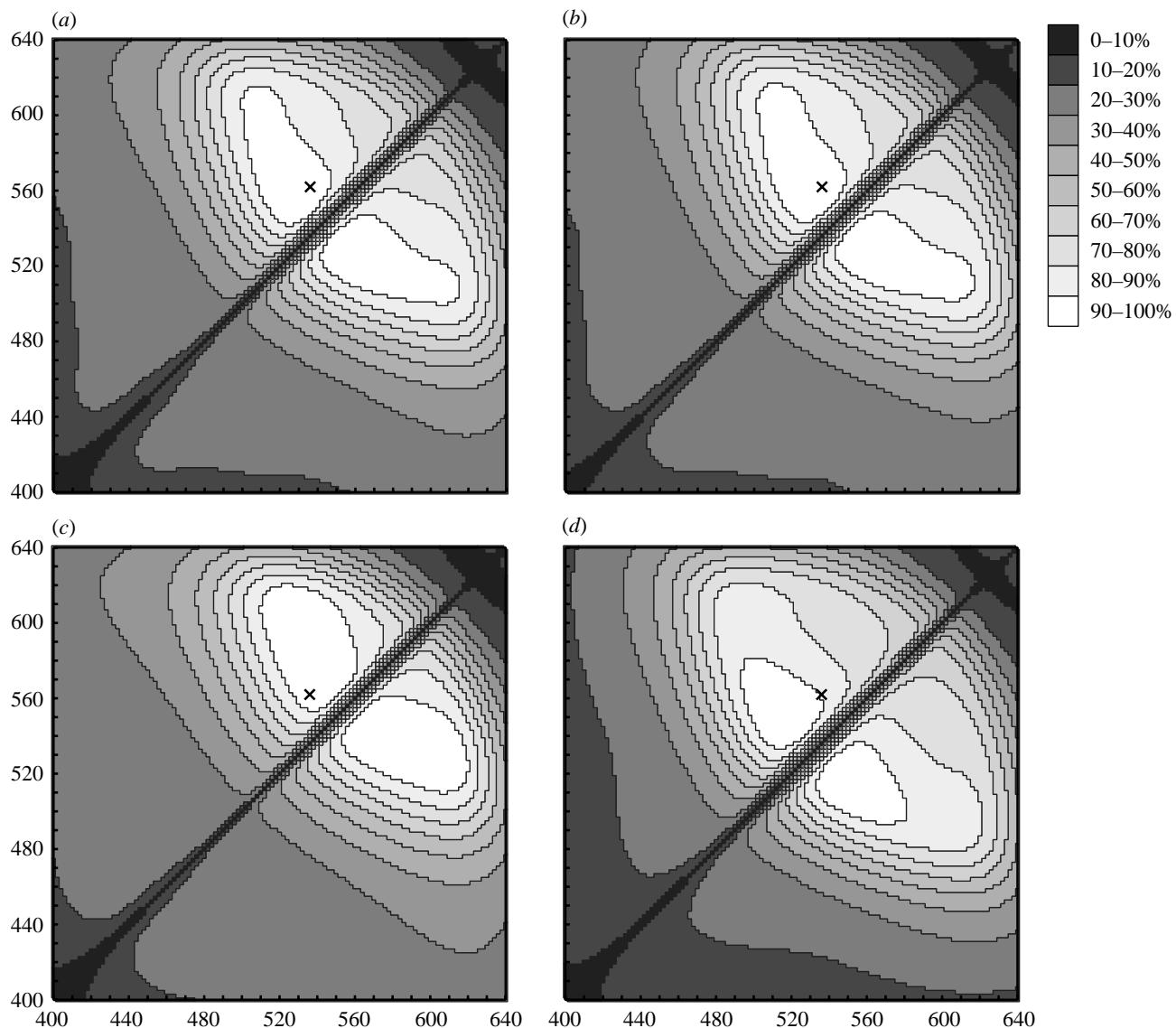


Figure 17. Effect of pre-receptoral filtering on signal-to-noise ratios for detecting fruits against a background of leaves. The analysis shown in figure 14 for *Alouatta seniculus* was repeated using: (b) no correction for lens pigment; (c) no correction for macular pigment; (d) correction for a macular pigment with twice the normal optical density. For comparison, (a) shows the same data as in figure 14, calculated using normal lens and macular pigment.

the ‘canopy, cloudy’ illuminant. At these lower light levels, quantum noise becomes a significant factor impairing detection, and the closer together the pigments performing the detection task are, the greater the impairment. Note, however, that these are extreme examples, being amongst the dimmest illuminant measurements that we took during the daytime, even amongst shade illuminants. Primates at Les Nouragues would seldom experience signal-to-noise levels as low as these.

Despite the large differences in signal-to-noise ratio under the different illuminants, there is no obvious interaction between the illuminants and the three phenotypes. In all three illuminants, the 430, 536 and 562 nm phenotype achieves a higher signal-to-noise ratio than the other two phenotypes; and neither of the latter phenotypes has an advantage over the other.

#### (v) *The illuminant, and the different trichromatic platyrhine phenotypes*

The great unsolved mystery in platyrhine visual science is why so many species exhibit polymorphic colour vision. If platyrhine colour vision evolved to assist monkeys in foraging for fruit, one possibility is that different phenotypes might be better at searching for different fruits, or even that certain fruits might be metamerically with the foliage background for one phenotype but distinct from the foliage background for another. Furthermore, any differences between phenotypes might depend upon the ambient illumination: one phenotype might have the advantage searching for a particular fruit under one illuminant, but not under another. Because the signal-to-noise ratio plots shown in figures 14, 17 and 19 are averages for all the fruits in the primates’ diets,

Table 5. Statistics of the distributions of leaf chromaticities using different illuminant spectra. The distributions were calculated for a trichromatic phenotype with cone pigment  $\lambda_{\max}$ -values at 430, 536 and 562 nm

( $\mu_{L/M}$ ,  $\mu_S$ ,  $\sigma_{L/M}$  and  $\sigma_S$  are means and standard deviations of the leaf distributions along the L/M and S cone axes;  $r_1$  is Pearson's product-moment correlation coefficient between values on S and L/M axes, and  $r_2$  Pearson's product-moment correlation coefficient between values on S and luminance axes.)

data set	$N$	$\mu_{L/M}$	$\sigma_{L/M}$	$\mu_S$	$\sigma_S$	$r_1$	$r_2$
430, 536, 562 nm, canopy, cloudy	155	0.5436	0.0056	0.0375	0.0106	-0.210	-0.057
430, 536, 562 nm, canopy, direct sun	155	0.5470	0.0058	0.0342	0.0095	-0.169	-0.058
430, 536, 562 nm, canopy shade	155	0.5314	0.0049	0.0505	0.0144	-0.385	-0.050
430, 536, 562 nm, forest floor, shade	155	0.5427	0.0049	0.0276	0.0078	-0.117	-0.055
430, 536, 562 nm, evening, clear sky	155	0.5212	0.0051	0.0660	0.0182	-0.515	-0.032

potential differences of this nature may be masked. We have therefore calculated signal-to-noise ratios for individual fruits eaten by *Cebus apella* seen against a foliage background, rather than calculate the mean ratios for all the fruits in the diet. To simplify matters, we have ignored quantum noise in these calculations, so the signal-to-noise ratio is here taken as the difference between the fruit chromaticity and the mean leaf chromaticity on the L/M axis, divided by the standard deviation of leaf chromaticities on the L/M axis.

The data are plotted in figure 20 in three separate panels, for the three different illuminants used (the same three that were used for figure 19). We have plotted data only for those fruit reflectance spectra where there is a difference of at least 1.0 between signal-to-noise ratios for any two phenotypes. For the 'canopy, cloudy' illuminant (figure 20a) this has occurred for 80 spectra out of the 372 included. For the 'forest floor, shade' illuminant (figure 20b), this occurs for 49 spectra; and for the 'canopy shade' illuminant (figure 20c), for 58 spectra. The three signal-to-noise ratios for each fruit reflectance spectrum are plotted as a triplet of points joined with a line, with the 430, 536 and 550 nm phenotype first, the 430, 536 and 562 nm phenotype second, and the 430, 550 and 562 nm phenotype third. In each panel, the plant species have been divided into two groups on the abscissa: those whose fruits give the highest signal-to-noise ratios to the 430, 536 and 550 nm phenotype (and are thus most detectable to this phenotype), and those whose fruits give the highest signal-to-noise ratios to the 430, 550 and 562 nm phenotype (and are most detectable to this phenotype). The data triplets for the former group slant upwards and left, and for the latter group, upwards and right. Within these two groups, the data triplets have been arranged so that data from all the samples of any given plant species included on any given panel appear in one cluster on that panel. The ordering of plant species on the abscissa has no further significance. We emphasize that the amount of space devoted to each plant species on each panel simply reflects the number of spectral measurements of each species that gave a difference in signal-to-noise ratio of more than one unit between any two phenotypes under the illuminant used for that panel. This is why the species included on each panel are different, and also why the number of measurements for each species varies between the three panels.

The most obvious point about figure 20 is that there are no triplets of points in a 'V'- or an inverted 'V'-shape:

for the fruits in these diagrams, the signal-to-noise ratio for the 430, 536 and 562 nm phenotype always lies in between the signal-to-noise ratios for the other two phenotypes. (Fruits do exist for which the signal-to-noise ratio is greatest for the 430, 536 and 562 nm phenotype; but the differences in signal-to-noise ratios for such fruits are much smaller than 1 unit.) Examining figure 20a shows that under the 'canopy, cloudy' illuminant, the biggest advantage accrues to the 430, 536 and 550 nm phenotype: for 65 fruits, the signal-to-noise ratio is at least 1 unit larger for this phenotype than the 430, 550 and 562 nm phenotype, whereas the reverse is true for only 15 fruits. The 430, 536 and 550 nm phenotype is still at an advantage under the 'forest floor, shade' illuminant (figure 20b), although the advantage is less: here, the signal-to-noise ratios are highest for this phenotype for 35 fruits, but highest for the 430, 550 and 562 nm phenotype for 14 fruits. In contrast, under the 'canopy shade' illuminant the pattern is reversed and the 430, 550 and 562 nm phenotype attains the highest signal-to-noise ratios for 48 fruits, compared with only ten for the 430, 536 and 550 nm phenotype.

It may seem on first inspection that the differences in signal-to-noise ratios are small compared with the absolute ratios, and that such relatively small differences would not give one phenotype much of an advantage over another. But the extreme right-hand edge of the leaf distribution in fact lies four standard deviations to the right of the mean leaf chromaticity on the L/M axis; so a signal-to-noise ratio of at least four is necessary for a fruit to be distinct from the leaves, even without allowing for quantum noise. The variations in signal-to-noise ratio shown here probably make a considerable difference in the detectability of these fruits to different phenotypes.

Comparing figure 20a-c shows that the plant species for which the 430, 536 and 550 nm phenotype has the advantage are more or less the same under both the 'canopy, cloudy' and 'forest floor, shade' illuminants. Likewise, the few species for which the 430, 550 and 562 nm phenotype has the advantage under the 'canopy, cloudy' and 'forest floor, shade' illuminants are a subset of the species for which this phenotype has an advantage under the 'canopy shade' illuminant. So there are some kinds of fruit that the 430, 536 and 550 nm phenotype should consistently be able to detect better than the 430, 550 and 562 nm phenotype, and vice versa. What are the properties of these fruits? Figure 21 shows the chromaticities of those fruits viewed under the 'canopy, cloudy'

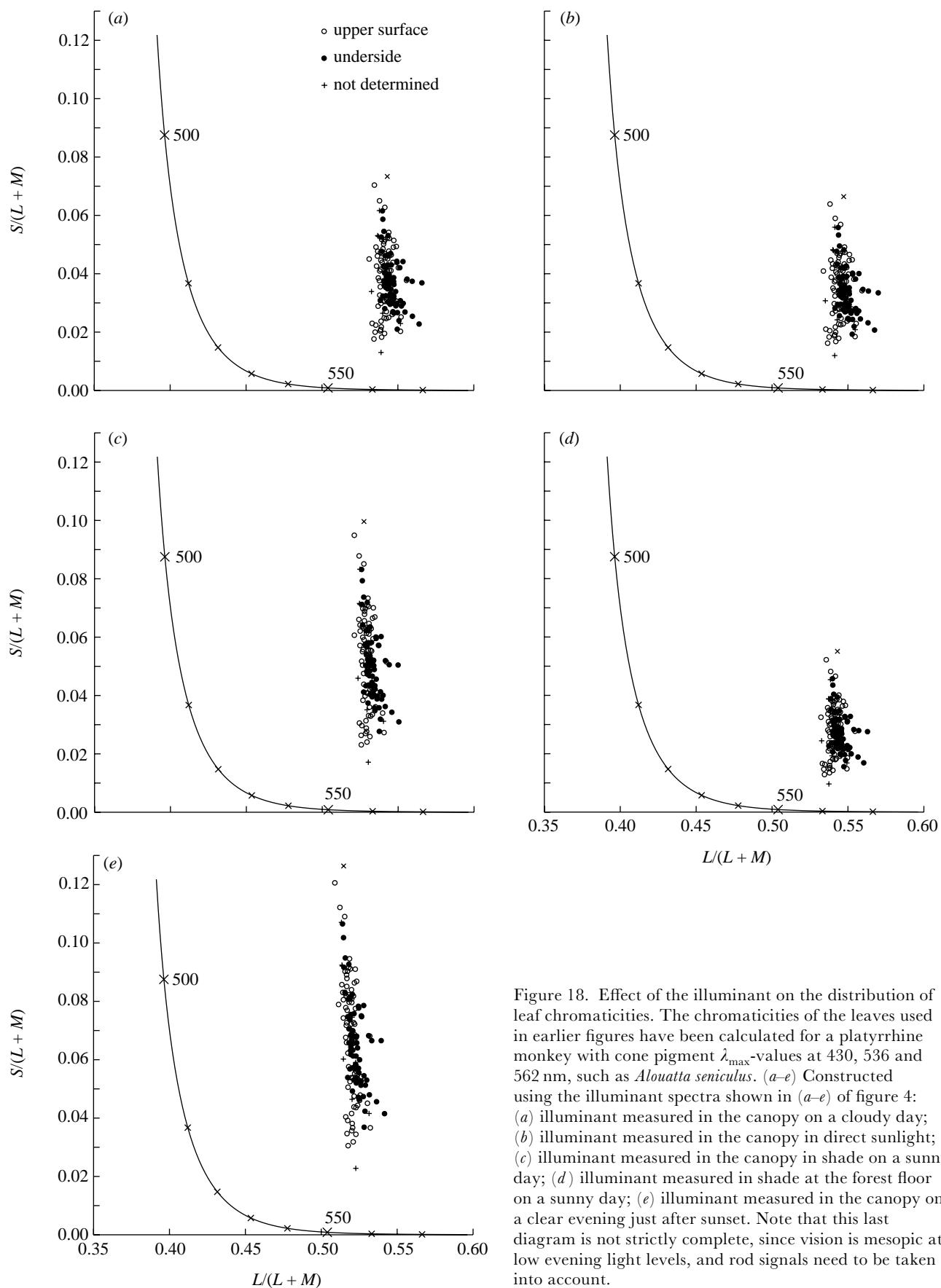


Figure 18. Effect of the illuminant on the distribution of leaf chromaticities. The chromaticities of the leaves used in earlier figures have been calculated for a platyrhine monkey with cone pigment  $\lambda_{\max}$ -values at 430, 536 and 562 nm, such as *Alouatta seniculus*. (a–e) Constructed using the illuminant spectra shown in (a–e) of figure 4: (a) illuminant measured in the canopy on a cloudy day; (b) illuminant measured in the canopy in direct sunlight; (c) illuminant measured in the canopy in shade on a sunny day; (d) illuminant measured in shade at the forest floor on a sunny day; (e) illuminant measured in the canopy on a clear evening just after sunset. Note that this last diagram is not strictly complete, since vision is mesopic at low evening light levels, and rod signals need to be taken into account.

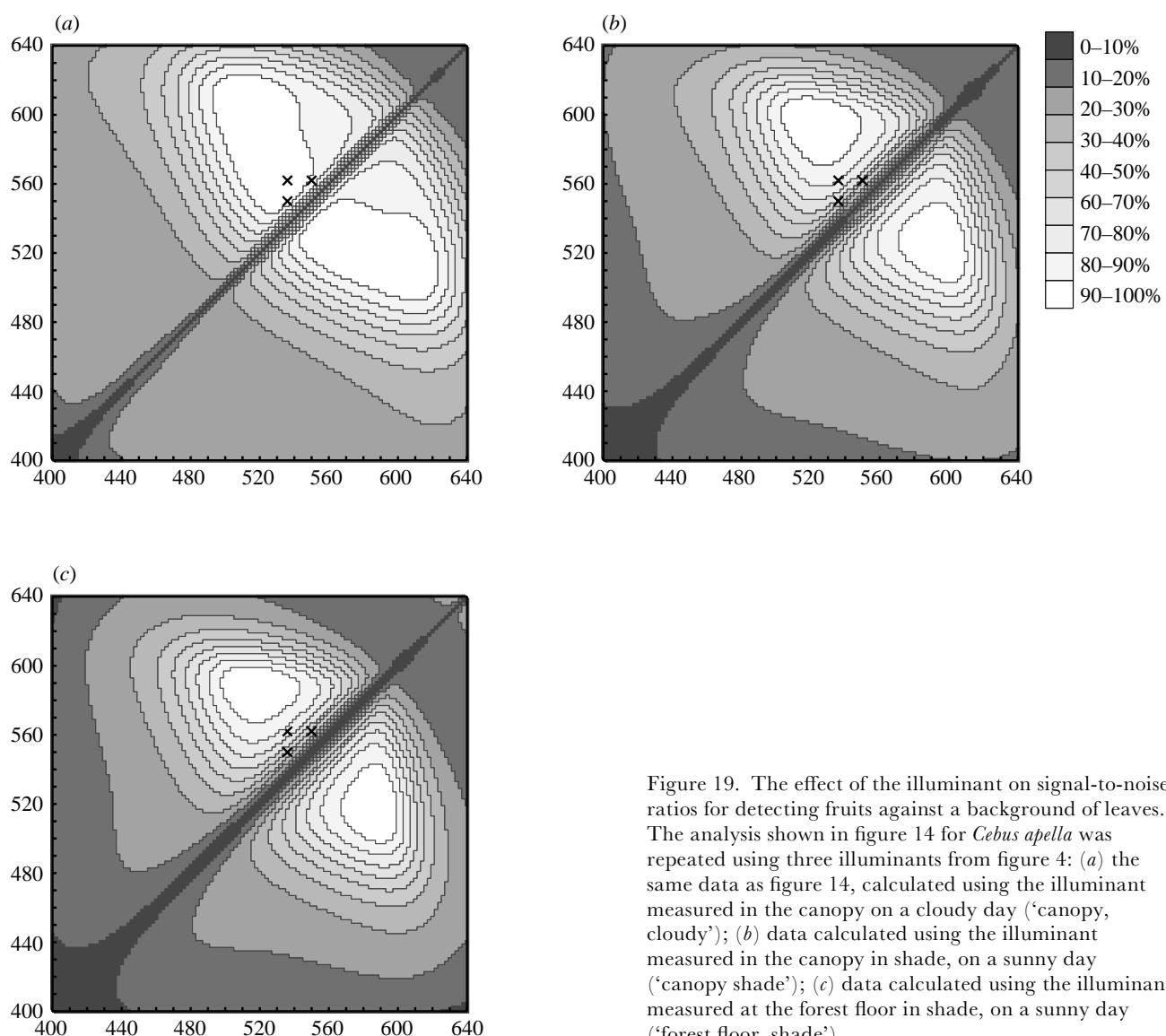


Figure 19. The effect of the illuminant on signal-to-noise ratios for detecting fruits against a background of leaves. The analysis shown in figure 14 for *Cebus apella* was repeated using three illuminants from figure 4: (a) the same data as figure 14, calculated using the illuminant measured in the canopy on a cloudy day ('canopy, cloudy'); (b) data calculated using the illuminant measured in the canopy in shade, on a sunny day ('canopy shade'); (c) data calculated using the illuminant measured at the forest floor in shade, on a sunny day ('forest floor, shade').

illuminant for which the 430, 536 and 550 nm phenotype has the advantage, and also the chromaticities of those fruits under the 'canopy shade' illuminant for which the 430, 550 and 562 nm phenotype has the advantage. The chromaticities are shown in two diagrams, on the left (a,c) for the 430, 536 and 550 nm phenotype, and on the right (b,d) for the 430, 550 and 562 nm phenotype.

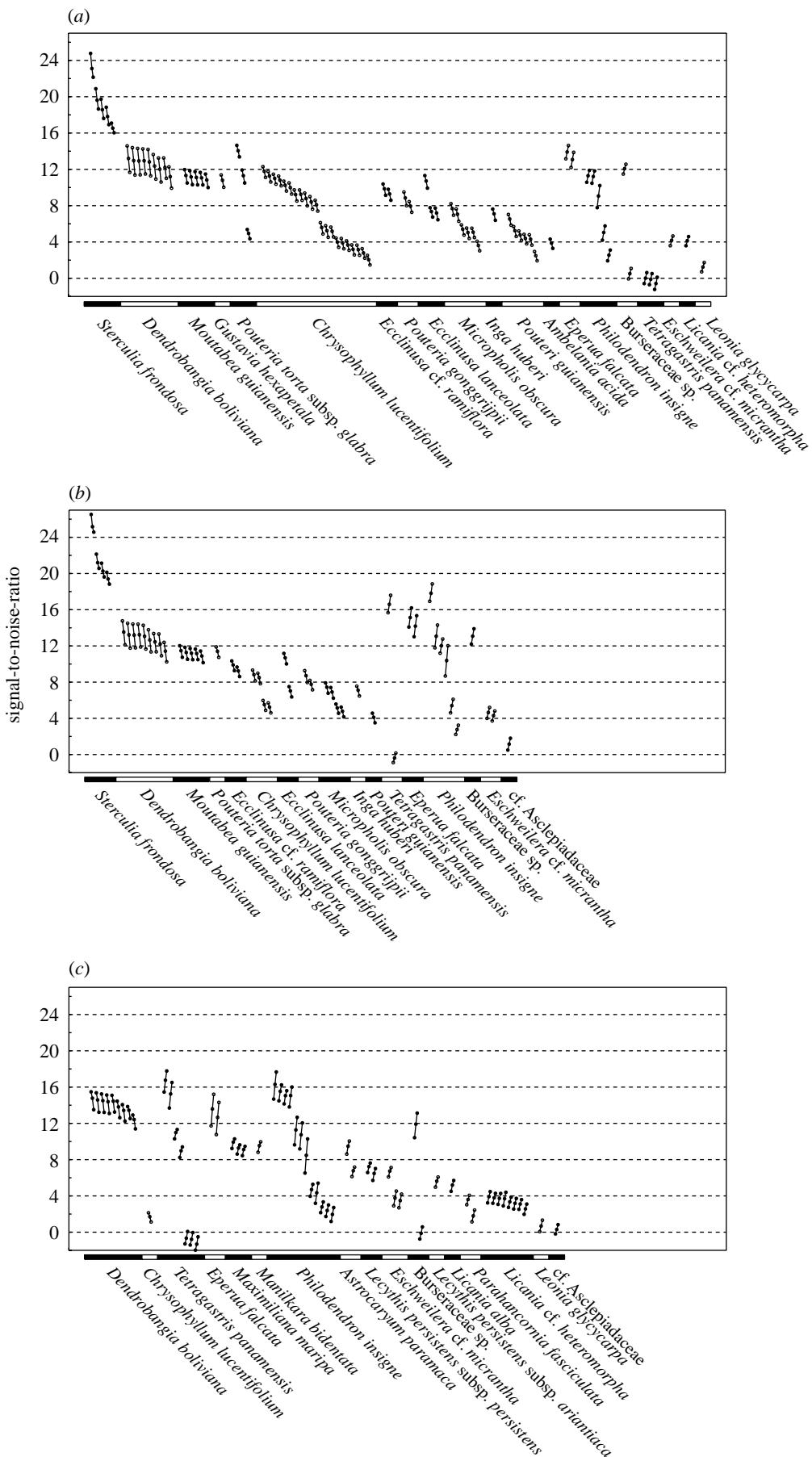
The chromaticities of the fruits that are more detectable for the 430, 536 and 550 nm phenotype lie at the bottom and to the right of the leaf distribution, and these fruits appear yellow, green or orange to human observers. The fruits that are more detectable for the 430, 550 and 562 nm phenotype lie at the top and to the right of the leaf distribution, and appear purple or brown to human observers. The differences in signal-to-noise ratio arise because the leaf distribution is tilted away from the fruits for one phenotype, and towards them for the other, making the fruit and leaf distributions overlap more or less on the L/M axis. This effect, although slight, can be detected in the histograms beneath the chromaticity

diagrams, showing the leaf and fruit distributions projected on to the abscissa.

#### (vi) Seed dispersal and seed predation

Since Grant Allen wrote about the problem in 1879, cryptic and conspicuous fruit coloration have been regarded as adaptations for defence against predators, and for securing seed dispersal. We have asked whether our data meet Allen's expectations: in figure 22 the chromaticities of fruits whose seeds are destroyed by primates are compared with those of fruits whose seeds are dispersed by primates. Only those species whose seeds we are certain are dispersed by primates or destroyed by primates (as indicated in table 1) have been included.

The chromaticities of fruits whose seeds are dispersed by monkeys tend to lie below and to the right of the leaf distribution in the chromaticity diagram for trichromatic monkeys, and are often also lighter than the surrounding foliage. Many of these fruits are quite distinct from the leaves and would be conspicuous in a natural scene.



However, a considerable number of these measurements of fruits yield chromaticities very close to, or within, the leaf distribution.

The most surprising feature of figure 22 is that the chromaticities of most of the fruits whose seeds are destroyed by monkeys lie outside the leaf distribution. Many of them have chromaticities just to the right of the leaf distribution, which, coupled with their relatively low lightness, might make them relatively dull and inconspicuous, although they would certainly be detectable against foliage to a trichromat. But a significant proportion of the fruits whose seeds are destroyed are highly conspicuous to trichromatic primates: one example is the bright red *Sterculia frondosa*, illustrated in figure 10j. How can we reconcile this with the account of crypsis proposed by Allen (1879)? First, we should keep in mind the fact that dichromacy is a more common condition amongst platyrhines than trichromacy, and that other mammalian seed predators such as squirrels are all also dichromatic. Not one fruit whose seeds are destroyed by primates is distinguishable from the leaves by a dichromatic observer, for not one fruit gives an S cone excitation higher or lower than the leaves. This may be the most significant point of figure 22. Second, the presence of birds as dispersal agents may help to explain why some fruits whose seeds are destroyed by primates are nevertheless so conspicuous to trichromats: the colour may simply be aimed at attracting birds. In the case of *Sterculia frondosa*, it may be significant that the fruits are dehiscent as well as being bright red. These characteristics are typical of bird-dispersed fruits (Van der Pijl 1972).

#### (vii) The primate seed-dispersal syndrome

A subset of the fruits whose seeds are dispersed by primates may be classified as belonging to the primate seed-dispersal syndrome on morphological criteria other than colour. In French Guiana, Julliot (1994) has defined these characteristics: a hard, indehiscent pericarp; a few large seeds; a juicy pulp. Of the 38 species whose seeds are known to be dispersed by primates, 24 possess these characteristics and therefore belong to the neotropical primate dispersal syndrome of Julliot (1994). The remaining 14 do not possess these characteristics. In figure 23 the chromaticities of fruits whose seeds are dispersed by primates are plotted in two diagrams, one for those fruits that belong to the neotropical primate dispersal syndrome, and one for those fruits that do not.

It is evident that the combination of a chromaticity lying to the right of and below the leaf distribution,

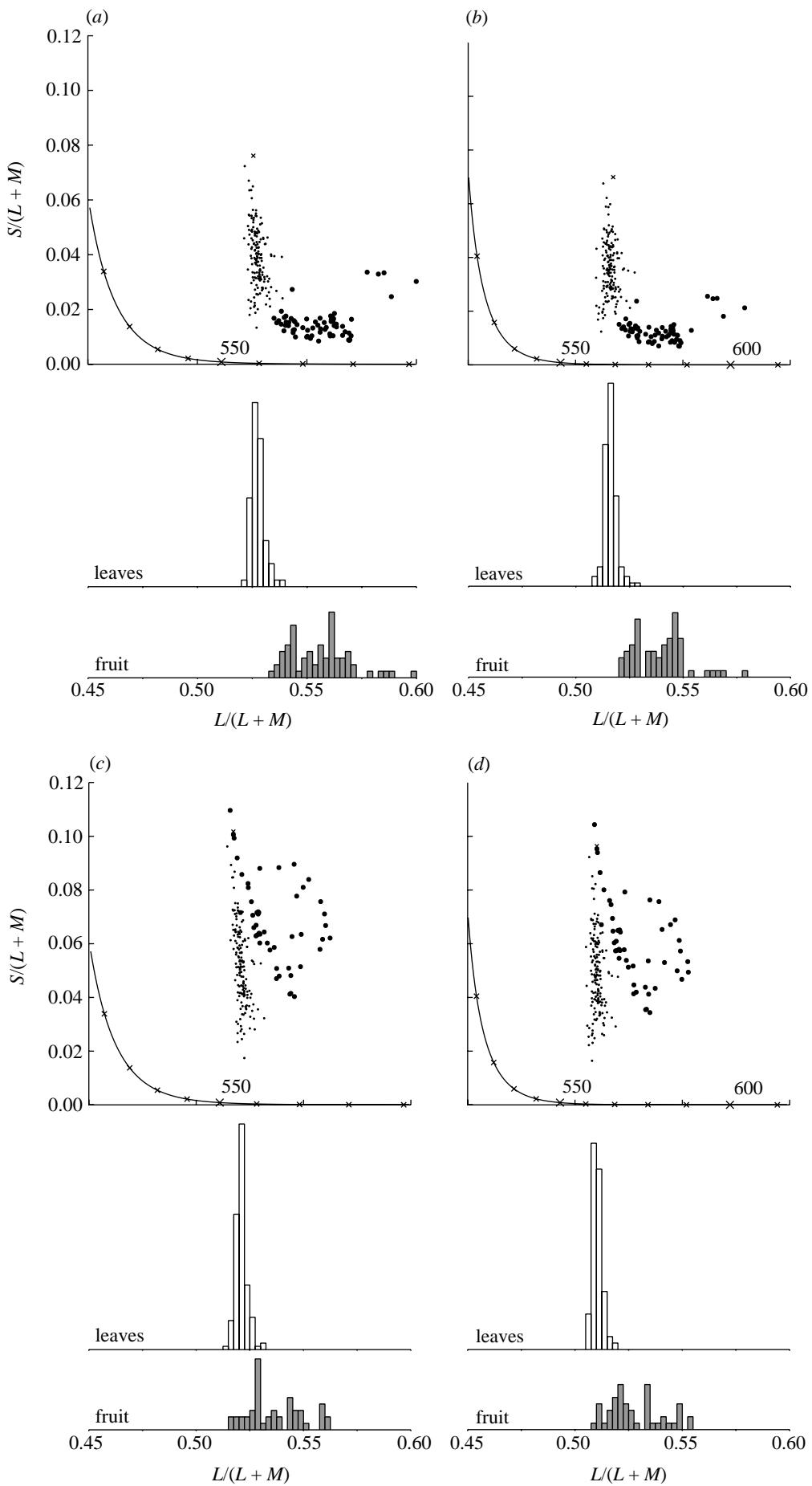
combined with a lightness greater than that of the leaf distribution, is typical of the primate dispersal syndrome. To a human observer these fruits appear light yellow or orange in colour. Many of these fruits distinguish themselves from leaves on the L/M axis, and to some extent on the S cone axis and on the luminance axis as well—in other words, along every primate visual dimension. Nevertheless, a number of fruits belonging to the primate dispersal syndrome have chromaticities that lie within the foliage distribution. Some of these represent fruits that were consumed before conspicuous coloration developed (e.g. *Pouteria guianensis*), while others represent fruits that remain green at maturity (e.g. *Inga* spp.).

It is particularly striking that the fruits belonging to the primate seed-dispersal syndrome occupy a well-defined region of colour space. With few exceptions, these fruits appear green, yellow or orange to human observers. In contrast, the fruits whose seeds are dispersed by primates, but that do not belong to the primate dispersal syndrome, are much more scattered in colour space, although most are still quite conspicuous to trichromats. Many of these exhibit adaptations for dispersal by animals other than primates. For example, *Virola michelii* and *Iryanthera sagotiana* (figure 10d,e) are both dehiscent fruits with red arillate seeds, characteristic of dispersal by birds (Van der Pijl 1972). For fruits with large numbers of small seeds and no hard external protection, such as the orange *Solanum* sp. and *Mouriri crassifolia*, and the yellow *Ludovia lancifolia*, bats are probably important seed dispersers, as well as birds and monkeys. A variety of selection pressures will act on the fruits of plants whose seeds are dispersed by a variety of consumers. Such fruits may have a characteristic odour, perhaps as an adaptation to attract bats; they may be conspicuously coloured, to attract primates and birds; their seeds may be highly accessible, for consumption by bats and birds; and so on (Van der Pijl 1972). The entire guild of dispersers must be considered when interpreting the colours of these fruits, bearing in mind that for any particular fruit, some dispersers may be more effective than others (and have more influence on that fruit's characteristics).

#### (viii) The nature of ripening

If the colour signals presented by fruits have evolved to help secure seed dispersal, we might expect these colour signals to change as the fruits ripen, in order to prevent consumers from picking unripe fruits and wasting the seeds within. The meaning of ripeness, however, differs for the plant and for the consumer: from the plant's point

Figure 20. The interacting effect of phenotypes and illuminants on signal-to-noise ratios for detecting individual fruits against leaves. Data in (a) were calculated using the 'canopy, cloudy' illuminant, in (b) using the 'forest floor, shade' illuminant, and in (c) using the 'canopy shade' illuminant. (The illuminants used were those used in figure 19 and are illustrated in figure 4.) For each of the 372 fruits that we measured in the diet of *Cebus apella*, and for each illuminant, we calculated signal-to-noise ratios as the distance on the L/M axis between the fruit chromaticity and the mean of the leaf chromaticities, divided by the standard deviation of the leaf L/M chromaticities. We calculated these ratios for the three trichromatic phenotypes of *Cebus apella* (430, 536 and 550 nm; 430, 536 and 562 nm; 430, 550 and 562 nm). If the difference in signal-to-noise ratios between any two phenotypes exceeds 1.0, we have plotted the ratios as triplets of points joined by lines, for the 430, 536 and 550 nm phenotype first, the 430, 536 and 562 nm phenotype second, and the 430, 550 and 562 nm phenotype third. The triplets have been grouped so that data from all the samples of a particular plant species appear together: successive groups, representing different species, are shown with alternating solid and open symbols. Species names are indicated below the bar at the bottom of each panel. Note the absence of inverted 'V' shapes, indicating that there are no fruits for which the signal-to-noise ratio for the 430, 536 and 562 nm phenotype greatly exceeds the signal-to-noise ratio for both the other phenotypes.



of view, a fruit is ripe when the seeds within are mature and capable of germination, whereas from the consumer's point of view, a fruit is ripe when the nutritive and/or sensory reward offered by consuming it outweighs the cost of processing the fruit and dealing with its seeds. We cannot, therefore, determine whether a fruit is ripe without determining the viability of the seeds or the potential reward to the consumer. In addition, the colour change occurring in fruits is not always related in a simple way to ripeness, for some fruits exhibit more than one colour change as they mature. One example is the blackberry, *Rubus*, which changes first from green to red while still unpalatable, and then to black when fully mature. Unripe fruits that exhibit conspicuous colours have been interpreted as 'fruit flags', whose function is to alert consumers to the presence of ripe fruits without indicating the amount of ripe fruit available. Plants that use fruit flags may offer only a few fully mature fruits each day, but the fruit flag may ensure that these fruits are rapidly removed by frugivores. This reduces the amount of time that ripe fruits are available for attack by microbes, and may also result in a wider dispersal of seeds than would occur if most of the plant's fruits were taken by a small number of frugivores over a short period of time (Stiles 1982; Willson & Thompson 1982).

Because of these difficulties, we have not attempted to classify individual fruits into 'ripe' and 'unripe' categories in order to compare their colours. Instead, we have simply illustrated the changes in chromaticity and lightness that occur in fruits at different stages of maturation. Figure 24 shows these changes in fruits of seven plant species found at Les Nouragues.

The fruits included in figure 24 all belong to the neotropical primate dispersal syndrome, except for *Glycydendron amazonicum*, which lacks a hard pericarp, and *Tetragastris panamensis*, which is dehiscent. In ripening, fruits from all species except *Tetragastris panamensis* take on the characteristic colour of fruits belonging to this dispersal syndrome, changing from a chromaticity lying near the centre of the leaf distribution to one lying below and to the right. Many of the fruits (*Chrysophyllum lucentifolium*, *Pouteria guianensis*, *Lacistema aculeata* and *Glycydendron amazonicum*) also increase in lightness.

### (e) Discussion

#### (i) Has coevolution between primate colour vision and fruit coloration occurred?

We have seen that the colour vision of trichromatic platyrhine monkeys is well matched to the task of detecting fruits against a background of leaves, under normal daytime illumination levels. This fact by itself

does not prove coevolution between primate colour vision and the reflectance functions of fruits. For example, it might be that primate trichromacy evolved for detection of pre-existing fruit signals, or that fruits adapted themselves for pre-existing properties of primate colour vision. Coevolution requires reciprocal evolution of traits in each party in response to changing traits in the other (Janzen 1980): thus, the fruits that are disseminated by primates, and primate colour vision, must each have changed in response to the other for coevolution to have occurred.

A crucial observation is that the great variety of fruits with the physical characteristics of the primate dispersal syndrome (a tough pericarp surrounding a few large seeds embedded in a juicy pulp) occupy a fairly small region of colour space (figure 23), and if they change colour when ripening, they change in the same way (figure 24). Despite this, these fruits come from quite different botanical families: in our sample, they are drawn from the Sapotaceae, Lecythidaceae, Apocynaceae, Rubiaceae and Polygalaceae, amongst others. These plant families diverged early in the evolution of flowering plants. In particular, the Polygalaceae belong to the 'Rosid' clade and the other four families to the 'Asterid' clade. A recent study using molecular genetic evidence to derive an angiosperm phylogeny (Soltis *et al.* 1999) confirms that these two clades belong to distinct branches of the phylogenetic tree. It is therefore likely that these several lineages have all developed similar fruit coloration in response to the same selection pressure—namely, to be conspicuous to primate seed dispersers.

On the other hand, it is much harder to show that the evolution of primate colour vision was driven specifically by these fruits. In particular, we note that the vertical distribution of leaf chromaticities in trichromatic platyrhine colour spaces (figure 7) effectively maximizes the detectability not only of fruits, but also of any other objects that differ in spectral reflectance from the foliage background. Primate trichromacy could first have evolved to detect any fruit against leaves (rather than specifically those disseminated by primates), to detect edible yellow or red young leaves against mature leaves (Lucas *et al.* 1998), or to detect conspecifics. Colobine monkeys are among the most folivorous of catarrhines, yet uniform trichromacy seems to be present in those species that have been examined (Jacobs 1999). A more recent study from our group, carried out in Uganda (Sumner & Mollon 2000) has indeed shown that trichromacy is an advantage for detecting yellowish young leaves against mature foliage, and that whether the task be to detect fruits against foliage or young leaves against foliage, the optimal spectral tuning of the L/M cone

Figure 21. Chromaticities of fruits eaten by *Cebus apella* for which the signal-to-noise ratios differ by more than one unit between trichromatic phenotypes (large solid circles). Foliage chromaticities are also plotted (small points). (a,b) Fruits for which the signal-to-noise ratios are greatest for the 430, 536 and 550 nm phenotype under the 'canopy, cloudy' illuminant, calculated using that illuminant, in chromaticity diagrams (a) for the 430, 536 and 550 nm phenotype and (b) for the 430, 550 and 562 nm phenotype. (c,d) Fruits for which the signal-to-noise ratios are greatest for the 430, 550 and 562 nm phenotype under the 'canopy shade' illuminant, calculated under that illuminant, in diagram (c) for the 430, 536 and 550 nm phenotype and in (d) for the 430, 550 and 562 nm phenotype. The histograms below each graph show the chromaticity distributions of fruits and leaves projected on to the abscissa. Although the effect is fairly slight, the distributions of fruit and foliage overlap more in (b) compared with (a) and in (c) compared with (d); and the fruit chromaticities extend further from the foliage chromaticities in (a) compared with (b), and in (d) compared with (c).

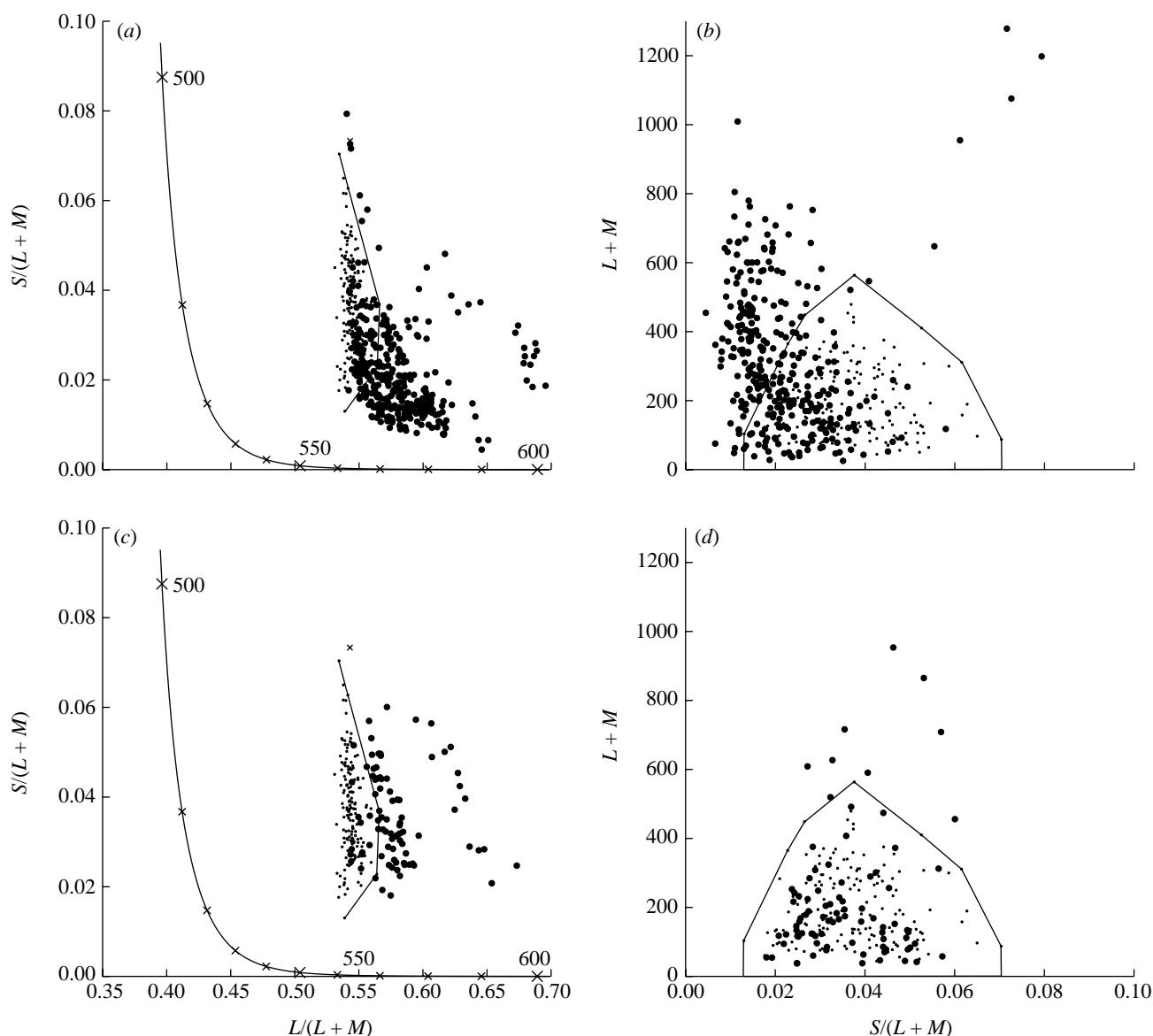


Figure 22. Chromaticities of fruits whose seeds are dispersed by primates, and fruits whose seeds are destroyed by primates. (a, b) Data for the fruits of 38 species whose seeds are known to be dispersed by primates in the Guianas (reconstructed from 342 reflectance spectra). (c, d) Data for the fruits of 22 species whose seeds are known to be destroyed by primates at Les Nouragues (reconstructed from 86 reflectance spectra). Leaf data are plotted as points and fruits as filled circles, and for clarity, the limit of the leaf distribution is indicated with a line on each diagram.

pigments is the same. Thus, the spectral tuning of the L/M pigments may have been determined by the properties of the canopy background against which targets must be distinguished, rather than by the targets themselves.

In sum, our quantitative results are consistent with the coevolution hypothesis but do not require it. It seems that plants have been influenced by primates, for many plants from different evolutionary radiations produce similar fruits with the characteristics of the primate seed-dispersal syndrome. But there is no direct evidence that trichromacy in primates evolved specifically for detecting these fruits: although primate trichromacy is well matched to the task of detecting fruits against a background of foliage, it seems equally well matched to detecting conspecifics or young leaves against mature leaves. However, the fact that primates are the only

mammalian trichromats remains a provocative one: if trichromatic colour vision is generally beneficial to forest-dwelling animals, then where are all the other trichromatic mammals?

#### *Other factors influencing the colours of fruits*

Although many fruits that are dispersed by primates are conspicuously coloured, some are not. Why might this be? In some cases, green fruits whose seeds are dispersed by primates probably would be conspicuously coloured if allowed to mature further, but they are eaten before the coloration has fully developed. We have observed this at Les Nouragues when monkeys have eaten green fruits of *Pouteria guianensis* and *Chrysophyllum lucentifolium*. Fruits of these species eaten by monkeys when green tend to be full-sized, contain at least some edible pulp, and may

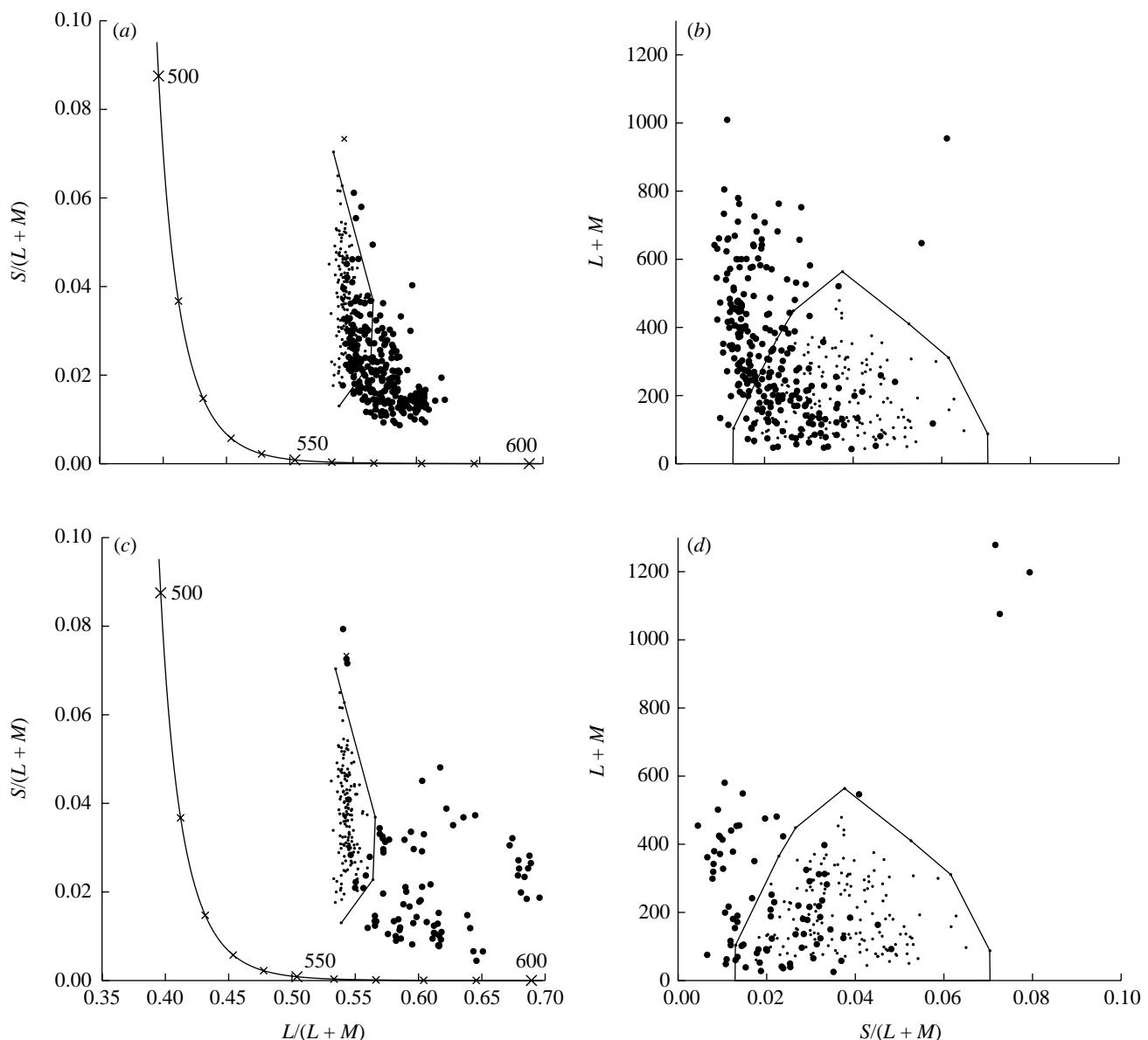


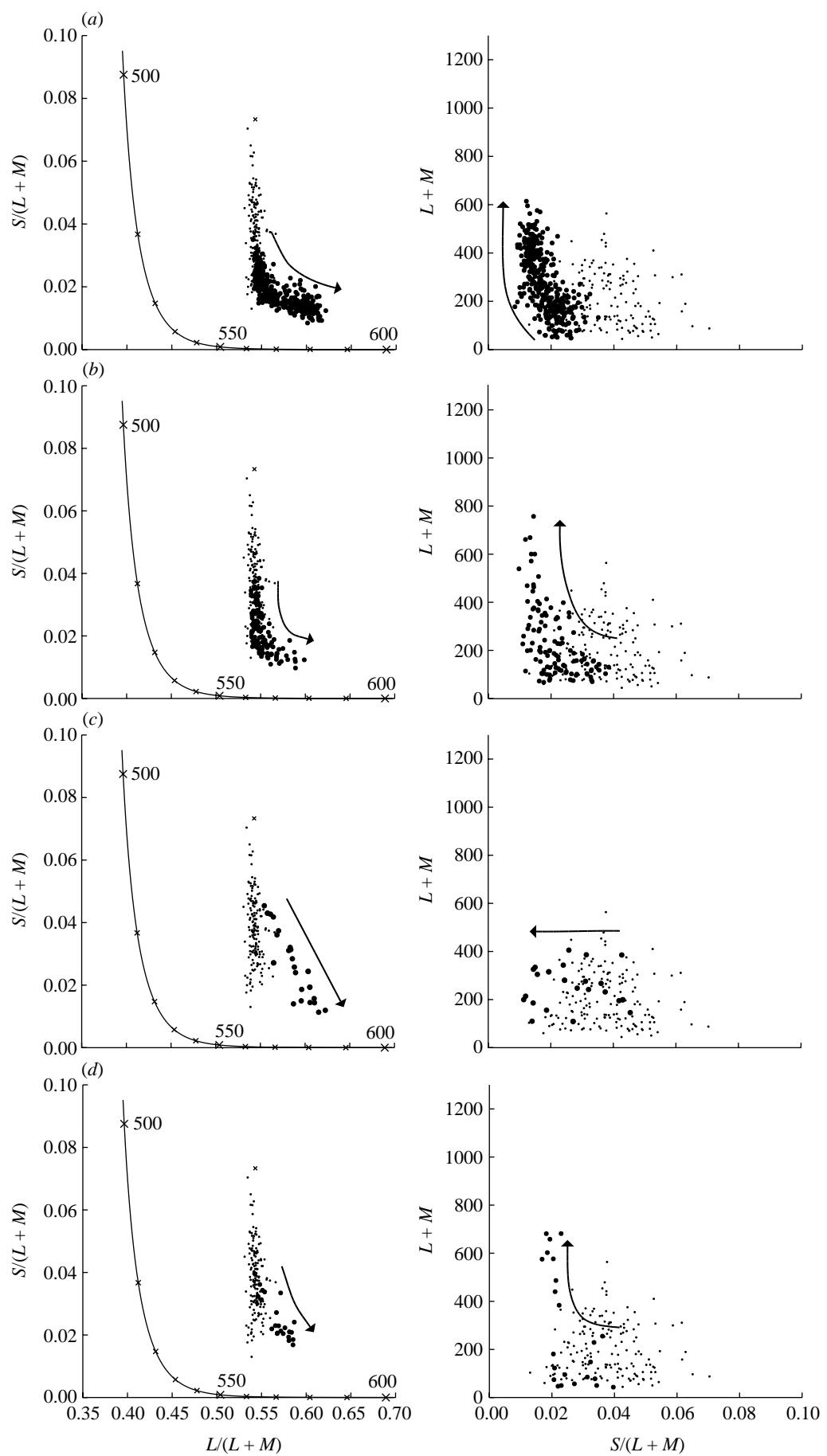
Figure 23. Fruits that belong to the primate dispersal syndrome, and fruits that do not. This figure shows data from 38 species whose seeds are known to be dispersed by primates (the same data shown in figure 22, calculated using the same illuminant, for the same 430, 536 and 562 nm phenotype). These have been classified into 24 species that belong to the 'primate dispersal syndrome' of Julliot (1994) on morphological grounds ((a,b), 258 measurements), and 14 species that do not belong to this syndrome ((c,d), 84 measurements). Leaves are plotted as points, and fruits as filled circles.

contain viable seeds (Regan 1997). Similarly, Fleming *et al.* (1985) found that bats would eat some green fruits of *Muntingia calabura*, even though these fruits would ultimately change from green to red. They also found that the seeds of those green fruits that were consumed by bats were viable after passing through the bats' digestive tracts. Both Fleming *et al.*'s observations and our own suggest that external colour is sometimes one of the last aspects of fruit morphology to change with maturation. Fruits may become ripe, both in terms of viable seeds and in terms of nutritional reward to a consumer, before the colour change associated with maturation has been completed.

Nevertheless, there are some green fruits that are genuinely cryptic when mature, but whose seeds are dispersed by primates (e.g. some *Inga* spp., *Ficus* spp. and *Passiflora* spp.). Fruit production may exert a considerable energy burden on

plants, but this burden can be lightened if fruits photosynthesize. This, rather than crypsis, may be the main reason why many immature fruits are green (Janzen 1983), as immature fruits usually have chemical means of protecting themselves from predation anyway. For some mature fruits also, the advantages of photosynthesis may outweigh the disadvantages of inconspicuousness.

We should also remember that many plants whose fruits are consumed by primates may be adapted for non-primate dispersers, or have a generalized dispersal strategy, producing fruits available to a wide range of consumers. For example, the fruits of *Ficus* spp. and *Pourouma* spp. usually appear cryptic to primates. In the case of *Ficus* spp., the small seeds and soft pericarp make the fruit available to bats as well as to primates and birds. In the case of *Pourouma* spp., the fruits have the waxy bloom on their surface that is characteristic of fruits that



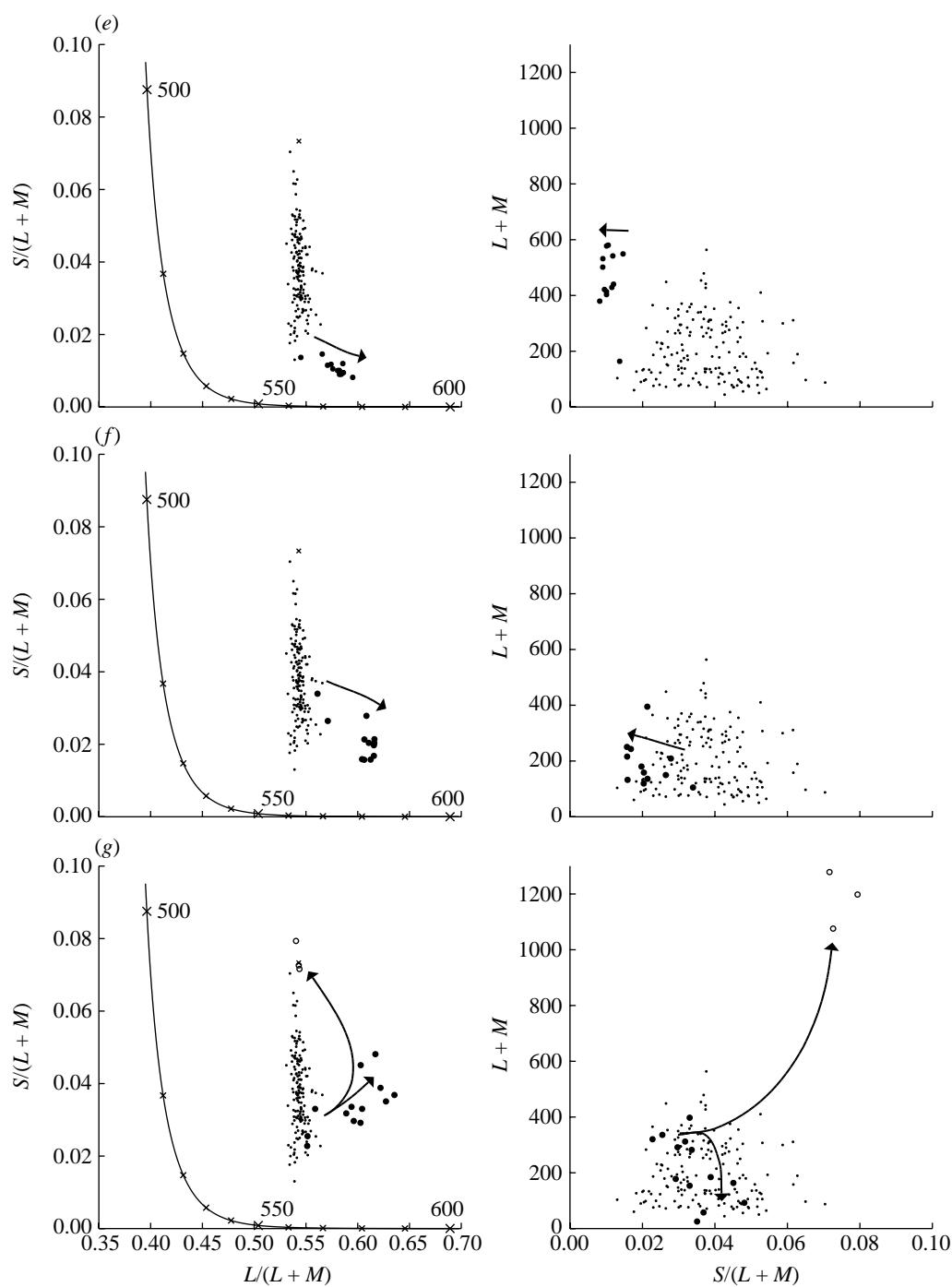


Figure 24. Ripening. Chromaticities of fruits of seven species consumed by primates at Les Nouragues, showing measurements made at varying states of maturity. The arrows show the overall direction in which the chromaticities and luminances change with increasing maturity. (a) Three hundred and seventy-one measurements of *Chrysophyllum luculentifolium* (Sapotaceae); (b) 117 measurements of *Pouteria guianensis* (Sapotaceae); (c) 23 measurements of *Pradosia ptychandra* (Sapotaceae); (d) 23 measurements of *Lacistema aculeata* (Apocynaceae); (e) 13 measurements of *Glycydendron amazonicum* (Euphorbiaceae); (f) 12 measurements of *Gustavia hexapetala* (Lecythidaceae); (g) 16 measurements of *Tetragastris panamensis* (Burseraceae). Arils (visible only after dehiscence) are shown as open circles, exteriors of valves as filled circles.

reflect in the ultraviolet (Burkhardt 1982). Many birds have ultraviolet-sensitive receptors (Bowmaker 1991) and these fruits are probably also dispersed by birds.

It is also true that a few fruits whose seeds are predated by primates are conspicuously coloured, which may seem counter-intuitive. However, as we have already mentioned, the colour of some such fruits (e.g. *Sterculia frondosa*) may be aimed at avian dispersers. It is also possible that coloured carotenoid pigments in these fruits

act as a chemical defence against insect predators that could ultimately be more damaging than primates (Willson & Whelan 1990).

#### *Other factors influencing the spectral tuning of primate cone pigments*

Our results show that the spectral tuning of the L and M cone photopigments in trichromatic platyrhine monkeys is well matched to the task of detecting fruits against foliage. However, figure 14 suggests that within

the constraints imposed by this task, a number of photopigment pairings might be equally effective: the ‘plateau’ of optimal pigment pairings (producing a signal-to-noise ratio 90% or more of the maximum possible) is quite wide, and photopigments with  $\lambda_{\max}$ -values separated by as much as 100 nm may be as effective as the L and M pigments actually seen in trichromatic platyrhines. Furthermore, a wider separation of the L and M pigments would produce larger signal-to-noise ratios under dim illumination (see, for example, figure 19); so it is likely that the spectral tuning of these pigments has been constrained by a number of other factors, in addition to the needs of detecting fruit.

One factor that may limit the spectral separation of the L and M cones is longitudinal chromatic aberration. At any time, the retinal image can be in focus for only one wavelength, and the more the peak sensitivity of a photoreceptor class differs from the wavelength in focus, the more blurred will be the image sampled by that photoreceptor class. If the L and M cones are both to contribute to spatial resolution, they must have similar spectral sensitivities: otherwise, the image sampled by one cone class would be more blurred than that sampled by the other, which would impair visual acuity.

Colour vision imposes further costs on spatial vision (Hunt 1967; Geisler 1989; Mollon 1991; Williams *et al.* 1991; Nagle & Osorio 1993; Osorio *et al.* 1998). A difference between the outputs of two neighbouring cones of different spectral sensitivity may arise either because the two cones are viewing points of differing luminance on an achromatic surface, or because they are viewing a uniform chromatic surface that has a higher luminous efficiency for one cone type than for the other. At the highest spatial frequencies, chromatic and luminance signals will therefore be confounded (Nagle & Osorio 1993); and spatial resolution will be poorer for chromatic contrast than for achromatic contrast (Hunt 1967). Williams *et al.* (1991) considered this as the origin of the spurious coloured patches known as ‘Brewster’s colours’ that are sometimes seen when viewing achromatic gratings of high spatial frequency: some patches of grating may be viewed predominantly by L cones, and others by M cones. This effect is restricted to high spatial frequencies, but Osorio *et al.* (1998) suggested that chromatic signals can also interfere with low spatial frequency luminance signals in the magnocellular pathway. Ganglion cells of the magnocellular pathway probably take input from L and M cones unselectively, and therefore the response of different magnocellular units to an identical stimulus may differ depending on the exact composition of L and M cones making up the inputs to each unit. Finally, Mollon (1991) has argued that spatial vision is impaired at all chromatic edges that are close to equiluminance. At most edges in the natural world there is a luminance difference, and the output of both L and M cones is lower on the darker side of the edge. At edges that are close to equiluminance, however, the L cone signal may decrease across the edge at the same time as the M cone signal increases. Midget ganglion cells with L cone centres may signal a luminance decrement, while those with M cone centres signal an increment. Mollon (1991) argued that this ‘contradiction of normally yoked signals’ is why secondary visual functions, such as

stereopsis and movement perception, are impaired at equiluminance: these visual functions rely on the primary process of detecting edges.

These costs to spatial vision arise because both L and M cones, although spectrally distinct, contribute similar inputs to post-receptoral luminance channels. If the spectral separation between L and M cones were increased, a given chromatic difference would have a bigger effect on the relative outputs of the L and M cones, and these effects would become more pronounced. Limiting the spectral separation of the L and M cones may allow them to be treated alike for the purposes of spatial vision (Barlow 1982). The spectral tuning of the L and M cone pigments observed in primates may therefore be a trade-off, maintaining a certain minimum separation between the L and M pigments in order to counter quantum noise and detect fruits against foliage, while causing the least possible impairment in spatial vision.

#### (ii) *The mystery of platyrhine polymorphism*

The variety in colour vision amongst platyrhine monkeys remains mysterious. If trichromacy is an advantage, why is it not ubiquitous? And why are there many different trichromatic phenotypes?

#### *Advantages of dichromacy*

One possible explanation for the high incidence of dichromacy amongst platyrhines is that dichromatic colour vision is not necessarily a handicap. One potential advantage of dichromacy is in breaking camouflage: when an object is camouflaged with large, irregular patches of colour, a trichromat may fail to detect it because the camouflage patches offer a powerful cue for perceptual organization, and the overall contour of the object is lost in the jumble of these patches. A dichromat, on the other hand, may be less sensitive to the variegated colours of the camouflage patches—especially those that lie along an L/M axis of colour space—and thus may detect the object more readily (Anonymous 1940). The ability of dichromats to break camouflage has been exploited by designers of colour vision tests, who have sometimes created pseudoisochromatic plates with figures visible to the dichromat but not to the normal trichromat. For example, in Ishihara’s (1917) test, there are plates with figures that are subtly bluer than the background. These figures are masked for the normal trichromat by a pattern of green, orange and brown patches. Dichromats, however, are often able to detect these figures. Morgan *et al.* (1992) have also demonstrated this advantage of dichromacy in breaking camouflage: in their experiment, subjects were required to determine the location of a patch of texture elements that was defined by orientation, but masked by random variations in colour on a red-green dimension. Dichromats perform this task better than trichromats.

A further advantage of dichromacy is improved spatial vision. As discussed earlier, dichromats lack spectrally distinct L and M cone classes and therefore do not suffer ‘chromatic noise’ in post-receptoral luminance channels (Williams *et al.* 1991; Osorio *et al.* 1998). Dichromats would also not suffer the ‘contradiction of normally yoked signals’ at borders between regions differing in colour but close to equiluminance (Mollon 1991), where ganglion

cells driven by L cone centres send signals of contradictory sign to ganglion cells driven by M cone centres. At such edges the dichromat will normally see a clear luminance difference, and the edge will be more distinct than to the trichromat. Of course, there exist rare edges where the two regions are exactly equiluminant to the residual L/M cone class of the dichromat, and the edge will be detectable only by S cone signals. But dichromats are only impaired at detecting the border between two regions that are exactly equiluminant to them, whereas trichromats are impaired at detecting the border whenever the transients from L and M cones across the edge contradict each other.

Dichromatic platyrhine monkeys may therefore have an advantage at natural tasks dependent on breaking camouflage and detecting edges. In particular, one might imagine that dichromatic monkeys are better than trichromats at detecting camouflaged prey, such as insects and small vertebrates. The polymorphism of platyrhine monkeys might then be maintained by frequency-dependent advantage (Clarke 1979; Mollon *et al.* 1984): the advantage of the individual dichromat in certain foraging tasks over trichromatic conspecifics.

#### *Advantages of different trichromatic phenotypes*

Just as dichromats may have the advantage over trichromats at some tasks, different trichromatic phenotypes may have advantages over each other. In particular, we have shown that under the different illuminants that may be encountered at different times and locations in the forest, certain fruits may be more detectable by one platyrhine phenotype than another (figure 20). In extreme cases, the chromaticity of a fruit, when projected on to the L/M axis, may fall within the leaf distribution for one phenotype but not for another: in our sample, this occurred for fruits of *Chrysophyllum lucentifolium*, *Pouteria guianensis*, *Micropholis obscura*, *Ambelania acida*, *Philodendron insigne*, *Parahancornia fasciculata*, *Licania cf. heteromorpha* and *Eschweilera cf. micrantha*. Different phenotypes might therefore be better suited to different microhabitats. The data of figure 20 suggest that a phenotype with  $\lambda_{\max}$ -values at 430, 550 and 562 nm might have a slight advantage under the bluish 'canopy shade' illuminant, whereas a phenotype with  $\lambda_{\max}$ -values at 430, 536 and 550 nm might have a slight advantage under the whitish 'canopy, cloudy' illuminant, or in the deep green shade near the forest floor. Although our reflectance measurements were largely restricted to fruit, the argument applies equally to prey: one might envisage camouflaged insects or other animals that are exactly metameristic with their background for one trichromatic platyrhine phenotype in a particular light environment, but not for another phenotype. Both for detecting fruit and for detecting prey, a frequency-dependent advantage may help to maintain the variety of trichromatic phenotypes.

Moreover, most platyrhine monkeys are not solitary, but forage in groups (Wrangham 1987), and in some cases, individuals may actively signal to other members of the group when they find food (Menzel & Juno 1985). It is therefore possible that the most successful groups contain a variety of different dichromatic and trichromatic individuals, each with advantages and disadvantages at particular foraging tasks, and that the

maintenance of polymorphic colour vision in platyrhine monkeys is by kin selection, giving a net group benefit for the detection of resources (Mollon *et al.* 1984).

#### *Polymorphic colour vision as an intermediate step in the evolution of uniform trichromacy*

A final explanation for the rarity of uniformly trichromatic colour vision in primates is that the required opsin-gene duplication may, as discussed earlier, have occurred only twice in primate ancestry: once during the evolution of catarrhine monkeys, and a second time in the howler monkey lineage. In platyrhine species with polymorphic colour vision, the variation among dichromatic males may simply be maintained by heterozygous advantage (Mollon *et al.* 1984): the advantage of trichromatic females at detecting fruits and conspecifics against a background of foliage.

The last word should go to Grant Allen:

'If we would learn fully the whole history of the colour-sense... we must see by what steps the hues of flowers, and seeds, and fruits, and small animal prey caused the growth of a distinctive colour-perception in the creatures which fed upon them.... We may hope to show, furthermore, that the existence of bright colouring in the world at large is almost entirely due to the influence of the colour-sense in the animal kingdom... we do owe to the colour sense... the diverse artistic wealth of oranges, strawberries, plums, melons, brambleberries, and pomegranates.'

(Allen 1879, pp. 2–5)

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