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CHROMATICITY AS A SIGNAL OF RIPENESS IN FRUITS TAKEN BY PRIMATES

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Summary

We have measured the reflectance spectra of many samples of fruit eaten by chimpanzees and three frugivorous monkey species. If the fruit are plotted in a colour space appropriate for catarrhine primates, several distinct ripening patterns are evident. The degree of ripeness of many species would be discernible by dichromatic primates, but for most fruit a trichromatic consumer would be at an advantage. However, by calculating which set of possible photopigments would maximise the chromatic distance between samples of each fruit species, we show that the spectral positions of the primate long- (L) and middle-wavelength (M) cone pigments are not optimised for this task.

Key words: colour vision, trichromacy, opsin, visual ecology, Old World primate, frugivory, fruit, ripening, fig, evolution, Kibale, Uganda.

Introduction

It is a long-standing hypothesis that primate trichromacy evolved to aid frugivory (Allen, 1879; Mollon, 1991; Polyak, 1957). Not only must frugivorous primates find fruits in foliage, they must discern whether they are ripe. Many fruits undergo a small or large change in spectral reflectance as they ripen, and colour vision therefore has the potential to provide a reliable cue for discriminating between ripe and unripe fruits. It may be that this important task has influenced the evolution of primate photopigments.

The appropriate definition of ripeness depends on whether we take the point of view of the plant or that of the consumer. For the plant, fruits are ripe when the seeds have a maximum chance of germination. For the consumer, fruits are ripe when they contain desirable nutrients that are not made inaccessible by the presence of toxins or physical barriers. The definition may differ between consumers of different species, or even between individuals of the same species. For example, some primates might find a particular level of toughness a disincentive, whereas primates with more powerful jaws would not; and colobines have stomachs capable of digesting less ripe fruits than do guenons. The present study does not attempt to deal with the point of view of the plants, but treats fruits simply as natural visual stimuli presented to primates (for a review that takes the plants' perspective, see Janzen, 1983). To be an important signal to a consumer, a change in surface reflectance properties of a fruit must be correlated with a change in unseen properties such as toughness or the levels of nutrients or toxins. As our independent measures of ripeness, we have measured toughness, size and, where appropriate, latex content. Analysis of nutrients and toxins in each sample of each fruit species was beyond the scope of this study and, for the present purpose, we assume that changes in these are correlated with changes in our chosen measures. We do not claim to know when a primate would consider a particular fruit 'ripe', but we have measured a wide range of maturity stages for each fruit species, and we assume that the primate would benefit by having a visual system sensitive to the different stimulus spectra that the fruits can present.

The present paper has three distinct aims. (i) We seek to describe the ripening process of fruits in colour coordinates appropriate to their primate consumers. We ask whether most fruits taken by primates present the same sequence of signals or whether there are different patterns of chromaticity change. The fruits measured in Uganda are compared with each other and also with those measured in French Guiana by Regan (1997). (ii) We ask what advantage the existing trichromacy of catarrhine primates offers in this discrimination task, relative to the supposed ancestral dichromacy. (iii) We assume that the long-wavelength (L) and middle-wavelength (M) photopigments of catarrhines could have evolved to have any λ_{max} value between 400 nm and 700 nm, and ask which peak sensitivities would be optimal for discriminating ripe fruits from unripe fruits. To answer this question, we investigate which possible set of photopigments would maximise the dispersion in an appropriate colour space between fruits of differing ripeness state. The use of colour vision for the task of discriminating between objects in front of the subject is distinct from the use of colour vision for detecting objects against a background of distracting elements (the latter task has been examined by Sumner and Mollon, 2000). There are other possible visual or non-visual cues, besides colour vision, for discerning the ripeness of fruits (for example, chimpanzees

have been seen to smell or squeeze certain fig species), but just because a task might be done another way in some cases does not mean that an animal's colour vision should not be optimised for that task.

Osorio and Vorobyev (1996), using an analysis different from ours, have found that for dichromatic primates with a short-wavelength (S) pigment with λ_{max} fixed at 430 nm, a second pigment with λ_{max} anywhere in the range 510–580 nm (beyond 580 nm was not tested) would nearly maximise the number of fruits that could be distinguished from each other. For trichromatic primates with pigments with λ_{max} at 430 and 565 nm, a third pigment with λ_{max} between 460 and 520 nm was found to be optimal (they did not test the effect of changing the spectral position of the L pigment). They used 78 spectra of cultivated 'edible fruit' that were 'mainly tropical and subtropical species purchased in London and Berlin. Species used included mango, pawpaw, banana, lychee, figs and loquats'. It seems likely that some of the species included had been bred for enhanced colour or had been selected on the basis of colour before marketing and thus may not have represented stimuli that primate vision has experienced on an evolutionary time scale. Osorio and Vorobyev (1996) concluded that, for identifying fruits, 'the dichromat's eye is almost as good as a trichromat's', a conclusion different from the one we reach here. They were interested in identification of fruit species, not stages of ripeness, and thus compared fruits between species, whereas we compare different samples of fruit within a species.

Materials and methods

The field work in Uganda has been described in the previous paper (Sumner and Mollon, 2000), and the methods of analysis used here have much in common with those of that study. The quantum catches of putative cones have been calculated in the same way, and the stimuli have been plotted in a colour space most appropriate for catarrhine monkeys: the λ_{max} values were 430, 531 and 561 nm, the lens filtering adjustment used average data from baboon and macaque (Cooper and Robson, 1969) and the 'stimulus spectra' were reconstructed from the reflectance spectra using the same standard illuminant measured in the canopy in cloudy conditions. However, here we introduce a different analysis that seeks the pigments that maximise the chromatic distances between all the stimuli rather than those that maximise the signal-to-noise ratio. Both subsystems of colour vision are considered in the analysis and, by holding the S cone λ_{max} constant and varying the λ_{max} values of the other cones, we discover which pair of possible L and M pigments would be optimal for discriminating amongst stimuli (rather than detecting stimuli against a background). In this case 'optimal' is defined as the maximum possible weighted sum of the variances in the two chromatic channels.

For each possible set of λ_{max} values for the L, M and S pigments, the corneal sensitivity curves were calculated as detailed in Sumner and Mollon (2000). For each chosen stimulus spectrum, the quantum catches ('*L*', '*M*' and '*S*') and the chromaticity values $\log[S/(L+M)]$ and $\log(L/M)$ were calculated. The variance on each of these chromaticity axes was then found, and the two variances were summed according to a weighting factor discussed briefly below. These steps were repeated for different sets of cone sensitivities. The λ_{max} value of the S cone pigments was held at 430 nm, and the L and M cone pigments took λ_{max} values that varied in 5 nm steps between 400 nm and 700 nm. The results are plotted as a contour map in the same way as the results for the signal-to-noise analysis described in Sumner and Mollon (2000), the axes being the λ_{max} values of the hypothesized L and M pigments.

A set of photopigments that increases the chromatic distance between stimuli may not be advantageous if it also increases the noise in the chromatic channel. Therefore, the variance in each chromaticity value due to 'quantum noise' was calculated, and the mean value on each axis for each photopigment set was used to scale the results. Since the variance of $\log X$ is $1/X^2$ times the variance of X, the 'quantum noise' was $1/S+1/(L+M)$ for $\log[S/(L+M)]$ and $1/L+1/M$ for $\log(L/M)$. However, there were found to be only very small and non-important differences between the scaled and non-scaled results, and so the inclusion of quantum noise in this analysis will not be further discussed.

The logarithm of $S/(L+M)$ was taken because chromatic discriminations along the $S/(L+M)$ axis conform to Weber's law: threshold increases with higher $S/(L+M)$ values but is approximately constant for $\log[S/(L+M)]$ (Krauskopf and Gegenfurtner, 1992; Le Grand, 1949). For consistency with the other axis, the second colour subsystem was represented as $\log(L/M)$, but calculations for each fruit species in terms of $L/(L+M)$ produced extremely similar results. The axes were scaled so that the S direction was 4.6 times less sensitive than the L/M direction, in accordance with the values of 8.7 and 1.9 given for Weber fractions for detection of short-wavelength and long-wavelength targets by Wyszecki and Stiles (1982). It is not known exactly what the appropriate scaling factor should be, but we tested a range of values and found that the results were virtually unchanged when any scaling factor higher than 1.0 was used.

Using this method, we have calculated, for each fruit species, which set of possible cone pigments would maximise the factor by which the relative cone signals change as the fruits ripen. This set of pigments is taken to be optimal for discriminating the ripeness stages of the fruits. Both ripe and unripe samples were present in every case, but no distinction between these categories was made in the present analysis. However, we did check that the 'optimal' pigments produced an ordering in chromaticity space that reflected the order given by the independent measures of ripeness: penetrometer measurements, size and the presence of latex.

We have also calculated, for each fruit species, which cone pigments would yield the highest signal-to-noise ratio for detecting ripe fruits amongst unripe fruits following the method described by Sumner and Mollon (2000). The ripe samples were 'targets' and the unripe samples were

'background'. The classification of 'ripe' and 'unripe' samples has been discussed in the description of the fieldwork in Sumner and Mollon (2000). The task of discriminating fruits is different from that of detecting fruits, and maximising the variance among fruit signals seems to be a more appropriate approach than does maximising the signal-to-noise ratio. However, the justification for also calculating the latter was twofold: first, the signal-to-noise ratio can be a measure of the confidence with which an object can be classified as a target (ripe fruit) and not a distractor (unripe fruit or leaf) and, second, more direct comparison with the results for detecting targets against leaves would be possible. The results and conclusions for the task of discriminating fruits turn out to be strikingly different from those reported in Sumner and Mollon (2000) for detecting targets against leaves, and it is important to show that this effect is not dependent on the different kind of analysis employed.

Results and discussion

Patterns of ripening

Figs 1, 3 and 5 show photographs of 14 of the 51 fruit species that were measured from the diets of *Pan troglodytes*, *Lophocebus albigena*, *Cercopithecus mitis* and *C. ascanius* (the primates in Kibale Forest, Uganda, that are conventionally classified as frugivores). Reflectance spectra of samples of differing ripeness are also shown. Individual species are discussed below.

Figs 2, 4 and 6 show colour space diagrams for 11 of the species in the photographs. The samples are marked as unripe (filled circles), mid-ripe (open squares) or ripe (filled triangles) to illustrate the changes in chromaticity and luminance that occur during ripening (some species have been separated into only two categories owing to the small number of samples). The ripeness categories are based primarily on the force required to puncture the skin (measured by a penetrometer) and also the size of the samples. In the case of the figs, described below, the presence of latex was taken into account as well. In the accompanying paper (Sumner and Mollon, 2000), we divided fruit into only two categories, and the same two categories were used for the signal-to-noise analyses in this paper. No categorisation was employed in the analysis of chromaticity variance (see below). The boundaries between categories are necessarily arbitrary, so that the mid-ripe stage for one fruit species cannot be directly compared with the mid-ripe stage for other fruits: the aim was simply to show the ripening process in each species. In many cases, the frugivorous primates have been observed by the first author and other researchers at the site (see Materials and methods in Sumner and Mollon, 2000) to eat fruits resembling the 'ripe' category and the 'mid-ripe' category (*Colobus guereza* and *Colobus badius* have been observed to eat the unripe fruits). Whatever the exact ripeness state of the fruits actually chosen by the primates, it is assumed for the purposes of this study that being able to discriminate the ripeness stages using vision would offer a selective advantage.

Many species show very little or no change in reflectance properties as they ripen. Some of these that are important to primates include: *Warburgia ugandensis*, Canellaceae, *Tabernaemontana holstii*, Apocynaceae, *Pterygota milbraedii*, Sterculiaceae, *Ficus brachylepis* and *Morus lactea*, both Moraceae. These fruits tend to be larger than average (35, 120, 110, 30 and 20 mm in diameter respectively) and we shall return to this observation later.

Non-fig species

Chrysophyllum albidum, Sapotaceae (Fig. 1Ai), typifies the type of fruit thought to be specialised for dispersal by primates (Gautier-Hion et al., 1985; Janson, 1983; Julliot, 1996; McConkey, 1999): the fruits are approximately 40 mm across, and a few large seeds are surrounded by fleshy pulp and a tough pericarp. In Kibale, fruits of *Chrysophyllum* species are commonly eaten by the four frugivorous primates, and seeds from chimpanzee dung have been shown to germinate, while those from fruits picked direct from a tree did not germinate (Wrangham et al., 1994). Similar fruits from trees of the same genus are commonly eaten by *Alouatta seniculus*, *Ateles paniscus* and *Cebus apella* in French Guiana (Regan, 1997; Regan et al., 1998; B. C. Regan, C. Julliot, B. Simmen, F. Viénot, P. Charles-Dominique and J. D. Mollon, in preparation). The reflectance spectra of the unripe fruits (Fig. 1Aii) resemble those of leaves, showing the characteristic chlorophyll absorbance regions: below 500 nm and between 600 and 700 nm. The ripe fruits show much greater, and rising, reflectance in the latter region, owing to the removal of chlorophyll and the presence of pigments such as carotenoids. A dip at 670 nm does survive, presumably because some chlorophyll remains. The chromaticity diagram in Fig. 2A shows that the fruits exhibit a very strong correlation between ripeness and each chromaticity coordinate. Reliable cues to ripeness could, therefore, be provided by either colour subsystem. The plot of $L+M$ *versus* $S/(L+M)$, to the right of the chromaticity diagram, shows that the fruits also increase in lightness (luminance) upon ripening. Lightness could also, therefore, be used to discriminate ripeness.

Celtis durandii, Ulmaceae (Fig. 1B), is a very abundant tree around the field station in Kibale (more than 30 stems per hectare are reported in Isabirye-Basuta, 1989) and has featured in the top three species in most of the dietary studies of the four frugivorous primates. At 6 mm across, the fruits are very much smaller than those of *Chrysophyllum albidum*, but they display a very similar pattern of changing reflectance, and they therefore show a similar journey through colour space in Fig. 2B. We found that several other species of fruits that are eaten by the frugivores in Kibale Forest, and which are from diverse botanical families, also follow this pattern of chromaticity and luminance change as they ripen, e.g. *Celtis africana* (5 mm), Ulmaceae, *Cordia millenii* (25 mm), Boraginaceae, *Mimusops bagshawei* (20 mm), Sapotaceae, *Phoenix reclinata* (20 mm), Palmae, and *Strychnos mitis* (13 mm), Loganiaceae. All these fruits have a single seed, and germination success of seeds from chimpanzee dung has been

demonstrated for each species (except the two *Celtis* species, which were not tested) (Wrangham et al., 1994). In contrast, seeds that were collected directly from trees did not germinate (only *Cordia* and *Mimusops* were tested). Some other fruits make a transition in the same direction in colour space (from green to yellowish), but do not progress quite so far from their unripe appearance (e.g. *Bosqueia phoberos*, 15 mm, Moraceae). The very small fruits of *Ehretia cymosa* (6 mm), Boraginaceae, become an orange colour that contains slightly more S cone signal than the colour of *Chrysophyllum* and *Celtis* species.

Fig. 1Ci shows the fruits of *Diospyros abyssinica*, Ebenaceae, which was the food most frequently eaten by *Lophocebus albigena* in the studies of Olupot (1998) and Waser (1977). However, these monkeys act as predators, destroying the single seed as they eat the small fruits (9 mm). The guenons (*Cercopithecus mitis* and *C. ascanius*) also commonly take these fruits, but the chimpanzees have not been seen to do so. It seems likely that birds are responsible for the majority of seed dispersal in this case. The same change in chromaticity displayed in the species discussed above is evident at the beginning of the ripening process of *Diospyros abyssinica* (Fig. 2C), but the fruits show a different change in reflectance (compare Fig. 1Cii with Fig. 1Bii): the yellow/orange colours of ripe *Celtis durandii* and mid-ripe *Diospyros abyssinica* are not produced by the same reflectance spectra (and therefore might appear different from each other to animals with colour vision unlike that of extant catarrhine primates). The fruits of *Diospyros abyssinica* are still hard at this yellow stage and continue changing colour until they appear dark red and have very little reflectance at wavelengths shorter than 560 nm. The chromaticity diagram shows that the second catarrhine subsystem would provide a good cue to ripeness, whereas the ancient colour subsystem could not help. Discrimination might be based also on the decrease in luminance.

The ripening process of *Uvariopsis congensis*, Annonaceae, is very different from that of all the fruits discussed above. The fruits do not change colour gradually, but instead a red patch appears and quickly spreads (Fig. 1Di). This is evident from the lack of samples between the ‘unripe’ and ‘ripe’ categories on the chromaticity diagram (Fig. 2D). The colour space plot shows also that it would be difficult to make the ripeness discrimination on the basis of luminance or the S cone channel, but it would be easy on the basis of comparing the L with the M cone signal. This small tree provides all the frugivorous primates in Kibale with a large part of their diet, often being the most frequently eaten food, and being in the top five species in nearly all studies. Wrangham et al. (1994) found that seeds from chimpanzee dung germinated, but those taken directly from trees did not.

A fourth distinct type of colour distribution of ripening fruits is displayed by some species in Kibale Forest that turn from green to dark purple without any intermediate colours: *Bridelia micrantha*, Euphorbiaceae, *Polyscias fulva*, Araliaceae, and *Prunus africana*, Rosaceae (Fig. 1Ei). All these fruits are small (10, 3 and 11 mm, respectively) and are not taken by chimpanzees (they are eaten by monkeys and birds). Unlike the species discussed above, the major change in reflectance occurs between 500 and 600 nm, with little change beyond 600 nm. A patch of the ripe colour appears on the unripe fruits quite early, which is why one of the unripe reflectance spectra shown is similar to that for the ripe fruits (Fig. 1Eii). Unfortunately, since the ripe fruits are dark and glossy, their reflectance spectra are prone to contamination by specular reflection, and we therefore obtained very few reliable measurements. For this reason, colour space diagrams are not shown, and these species were not subjected to any further analysis.

Fig species

Fig. 3Ai,Bi shows fruits of two *Ficus* species that are consumed in large quantities by chimpanzees, mangabeys and guenons in Kibale Forest. The colobines have also been seen to eat them. The crop of a single tree can be very large, and Isabirye-Basuta (1989) found that, during the months in which fruiting trees of either species could be found, some chimpanzees relied almost exclusively upon them. Wrangham et al. (1994) concluded that chimpanzee-dispersed seeds germinated for all *Ficus* species. They repeatably found that *Ficus* seeds from chimpanzee dung germinated, and on average they germinated sooner than seeds taken directly from the trees, but the study did not distinguish between fig species.

The reflectance spectra in Fig. 3Aii,Bii show that the colour change associated with ripening is produced in a clearly different way from the colour change in fruits such as *Chrysophyllum albidum*: in the latter case, reflectance is increased at wavelengths beyond 550 nm, whereas for these figs, reflectance is reduced between 500 and 600 nm and does not change very much outside this region. The samples of *F. exasperata* and *F. natalensis* exhibit a very strong correlation between ripeness and each of the three colour space coordinates (Fig. 4A,B). Therefore, reliable cues to ripeness could be provided by luminance and by both colour subsystems. However, unlike the case of the fruits shown in Fig. 2, the relative S cone signal increases rather than decreases during ripening. The fruits remain the yellowish-green colour of the unripe state until very late. These ‘mid-ripe’ fruits are full-size, soft, do not contain latex and have been seen to be eaten (at least by chimpanzees). It is interesting that these fruits, as well as several other species in Kibale (e.g. *Diospyros abyssinica*, discussed above), darken as they ripen, because very few of the fruits measured by Regan in South America showed this property (Regan, 1997). There is one fig species in Kibale, *Ficus mucuso* (45 mm), Moraceae, that becomes an orange colour (that contains slightly more S cone signal than the colour of *Celtis durandii*).

Of all the fruits measured that do change colour, *Ficus dawei* (Figs 3C, 4C) was the only species for which the ripening process would hardly be evident in the second catarrhine colour subsystem, which compares the signal in the M and L cones. Nor is there much change in luminance. However, the

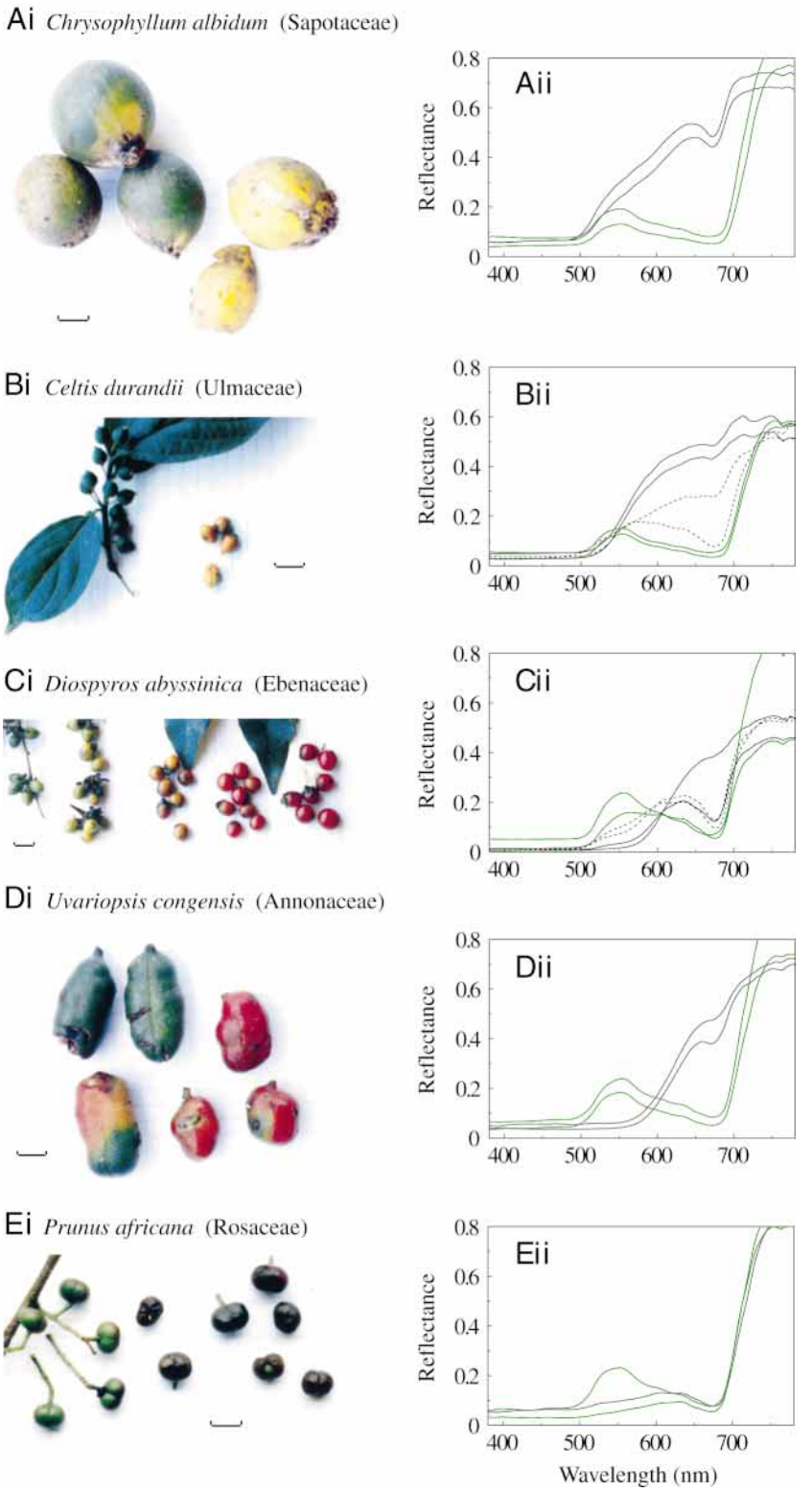

Fig. 1. Photographs (Ai–Ei) and reflectance spectra (Aii–Eii) of fruits of five species commonly eaten by primates at Kibale Forest, Uganda. The unripe fruits are shown on the left of the photographs, and their reflectance spectra are drawn in green. The ripe fruits are shown on the right of the photographs, and their reflectance spectra are drawn as solid black lines. The dashed lines are for mid-ripe fruits. Note that primate long-wavelength (L) cones have extremely low sensitivity beyond 700 nm, and therefore the sharp rise in many spectra at around 700 nm is of very little importance to extant primates. However, it does become important in the analysis that seeks optimal pigments. Scale bars, 10 mm.

ripeness categories seem to produce diagonal striations in the chromaticity diagram, and so ripeness might be discriminated using a combination of the two colour channels. Interestingly, the colour change was much less evident on the outside than it was if the fruits were cut open (only measurements of the outside are analysed here).

The fruits of *Ficus capensis* (Figs 3D, 4D) do not grow on branches amongst leaves, but grow off the trunk instead. In this case, only the second catarrhine colour subsystem would reliably make the ripeness distinction, although there is an average luminance decrease too. The fruits on different trees did not all follow exactly the

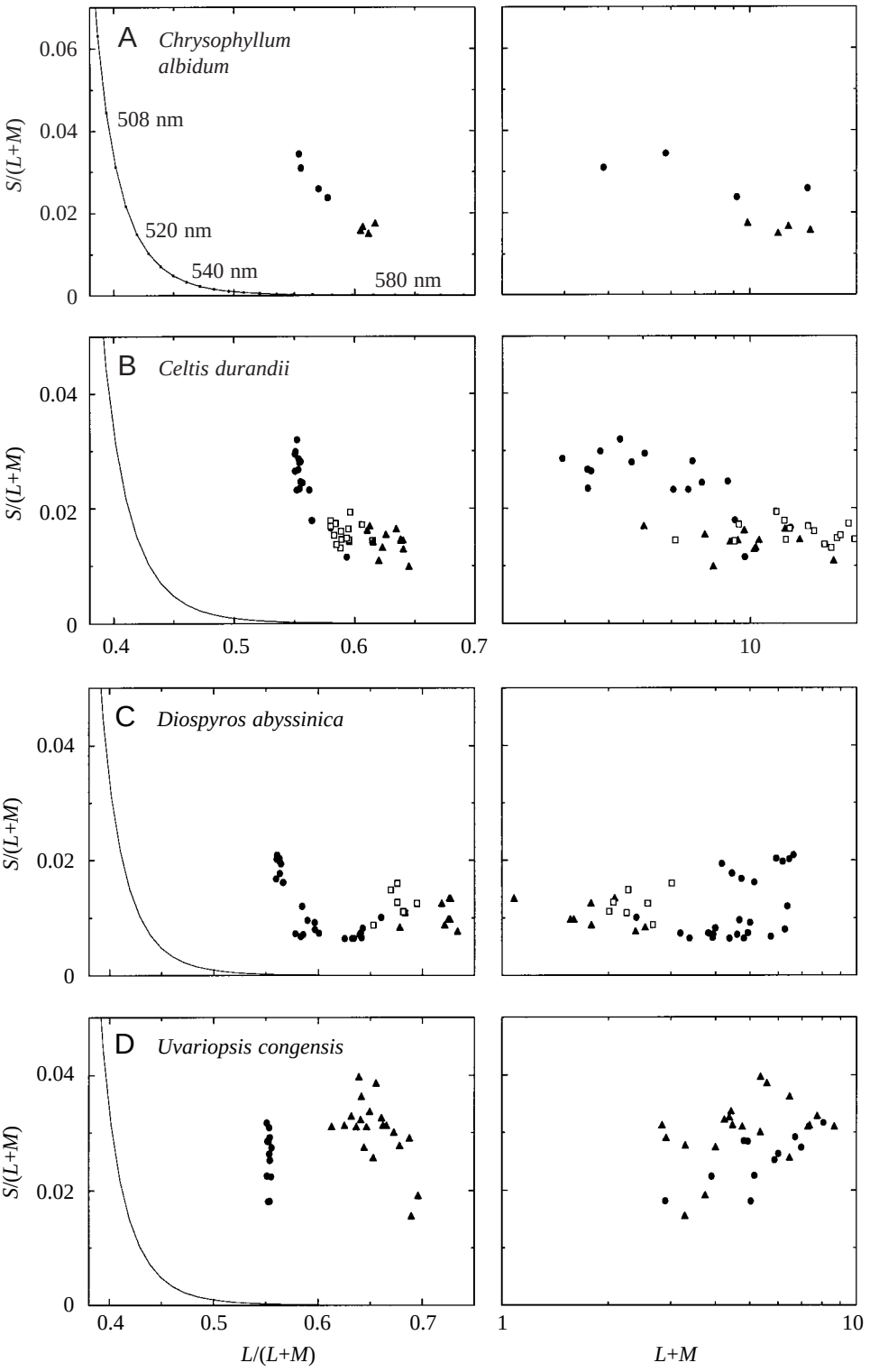

Fig. 2. (A–D) The chromaticity (left) and luminance (right) of unripe (filled circles), mid-ripe (open squares) and ripe (filled triangles) fruits of the fruit species shown in Fig. 1A–D, plotted in catarrhine monkey colour space. The locus of monochromatic lights is marked by the curve, and the cross (×) in A marks the chromaticity of the illuminant that was combined with the reflectance spectra. In subsequent diagrams, the vertical axis extends only to 0.05 because all fruit samples had values below this. Note that the chromaticity axes are not logarithmic, but that the $L+M$ axis is logarithmic and runs from 2 to 20 for A and B, but has been shifted to 1 to 10 in C and D. This axis is relative, and the actual values have no meaning except for comparison with other diagrams in this paper and diagrams in Sumner and Mollon (2000). Note also that the $L/(L+M)$ axis has been extended in C and D. See Materials and methods for an explanation of L, M and S.

same pattern of spectral change (the reflectance spectra illustrated in Fig. 3Dii indicate some of the variation): the ripe fruits shown in Fig. 3Di appear pinkish, but some samples from other trees were more yellow or brown than any shown in that photograph and could fulfil the criteria of 'ripe', being just as soft and having no latex, without appearing pink at all.

Understorey species

The fruits shown in Fig. 5 come from plants that do not grow over 5 m in height. All five species are eaten by *Pan troglodytes* and the first three by *Cercopithecus ascanius* (see the description of fieldwork in the accompanying paper, Sumner and Mollon, 2000, for a list of sources of dietary information). It is possible that the other frugivores also eat these fruit when

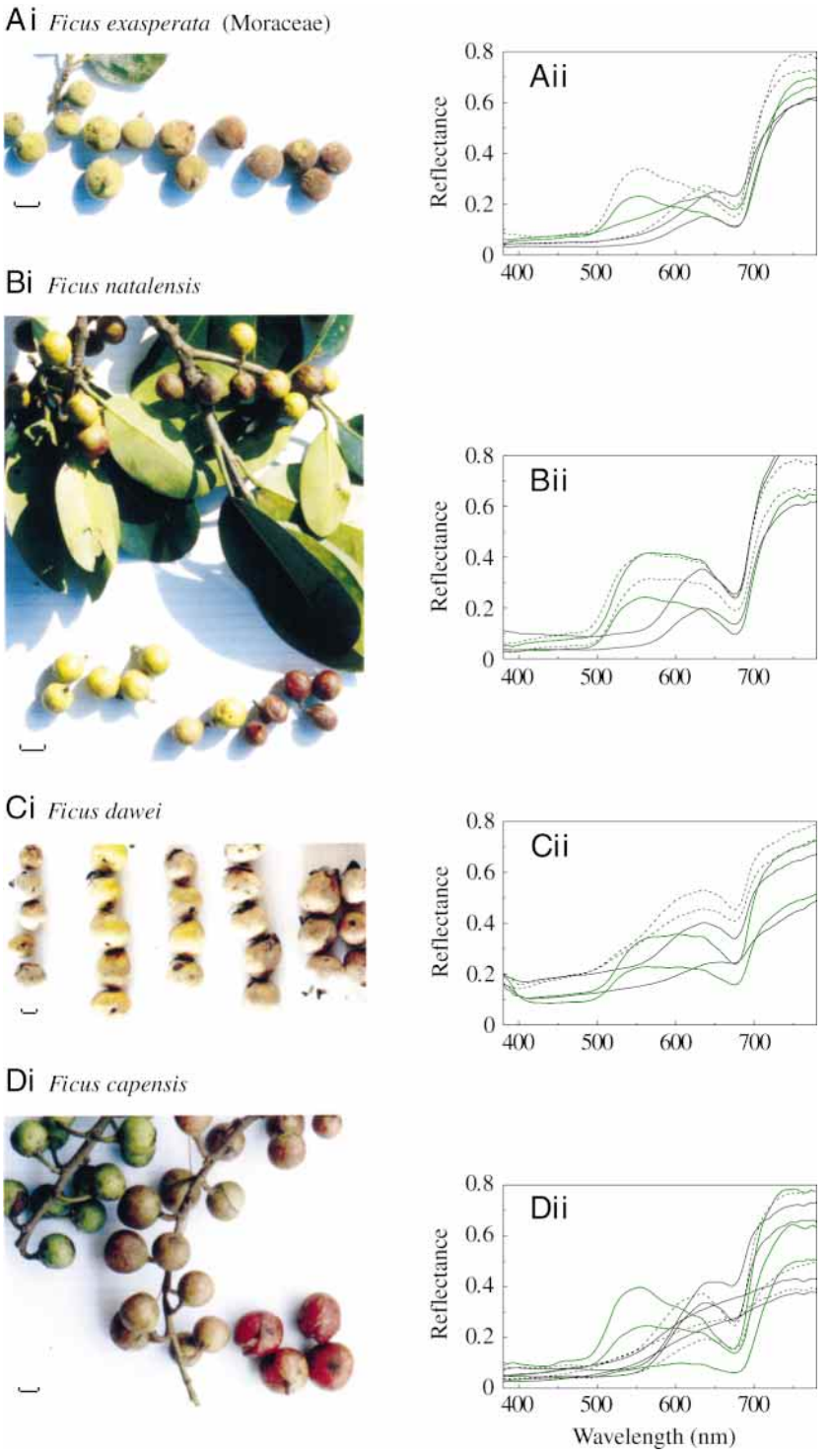

Fig. 3. Photographs (Ai–Di) and reflectance spectra (Aii–Dii) of fruits of four species of fig commonly eaten by all four frugivorous primates in Kibale Forest. Explanation as for Fig. 1. Scale bars, 10 mm.

researchers are not present to discourage them from descending to the understorey.

The samples of *Ficus asperifolia* fill a large area in colour space (Fig. 6A) and, although there is a general trend to become darker and redder while ripening, many unripe fruits have patches of the same colours that ripe fruits display. It seems that, since there will be very few ripe fruits on the small shrub at any one time, the plant adopts a strategy of 'flagging' (Stiles, 1982) all its fruits to attract potential disseminators, who could then discern ripeness by size, softness and whether the red or orange colour covered the whole fruit or was only on the tip. The lightness of many samples might be an adaptation to the lower light levels of the understorey.

Fig. 5B shows the fruits of *Rubus apetalus*, Rosaceae, and Fig. 6B shows their chromaticities. The ripening process begins by following the typical chromaticity change discussed for canopy fruits such as *Celtis durandii*, but upon becoming fully ripe these understorey fruits increase in relative S cone

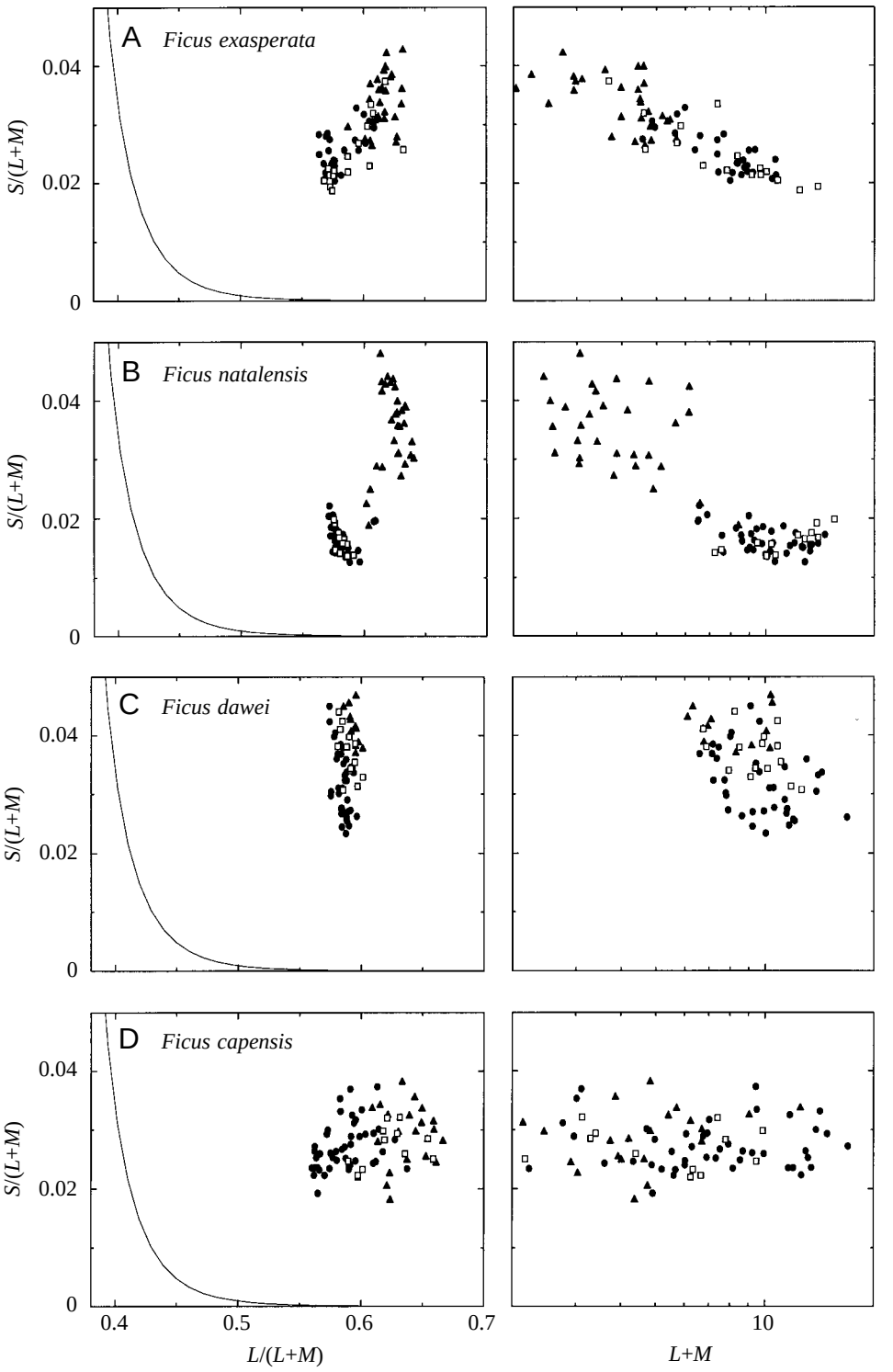

Fig. 4. (A–D) The chromaticity (left) and luminance (right) of unripe (filled circles), mid-ripe (open squares) and ripe (filled triangles) fruits of the fig species shown in Fig. 3A–D. Further explanation as for Fig. 2.

signal without further increase in the *L*:*M* ratio, so describing a hemicircle in chromaticity space. They also decrease slightly in lightness. The fruits of *Dovyalis macrocalyx*, Flacourtiaceae (Figs 5C, 6C), become orange, also following the same trend as *Celtis durandii*, except that they do not get lighter. The interesting feature of this species is the light green calyx that remains and provides a striking contrast (in both colour subsystems) to the orange fruit peeping out from within.

Marantochloa leucantha, Marantaceae, shown in Fig. 5Di, is an understorey herb species eaten by chimpanzees. A colour space diagram is not shown because the ripening fruits display a very similar chromaticity pattern to that of *Diospyros abyssinica* shown in Fig. 2C. However, comparison of Fig. 5Dii with Fig. 1Cii reveals that the changes in reflectance are not identical. Fig. 5Ei shows a photograph of an *Aframomum* sp. (probably *zambesiacum*). The two reflectance

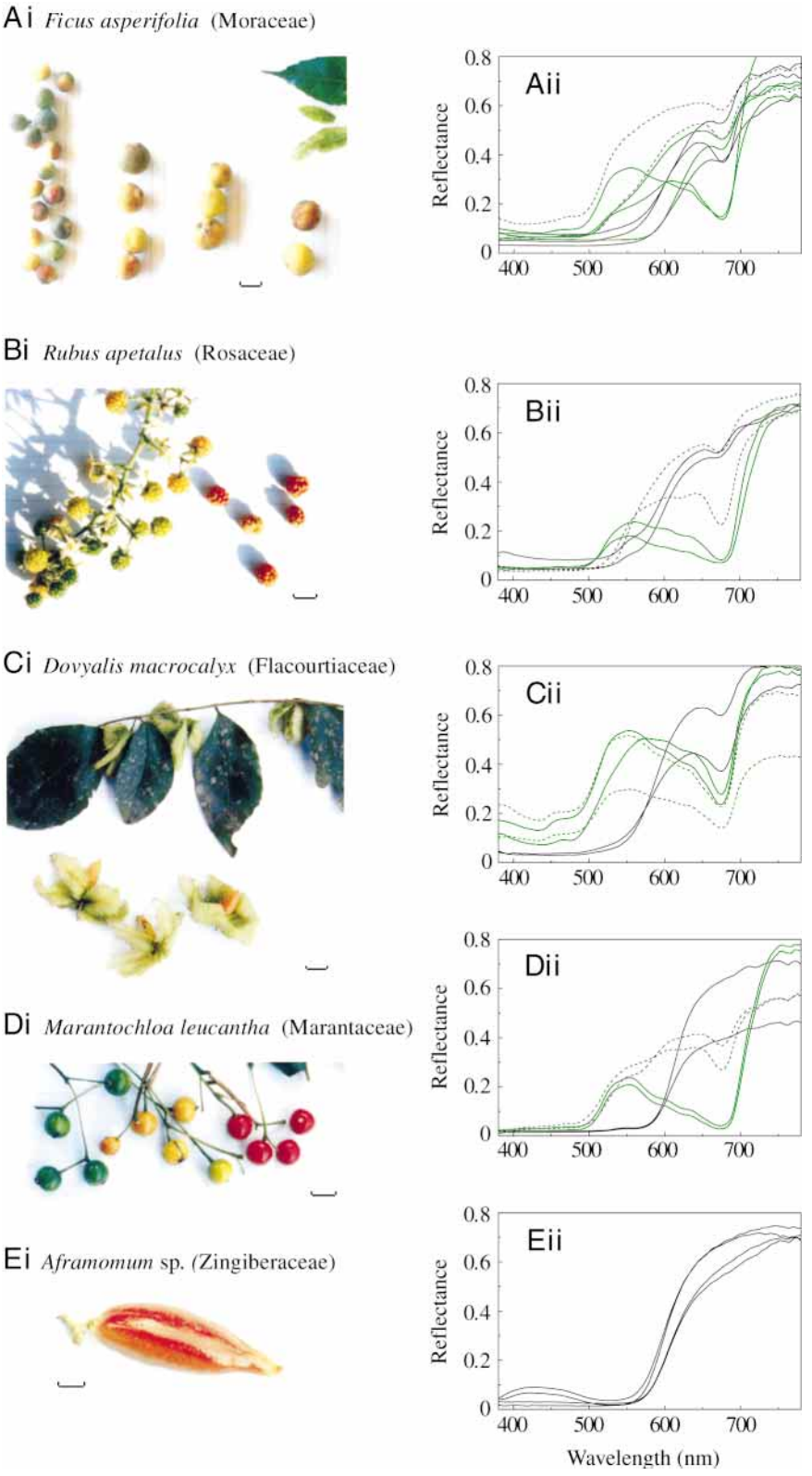

Fig. 5. Photographs (Ai–Ei) and reflectance spectra (Aii–Eii) of fruits of five understorey species. Explanation as for Fig. 1, except that the green dashed lines in C are reflectance spectra for the calyx of *Dovyalis macrocalyx*. Scale bars, 10 mm.

spectra in Fig. 5Eii with least reflectance between 400 and 500 nm are from this species, and the two spectra that show an increase in reflectance in this region are from another *Aframomum* sp. (probably *milbraedii*). The latter are slightly smaller (63 mm in length instead of 70 mm) and appear pink rather than red. These two species produce the only large fruits in the present study that turned red or pink. Wrangham et al. (1994) have repeatably found that *Aframomum* seeds collected from chimpanzee dung germinated (but, as in the case of the figs, they did not distinguish between *Aframomum* species). All

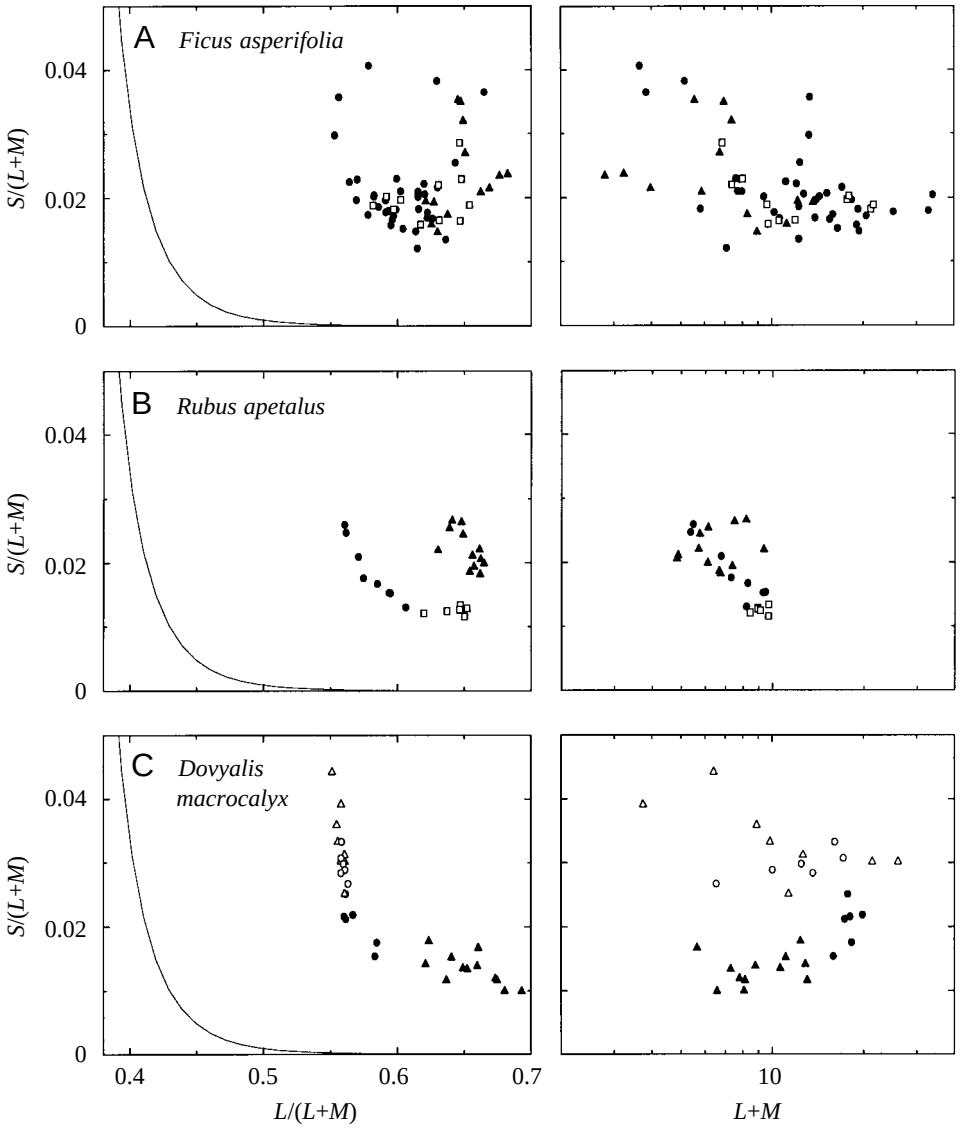

Fig. 6. (A–C) The chromaticity (left) and luminance (right) of unripe (filled circles), mid-ripe (open squares) and ripe (filled triangles) fruits of the fruit species shown in Fig. 3A–C. Further explanation as for Fig. 2. The open circles in C represent the calyx surrounding the unripe fruits and the open triangles represent the calyx surrounding the ripe fruits of this species. Note that the *L+M* axis extends from 2 to 40.

measured reflectance spectra were from fruits found and consumed by chimpanzees, which discarded the tough pericarp, which could then be collected. The sample in the photograph was found by the first author. Unfortunately, the sparseness of the fruits meant that no unripe samples were found, and therefore we do not present a colour diagram or any further analysis for these species.

The advantage of trichromacy

Most fruits important to primates in Kibale Forest show changes in reflectance properties as they ripen and, in each case discussed above, we have indicated whether these changes would be visible to the luminance and colour channels possessed by extant catarrhine primates. A dichromatic primate, possessing the ancient colour subsystem and a luminance channel, would be able to discriminate the different ripeness stages of most fruits in its diet. The discussion has been for luminance taken as *L+M*, but the results hold for the luminance channel in the putative dichromatic ancestral primate (with λ_{max} anywhere between 531 and 561 nm). However, the second catarrhine colour subsystem certainly offers an added advantage in nearly all cases, and there are some fruits whose ripeness would not be discernible without it. In addition, only in the second colour subsystem is there a unidirectional relationship between signal and ripeness of all fruit species: a higher *L*/*M* ratio means riper fruit. In the ancient colour subsystem and the luminance channel, ripeness is signalled by an increase in relative S cone absorbance for some fruit species, but a decrease for others. These channels could not, therefore, be used to discern the ripeness of unfamiliar fruits. We conclude that judging ripeness may have been an important selective pressure for developing and maintaining trichromacy in Old World primates.

Optimal cone pigments for discriminating amongst stimuli

We now turn to the question of which hypothetical photopigments would be optimal for discerning fruit ripeness.

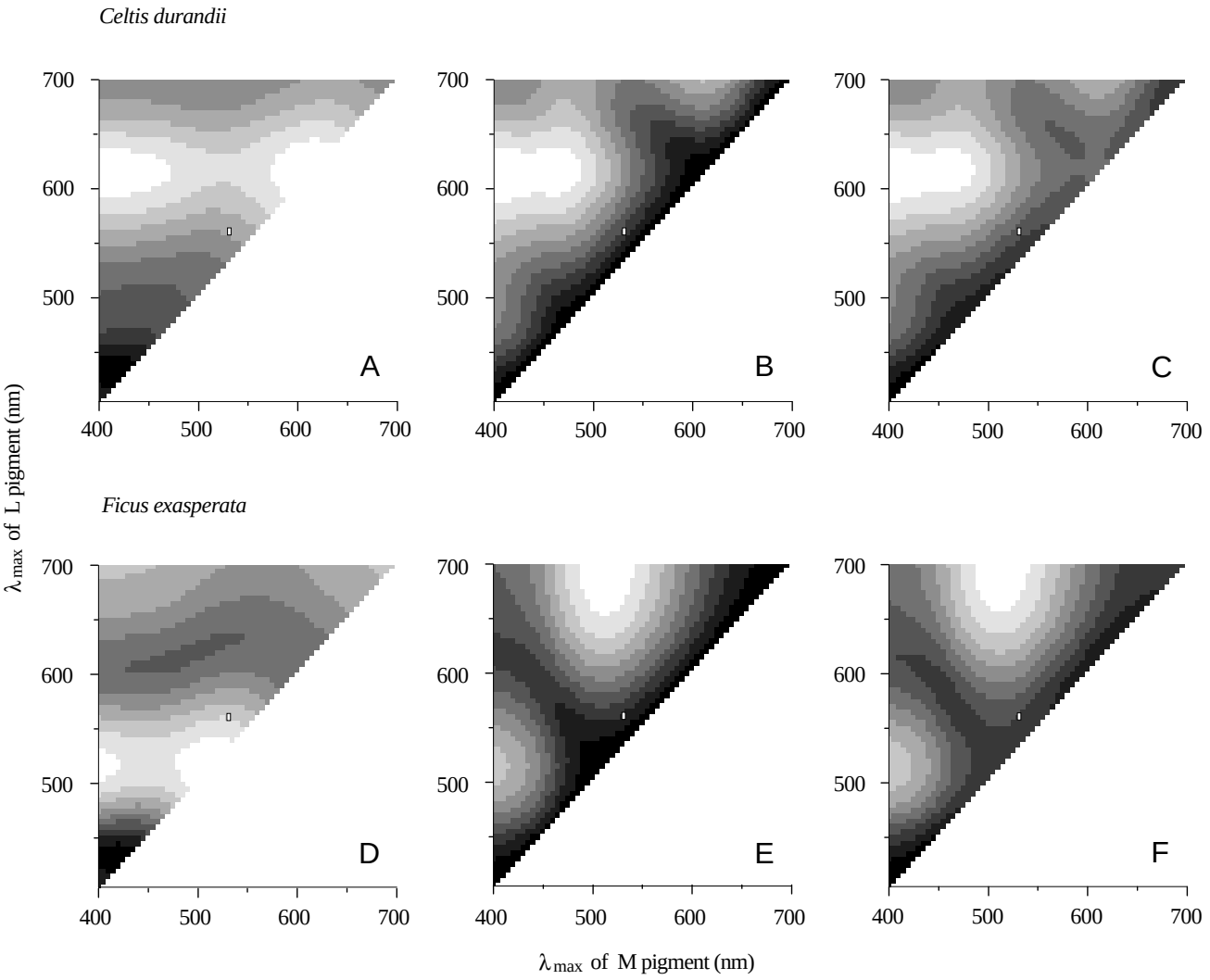

Fig. 7. The results of the chromaticity variance analysis for discriminating among fruits of *Celtis durandii* (A–C) and *Ficus exasperata* (D–F). The possible pairs of middle-wavelength (M) and long-wavelength (L) pigments had peak sensitivity (λ_{max}) values between 400 nm and 700 nm. The lighter the pixel, the larger the chromaticity variance. The white squares mark the pigment pair with λ_{max} values of 531 nm and 561 nm. (A,D) The standard deviation of chromaticities in log[*S*/(*L*+*M*)] as the L and M pigments vary in λ_{max}. (B,E) The standard deviation of chromaticities in log(*L*/*M*) as the L and M pigments vary in λ_{max}. (C,F) The square root of the weighted sum of the variance of chromaticities in each subsystem. The greyscale ranges from white (90–100% of the maximum variance) to black (0–10 % of the maximum variance).

The results of the chromaticity variance analysis are shown in Fig. 7 for *Celtis durandii* and *Ficus exasperata*. No species showed important variation from these patterns of results, except where noted below. Fig. 7A,D show how the variance in fruit chromaticities in the ancient mammalian colour subsystem was affected by the λ_{max} values of the L and M pigments (the λ_{max} value of the S cone was held at 430 nm). The 'optimal' pigments had λ_{max} values of 610 and 615 nm for *C. durandii* and of 510 and 515 nm for *F. exasperata*. It is unsurprising that these values are close together because this channel does not distinguish between L and M cones but, as long as the L pigment λ_{max} takes the optimal value, it does not matter whether the peak sensitivity (λ_{max}) of the M cone is at the same value or at much shorter wavelengths: in Fig. 7A,D, there are two light areas that represent large chromaticity differences between ripe and unripe fruit, and the same was true for all the other fruit species.

Fig. 7B,E shows how the chromaticity variance in the second catarrhine colour subsystem was affected by the λ_{max} values of the L and M pigments. For *C. durandii*, the 'optimal' L pigment had a λ_{max} value of 615 nm, and the λ_{max} of the M pigment would best be anywhere between 400 nm and 480 nm. In this case, therefore, the optimal pigments for the recent colour subsystem are no different from those for the ancient colour subsystem that has an S cone fixed at 430 nm. For *F. exasperata*, the situation is different: the optimal λ_{max} for one cone was still 510 nm, but the λ_{max} of the other would best be at very long wavelengths of 670–700 nm (although Fig. 7E does show a secondary rise in chromaticity variance when a short-wavelength pigment accompanies one with λ_{max} at 510 nm).

Table 1. *Summary of optimal peak sensitivity (λ_{max}) values for the middle-wavelength (M) and long-wavelength (L) pigments for discriminating fruit ripeness using each colour subsystem alone or using both subsystems*

	Peak sensitivity, λ_{max} (nm)					
	S-cone subsystem		M–L subsystem		Both subsystems	
	M	L	M	L	M	L
Chrysophyllum albidum	610	615	400	615	400	615
Celtis durandii	610	615	400	615	400	620
Diospyros abyssinica	625	630	495	635	495	635
Uvariopsis congensis	635	640	500	630	500	635
Ficus exasperata	510	515	510	700	510	700
F. natalensis	520	525	400	525	400	525
F. dawei	545	550	400	550	400	550
F. capensis	400	700	500	700	500	700
F. asperifolia	695	700	505	700	505	700
Dovyalis macrocalyx	645	650	465	650	465	650
Rubus apetalus	695	700	480	640	475	640

Fig. 7C,F shows the combination of the variances in each subsystem and is a measure of the spread in the two-dimensional chromaticity diagram as the λ_{max} values of the L and M pigments vary. It is clear that the signal in the second colour subsystem dominates, and this is not just a result of the relative weighting favouring the second subsystem: it was true even when the relative sensitivity weightings of the two subsystems was reduced to 1:1, which is outside the plausible range. It is equally clear that, for discriminating amongst fruits of these species, the photopigments possessed by the primates (marked by the white square at 531, 561 nm) are a long way from optimal for either subsystem or for the combination of colour subsystems. Therefore, it can be concluded that catarrhine photopigments are not optimised for discriminating the ripeness of these fruits. The pigments possessed by the primates could not be made to appear optimal no matter how the weightings were changed. In the case of *C. durandii*, the optimal pigments remained in the top half of the plot, whereas for *F. exasperata* further increases to the S cone sensitivity produced two peaks of maximum variance, corresponding to the peaks for each subsystem, leaving a trough between them into which the primates' pigments fall.

Table 1 summarizes the results for the fruits whose colour space distributions have been presented above. In general, the ancient colour subsystem, with an S pigment at 430 nm, requires M and L pigments at very long wavelengths for optimal discrimination of fruit ripeness. The exceptions are *Ficus exasperata* and *F. natalensis*, which require M and L pigments centred on about 515 nm, and *F. dawei*, which requires pigments centred on about 545 nm (this is the only case, for any fruit species and either colour subsystem, in which the optimal pigments correspond closely to those possessed by catarrhines). This pattern of results can be explained by reference to the reflectance spectra shown in Figs 1, 3 and 5. For most fruit species, the largest change in reflectance occurs between 600 and 700 nm, and the largest difference in signal in the S cone channel between ripe and unripe fruits would therefore be produced by comparing a pigment sensitive in this spectral region with the S cone pigment (which is sensitive to a range of wavelengths where there is little change). However, in the case of the three fig species mentioned as exceptions, the largest change in reflectance occurs between 500 and 600 nm.

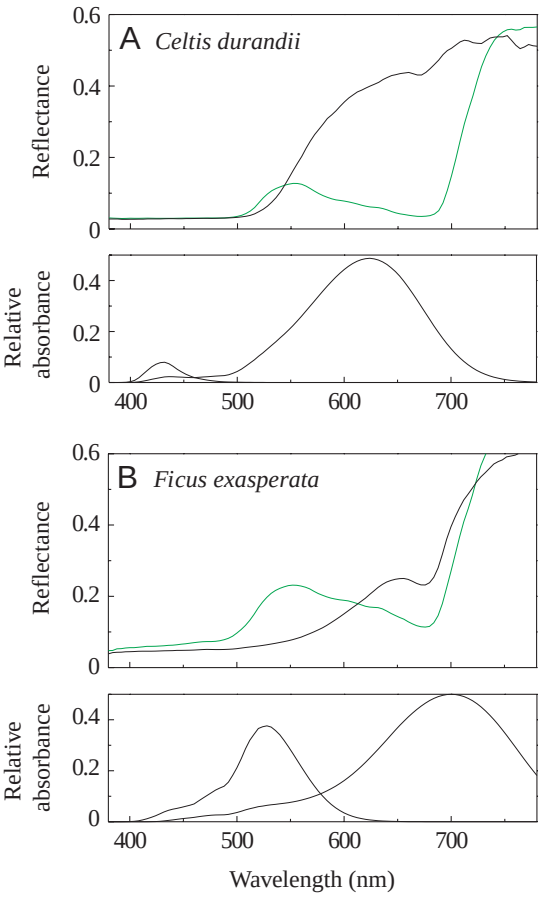

Fig. 8. The spectral positions of the optimal middle-wavelength (M) and long-wavelength (L) pigments (lower panels) for (A) *Celtis durandii* and (B) *Ficus exasperata* compared with sample reflectance spectra (upper panels) of unripe fruits (green line) and ripe fruits (black line).

The second colour subsystem always required widely spaced M and L pigments for optimal discrimination of fruit ripeness, and the results can again be explained by reference to the reflectance spectra. In cases such as *Chrysophyllum albidum* and *Celtis durandii*, which show no significant decrease in reflectance in any spectral region as they ripen, the largest difference in signal between ripe and unripe fruits is produced by comparing a pigment sensitive to wavelengths where there is most change (between 600 and 700 nm) with a pigment sensitive to the spectral region that shows least change below 500 nm. This is illustrated in Fig. 8A. In cases such as *Diospyros abyssinica*, *Uvariopsis congensis* and *Ficus exasperata*, in which a decrease in reflectance at some

wavelengths accompanies an increase at others, the largest contrast between ripe and unripe fruits is produced by comparing a pigment sensitive to the spectral region where most decrease occurs with a pigment sensitive to the region that shows most increase. As illustrated in Fig. 8B, for *F. exasperata*, the pigment sensitive to the wavelengths that show a decrease in reflectance should be positioned on the short-wavelength side of this region so that it is not sensitive where any increase in reflectance occurs. The other pigment should be positioned to the long-wavelength side of the region showing an increase in reflectance, in order to be sensitive to this increase but minimally sensitive where there is a decrease in reflectance. As expected, the results for *Ficus natalensis* were very similar to those for *F. exasperata*, but in Table 1 they do not appear to be so. This is because the results showed a 'double hump' for the second colour subsystem: large variances in fruit chromaticities were produced by positioning one pigment with λ_{max} at approximately 520 nm and having the other at either very long wavelengths or short wavelengths, and whereas for *F. exasperata* the long-wavelength hump was higher, for *F. natalensis* the humps were of equal height so that the optimal pigments happened to be 400 nm and 525 nm, but the second optimal pair was 525 nm and 700 nm.

As Fig. 7 shows, if the M and L pigments are constrained to be only 30 nm apart by other factors, it matters little what the values of their λ_{max} actually are for the task of discerning fruit ripeness using the second colour subsystem, whereas the S cone subsystem would favour longer-wavelength pigments for most fruit species for which the pattern of results were similar to those of *Celtis durandii*.

The results of the signal-to-noise analysis are not shown, but they conform to the above conclusions. In most cases, the pigments found to be optimal had λ_{max} values at much longer wavelengths than those possessed by the primates, and in the few exceptions for which the primates' pigments produced relatively high signal-to-noise ratios, pigments with λ_{max} values at longer wavelengths produced equally high ratios.

Unripe fruits contain chlorophyll, and their reflectance spectra are often indistinguishable from those of leaves. It might, therefore, have been expected that discriminating ripe fruit from unripe fruit would require the same photopigments as detecting fruit amongst leaves. However, for most species, only a subset of unripe samples has leaf-like reflectance because the fruits begin changing colour before the primates consider them ready to eat and, second, only a subset of leaf reflectance spectra resembles any unripe fruit spectra. In other words, the chromaticity distributions of leaves and unripe fruit overlap, but both categories contain samples that are unlike any in the other category. [Osorio (1996) has previously assumed that the spectra of unripe fruit can represent leaves.]

Size of fruits

The fruits in the diets of the Kibale primates ranged in size from 3 mm in length to nearly 200 mm, although the smallest ones tend to grow in clumps so the target size presented to the primate would be larger than the individual fruits. Nevertheless, for any given difference from the background in chromaticity or luminance, the larger fruits would be more visible. Therefore, assuming that there is a cost to the plant in changing the colour of fruits from that given by chlorophyll (either a manufacturing cost of a different pigment, or because photosynthesis in the fruits is impeded) for the fruits that are disseminated by primates, we should predict an inverse correlation between the size of the ripe fruits and the chromaticity or luminance difference from the leaves or the unripe fruits: small fruits need to be more different from their background if they are to be equally visible to a primate. In addition, it would be much more time-consuming to test small fruits by touch than it would to test large fruits. We have calculated the correlations between ripe fruit size (average of length and width) and the absolute difference between the ripe fruit value and the average mature leaf value on the three axes of the catarrhine colour space (the understorey fruit were not included because they tend to have large colour signals regardless of size, presumably because of the lower light levels of their environment). There was no correlation between size and luminance, a small negative correlation between size and S axis signal (Spearman rank correlation coefficient, s_r=–0.28, P<0.05 one-tailed) and a more significant negative correlation between size and the signal in the $L/(L+M)$ axis (s_r=–0.39, P<0.005). Luminance and S cone signal would not be good cues for detecting fruits in mature leaves because of the large variance of the leaves on these axes. The axis that does provide a good cue for spotting fruits, $L/(L+M)$, shows a negative correlation between the magnitude of the signal and fruit size.

We have also calculated the correlations between fruit size and the absolute ripe fruit–unripe fruit difference, for all three colour space axes. There was a significant (P<0.005) negative correlation in each case [s_r=–0.53, –0.73 and –0.52 for $S/(L+M)$, $L/(L+M)$ and $L+M$, respectively]. It was concluded above that the signal in both colour subsystems and also in luminance could be useful for discriminating ripe from unripe fruits in many plant species, and here it is shown that the magnitude of these signals tends to be larger if the fruits are smaller.

An alternative explanation for the correlation between size and chromaticity would be that the large and small fruits are part of different 'dispersal syndromes'. The fruits that birds take tend to be small and red, whereas the fruits commonly taken by primates are often larger and yellow (Gautier-Hion et al., 1985; Janson, 1983; Julliot, 1996). Therefore, rather than being directly dependent on each other, the colour and the size of a fruit would be seen as both being dependent on another factor, the disperser, for different reasons: the vision of the disperser might determine the colour of the fruit, but the size of the fruit would be determined by the ability of the disperser to carry it, bite it or digest it, and not by any visual factors.

Concluding remarks

Although the ripeness state of many fruit species can be discriminated using luminance or the ancient colour subsystem, when the catarrhine M and L pigments first diverged, the newly possible second colour channel would

have offered an additional advantage in discriminating the ripeness of most fruits. Nevertheless, the sensitivities of the M and L cones have not been selected to maximise the variation in the fruit signals. The ability to discern fruit ripeness may, therefore, have been an important selective pressure in catarrhines for the development and maintenance of trichromacy over the supposed ancestral dichromacy, but other factors must have been important in determining the exact form that catarrhine trichromacy has taken.

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