

EVOLUTION AND FUNCTION OF ROUTINE TRICHROMATIC VISION IN PRIMATES

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Abstract.—Evolution of the red-green visual subsystem in trichromatic primates has been linked to foraging advantages, namely the detection of either ripe fruits or young leaves amid mature foliage. We tested competing hypotheses globally for eight primate taxa: five with routine trichromatic vision, three without. Routinely trichromatic species ingested leaves that were “red shifted” compared to background foliage more frequently than species lacking this trait. Observed choices were not the reddest possible, suggesting a preference for optimal nutritive gain. There were no similar differences for fruits although red-greenness may sometimes be important in close-range fruit selection. These results suggest that routine trichromacy evolved in a context in which leaf consumption was critical.

Key words.—Cone, diet, folivory, foraging, frugivory, opsin, retina.

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Color perception requires photoreceptors with differing spectral sensitivities and opponency mechanisms for comparing their outputs (Dacey 2000). Four photopigment opsins in birds, reptiles, and teleost fish indicate that the common ancestor of tetrapods and amniotes had tetrachromatic vision (Bowmaker 1998). Today, most mammals possess dichromatic vision, having only two opsins maximally sensitive to short and long wavelengths (Kelber et al. 2003). Because color vision is relatively poor at low light levels, it is reasoned that mammals lost opsins during the nocturnal phase of their evolution. Primates, however, are unique among eutherians for possessing as many as three opsins (Ahnelt and Kolb 2000; Arrese et al. 2002). Remarkably, the anatomy varies greatly within the order (SurrIDGE et al. 2003).

Variation in Primate Color Vision

Catarrhines (Old World monkeys, apes, and humans) are considered routinely trichromatic. That is, both males and females possess three opsins maximally sensitive to short (about 430 nm), middle (about 530 nm), and long (about 560 nm) wavelengths (Bowmaker et al. 1991; Jacobs and Deegan 1999). The genes coding for each opsin (conventionally abbreviated as S, M, and L) are located on chromosome 7 and adjacent sites on the X-chromosome, respectively (Nathans et al. 1986). Cone outputs are processed into two separate visual systems: the S-cone mediated “blue-yellow” subsystem and the phylogenetically recent “red-green” subsystem (Regan et al. 2001). Colorblind males (i.e., those lacking a cone pigment) are few, suggesting that strong selective pressures are maintaining catarrhine trichromacy (Onishi et al. 1999; Jacobs and Williams 2001).

In platyrrhines (New World monkeys), color vision varies dramatically. Although they share an S photopigment encoded by an autosomal gene with catarrhines, platyrrhines have only a single X-chromosome M/L opsin gene locus. Males always receive one M/L photopigment, which when added to the S photopigment yields dichromatic vision. However, this gene locus is often polymorphic with two to three alleles, rendering a proportion of platyrrhine females heterozygous (Jacobs and Nietz 1987; Jacobs and Deegan 2001) with trichromatic vision (Mollon et al. 1984). Three alleles in a population produce up to three dichromatic and three trichromatic phenotypes and thus six distinct kinds of color vision in females (SurrIDGE et al. 2003). Although this polymorphism appears to be maintained by a selective advantage, the mechanism is unclear (Cropp et al. 2002; SurrIDGE and Mundy 2002). Here we use the term “non-routine trichromatic species” to describe this state.

Among platyrrhines there are two exceptional genera. Night monkeys (*Aotus*) have lost functional S photopigments and polymorphic variation of the M/L opsin gene. Accordingly, these nocturnal anthropoids possess a single L pigment and cannot perceive color (Jacobs et al. 1993). Equally intriguing are howling monkeys (*Alouatta*), which are routinely trichromatic (Jacobs et al. 1996a). The opsin gene duplication in *Alouatta* is similar to catarrhines but exists independently (Boissinot et al. 1998; Kainz et al. 1998; Dulai et al. 1999).

Lastly, allelic variation has been reported in tarsiers and strepsirrhines (Tan and Li 1999). The presence of both M and L alleles in Coquerel's sifakas (*Propithecus verreauxi coquereli*) and red ruffed lemurs (*Varecia variegata rubra*) predicted trichromacy in heterozygous females. This was later confirmed in *P. v. coquereli* and *V. v. variegata* (Jacobs et

TABLE 1. The primate species studied and a summary of their diets during the study period. The fruit category includes fruits and seeds; the leaf category includes petioles and stalks.

Species	Field site	Hours of observation	Diet (% feeding time)			Leaf detection sample size	Fruit detection sample size
			Fruit	Leaves	Flowers		
Non-routine trichromats/dichromat							
<i>Lemur catta</i> (ring-tailed lemur)	Beza Mahafaly (Madagascar)	247	31	44	15	113	40
<i>Propithecus verreauxi verreauxi</i> (sifaka)	Beza Mahafaly	242	16	69	15	259	36
<i>Ateles geoffroyi</i> (red spider monkey)	Marengo (Costa Rica)	460	56	15	27	19	77
	Murcielago (Costa Rica)	503	75	18	2	32	249
Routine trichromats							
<i>Alouatta palliata</i> (mantled howler monkey)	Marengo	456	19	81	0	25	96
	Murcielago	595	29	63	6	200	129
<i>Pan troglodytes</i> (chimpanzee)	Kibale (Uganda)	58	83	8	0	18	32
<i>Cercopithecus ascanius</i> (red-tailed monkey)	Kibale	330	42	41	7	63	20
<i>Ptilocolobus badius</i> (red colobus)	Kibale	412	86	11	2	69	13
<i>Colobus guereza</i> (black and white colobus)	Kibale	378	91	7	1	141	16

al. 2002; Jacobs and Deegan 2003a). However, reduced cone densities and the absence of a *fovea centralis* may yield a trichromacy inferior to that in heterozygous platyrrhines. Notably, the prosimian M/L cone opsin polymorphism is not inexorably linked to diurnality; *Lemur catta* lacks the potential for allelic trichromacy (Jacobs and Deegan 2003b). Finally, the bush babies (Galagonidae) are monochromatic: they lack S photopigments and possess only a single cone maximally sensitive to 543 nm (Deegan and Jacobs 1996; Jacobs et al. 1996b; Zhou et al. 1997).

Adaptive Hypotheses

What selective advantage does trichromacy bestow on a primate species (or individuals within a species)? Suggestions have focused on feeding, with the oldest advocating advantages of detecting ripe fruits against a verdurous background of mature foliage (Allen 1879; Mollon 1989). Most large primates have a fruit-dominated diet (Fleagle 1999), offering apparent support, but a recent alternative suggestion submits that trichromacy evolved to recognize young leaves against the same background (Lucas et al. 1998). Here we examine these hypotheses on an unprecedented scale, reporting globally on the visual feeding ecology of eight primate taxa: five with routine trichromacy, three without.

MATERIAL AND METHODS

Ripening fruits and developing leaves of tropical plants often produce red-green signals distinct from mature leaves, possibly supporting both hypotheses (Sumner and Mollon 2000a,b; Dominy and Lucas 2001). Of course, in either case the unique selective advantage of trichromacy is likely to lie in detecting foods at distances (≥ 20 m in a forest) beyond the useful range of most other senses (Dominy et al. 2001). Color may also be useful at much shorter distances (< 1 m), but then it complements other senses (Dominy et al. 2001). Therefore, we focus here on long-distance color cues for identifying potential food targets against background scenery. We refer to this as "food detection" and distinguish it from close-range decisions regarding several similar items, which we call "food selection."

We studied annual feeding behaviors in eight primate species at four tropical sites; observational protocol was standardized and totaled 3681 h (Table 1). Focal animals were observed and selected randomly every 10 min at Beza Mahafaly, Madagascar, and Kibale, Uganda, whereas at Marengo and Murcielago, Costa Rica, observational bouts were reduced to 2 min because animals were frequently lost quickly from view. Five primate taxa possessed routine trichromacy and three did not. Each site had an approximate frugivore: folivore balance and sympatric spider and howling monkeys were studied in both wet (Marengo) and dry (Murcielago) forests (Table 1). Reflectance spectra, toughness, and protein of selected food specimens, nonselected food items, and background foliage were recorded (Lucas et al. 2001). Fruit sugars were estimated from total fructose, glucose, and sucrose concentrations present in extracts (Lee 1990).

To permit color comparisons on a uniform basis, we decoded reflectance spectra into the color signals of routine trichromats (Osorio and Vorobyev 1996) and calculated color differences for consumed fruits and leaves from their collective background. Some foods were sensed against other backgrounds, principally in Beza and Murcielago, where many plant species are deciduous during the dry season. These data are excluded from our analysis. Specimens defined as food were usually partially consumed items mishandled by primates: these were detected on a visual basis. Additional samples were obtained by ascending vacated trees, by sling-shot, or, at sites with low canopies (e.g., Beza and Murcielago), with extendable shears, looking for items with fresh evidence of primate incision. Mature foliage and nonselected items were collected whenever possible, but the latter were difficult to obtain. The study was observational, not experimental, so it must be expected that dichromats, without red-green capability, would consume foods with red-green values distinct from their background. They would not be cognizant of doing this, but the differences can be explained as a correlate of some other sensory characteristic. Support for either feeding hypotheses therefore cannot simply postulate the existence of these differences, but rather a statistically greater frequency of food items with distinct red-green signals in the diet of routine versus nonroutine trichromats.

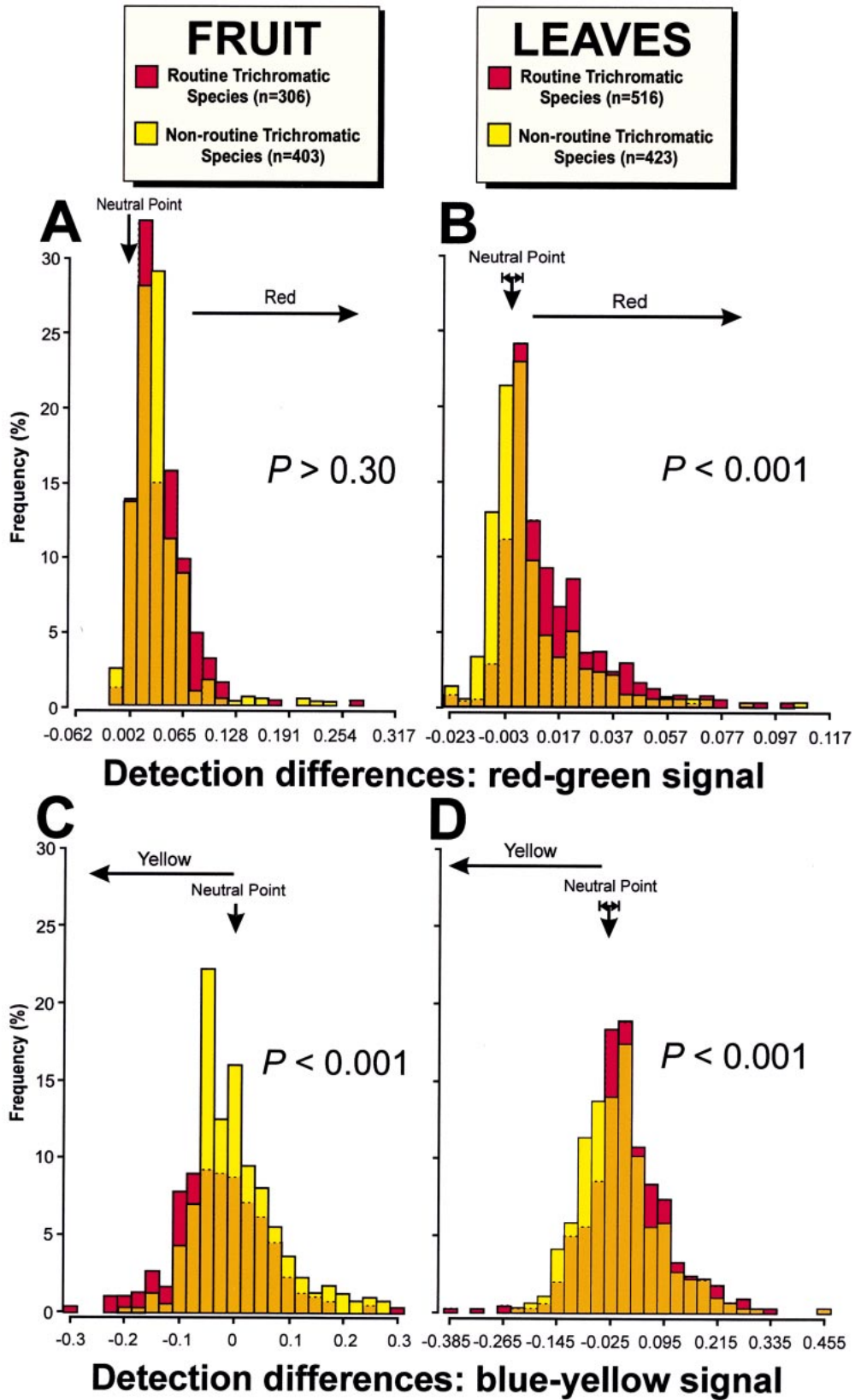


FIG. 1. Routinely trichromatic primates make differential use of the red-green signal (top row) for detecting leaves (right column), not fruits (left column). Histograms show chromatic differences between individual foods and the foliage background for that food. Choice overlap between the two primate groupings is shown as brown: trends can be spotted by looking for directionality in yellow or red bin tips with respect to neutral. The vertical arrow represents chromatic identity between food item and mature leaf. Background variability

RESULTS

Red-green differences were heavily skewed toward red. Routine trichromatic taxa consumed significantly greater quantities of “red-shifted” leaves than nonroutine trichromats (Fig. 1B), but there were no significant differences for fruits for this color channel (Fig. 1A) despite these fruit signals being more variable. Blue-yellow differences were not skewed. Routine trichromats chose significantly yellower fruits (Fig. 1C), but nonroutine trichromats chose yellower leaves (Fig. 1D). Detection differences corresponded with nutritional value. Leaves consumed by both groups of primates had a protein:toughness ratio—a key indicator of leaf quality (Dominy and Lucas 2001)—twice as large as those of the mature leaves against which they were detected. These ratios were significantly larger in leaves consumed by routine trichromats than the other primates (Kolmogorov-Smirnov $Z = 1.393$; $P < 0.05$) and, in the entire sample, positively correlated with red-green differences ($r = 0.31$, $P < 0.001$; $n = 110$), but not with blue-yellow ($r = 0.09$, $P > 0.09$).

Intuitively, intracrop selection of either fruits or leaves involves finer color distinctions than detection (Fig. 2). Significant differences in the use of the red-green color signal between primate groupings were found for both fruits and leaves, but differences for selection were much less skewed than for detection (compare Fig. 1D with Fig. 2D). Routine trichromats selected red-shifted fruits significantly more frequently than neighboring alternatives (Fig. 2B), but selected significantly greener leaves (Fig. 2C), although these were still redder than the background. Differences in total sugars between selected and non-eaten fruits were significantly positively correlated with differences in both color signals (red-green: $r = 0.38$, $P < 0.001$; $n = 81$; blue-yellow: $r = 0.42$, $P < 0.001$; $n = 84$).

DISCUSSION

Nutritional data support the value of foraging for tropical leaves on a trichromatic basis. Many tropical plants delay greening their leaves until full expansion, probably to evade invertebrate herbivory (Kursar and Coley 1992). When young, these tender leaves are pale or red, but have little nutritive content (Coley and Kursar 1996). The subsequent extensive development of active chloroplasts results in a strong red-green signal (Lucas et al. 1998; Sumner and Mollon 2000a). Most herbivory, whether by vertebrates or invertebrates, is conjectured to occur at this stage, when nutrients are both readily assimilated and easily accessed, because toughness remains low. The capacity to detect red-shifted leaves at a distance may alert a primate to the greening process. At close quarters, however, the differentiation of greening leaves from those at younger stages requires preference for a green shift (i.e. using the red-green signal, but

reversing the direction of attention). Accordingly, red-green changes in leaves are small compared to fruits, which may account for the increased foveal acuity of the red-green subsystem (Roorda and Williams 1999; Mullen and Kingdom 2002).

Fruits, however, are initially “leaf green” but ripen to a wide variety of colors in which a red shift is only one possibility (Willson and Whelan 1990). In this regard, few fruits are probably specifically targeted at primates. Indeed, primates evince no fidelity to any specific fruit hue, regardless of the proportion of trichromatic individuals (Dominy 2004). The adaptive value of red-green color sensitivity may thus lie in the spatial distributions of potential foods. In tropical rain forests, tree crowns generally releaf asynchronously. Small crown areas flush leaves, which then develop rapidly, quickly passing the stage at which primates target them as a food source. This results in crowns with highly variegated, even dappled, appearances. Nearby conspecifics may not releaf in unison, and so the advantage of perceiving red-greenness in a tropical forest may be to identify small, spatially irregular, leaf-food patches large enough to accommodate one to two individuals. This would result in selective pressure on individual pairs of eyes within a troop. Fruit patches, in contrast, are larger because their development is generally synchronized at the species taxonomic level. Thus, if a primate group locates just one fruiting tree at an acceptable developmental state, individuals may use spatial memory (Garber 1989; Janson 1998) to locate additional conspecifics. One heterozygous female in a troop might suffice to locate this hypothetical “first tree,” identifying a food patch capable of accommodating most group members. Indeed, the emission of food-related vocalizations is common among platyrrhines (Dominy et al. 2001). Accordingly, nonroutine trichromacy may be sufficient for frugivory on well-synchronized sources.

Why Not Routine Trichromacy in All Primates?

The gene duplication producing routine trichromacy may be improbable, occurring independently among catarrhines and *Alouatta*, but not other lineages. Under this hypothesis, platyrrhine variation is maintained by *heterozygous advantage*. That is, the female heterozygote enjoys advantages for detecting conspicuous foods, such as ripe fruits (Mollon 1989) or insects (Surrige and Mundy 2002). The latter suggestion (an advantage to female heterozygotes in detecting insects) seems implausible given that several platyrrhine genera (including *Ateles*, *Cebus*, *Chiropotes*, *Lagothrix*, and *Pithecia*) possess an allelic trichromacy but seldom consume isolated insects (Rosenberger 1992; Jacobs and Deegan 2003c). With respect to fruits, the experiments of Caine and Mundy (2000) demonstrate that trichromatic marmosets do have an advantage in detecting orange objects against a green

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(horizontal range, illustrated in the right column only, shows 1 SD) was comparatively negligible. Distributions were obtained by calculating cone excitations from individual reflectance spectra relative to a standard white reflector. Red-green [$L/(L + M)$] and blue-yellow [$S/(L + M)$] signals are the (dimensionless) ratios of short (S), medium (M) and long (L) wavelength cone outputs (Osorio and Vorobyev 1996; Regan et al. 2001). Histograms show the color difference that separates the background mature foliage from the food item. P -values are from Mann-Whitney tests.

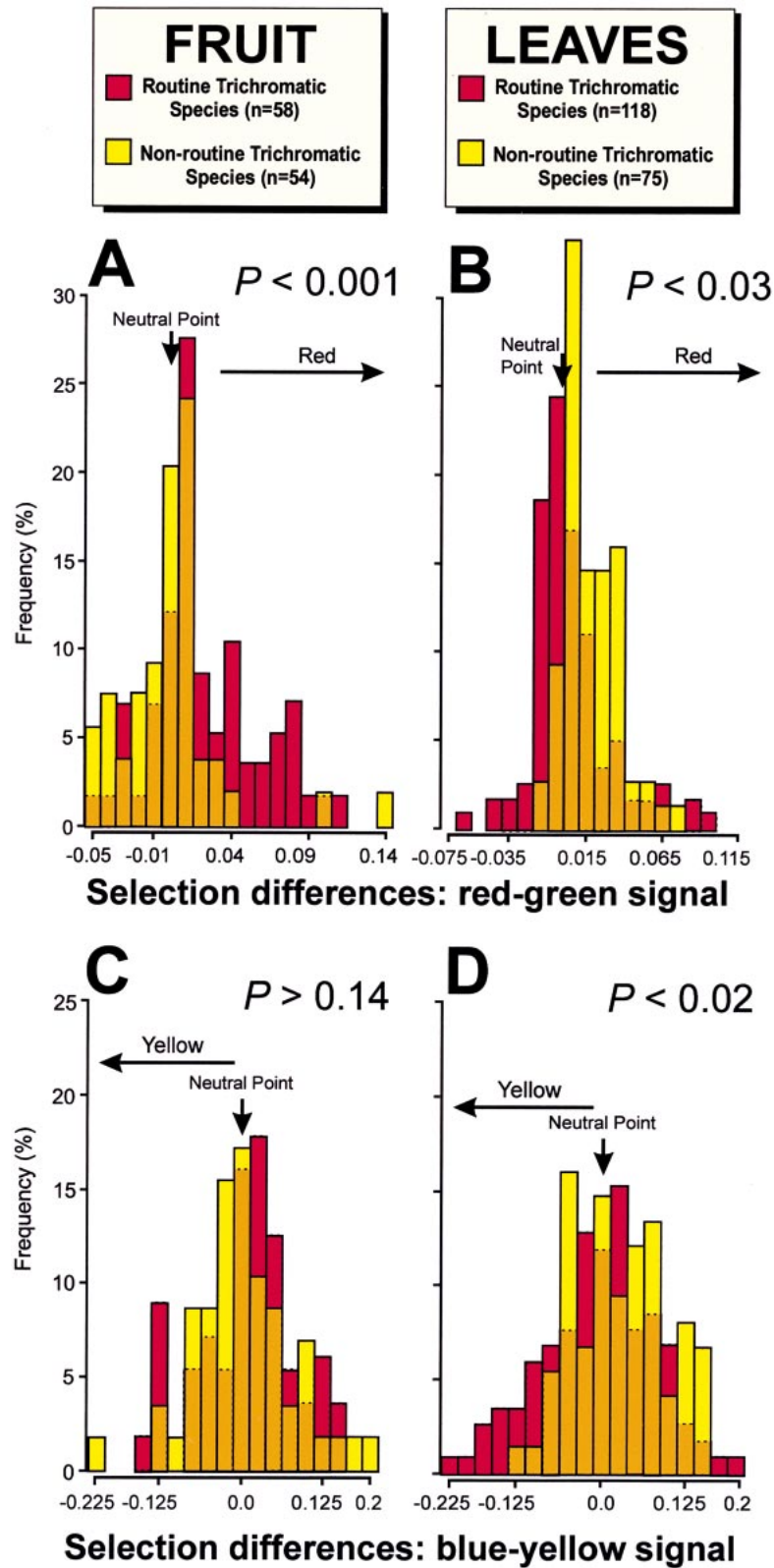


FIG. 2. Chromatic differences between selected (eaten) and nonselected (presumptively rejected) fruits and leaves. Routine trichromatic primates more frequently ate red-shifted fruits, but green-shifted leaves, than neighboring alternatives. P -values are from Mann-Whitney tests.

background at distances >0.5 m. However, recent foraging experiments with tamarins failed to support the ripening fruit hypothesis with respect to improved detection of bananas (Dominy et al. 2003a). Accordingly, the evolutionary persistence of allelic trichromacy in highly frugivorous primates (SurrIDGE and Mundy 2002) may be associated with seasonal periods of fruit dearth, when orange and red fruits could represent important fallback resources to heterozygous females. Although nonhuman primates seldom prefer fruits of these hues (Dominy 2004), such fallback foods may play a key role in determining the feeding adaptations of primates (Terborgh 1983). Indeed, in birds, feeding adaptations to critical resources can occur rapidly (Grant and Grant 2002).

Alternatively, the M/L cone opsin polymorphism may be maintained by *frequency-selective advantage*. That is, conspecific dichromats may incur some advantages over individual trichromats. A variety of anecdotes and one empirical study suggest that reduced “chromatic noise” enables dichromats to better break camouflage (Morgan et al. 1992), including, potentially, cryptic predators or foods (Caine 2002). In this regard, the primate M/L cone opsin polymorphism may be maintained by advantages conferred on both dichromats and trichromats. Kin selection could favor a diversity of phenotypes within a foraging group because detection of all foods, both cryptic and conspicuous, is improved (Tovée 1993).

Evolutionary Synthesis

Climatic changes during the Eocene–Oligocene transition may be linked to the global variation in primate color vision. Dominy et al. (2003b) proposed that primates invaded Paleogene forests characterized by figs and palms, the fruits of which played a keystone function (Terborgh 1986). On the basis of character optimization, Paleogene primates were routine dichromats or allelic trichromats (Heesy and Ross 2001; SurrIDGE et al. 2003). They may have relied on figs and palms and provided high-quality seed dispersal. In turn, figs and palms lost or simply did not evolve conspicuous hues (Dominy et al. 2003b), as this conferred little advantage for attracting mammals. Accordingly, advantages may have been conferred on dichromats for detecting cryptic figs and palms as well as on heterozygous females for detecting conspicuous fruits. The abundance and hue of figs and palms may have offered a selective advantage to foraging groups with mixed capabilities for chromatic distinction. However, by the end of the Eocene and into the Neogene, climatic cooling resulted in widespread regional extinction or decimation of palms and (probably) figs (Morley 2000). These changes attended dietary shifts among paleotropical mammals: terrestrial frugivores gradually shifted to grazing (Collinson and Hooker 1991) and arboreal primates began to rely on leaves (Kirk and Simons 2001).

Thus, in regions where figs and palms became scarce, primates appear to have evolved routine trichromatic vision in order to exploit proteinaceous young leaves as a fallback resource. A survey of the color and biogeography of extant figs and palms provides empirical support (Dominy et al. 2003b). Where these resources are infrequent, primates are routinely trichromatic and consume young leaves during sea-

sonal periods of fruit dearth (Doran 1997; McConkey et al. 2003). In fact, at least one gene duplication facilitating folivory in colobines is well established (Zhang et al. 2002), indicating that adaptations to leaf consumption play an important role in catarrhine evolution. The results reported here are consistent with this scenario, suggesting that routine trichromacy evolved in a context in which leaf consumption was critical.

Future Directions

Exceptions provide important tests: sifakas are folivores with nonroutine trichromacy. The sifaka studied here lives at the extremes of the tropics in a dry forest site with many deciduous trees. We predict from the above that the synchrony of releasing far from the equator reduces pressure for all individuals to be trichromatic. Delayed greening appears to be rare in such sites (Dominy et al. 2002). We conclude that the red-green signaling pathway evolved for leaf consumption and that any specific targeting of primates as fruit dispersers by color postdates the advent of routine trichromacy. However, food resource synchronization is of paramount importance. Finally, whether allelic trichromacy is maintained by frequency-selective advantages in detecting camouflaged prey/predators (Tovée 1993; Caine 2002) or keystone fruits (Dominy et al. 2003b) remains to be determined.

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