



Do female tamarins use visual cues to detect fruit rewards more successfully than do males?

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Primates are unique among eutherian mammals for possessing trichromatic colour vision. It is generally proposed that trichromacy evolved to aid detection of ripe fruits against mature foliage. However, while trichromacy is routine in all Old World monkeys and apes (the catarrhines), a cone opsin polymorphism in New World monkeys (the platyrrhines) results in foraging groups with mixed capacities for chromatic distinction. Although 50–66% of female platyrrhines are trichromatic, all males are dichromatic. Here, we test the hypothesis that trichromatic platyrrhines use visual cues to detect fruit rewards more successfully than do males. Specifically, we ask whether female emperor tamarins, *Saguinus imperator imperator*, and saddleback tamarins, *S. fuscicollis weddelli*, are the first members of their foraging group to locate food patches; and, furthermore, whether they are more successful than males in using colour, shape and size cues to discriminate between sham and reward feeding sites. Our results show that females and males do not differ in their ability to locate or discriminate between feeding sites. We conclude that trichromatic vision in female tamarins does not confer an advantage for detecting yellow fruit rewards against mature foliage.

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Colour vision is based on the presence of multiple cone photoreceptors maximally sensitive, or tuned, to different regions of the spectrum. Among eutherians, only primates possess trichromatic vision, or three types of cone opsin sensitive to 424–434, 531–539 and 562–568 nm (Ahnelt & Kolb 2000; Arrese et al. 2002; Kelber et al. 2003). However, there is considerable variation in the spectral tuning and number of cone opsins among primates (Surridge et al. 2003). Accordingly, the colour perception that different combinations of cone opsins render (and why) is a central issue in primate behaviour and evolution (Dominy et al. 2001).

Among anthropoids, trichromatic vision is routine in catarrhines (Old World monkeys, apes and humans). That is, trichromatic vision is uniform in both males and females because the genes coding for each opsin (abbreviated as S, M and L due to their short-, middle- or long-wavelength absorption) are located on chromosome 7 and neighbouring sites on the X chromosome (Nathans et al. 1986; Jacobs & Deegan 1999). Dysfunction of M/L cone opsins seldom occurs in nonhuman catarrhines (Onishi et al. 1999; Jacobs & Williams 2001).

In platyrrhines (the New World monkeys), the nature of colour vision is quite different. Although platyrrhines share with catarrhines the S opsins specified by an autosomal gene, they possess only a single X chromosome opsin gene locus. This results in polymorphic variation such that males and females differ in their capacity for colour perception. In males, the S opsin allele conjoins with a single type of M/L opsin allele. Accordingly, all males possess dichromatic colour vision. Among females, however, approximately 50–66% of individuals are heterozygous for the M/L opsin allele and possess three dissimilar cone opsins, a condition rendering full dichromacy (Mollon et al. 1984; Jacobs & Deegan 2001).

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Finally, in platyrrhines thoroughly studied, there is di- or triallelic variation on the X chromosome (i.e. there are as many as three dichromatic and three trichromatic phenotypes, rendering up to six distinct kinds of colour vision; Jacobs & Deegan 2001 and references therein). Although the mechanisms remain unclear, allelic trichromacy in callitrichines and squirrel monkeys (*Saimiri* spp.) appears to be maintained by an adaptive advantage (Cropp et al. 2002; Surridge & Mundy 2002). In callitrichines, the M/L opsin alleles are maximally sensitive to 543 nm, 556 nm and 563 nm (Surridge & Mundy 2002).

Among platyrrhines there are two exceptions to this general pattern. Night monkeys (*Aotus*) have not only lost functional S cone pigments, but also polymorphic variation in the M/L opsin gene. Accordingly, they possess a single pigment and cannot perceive colour (Jacobs et al. 1993). This inability to perceive colour is likely to be associated with the fact that night monkeys are secondarily nocturnal and are the only species of anthropoid habitually active at night (Wright 1989). Equally intriguing are the howling monkeys (*Alouatta*), which are routinely trichromatic (Jacobs et al. 1996a). The gene duplication of the X-chromosome opsin in *Alouatta* is similar to that in catarrhines, but occurred independently (Boissinot et al. 1998; Kainz et al. 1998).

Tan & Li (1999) reported allelic variation of the M/L opsin gene in tarsiers and some prosimians. Their results predicted allelic trichromacy in Coquerel's sifaka, *Propithecus verreauxi coquereli*, and red ruffed lemurs, *Varecia variegata rubra*. Jacobs et al. (2002) and Jacobs & Deegan (2003a) have since confirmed this potential in the heterozygous females of *P. v. coquereli* and *V. v. variegata*. Notably, some diurnal prosimians lack the potential for allelic trichromacy (e.g. *Lemur catta*; Jacobs & Deegan 2003b). Lastly, galagos possess only one cone opsin tuned to 543 nm (Jacobs et al. 1996b; Zhou et al. 1997).

The maintenance of three opsin alleles among callitrichines for 14 million years implies an adaptive advantage (Surridge & Mundy 2002). Because trichromatic vision allows individuals to discriminate between foliage and objects reflecting long, yellow to reddish wavelengths (Osorio & Vorobyev 1996; Regan et al. 2001; Párraga et al. 2002), a heterozygous advantage in detecting ripe fruits is hypothesized to maintain the M/L cone opsin polymorphism in primate populations (Mollon 1989). Indeed, Caine & Mundy (2000) recently reported a foraging advantage for trichromatic marmosets (*Callithrix geoffroyi*). In their experiment, captive marmosets competed for orange- and green-coloured breakfast cereal scattered or concealed in green pine shavings from varying distances. Trichromatic females detected more orange cereal within 6.0 m than did dichromats, but did not differ from dichromats in their rate of detection and ingestion of orange cereal within 0.5 m. Although these results are intriguing, and although female *Varecia* lead foraging groups to food patches (Erhart & Overdorff 1999; Overdorff et al. 2002), no study has explicitly evaluated the hypothesis that heterozygous females use visual cues to detect fruits more successfully than do males (but see Smith et al. 2002).

Here we report the results of an experimental field study of foraging strategies in two species of tamarin in northwestern Brazil. Specifically, we examined the ability of males and females to use ecological information when foraging. We addressed the following questions.

(1) Are female tamarins the first member of their foraging group to locate feeding sites?

(2) Are female tamarins more successful than male tamarins in using available visual cues to discriminate between reward and sham feeding sites?

(3) Does tamarin foraging behaviour support the hypothesis that trichromatic colour vision in females results from an advantage in detecting fruit resources?

METHODS

Study Site and Species

We studied saddleback tamarins, *Saguinus fuscicollis weddelli*, and emperor tamarins, *S. imperator imperator*, at the Zoobotanical Park (9°56'30"–9°57'19"S, 67°52'08"–67°53'00"W), a 100-ha protected research facility administered by the Federal University of Acre (UFAC), Rio Branco, Acre, northwestern Brazil. In addition to the tamarins, four other primate species also inhabit the site: red titi monkeys, *Callicebus cupreus cupreus*, southern red-necked night monkeys, *Aotus nigriceps*, pygmy marmosets, *Cebuella pygmaea*, and Bolivian squirrel monkeys, *Saimiri boliviensis boliviensis* (C. Calegario-Marques & J. C. Bicca-Marques, unpublished observations).

We studied three social groups of emperor tamarins (IMP 'A': 4–5 individuals; IMP 'B': 5 individuals; IMP 'K': 7–8 individuals) and three social groups of saddleback tamarins (FUS 'A': 4–6 individuals; FUS 'C': 5–6 individuals; FUS 'E': 9–10 individuals; Table 1). Individuals were captured, identified by age and sex, and individually marked with colour-coded beaded collars (Bicca-Marques 2000).

Research Design

The research design involved the construction of feeding stations within the home range of all study groups. Feeding stations were positioned 58–256 m apart, and each represented an independent food patch with its own distribution of food items and patterns of resource renewal. Each feeding station contained eight visually identical feeding platforms (30 × 45 cm) in a circular arrangement. Adjacent platforms were approximately 5 m apart and placed 1.5 m above ground. A blind placed 5 m from the nearest platform was used to observe the behaviour of the monkeys at each feeding station.

After a 10-day period of prebaiting, we initiated a series of field experiments (feeding trials; Bicca-Marques 2000) to test the tamarins' abilities to use visual and spatial information to locate feeding sites. In each experiment, we systematically manipulated the information available to the monkeys in order to present them with a set of foraging problems analogous to those naturally encountered in the wild. In each experiment, two platforms at

Table 1. Age and sex composition of the emperor and saddleback tamarin study groups (excluding dependent young)

Species/group	Age-sex class	ID	%Total group searches*	
Emperor tamarins	IMP A	Adult male	IA-AMA	
		Adult female	IA-PNK	Finder (40.0%) $P < 0.001$
		Subadult male	IA-BRA	Finder (45.2%) $P < 0.001$
	IMP B	Juvenile male	IA-LAR	
		Adult male	IB-VRM†	
		Adult male	IB-VEP	Finder (23.4%) $P < 0.05$
		Adult female	IB-REP	
		Adult female	IB-AZL	Finder (30.8%) $P < 0.001$
	IMP K	Juvenile female	IB-PRO	
		Adult male	IB-VRM†	Finder (43.2%) $P < 0.01$
		Adult male	IK-CAZ	
		Adult male	IK-CAC	
		Adult female‡	IK-CRO	
		Adult female	IK-COX	
		Subadult male	IK-CLA	
Saddleback tamarins	FUS A	Juvenile female	IK-CVE	
		Juvenile female	IK-CBR	
		Adult male	FA-AZL	
	FUS C	Adult male	FA-BRA	Finder (43.0%) $P < 0.001$
		Adult female	FA-ROS	Finder (30.2%) $P < 0.001$
		Immature male	FA-AMA	
		Adult male§	FC-VER	
		Adult male	FC-VRM	
		Adult female	FC-AEP	
		Adult female	FC-COR	
	FUS E	Juvenile female	FC-LAR	Finder (66.7%) $P < 0.001$
		Juvenile female	FC-REB	
		Adult male	FE-AMC	
		Adult male	FE-AZA	
		Adult male	FE-ROV	
		Adult male	FE-VBV	
		Adult male	FE-VRA	
		Adult female**	FE-ROA	
		Subadult male	FE-AZB	
		Subadult male	FE-VEB	
Subadult female††	FG-CIV			
Juvenile female	FE-MAM			

*Values in parentheses represent the percentage of total group searches performed by the individual that was statistically significant ($P < 0.05$) by a Z test of two percentages for that group, based on the assumption that all group members search equally. See text for details.

†IB-VRM was originally a member of group IMP B, but became a member of group IMP K when group IMP K occupied part of the same range that was previously occupied by group IMP B. IB-VRM was the only individual that was present in a study group in both 1998 and 2001.

‡Emperor tamarin adult female IK-CRO disappeared from the group during the study.

§Adult male FC-VER died and therefore was present in the group during only 31 of 125 days of data collection. Data from this adult male were not used in the analysis.

**Saddleback tamarin adult female FE-ROA disappeared from the group during the study.

††Saddleback subadult female FG-CIV migrated into the group during the study.

each feeding station contained a food reward (a real banana) and the remaining six platforms were baited either with plastic (sham) bananas or with inaccessible real bananas inside wire mesh cages depending on experimental protocol. Both plastic bananas and inaccessible real bananas inside wire mesh cages are referred to as 'sham sites' because each fails to provide foragers with a food reward. To simulate a natural foraging task, all bananas were placed against a background simulating the colour and shape of a large mature leaf.

Although the appearance of real bananas may reflect the attentions of plant breeders aiming for a highly

saturated hue, we used real and sham bananas because of their availability, their appeal to tamarins and their chromatic similarity to fruits frequently consumed by platyrrhines (Janson 1983; Defler & Defler 1996), including tamarins (Lambert & Garber 1998). Moreover, the hue of ripe bananas appears suited to testing the sensory differences between dichromats and trichromats. Despite the impossibility of reconstructing the perceptual world of a tamarin, studies modelling primate photoreceptors are informative. For example, the yellow-blue visual subsystem of dichromats, which is mediated by S cone photoreceptors, may allow individuals to distinguish

some fruits as slightly more yellow than mature foliage (Sumner & Mollon 2000a, b; Dominy & Lucas 2001), but the spatial resolution is considerably lower than the red-green subsystem unique to trichromats (Regan et al. 2001). This is especially true at the centre of the fovea (Mullen & Kingdom 2002), where S cones are few and peripherally arranged (Wikler & Rakic 1990; Roorda & Williams 1999). Accordingly, several studies report that trichromacy is superior, if not optimized, for detecting yellow, orange and red targets against mature foliage (Osorio & Vorobyev 1996; Regan et al. 1998; Sumner & Mollon 2000a, b; Párraga et al. 2002).

In each experimental trial, the amount of food available was sufficient to feed more than a single individual (bananas averaged 100 g), but was generally not enough to satiate all members of a social group. In a separate set of experiments conducted only on groups IMP K and FUS E, the two reward platforms each contained approximately 15 g of bananas each. This was not sufficient to satiate more than a single group member. Given the small amount of food on a reward platform in this final experiment, there was a significant advantage to the finder of a reward platform and a significant cost to other group members selecting a nonreward platform.

Data Collection and Analyses

Feeding stations were monitored daily from 0500–0600 (depending on time of sunrise) to 1500 hours from 22 September 1997 to 29 January 1998 (totalling 125 days of data collection) and 14 to 29 August 2001 (totalling 12 days of data collection). Approximately 4200 person-hours were spent in blinds monitoring the feeding stations. Behavioural observations and data collection began when tamarin vocalizations were heard or animals were visually detected within 10 m of the feeding station. The data that were collected included: species, times of arrival and departure from the feeding station, direction from which the group came and direction taken after leaving the station, number and identity of individual(s) visiting each feeding platform and social interactions.

We recorded a platform visit if an individual was observed (1) sitting or standing on the platform and searching it for food, or (2) hanging on a substrate adjacent to the platform (≤ 1 m distant) and searching it for food (see Garber & Dolins 1996; Garber & Paciulli 1997). We recorded all platform visits and scored visits to platforms containing real bananas as correct choices. Visits to platforms with sham bananas were scored as incorrect choices (see Garber & Dolins 1996; Garber & Paciulli 1997). Information presented here represents 6089 initial visits to real and sham feeding platforms.

Individual searching investment was defined as the number of times a given individual was the first member of its group to arrive at a previously noninspected feeding platform (hereafter termed the 'Finder'). The performance of the Finder is important because platform selection by subsequent group members is likely to be affected by the success or failure of earlier foragers in locating reward platforms. We consider Finders to be those individuals that search for or locate reward platforms at a signifi-

cantly greater frequency than expected based on the number of foragers present in the group. Finders probably serve an important social role by providing information to other group members seeking food.

To evaluate the ability of an individual to use visual information and spatial cues during foraging, we also compared the proportion of times an individual was the first group member to visit reward and nonreward platforms during each experimental condition. We analysed the data using the test of two percentages (Z) and observed versus expected performances. We considered a chance level of 25% (two reward platforms out of eight feeding platforms) for choosing a reward platform and applied a Fisher's exact test when the sample size was too small (Lehner 1996). A 0.05 level of confidence is used throughout.

RESULTS

Our results indicate that tamarin social groups are characterized by one or a few individuals who are responsible for the majority of food searches (i.e. Finders; Barnard & Sibly 1981). Finders were commonly the first member of their group to arrive at experimental platforms (at a rate significantly greater than expected based on the number of foragers in the social group); and they invested greater search effort in locating feeding platforms than did other group members (Table 1). Given the sex ratio of adult tamarins in our study groups (1.6:1 males:females), Finders were no more likely to be females than males. Of the eight Finders identified in six tamarin social groups, three were adult males, three were adult females, one was a subadult male and one was a juvenile female (Table 1). Moreover, in the case of emperor tamarin group K, for which the advantage to the Finder of locating a reward platform was greatest (exclusive access to 15 g of banana on each of two reward platforms), an adult male was commonly the first group member to arrive on a reward platform (Table 1). Under these same experimental conditions, in saddleback tamarin group E, females were no more likely than males to be the first to locate the food reward. Notably, tamarins are unusual among primates in their evolution of a cooperative breeding system. Adult males devote considerable time and energy in provisioning, carrying and protecting the young (Garber 1997). Given the extent of male caregiving behaviour, male and female tamarins may be under similar foraging constraints (Gaulin & Sailer 1985).

We also examined the degree to which females successfully used visual cues (colour, shape and size) to locate baited feeding sites. In this experiment, we controlled the availability of olfactory cues (banana skins were concealed under leaves on nonreward platforms) and spatial information (we randomized which two of eight platforms contained real bananas) presented to the forager. Performance depended on an individual's ability to visually discriminate real bananas from similarly hued plastic bananas. Despite the advantage of trichromacy for detecting bananas against mature foliage (Osorio & Vorobyev 1996), the results of this experiment indicate that some individual males performed above chance levels (2/8 or

Table 2. Experiment testing the ability of tamarin foragers to use visual cues to discriminate reward from nonreward feeding site (real banana versus sham banana)

Species/group	Reward	Nonreward	Total	%Correct	P	Test	Males versus Females
Emperor tamarins							
IMP A							
Adult male (N=1)	3	1	4	75.0	NS	Fisher's exact	
Adult female (N=1)	7	1	8	87.5	0.03	Fisher's exact	Fisher's exact, NS
All males (N=3)	15	15	30	50.0	<0.05	Z	
All females (N=1)	7	1	8	87.5	0.03	Fisher's exact	Chi-square, NS
IMP B							
Adult males (N=2)	9	12	21	42.9	NS	Z	
Adult females (N=2)	10	11	21	47.6	NS	Z	Chi-square, NS
All males (N=2)	9	12	21	42.9	NS	Z	
All females (N=3)	18	13	31	58.0	<0.01	Z	Chi-square, NS
Saddleback tamarins							
FUS A							
Adult males (N=2)	21	27	48	43.7	NS	Z	
Adult female (N=1)	9	16	25	36.0	NS	Z	Chi-square, NS
All males (N=3)	23	29	52	44.2	<0.05	Z	
All females (N=1)	9	16	25	36.0	NS	Z	Chi-square, NS
FUS C							
Adult males (N=2)	6	3	9	66.7	NS	Fisher's exact	
Adult females (N=2)	4	9	13	30.7	NS	Fisher's exact	Chi-square, NS
All males (N=2)	6	3	9	66.7	NS	Fisher's exact	
All females (N=4)	9	32	41	21.9	NS	Z	Chi-square, P<0.05

25%) in using colour information to solve the foraging problem (Table 2). A sex comparison of all group members indicated that, in three of four study groups, adult males and females did not differ significantly in their search accuracy (percentage of correct choices) or in their ability to use visual cues (Table 2). In the remaining case (FUS C), the two male group members scored significantly higher than the four female group members in discriminating real versus sham banana feeding sites. Although it was not possible to determine which females in the study groups were trichromatic, taken together, these data fail to support the hypothesis that heterozygous females enjoy a foraging advantage over dichromats when discriminating between yellow fruit rewards.

DISCUSSION

Studies on search strategies and feeding ecology among social animals indicate that foragers face several problems in successfully acquiring food resources (Giraldeau & Caraco 2000). These include the ability to use ecological information to locate potential feeding sites, as well as obtaining access to resources also sought by other group members (Vickery et al. 1991). In general, two primary forms of feeding competition have been recognized. In the case of contest competition, dominance and aggression play a direct role in obtaining resources. Dominant animals may act as finders and rely on ecological information to locate feeding sites, or they may act as joiners and rely on social cues to usurp feeding sites found by subordinate group members. In the case of scramble competition, however, individuals who arrive first at a feeding site may obtain a 'finder's advantage' (Rita et al. 1997) and thereby increase their feeding success regard-

less of social rank. Animals adopting a finder strategy may incur significant costs associated with increased conspicuousness to predators and/or reduced feeding rates in response to vigilance (Treves 1998). Finders, however, may receive important feeding benefits by obtaining first or exclusive access to resources (Barnard & Sibly 1981). Given the importance of fruit in the diet of most platyrrhines, finders are hypothesized to be female in light of the advantage that trichromatic vision affords in detecting Neotropical fruits (Mollon 1989; Regan et al. 1998, 2001).

However, there was no significant difference in the ability of male and female emperor and saddleback tamarins to act as finders of bananas (Tables 1, 2). In experiments in which food rewards were small and the finder's advantage high, females did not locate feeding sites more accurately than did males (IMP K and FUS E; Table 1). Similarly, in experiments where visual information (colour, size and shape differences between real versus sham bananas) provided the only available cue to discriminate between reward and nonreward platforms, females did not outperform males (Table 2).

Why, then, do most platyrrhines (and at least two prosimians) possess an M/L cone opsin polymorphism? One hypothesis suggests that the gene duplication rendering routine trichromacy is a low probability event, occurring independently among catarrhines and *Alouatta*, but not other lineages. Under this hypothesis, variation between platyrrhines is maintained by a heterozygous advantage: the female heterozygote has advantages in distinguishing ripe fruits from foliage (Mollon 1989) or in detecting insects that are motionless against a green background (SurrIDGE & Mundy 2002). Although this latter hypothesis (an advantage to female heterozygotes in

detecting insects) needs to be tested, there exist several platyrrhine genera (e.g. *Ateles*, *Cebus*, *Chiropotes*, *Lagothrix* and *Pithecia*) with an M/L cone opsin polymorphism that are reported to seldom consume insects, or to consume principally colonial or embedded insects (Janson & Boinski 1992; Rosenberger 1992; Strier 1992; Walker 1993).

Our results from a naturalistic foraging experiment failed to support the ripening fruit hypothesis with respect to improved detection of bananas. The experiments of Caine & Mundy (2000), however, demonstrate that trichromatic females have an advantage in detecting orange objects against a green background at distances greater than 0.5 m. Paradoxically, orange and red fruits are not nutritionally superior to fruits of other hues and are seldom preferred by nonhuman primates (Wheelwright & Janson 1985; Dominy, in press). Accordingly, the repeated maintenance of the M/L cone opsin polymorphism in callitrichines (SurrIDGE & Mundy 2002) may be associated with seasonal periods of fruit dearth, when orange and red fruits could represent important fallback resources to heterozygous females. Indeed, fallback resources may play an important role in the evolution foraging adaptations (Grant & Grant 2002).

Another possibility is that the M/L cone opsin polymorphism is maintained by a frequency-selective advantage: the advantage of individual dichromats over trichromatic conspecifics. In the absence of chromatic noise, dichromats may better detect the edges and contours of predators or foods, such as camouflaged arthropods or cryptic fruits (Morgan et al. 1992; Caine 2002). Alternatively, primate M/L cone opsin polymorphisms may be maintained by balanced, complimentary advantages conferred on both dichromats and trichromats. In this regard, kin selection could favour a diversity of phenotypes within a foraging group because detection of all foods, both cryptic and conspicuous, is improved (Tov e 1993). Similarly, variations in ambient illumination may render advantages to some phenotypes and not others, thus improving overall food detection (Regan et al. 2001). Our results showing that male and female tamarins were equally likely to represent finders that located and shared resources with other group members are consistent with these views. Note, however, that although dichromats may enjoy perceptual advantages under low-light conditions (Reimchen 1987; Verhulst & Maes 1998), such as those representing our experimental design (light incident on feeding platforms was approximately 1–5% of that on the canopy; Chazdon 1988), they can also be particularly sensitive to differences in psychophysical properties of colour, such as value (lightness) and chroma (saturation) (see e.g. Jacobs 1999). Thus, although we attempted to control for hue, other psychophysical properties of colour may have influenced a foragers' selection of feeding platforms.

Recently, Dominy et al. (2003) suggested a link between the climate changes of the Eocene–Oligocene transition and the global variation in primate colour vision. They surveyed the hue and biogeography of keystone fruits and proposed that their hue and historical biogeography played an important role in primate evolution. Specifically, they suggested that primates invaded

Paleogene forests characterized by figs (*Ficus* spp.) and palms (Arecaceae), the fruits of which played a keystone function (Terborgh 1986). Primates probably relied on such resources and provided high-quality seed dispersal. In turn, figs and palms lost or simply did not evolve conspicuous coloration, because this would have conferred little advantage for attracting dichromatic mammals. On the basis of character optimization, Paleogene primates were probably routinely dichromatic or possessed an M/L cone opsin polymorphism (Heesy & Ross 2001). Accordingly, the abundance and cryptic coloration of figs and palms may have offered a selective advantage to foraging groups with mixed capabilities for chromatic distinction. Advantages may have been conferred on heterozygous females for detecting conspicuous fruits and dichromats for detecting cryptic figs and palms. However, climatic cooling at the end of the Eocene and into the Neogene resulted in widespread regional extinction or decimation of palms and (probably) figs. In regions where figs and palms became scarce (Morley 2000), primates appear to have evolved routine trichromatic vision in order to exploit proteinaceous young leaves as alternative, fallback resources. A survey of the colour and biogeography of extant figs and palms provides some empirical support. Where these resources are infrequent, primates are routinely trichromatic and consume young leaves during seasonal periods of fruit dearth.

Furthermore, edible leaves are not divisible resources to the same extent as fruits. Whereas fruit development is usually synchronized within a tree crown, young leaves often flush in variegated patches. Selection and consumption of young leaves is therefore more clearly an individual task for which dichromatic vision offers no foraging advantage (Dominy & Lucas 2001). The near uniform distribution of routine trichromacy in catarrhines is consistent with a common reliance on leaves as a primary or secondary source of nutrients (Terborgh & van Schaik 1987). In fact, since the Eocene–Oligocene transition, seasonal folivory is a continuous theme in catarrhine evolution, from the earliest fossils (Kirk & Simons 2001) to extant apes (Doran 1997; McConkey et al. 2003). The exceptional evolution of routine trichromacy in *Alouatta* is compelling: they are not only well known to favour young leaves, but express a variety of behavioural, dental and digestive adaptations for this purpose.

Insofar as routine trichromacy in primates probably evolved to detect young leaves (Lucas et al., in press), the evolution of the balanced M/L cone opsin polymorphism is considerably more perplexing. We show here that female tamarins do not have a foraging advantage in a naturalistic experiment using ripe bananas. We suggest that selective pressures may favour a preponderance of dichromatic individuals in the population. Whether these involve advantages conferred by detecting camouflaged prey, predators or fruit remains to be determined.

Addendum

After this article went to press, a study comparing the foraging efficiency of di and trichromatic tamarins was

published. It bears so centrally on the topic of this article that it warrants mention. In an elegant experiment designed to mimic a natural foraging task, Smith et al. (2003) compared the foraging efficiency of captive saddleback, *Saguinus fuscicollis weddelli*, and red-bellied tamarins, *S. labiatus labiatus*. Although males and females did not differ in their capacity to detect 'ripe'-coloured food rewards, trichromatic individuals outperformed dichromats when detecting six or fewer fruits. At the end of each experimental trial, however, all rewards were detected, regardless of the visual status of the individual tamarin being tested.

Furthermore, it is notable that the fruits and leaves being simulated were those of *Abuta fluminum* (Menispermaceae), a common liana. In tropical forests, liana species are often patchily distributed, ephemeral resources. It is compelling, then, that trichromatic vision may be advantageous for detecting such resources, which could represent important fallback foods. Smith et al. report that many important fruits in the tamarin diet are from large trees and appear not to require trichromatic vision for their detection.

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