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Effect of color vision phenotype on the foraging of wild white-faced capuchins, *Cebus capucinus*

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New World monkeys exhibit a color vision polymorphism. It results from allelic variation of the single-locus middle-to-long wavelength opsin gene on the X chromosome. Females that are heterozygous for the gene possess trichromatic vision. All other individuals possess dichromatic vision. The prevailing hypothesis for the maintenance of the color vision polymorphism is through a consistent fitness advantage to heterozygous trichromatic females. Such females are predicted to be more efficient than dichromats when detecting and selecting fruit. Recent experiments with captive callitrichid primates provided support for this hypothesis by demonstrating that color vision phenotype affects behavioral responses to contrived food targets. Yet, the assumptions that trichromatic females acquire more calories from fruit, or that number of offspring is linked to caloric intake, remain untested. Here, we assess if, in the wild, heterozygous trichromatic individuals in a group of white-faced capuchins (*Cebus capucinus*) enjoy an energetic advantage over dichromats when foraging on fruit. Contrary to the assumptions of previous theoretical and experimental studies, our analysis of *C. capucinus* foraging behavior shows that trichromats do not differ from dichromats in their fruit or energy acquisition rates. For white-faced capuchins, the advantage of trichromatic vision may be related to the detection of predators, animal prey, or fruit under mesopic conditions. This result demonstrates the importance of using a fitness currency that is relevant to individual animals to test evolutionary hypotheses. *Key words:* frugivory, M/L cone opsin polymorphism, primates, trichromatic vision. *[Behav Ecol 18:292–297 (2007)]*

Variation exists in the color vision of New World monkeys (Platyrrhini). Like most platyrrhines, the genus *Cebus* is characterized by a color vision polymorphism. The polymorphism results from allelic variation of the single-locus middle-to-long wavelength (M/L) opsin gene on the X chromosome (Mollon et al. 1984; Jacobs et al. 1993). The presence in the population of 3 alleles coding for different M/L photopigments results in a variety of color vision phenotypes. Females that are heterozygous for the M/L opsin gene possess trichromatic vision. All other individuals possess dichromatic vision (Jacobs and Neitz 1987; Lee et al. 2000; Jacobs and Deegan 2003). The polymorphism appears to be maintained by balancing selection (Boissinot et al. 1998; Surridge and Mundy 2002), although the major mechanisms acting to maintain allelic variation in platyrrhine populations are poorly understood (Surridge et al. 2003).

The prevailing hypothesis for the maintenance of the polymorphism is through a consistent fitness advantage to heterozygous trichromatic females (Mollon et al. 1984). Such females are predicted to have an advantage when foraging on fruit (Regan et al. 2001), particularly those characterized as yellow, orange, or red (Mollon 1989; Párraga et al. 2002). Recent experiments with captive callitrichid primates have provided some support for this hypothesis. For instance, Caine and Mundy (2000) demonstrated an advantage in feeding rate for trichromatic marmosets (*Callithrix geoffroyi*) competing for orange cereal balls scattered on the floor of their enclosure. The result suggests an advantage for trichromats based on food color, but in a second test where the food was presented at close range (<0.5 m), the difference between dichromats and trichromats disappeared. Similarly, Smith et al. (2003) demonstrated an advantage in feeding rate for trichromatic tamarins (*Saguinus fuscicollis* and *Saguinus labiatus*) scrambling for chromatically naturalistic food targets fixed to a background of simulated leaves. Interestingly, the total number of food targets acquired during the 15-min test period did not depend on the color vision phenotype, suggesting that a persistent dichromat may in the end acquire the same total harvest as a trichromat.

Such experiments demonstrate that color vision can affect behavioral responses to environmental stimuli, particularly the rate at which foods are acquired. Yet, the assumption that an advantage in food acquisition rate results in an energetic and fitness advantage remains implicit and untested. To achieve a more complete understanding of the evolution of platyrrhine color vision, it is necessary to observe the natural foraging behavior of primates and to select a currency that is relevant to individual fitness (Crone 2001). The currency should directly impact individual survival or reproduction and must not trade off with another relevant fitness currency (Burns 2005). For *Cebus capucinus*, which devotes 81–85% of its foraging time to consuming fruit (Chapman 1987; Vogel 2004), female fitness is likely to be closely linked to both the rate and the quality of fruit acquisition. It follows that energy-intake rates will be higher among phenotypes that learn the difference between rewarding and unrewarding fruits on the basis of color, and therefore make more accurate foraging decisions (Dall et al. 2005).

It stands to reason therefore that heterozygous trichromatic females may select fruits and acquire energy from fruits at faster rates than dichromatic phenotypes. Here, we test this prediction. We genotyped the M/L opsin genes of a group of wild white-faced capuchins (*C. capucinus*) to ask the following questions: first, do trichromatic females have a higher energy-intake rate than dichromats? And, second, does the energetic advantage, if it exists, extend to a particular species or class of fruit?

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METHODS

Study site and subjects

White-faced capuchins were studied in the Lomas Barbudal Biological Reserve and surrounding properties, Guanacaste Province, northwest Costa Rica (10°30′N and 85°22′W). The 2279-ha reserve is classified as a tropical deciduous forest (Frankie et al. 1988). Observational data were collected from 1 study group, Group QQ, from January to July 2002, for a total of 1950 h (Vogel 2005). Group QQ was composed of 4 adult males, 9 adult females, 1 subadult male and female, 7 juveniles, and 4–5 infants. Their home range covered 276 ha.

Behavioral and ecological data

During feeding bouts, 1-min feeding rate samples were recorded for as many individuals as possible within a tree (Vogel 2005). The tree species, the number of food items ingested, and the amount of time spent in processing foods were recorded. From these data, feeding rates (number of fruits ingested per min) were calculated. If more than 1 feeding rate was collected for an individual during a feeding bout, the feeding rates were averaged for the individual. The density of fruit in each tree and the density of the trees themselves were also calculated. The energy-intake rate was estimated as the product of the number of fruits ingested per min × g dry mass of each fruit × kJ/g dry mass of each fruit. This metric was calculated for 1–20 focal animals for each of 17 tree species (Table 1). The total energy available in a tree crown was calculated as the product of the abundance and kJ/g dry mass per fruit, divided by the tree crown volume. The hues of edible fruits are presented in Table 1; they were grouped into 2 classes based loosely on their chromatic conspicuousness to trichromatic primates: 1) yellow/orange/red fruits (conspicuous fruits) and 2) green and brown fruits (cryptic fruits).

Amplification and sequencing of the M/L cone opsin gene

Fecal samples (ca., 5 g each) were collected from individual animals. The samples were stored at ambient field temperatures in 50-ml tubes containing 20 g silica gel beads (Nsubuga et al. 2004). Samples were later transported to the University of Chicago and stored at 4 °C. We extracted genomic DNA with a QIAamp DNA Stool Mini Kit (Qiagen, Valencia, CA). We modified Step 2 of the manufacturer instructions: samples were mixed with 1.6 ml ASL buffer and incubated at room temperature for 3 h.

The λ_{max} of the M/L ospin gene can be predicted from the amino acid composition of 3 sites: site 180 encoded by exon 3 and sites 277 and 285 encoded by exon 5 (Nathans et al. 1986; Neitz M and Neitz J 1998). Amino acid changes from Ser to Ala at site 180 (denoted Ser180Ala), Tyr277Phe, and Thr285Ala shift the λ_{max} values by –7, –8, and –15 nm, respectively, although estimates of λ_{max} can vary slightly (Neitz et al. 1991; Merbs and Nathans 1992; Asenjo et al. 1994; Yokoyama and Radlwimmer 2001).

The polymerase chain reaction (PCR) was used to amplify exons 3 and 5 of the M/L opsin gene (Neitz M and Neitz J 1995). Exons 3 and 5 were amplified separately using the AmpliTaq Gold PCR kit per manufacturer instructions (ABI, Foster City, CA). Each 50-μl PCR reaction contained a final concentration of 1× Buffer, 1 mM $MgCl_2$, 600 nM of each primer, 50 μM each of dATP, dCTP, dTTP, and dGTP, and 1.25 units of AmpliTaq Gold (ABI). Exon 3 was amplified using the forward primer 5′ CGTCTGTCTGCTCTCCCCTA and the reverse primer 5′ TTGCCTCAGGGTCACAGAGT. One or 2 rounds of PCR were done in an ABI 2700 Thermal Cycler using cycling conditions of 94 °C for 9 min for 1 cycle, followed by 37 cycles of 94 °C for 45 s, 61 °C for 45 s, 72 °C for 45 s. Reactions were then incubated at 72 °C for 7 min and stored at 4 °C. Exon 5 was amplified using the forward primer 5′ GTGGCAAAGCAGCAGAAAG and the reverse primer 5′ CTGCCGGTTCATAAAGACATAG or using the forward primer 5′ TCCACCCCCCGACTCACTATCC and the reverse primer 5′ ACGGTATTTTGAGTGGGATCTGCT. The thermal cycling conditions were the same as those used to amplify exon 3 except that the 61 °C step was done at 59 °C. PCR products were directly sequenced using the same primers that were used to amplify the exons and the BigDye Terminator 3.1 kit (ABI). Sequencing reactions were analyzed on an ABI 3100 Avante.

Allelic dropout is a potentially confounding factor in this analysis (Knapp 2005). Because the possibility of allelic dropout could not be ruled out for one homozygous adult female, this female was excluded from all analyses. Accordingly, a total of 22 animals served as subjects for these analyses (9 adult/subadult females, 4 juvenile females, 7 adult/subadult males, and 2 juvenile males).

Statistical analyses

Our analysis is based on 481 feeding rates collected during 210 independent focal tree samples. Linear multiple regression models were used to predict the effect of visual phenotype (dichromatic or trichromatic) on the feeding and energy-intake rates of all individuals and for a separate analysis of adult females. The assumptions of homoscedasticity and normality of residuals were tested; in nearly all cases, taking the logarithm of the original data brought the data into conformity with these assumptions (Sokal and Rohlf 1995). All variables were checked for independence using pairwise correlation techniques.

We ran each model twice, once with fruit-intake rate as the dependent variable and once with energy-intake rate as the dependent variable. Because variables other than color vision phenotype can contribute to variation in individual foraging behavior, we included them in the multiple regression models. The variables were: 1) the percentage of aggression won, 2) sex, 3) fruit density within a tree, 4) total energy within a tree crown, and 5) tree species. The percentage of aggression won is a measure of dominance rank. It is calculated as the ratio of aggressive interactions won to the total number of interactions in which the individual participated (Janson 1985). These data were arcsine transformed. In a previous study, dominance rank correlated with both feeding and energy-intake rates (Vogel 2004, 2005). Fruit density and the energy available within a tree crown are also significant predictors of feeding rates and energy-intake rates, respectively (Vogel 2004, 2005). Accordingly, we included fruit density in models predicting feeding rates and crown energy density in models predicting energy-intake rates. Lastly, there is a large amount of variation in average feeding rates and average energy-intake rates for several tree species (Vogel 2005). Tree species were therefore included in the multiple regression models; the variable accounted for 49–85% of the variation in energy-intake rates among focal animal samples.

When categorical data were included in a model (e.g., species, phenotype, sex), JMP-SAS 5.0.1a converted the categorical values (levels) into internal columns of numbers and analyzed the data as a linear model. The program uses a sum-to-zero coding scheme to create indicator variables and provides information on how different the mean for a specific level was from the mean of the means for each level and also provides directional effects (Sall et al. 2001). Lastly, given our relatively small sample sizes, a power analysis was conducted for all tests. The one analysis with insufficient power

Table 1
Trees used in the analysis of Group QQ foraging behavior

Tree species	Fruit energy (kJ/g)[a]	Average feeding rate (fruits/min)[a]	Average energy-intake rate (kJ/min)[a]	Fruit hue[b]	Observed cases of feeding
Anacardium occidentale	15.20	3.50	37.70	Yellow	54
Bursera simaruba	5.77	11.03	7.41	Green	2
Doliocarpus dentatus	13.56	10.90	1.53	Red	10
Ficus sp.	8.00	11.65	16.40	Green	12
Garcinia edulis	8.47	4.98	19.46	Orange	22
Genipa americana	12.22	0.68	46.77	Brown	15
Guazuma ulmifolia	8.20	2.55	27.89	Brown	8
Luehea speciosa	7.73	1.41	0.19	Brown	31
Mangifera indica	14.33	0.47	105.63	Green	37
Manilkara chicle	11.66	15.96	119.92	Green	4
Muntingia calabura	10.41	6.21	19.46	Red	56
Psychotria pubescens	9.88	12.13	5.69	Red	10
Simarouba glauca	7.38	3.67	1.58	Red	15
Sloanea terniflora	24.92	2.64	2.46	Red	146
Spondias purpurea	12.49	4.09	45.97	Red	18
Ximenia americana	6.95	4.20	13.38	Yellow	11

[a] Methods and calculations are detailed in the text and in Vogel (2005).

[b] Hues were determined from personal observations and crosschecked with Enquist and Sullivan (2001) or the Área de Conservación Guanacaste website, www.acguanacaste.ac.cr.

to detect a significant result was the test for phenotypic differences in fruit and energy-intake rates among adult females. The analysis revealed that the number of data points in our sample was insufficient to achieve significance (least significant number = 519, 552, respectively) and that the overall power of the phenotype estimate was relatively low (power = 0.30, 0.28, respectively). All possibility levels are 2-tailed, and significance for all tests was set at alpha 0.05.

RESULTS

Variation in M/L opsin alleles

We detected varying residues at positions 180, 277, and 285 of the M/L opsin gene that are predicted to yield pigments with λ_{max} values of 535, 549, and 562 nm (Jacobs and Neitz 1987; Jacobs and Deegan 2003). Although the spectral peaks of *Cebus* pigments may vary somewhat depending on the measurement methodology employed, for example, electroretinogram flicker photometry (above), microspectrophotometry (535, 550, 563 nm; Bowmaker et al. 1983; Hunt et al. 1998), or in vitro pigment reconstitution (530, 545, 560 nm; Hiramatsu et al. 2005) their relative positions do not. Table 2 shows the distribution of alleles and inferred phenotypes among individuals in Group QQ. The allele frequencies of P535, P549, and P562 were 45%, 10%, and 45%, respectively, in a total of 29 X chromosomes examined for the group. Six out of 11 females (55%) were heterozygous and are thus predicted to have different types of M/L cone pigment. Two of the 3 possible trichromatic phenotypes (P535/P562 and P549/P562) were observed. The P549/P562 combination is equivalent to human anomalous trichromacy. As expected, all males examined were dichromats.

Phenotypic variation in foraging

The multiple regression models were significant ($P < 0.0001$). Overall, there was no difference between dichromats and trichromats in feeding rate and energy-intake rate (Table 3). There was a trend, although not statistically significant, toward an overall dichromatic advantage (Table 3).

Table 2
Distribution of alleles and inferred phenotypes (P) among individuals in Group QQ

	Female		Male		Unknown sex
Phenotype	Adult/subadult	Juvenile	Adult/subadult	Juvenile	Infant
Dichromat					
P535	2	0	3	0	1
P549	1	0	1	0	0
P562	2	0	2	1	1
Trichromat					
P535/P549	0	0	0	0	0
P535/P562	2	3	0	0	0
P549/P562	1	0	0	0	0
Unknown[a]	2	1	1	1	3
Total	10	4	7	2	5

[a] We were unable to extract DNA of 1 adult female; 1 subadult male, 1 juvenile male, and 2 infants; all other individuals ($n = 3$) are dichromatic but we could not differentiate between the 549 and 562 alleles. A total of 22 animals served as subjects for this analysis.

Table 3
Effect of phenotype on feeding and energy-intake rates for all individuals on all fruits

Parameter	Slope (beta)	Standard error (SE) (beta)	*F* ratio	r^2 (%)	*P* value
Feeding rates					
Focal tree species[a]			**45.2**	**98.7**	**<0.0001**
Percentage of aggression won	**0.084**	**0.040**	**4.29**	$\mathbf{5.86 \times 10^{-3}}$	**0.039**
Phenotype (dichromatic)[b]	0.026	0.031	3.22	4.39×10^{-3}	0.074
Sex (female)[b]	0.016	0.015	1.23	1.68×10^{-3}	0.268
Fruit density	0.026	0.031	0.699	9.55×10^{-4}	0.403
Energy-intake rates					
Focal tree species[a]			**287.1**	**99.4**	**<0.0001**
Crown energy density	**0.081**	**0.019**	**16.92**	$\mathbf{3.66 \times 10^{-3}}$	**<0.0001**
Phenotype (dichromatic)[b]	0.024	0.012	3.71	8.03×10^{-4}	0.054
Percentage of aggression won	0.065	0.034	3.61	7.81×10^{-4}	0.058
Sex (female)[b]	0.016	0.015	1.60	3.48×10^{-4}	0.205

Whole model test feeding rates: $F = 72.50_{20,439}$, $P < 0.0001$, $r^2 = 0.76$, $n = 440$; Whole model test energy-intake rates: $F = 249.49_{20,439}$ $P < 0.0001$, $r^2 = 0.92$, $n = 440$. The column "% of r^2" represents the percentage contribution of each variable to the total explained variance attributable to the additive effects of single variables. Variables that were significant at the P <0.05 level in the analysis are indicated in bold.

[a] Because there are 17 species included in the analysis, the slope and SE for each species were not included in the table because we were controlling for the effect of species, not species' effects on feeding/energy-intake rates (see Vogel [2005] for these effects).

[b] For categorical variables with 2 states, the effect is in the direction of the state in parenthesis (e.g., the mean feeding rate for dichromats is higher than for trichromats, although not significant).

When only yellow/orange/red (conspicuous) fruits were included in the model, there was no difference between dichromats and trichromats in feeding rates or energy-intake rates ($F_{1,324} = 2.50$, $P = 0.12$; $F_{1,324} = 3.03$, $P = 0.09$, respectively). The same result held for feeding rates and energy-intake rates when only cryptic were included in the analysis ($F_{1,102} = 0.81$, $P = 0.37$; $F_{1,102} = 0.22$, $P = 0.63$, respectively). The sex of the animal had no effect on feeding rate or energy-intake rate, a result consistent with past studies (Vogel 2005). In a separate analysis of adult females, there was no difference in feeding rates and energy-intake rates between dichromats and trichromats when all fruits were included in the analysis, when only yellow/orange/red fruits were included in the analysis, or when only cryptic fruits were included in the analysis (Table 4), although the overall power of this analysis was low.

DISCUSSION

We detected 3 M/L opsin gene alleles in a population of *C. capucinus* that are predicted to yield pigments with λ_{max} values of 535, 549, and 562 nm. This result is consistent with previous genetic examinations of *Cebus apella* (Hunt et al. 1998), *C. capucinus* (Hiramatsu et al. 2005), and *Cebus olivaceus* (=*Cebus nigrivittatus*; Shyue et al. 1998). An analysis of fruit foraging revealed no difference between trichromatic and dichromatic phenotypes when variables known to affect individual foraging success were controlled for statistically. In fact, there was a nonsignificant trend toward dichromats having an overall foraging advantage. Our findings are inconsistent with the hypothesis of heterozygote advantage, at least in the context of wild capuchins foraging on fruits, chromatically conspicuous or otherwise.

However, 2 methodological issues pertain to our analysis. First, the anthropogenic assignment of fruits into hue categories may be inadequate for testing hypotheses relating color signals to the perception of nonhuman receivers. Such hypotheses should be addressed by quantifying the color of targets and distracters in a way that is appropriate for the animals under consideration. Although yellow, orange, and red fruits are chromatically conspicuous to trichromatic capuchins (Regan et al. 2001), other aspects of the fruit, such as brightness contrast (Schmidt et al. 2004), may be salient to dichromats. It is estimated that dichromatic spider monkeys (*Ateles geoffroyi*) can detect 94–97% of fruit species detectable to trichromatic phenotypes (Riba-Hernández et al. 2004; Stoner et al. 2005). Second, our results are based on a retrospective analysis of genetic samples collected during a study of aggression (Vogel 2004). Variation in the selection of fruits within a tree crown was not recorded. It is possible that dichromats and trichromats selected fruits of different caloric values within a feeding tree. Although our protocol may have missed subtle intratree variation in individual foraging behavior, it has the advantage that the original observers were unaware of the hypothesis that was later tested.

If the above factors confounded our analysis—and if fruit color is a reliable signal of energy content within or between trees (Lucas et al. 2003; Riba-Hernández et al. 2005)—it follows that a comparatively high fruit-intake rate should exist among dichromats to compensate for the selection of lower energy fruits, that is quick-and-compulsive selection instead of a slow-and-accurate selection (Chittka et al. 2003; Dyer and Chittka 2004). This prediction was not met: dichromatic and trichromatic capuchins did not differ in their overall fruit-intake rates, although dichromats may have compensated by foraging longer overall, as they do in captivity (Saito et al. 2005). Our analysis of 8 females (5 dichromats and 3 trichromats) also failed to detect a difference in fruit-intake rate, although this result is best considered provisional due to the relatively low statistical power of our analysis. With so few females we cannot exclude the possibility of a Type II error; trichromatic females may in fact acquire fruit at faster rates than dichromatic females.

Our results are the first to suggest that trichromatic advantages observed among captive callitrichids (based on food-intake rate) may not extend more generally to wild primates. Such artifacts of captivity have been observed in birds. For instance, Schmidt and Schaefer (2004) reported an unlearned preference for red artificial fruits among ecologically naive blackcaps (*Sylvia atricapilla*), although no preference existed among wild-caught individuals. Overall, it is difficult to link the photopigments of primates, particularly those of cebid monkeys, with aspects of their foraging ecology (Cropp

Table 4

Log transformed feeding and energy-intake rates for adult females when feeding on all fruits ($n = 270$ feeding events), yellow/orange/red conspicuous fruits ($n = 213$ feeding events), and green and brown cryptic fruits ($n = 57$ feeding events)

	Dichromats ($n = 4$)			Trichromats ($n = 5$)			
Parameter	Mean ± SE	Lower 95%	Upper 95%	Mean ± SE	Lower 95%	Upper 95%	*P* value
Feeding rates							
All fruits	0.47 ± 0.02	0.42	0.51	0.43 ± 0.03	0.37	0.48	0.16
Conspicuous fruits	0.59 ± 0.02	0.55	0.64	0.55 ± 0.03	0.48	0.61	0.07
Cryptic fruits	0.21 ± 0.05	0.10	0.32	0.16 ± 0.07	0.01	0.30	0.37
Energy-intake rates							
All fruits	1.18 ± 0.02	1.15	1.22	1.14 ± 0.02	1.10	1.19	0.17
Conspicuous fruits	1.09 ± 0.02	1.05	1.23	1.05 ± 0.03	0.99	1.10	0.18
Cryptic fruits	1.35 ± 0.04	1.28	1.42	1.34 ± 0.05	1.25	1.43	0.90

Mean values are the least squares mean from the multiple regression models.

et al. 2002; cf., Talebi et al. 2006). Our results also raise questions concerning the maintenance of the M/L cone opsin polymorphism.

The factors contributing to the maintenance of the platyrrhine M/L cone opsin polymorphism are a puzzle, but selection for finding food may be important. It has long been hypothesized that the polymorphism is maintained because heterozygous females enjoy a fitness advantage when foraging for ripe, energy-rich fruit, and that the number of offspring is reasonably linked to calorie intake (Regan et al. 2001). The results of visual detection experiments with colorblind humans and callitrichid primates are consistent with this hypothesis (Caine and Mundy 2000; Smith et al. 2003; Cole et al. 2004; Rowe and Jacobs 2004). Here, we conclude that, in the wild, trichromatic phenotypes of *C. capucinus* may not enjoy the energetic advantages assumed in some of these studies. Yet, variations in particular allele frequencies suggest that a heterozygote advantage exists, particularly under dim light conditions (Osorio et al. 2004). Our results might therefore reflect a degree of phenotypic parity in the relatively high light conditions of a deciduous forest (Yamashita et al. 2005). Beneath a rain forest canopy, trichromatic females may well have a fitness advantage from the improved detection of fruit (Osorio et al. 2004), arthropod prey (Surridge and Mundy 2002), russet-colored predators (Coss and Ramakrishnan 2000), or any ecologically relevant object requiring high spatial resolution (Blessing et al. 2004).

The allele frequencies we observed are germane to this issue. The P535, P549, and P562 alleles were present, respectively, in 45%, 10%, and 45% of the 29 X chromosomes we studied. The infrequency of the P549 allele may have arisen because trichromatic vision favors a wide spectral separation between M/L pigments and equal frequencies of the P535 and P562 alleles, whereas in dichromats, long wavelength alleles are more fit (Osorio et al. 2004; cf., Surridge, Suárez, Buchanan-Smith, Smith et al. 2005). Yet, models of fruit detectability suggest that the advantage of the P562 allele to a dichromat is small and inconsistent between fruits (Osorio et al. 2004). Future studies with access to a larger data set should test if phenotypes with a wider spectral separation of M/L pigments enjoy energetic advantages. Importantly, the allele frequencies we observed differ from those reported from the nearby site of Santa Rosa National Park, Costa Rica. The combined frequencies of the P530, P545, and P560 alleles in 2 *C. capucinus* populations were 8%, 14%, and 78%, respectively (Hiramatsu et al. 2005). One group, CP, consisted of dichromats only ($n = 17$ individuals). The authors suggested that the allelic diversity of CP has been homogenized by genetic inbreeding. The avoidance of inbreeding may be one of the major factors contributing to the maintenance of M/L alleles among platyrrhines (Surridge, Suárez, Buchanan-Smith et al. 2005).

More research, particularly in the field, is needed to understand the maintenance of the color vision polymorphism of platyrrhine primates. Our study is the first to examine the hypothesized foraging advantage of trichromatic females in the wild. Contrary to the assumptions of previous theoretical and experimental studies, our analysis of *C. capucinus* foraging behavior suggests that trichromats may not enjoy an energetic advantage over dichromats when foraging on fruit in a tropical deciduous forest. The M/L cone opsin polymorphism of platyrrhines might instead allow for a wide range of visual advantages that could potentially serve to maintain the adaptation.

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