



# Trichromacy increases fruit intake rates of wild capuchins (*Cebus capucinus imitator*)

Amanda D. Melin<sup>a,b,c,1</sup>, Kenneth L. Chiou<sup>d,e</sup>, Emily R. Walco<sup>e,f</sup>, Mackenzie L. Bergstrom<sup>a</sup>, Shoji Kawamura<sup>g</sup>, and Linda M. Fedigan<sup>a</sup>

<sup>a</sup>Department of Anthropology & Archaeology, University of Calgary, Calgary, AB T2N 1N4, Canada; <sup>b</sup>Department of Medical Genetics, University of Calgary, Calgary, AB T2N 4N1, Canada; <sup>c</sup>Alberta Children's Hospital Research Institute, University of Calgary, Calgary, AB T2N 4N1, Canada; <sup>d</sup>Department of Psychology, University of Washington, Seattle, WA 98195-1525; <sup>e</sup>Department of Anthropology, Washington University in St. Louis, St. Louis, MO 63130-4899; <sup>f</sup>Department of Human Evolutionary Biology, Harvard University, Cambridge, MA 02138-2019; and <sup>g</sup>Department of Integrated Biosciences, Graduate School of Frontier Sciences, The University of Tokyo, Kashiwa, Chiba 277-8562, Japan

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Intraspecific color vision variation is prevalent among nearly all diurnal monkeys in the neotropics and is seemingly a textbook case of balancing selection acting to maintain genetic polymorphism. Clear foraging advantages to monkeys with trichromatic vision over those with dichromatic “red-green colorblind” vision have been observed in captive studies; however, evidence of trichromatic advantage during close-range foraging has been surprisingly scarce in field studies, perhaps as a result of small sample sizes and strong impacts of environmental or individual variation on foraging performance. To robustly test the effects of color vision type on foraging efficiency in the wild, we conducted an extensive study of dichromatic and trichromatic white-faced capuchin monkeys (*Cebus capucinus imitator*), controlling for plant-level and monkey-level variables that may affect fruit intake rates. Over the course of 14 months, we collected behavioral data from 72 monkeys in Sector Santa Rosa, Costa Rica. We analyzed 19,043 fruit feeding events within 1,602 foraging bouts across 27 plant species. We find that plant species, color conspicuity category, and monkey age class significantly impact intake rates, while sex does not. When plant species and age are controlled for, we observe that trichromats have higher intake rates than dichromats for plant species with conspicuously colored fruits. This study provides clear evidence of trichromatic advantage in close-range fruit feeding in wild monkeys. Taken together with previous reports of dichromatic advantage for finding cryptic foods, our results illuminate an important aspect of balancing selection maintaining primate opsin polymorphism.

sensory ecology | opsin genes | color vision | frugivory | platyrrhine

Intraspecific color vision variation is nearly ubiquitous among neotropical monkeys as a result of allelic variation of the X-linked M/L opsin gene (*OPN1LW*) (1). The enduring persistence of this polymorphism, its widespread occurrence across diverse taxa, and the extent of opsin gene diversity suggest that balancing selection maintains the allelic variation (2). The mechanism underlying balancing selection, however, is unresolved and remains a subject of extensive debate (3–7). Central to all current hypotheses is the prediction that trichromats will have an advantage over dichromatic group members, whether this advantage is global (heterozygote superiority hypothesis) or contextual (niche divergence, mutual benefit of association, or frequency-dependent hypotheses). It has long been suggested that trichromacy should assist the search for ripe fruit amid green leaves, given the stability of the color signal, even in the dappled lighting of forests (8, 9). For a majority of New World monkeys, fruit is an important dietary component, and many fruits have hues (yellowish-to-reddish) that are distinct from those of leaves (greenish) in the red-green range of the chromatic spectrum, thus making them more conspicuous to trichromatic animals (10–12). Because effective fruit detection and selection could improve foraging efficiency, natural selection favoring an enhanced

ability to perceive different fruit hues could be an evolutionarily significant force shaping primate sensory adaptation (11, 13).

To date, direct evidence of feeding advantages for trichromatic primates is absent in the wild. Some captive experiments have demonstrated clear differences between the intake rates of dichromats and trichromats (14, 15). Surprisingly, however, wild studies report similar intake rates among trichromats and dichromats (16–18), despite theoretical models predicting an increased ability for trichromats to find and select their dietary species (19, 20). Studies of the feeding rates of wild animals suffer a disadvantage relative to captive experiments, in that many stochastic variables influence the measures of interest. These variables include consumer-level factors, such as previous experience, skill, social dominance rank, sex, and body size, all of which may affect foraging ability and access to resources (21–23). For example, juvenile wedge-capped capuchins spend significantly more time foraging than adults (24), but are less efficient (22, 23, 25). In addition to consumer-level variables, food patch-level variables including plant species (fruit and seed size) and phenology (fruit abundance and ripeness) affect foraging rates of wild frugivorous birds and primates (26, 27). Nutritional reward also varies with plant species, making some fruits less profitable than others (28). Previous field studies evaluating the potential for trichromatic advantage in the wild have called attention to the relatively small number of monkeys in their studies and/or the limited number of plant species included (16–18, 29, 30), factors that have limited their power to detect small effect

## Significance

**Color vision variation is prevalent among neotropical monkeys. Captive studies indicate that trichromacy should confer a fruit feeding advantage. This hypothesis, however, has yet to be supported by field studies. We collected behavioral and genetic data from 72 capuchins and analyzed ca. 20,000 fruit intake events across 27 plant species. Controlling for plant species and phenological condition, we find that trichromats eat reddish, conspicuous fruits more quickly than do dichromatic (red-green colorblind) groupmates. We demonstrate an advantage of trichromacy for consuming fruit among wild monkeys. Previous research has revealed dichromatic advantage for cryptic tasks; our results suggest fruit foraging plays an important role in the maintenance of primate opsin polymorphism via balancing selection.**

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<sup>1</sup>To whom correspondence should be addressed. Email: amanda.melin@ucalgary.ca.

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sizes or generalize their results. Therefore, increased sample sizes and improvements in the ability to account for plant-level characteristics may reveal previously undetected effects of color vision phenotype on fruit intake rates of primates.

To address this possibility, we study a relatively large number of free-ranging white-faced capuchins (*Cebus capucinus imitator*;  $n = 72$ ; Dataset S1) and conduct foraging observations on males and females of varying age class and color vision phenotype. Male capuchins, as in other polymorphic platyrrhines, are dichromatic (red-green colorblind), whereas females can be either dichromatic (homozygous for the M/L opsin gene) or trichromatic (heterozygous; Fig. 1). We account for the conspicuity of ripe fruit color against a leaf background to different color vision types, the plant species, and the identities of individual food patches during foraging observations to control for patch-level variables (tree size, phenological state). Our overarching aim is to determine whether color vision phenotype affects fruit intake rates of wild primates once variation resulting from sex, age, or food patch characteristic is controlled for. We hypothesize that if discriminating among long wavelength hues is important for fruit detection and selection, then monkeys with different color vision types will eat fruits at the same rates. We predict that trichromatic advantage will be evident through increased numbers of conspicuous fruits eaten per duration of

foraging time (intake rate), and that this will result in increased nutritional uptake.

## Results

We collected behavioral data over the course of 14 mo from 72 monkeys in Sector Santa Rosa, Costa Rica. For 27 plant species, we had sufficient data to compare across color vision type and age class. In total, we analyzed 19,043 fruit intake events within 1,602 foraging bouts (Dataset S2). Twenty-one plant species, 77.78% of species in our study, produced ripe fruit we modeled to be more visually conspicuous to monkeys with trichromatic vision than dichromatic monkeys; three plant species produced relatively inconspicuously (cryptically) colored fruits that were similar in chroma and luminance to background leaves (Dataset S3). The final three species produced dark fruits that should be highly conspicuous to all vision phenotypes (31). Ripe fruits ranged in mean diameter from 0.08 to 5.16 cm, and differed in nutritional profile across species (Dataset S2). Considerable variation in nutrition was evident within each fruit color category (Dataset S2). However, fruits in different color categories did not differ significantly from each other in size of ripe fruit (Kruskal-Wallis test,  $\chi^2 = 1.2804$ ;  $df = 2$ ;  $P = 0.5272$ ), energy content per dry mass ( $\chi^2 = 1.6436$ ;  $df = 2$ ;  $P = 0.4396$ ), or energy intake rates ( $\chi^2 = 0.4783$ ;  $df = 2$ ;  $P = 0.7873$ ; Dataset S2).

To test for effects of sex on fruit intake rate, we ran a linear mixed model including only dichromats (Table 1, “Sex model”). We found that sex did not have a significant effect on fruit intake rates [ $\chi^2 = 0.002$ ;  $df = 1$ ;  $P = 0.965$ ; dichromatic females: least-squares mean  $\pm$  SE (LSmean) =  $-2.281 \pm 0.230$ ; dichromatic males: LSmean  $\pm$  SE =  $-2.279 \pm 0.229$ ]. Therefore, we treat data from male and female dichromats as belonging to a single color vision category for our linear mixed model and exclude sex from further analysis, as it is confounded with color vision type (i.e., it is not possible to have male trichromats).

Age class and color vision type had a significant effect on fruit intake rate (Table 1, “Main model”). Mature monkeys (LSmean =  $-2.153 \pm 0.195$ ) and large immatures (LSmean =  $-2.175 \pm 0.199$ ) fed at faster rates than small immatures (LSmean =  $-2.325 \pm 0.206$ ; Fig. S1). In addition to a significant main effect of color vision type on fruit intake rate ( $\chi^2 = 13.083$ ;  $df = 1$ ;  $P < 0.001$ ; Table 1), we found a significant interaction between color vision and fruit conspicuity ( $\chi^2 = 10.169$ ;  $df = 2$ ;  $P = 0.006$ , Table 1). When the intake rates of dichromats and trichromats are examined as least-squares means, controlling for the other variables in the model (i.e., plant species, fruit patch visit ID, monkey ID and age class), we see that trichromats (LSmean =  $-2.043 \pm 0.191$ ) consumed conspicuous fruits at a higher rate than did dichromats (LSmean =  $-2.388 \pm 0.196$ ; Fig. 2;  $t = 4.06$ ;  $df = 199.1$ ;  $P < 0.001$ ), but that there was no significant difference attributable to color vision type when cryptic (greenish) or dark fruits were compared (Fig. 2; cryptic:  $t = -0.03$ ;  $df = 197.5$ ;  $P > 0.999$ ; and dark:  $t = 0.33$ ;  $df = 270.2$ ;  $P > 0.999$ ). Similar effects of color vision are seen if analyses are restricted to only juvenile monkeys ( $n = 31$ ; main effect of color vision,  $\chi^2 = 6.984$ ;  $df = 1$ ;  $P = 0.008$ ), only mature monkeys ( $n = 41$ ; main effect of color vision,  $\chi^2 = 3.178$ ;  $df = 1$ ;  $P = 0.075$ ), or only females ( $n = 40$ ; main effect of color vision,  $\chi^2 = 2.683$ ;  $df = 1$ ;  $P = 0.100$ ). In all cases, trichromats had faster feeding rates for conspicuously colored fruits, although in the latter two subsets of data, the effect of color vision was not significant.

To demonstrate the effect of fruit conspicuity and plant species on intake rates, we plotted the values for dichromatic and trichromatic monkeys by plant species, with background shading indicating conspicuity category (Fig. 3). Species with larger fruits were among those consumed more slowly, including *Genipa americana*, *Randia monantha*, and *Zuelania guidonia*. The faster intake rate of trichromats is most evident for the reddish (conspicuous) fruits of *Krugiodendron ferreum*, and yellowish fruits of *Diospyros*



**Fig. 1.** Juvenile white-faced capuchins forage for the fruit of *Allorhaphys occidentalis* (A and B) and a katydid insect (C and D). Images simulate capuchin trichromacy (A and C;  $\lambda_{\max}$  532 and 561) and dichromacy (C and D;  $\lambda_{\max}$  532), using customized software (31), demonstrating the increased difficulty of visually discerning the ripe fruits, but not the leaf-camouflaged insect.

**Table 1. Results from linear mixed-effects models predicting fruit feeding rates of wild white-faced capuchin monkeys (*Cebus capucinus imitator*) in a tropical dry forest**

Model Name (dataset)	Variables and Interactions	$\chi^2$	df	P value
Sex model (only dichromats, $n = 47$ )				
	Age class	7.284	2	0.026*
	Sex	0.002	1	0.965
	Conspicuity	0.117	2	0.943
	Ripe fruit index	6.455	3	0.091
	Age class $\times$ sex	0.178	1	0.673
Main model (all, $n = 72$ )				
	Age class	6.280	2	0.043*
	Color vision type	13.083	1	<0.001*
	Conspicuity	0.743	2	0.690
	Ripe fruit index	7.877	3	0.049*
	Age class $\times$ Color vision type	2.805	2	0.246
	Color vision type $\times$ Conspicuity	10.169	2	0.006*
	Ripe fruit index $\times$ Color vision type	3.098	3	0.377
Dominance rank model (mature monkeys >5 y, $n = 41$ )				
	Color vision type	3.446	1	0.063
	Conspicuity	0.184	2	0.912
	Rank class	0.643	2	0.808
	Ripe fruit index	3.080	3	0.379
	Color vision type $\times$ conspicuity	7.182	2	0.028*
	Color vision type $\times$ rank class	3.441	2	0.179
	Ripe fruit index $\times$ color vision type	2.939	3	0.401

\*indicates statistical significance ( $P < 0.05$ ).

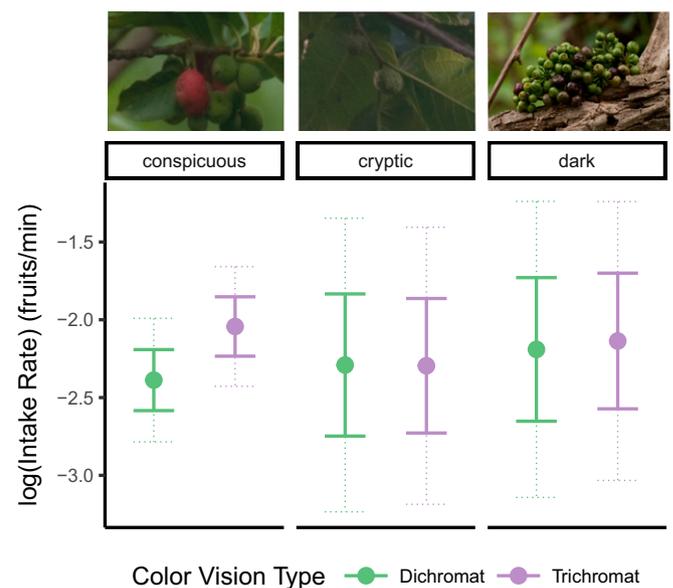
*salicifolia* and *Vachellia collinsii*. In contrast, dichromats had similar intake rates to trichromats for cryptic fruits, including the evergreen fruit of *Maclura tinctoria*, as well as for dark-fruited species (e.g., *Sciadodendron excelsum*).

To test for the possible influence of social dominance on foraging efficiency, we ran a model including dominance rank class along with color vision type, using the foraging data for mature monkeys that were old enough to have a dominance rank assigned (i.e., 6 y of age by the end of the study). We found that the main effect of color vision was not significant ( $\chi^2 = 3.446$ ;  $df = 1$ ;  $P = 0.063$ ), but there was a significant interaction between color vision type and fruit conspicuity ( $\chi^2 = 7.182$ ;  $df = 2$ ;  $P = 0.028$ ; Table 1, “Dominance rank model”), with trichromats having faster intake rates than dichromats for conspicuous fruits (trichromats:  $LS_{mean} = -2.178 \pm 0.242$ ; dichromats:  $LS_{mean} = -2.226 \pm 0.249$ ). Dominance rank class did not have a significant main effect on intake rate ( $\chi^2 = 0.428$ ;  $df = 2$ ;  $P = 0.808$ ). If we restrict the model to include only females (dichromats and trichromats) or only males (dichromats only), dominance still did not have a significant effect on intake rate (females:  $\chi^2 = 0.720$ ;  $df = 2$ ;  $P = 0.698$ ; and males:  $\chi^2 = 1.142$ ;  $df = 2$ ;  $P = 0.565$ ).

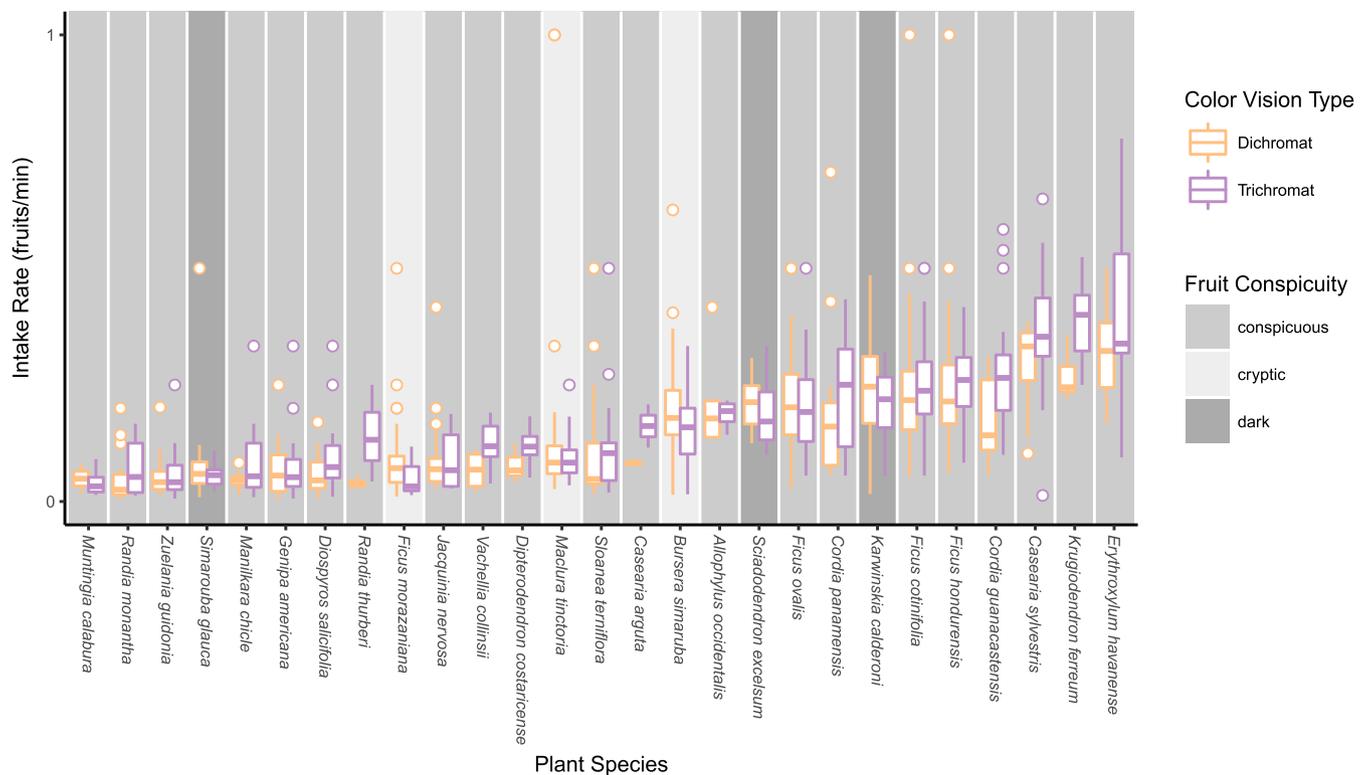
## Discussion

We demonstrate a significant difference in fruit intake rates of wild monkeys that is attributable to color vision phenotype. Overall, trichromats ate fruits at a faster rate than dichromats. However, differences between dichromats and trichromats were not present for all fruit color categories. This is likely because the chromatically cryptic fruits produced by some plants were relatively inconspicuous to both trichromats and dichromats, and the dark fruits were similarly visible to all visual systems, collapsing the performance gap between trichromatic and dichromatic monkeys for fruits in the cryptic and dark categories (17). For yellowish-to-reddish (conspicuous) fruits, trichromats had a higher intake rate. This effect held when we analyzed foraging data of juvenile monkeys, and for our analysis of mature monkeys, but only in the model in which social dominance rank was included. Color vision did not have a significant effect in analyses

that included only females (all ages). The juvenile result suggests effects of color vision type may be particularly strong during juvenescence, perhaps as a result of increased demands for resource acquisition in this critical window of development (23–25). In addition, as they age, capuchins may learn to effectively use nonvisual senses during foraging (18), lessening the importance of trichromacy among older monkeys. The lack of a significant effect of color vision in the female-only analysis may reflect decreased statistical power due to sample size, or possibly an undetected effect of sex, although we found the intake rates of



**Fig. 2.** Fruit intake rates [mean,  $\pm$ SE (bold lines) and 95% confidence intervals (dashed lines)] are plotted as least-squares (LS) means for dichromatic and trichromatic monkeys.



**Fig. 3.** Fruit intake rates (fruits eaten/second) of dichromatic and trichromatic wild capuchin monkeys across different plant species and fruit conspicuity categories of fruits consumed in Sector Santa Rosa, Costa Rica.

dichromatic males and dichromatic females were not significantly different. Overall, by controlling for phenological variation and tree species, as well as monkey age, an effect of color vision type on fruit intake is evident, mirroring results found in controlled captive experiments more than a decade ago (14).

We found no significant main effect of social dominance rank on intake rate in our study, although including dominance rank in the model improved our ability to detect an effect of color vision for mature monkeys. Dominance has previously been shown to affect aspects of foraging efficiency in capuchins and other primates, including priority of access to productive feeding trees, monopolization of central feeding locations, intake rates, and patch residence times (32–35). It is possible that we do not see a main effect of dominance in the present analyses because our method was to assess fruit intake efficiency once the monkey was already engaged in food searching behavior, and to control for food patch identity. By removing time spent in nonforaging behaviors (e.g., fleeing, waiting, other submissive behaviors) and controlling for plant-level variables, we removed many of the contexts in which dominant individuals have an advantage. Still, our dominance results should be treated with caution because of the limitations of our study. First, dominance hierarchies were assigned separately for females and for males. Thus, we could not create a linear numerical hierarchy including all mature monkeys, but used a within-sex calculation of dominance position followed by categorization as “high,” “mid,” and “low” rank. When we analyzed effects of dominance separately for males and females, sample size may have been an issue. We also did not consider the effect of tree size or quality on agonism rates, which can affect how dominance impacts intake rates (35). Finally, dominance hierarchies were constructed using social data collected in the months before, between, and after our three periods of foraging data collection. Although dominance hierarchies appeared to be stable across each of our 4-mo periods of observation,

dominance assessment should ideally coincide with the timing of foraging data collection. Additional studies should be conducted to further explore the relationship between dominance and vision type. However, trichromatic and dichromatic monkeys in our study were relatively evenly distributed across each dominance class (Dataset S1), so dominance rank is unlikely to have confounded our conclusions based on color vision phenotype.

The mean energy content per gram dry weight and net energy gain per minute feeding for conspicuously colored fruits was similar to the energy content of and gain from cryptic and dark fruits. Importantly, plant species with conspicuously colored fruits accounted for more than 75% of the species included in this study. Because of the high representation of conspicuous fruits in the capuchin diet and the higher intake rates by trichromatic monkeys, trichromacy likely confers an overall nutritional benefit in the context of fruit foraging. Other studies of capuchins and primates with polymorphic color vision similarly highlight the large proportion of chromatically conspicuous fruits in their natural diets (7, 16, 19, 30), suggesting trichromatic advantage in the context of frugivory could be widespread. However, while fruits comprise 50–80% of the annual diet for our study population (28, 36), alternative sources of nutrition are essential for capuchins and other primates. In future studies, the relative nutritional contributions of invertebrates and other dietary components, along with the intake of macro- and micronutrients by monkeys with differing color vision phenotypes, should be considered (37). Examination of the ratio of nonprotein energy to protein consumed would also be useful. This ratio is increasingly realized to be an important indicator of health outcomes among primates (e.g., ref. 38).

Our study adds insight to the mechanism of balancing selection that has preserved polymorphic color vision in New World monkeys for >20 My (39). This polymorphism is often described as an early (9) or intermediate stage (40) during the evolution of primate trichromatic vision. These terms risk teleological interpretation

and frame the search for a unifying visual target, such as ripe fruit, to account for the different expressions of trichromatic vision across primate lineages. In consequence, polymorphic color vision is often cast as a suboptimal, transitional trait on the path to uniform trichromatic vision. Our results affirm the value of trichromatic vision for discriminating natural fruits, but prior research has found that dichromats have a different foraging advantage: efficient gleanings of invertebrate prey attributed to an improved ability to break camouflage. This ability is hypothesized to contribute to the maintenance of polymorphic color vision (41, 42), and indeed, dichromatic and trichromatic females have similar levels of reproductive success, as measured by birth rates and infant survival rates (43).

This combination of findings is important because it indicates that the enduring preservation of polymorphic color vision cannot be attributed solely to the foraging advantages of trichromatic vision (heterosis), but rather to discrete foraging advantages associated with each visual phenotype. The polymorphic color vision of primates is perhaps best viewed as an alternative stable state that evolved under different ecological pressures than those that favored the evolution of uniform trichromatic vision in howling monkeys, Old World monkeys, and apes (44–48).

Future studies examining niche divergence within species with differing color vision types may reveal that differential foraging ability leads to divergent diets and decreased intragroup competition. A previous study examining the potential for niche divergence did not find large-scale differences in the diets of dichromats and trichromats (29), but a more refined level of examination with a larger sample size may generate new insight. The potential for mutual benefit of association among individuals with different phenotypes is also worthy of investigation (3, 4, 7). If trichromats are better able to locate profitable areas of a fruiting tree, dichromatic monkeys might benefit from foraging near them. Finally, detailed study of allele frequencies, variation within and between species, and social and ecological correlates may generate new insight into the mechanism of natural selection maintaining this intriguing color vision system.

## Materials and Methods

**Study Site and Subjects.** Data were collected in Sector Santa Rosa in the Área de Conservación, Guanacaste, Costa Rica. Sector Santa Rosa is a seasonal tropical dry forest (49). Annual rainfall is typically between 800 and 2,600 mm, with an average of 1,473 mm, and maximum temperatures vary between 21.6 °C and 34.4 °C (20, 50). Long-term field studies of white-faced capuchins in the park began in 1983 and have been ongoing (51).

White-faced capuchins are medium-sized omnivorous primates. They preferentially consume ripe fruits and have a highly diverse vegetative diet (52). In addition, they forage on invertebrates throughout the year, and seasonal variation in diet is common (20, 36, 53). Capuchins engage in extractive foraging and other complex behaviors, have relatively large brains, and are long-lived with extended periods of juvenile development (54, 55). We observed 72 white-faced capuchins (*Cebus capucinus imitator*) across four social groups: GN, CP, LV, and EX (Dataset S1). We classified our study subjects into three age classes: mature ( $\geq 6$  y), large-juvenile (3–5 y), and small-juvenile (1–2 y), and dominance status, categorized as high-, mid-, or low-ranking, was determined for individuals who reached 6 y of age by the end of the study (SI Materials and Methods). The color vision genotypes of all monkeys in the study have previously been reported (20). At the time of study, A.D.M. was aware that males would be dichromatic and knew the genotypes of five out of 24 adult females from a previous study (41); however, color vision types were intentionally not revealed to five assistants collecting behavioral data.

**Data Collection.** Research was conducted January–May 2007, September 2007–January 2008, and May–September 2008. When a monkey fed on fruit, we recorded a “fruit patch visit” and noted the plant species, diameter at breast height, and phenology, specifically the percentage of canopy coverage and the maturity of each phenophase (leaves, fruits, and flowers), using a five-point scale: 0%, 1–24%, 25–49%, 50–74%, 75–100% (see ref. 52 for detailed methods). Each fruit patch visit was given a unique ID. If a monkey returned on a subsequent day, we assigned a new fruit patch ID, as phenological conditions may have changed. We calculated a ripe fruit index for

each fruit patch by multiplying the fruit canopy coverage by the proportion of ripe fruit. Patches without ripe fruit received a score of 0, patches with <25% ripe fruit coverage a score of 1, patches with 25–49% ripe fruit coverage a score of 2, and patches with  $\geq 50\%$  ripe fruit coverage a score of 3. For 23 of the 27 fruit species, we were able to collect sufficient quantities of ripe fruit ( $>16$  g dry mass) for nutritional analyses at Dairy One Forage Lab. Using these data, combined with mean intake rates for each species, we calculated mean energy intake per minute as a measure of nutritive value for each fruit species (Dataset S2). Using spectral reflectance data and color models, we additionally classified fruits into one of three color categories: more conspicuous to trichromats than dichromats (“conspicuous”), similar in color to background leaves for both trichromats and dichromats (“cryptic”), or relative visible to both dichromats and trichromats due to strong luminance contrast (“dark”) (SI Materials and Methods and Dataset S3).

To record behavioral data, we conducted modified focal animal samples (56) ranging in duration from 1 to 5 min, depending on subject visibility, for as many individuals in the fruit patch as possible. We define a foraging bout as the time from when an individual began foraging in the fruit patch until the end of the last foraging state behavior. We recorded all fruit ingest events within this period. We ended the focal if the monkey ceased foraging for more than 30 s, began feeding on a different species, or exited the tree. Focal individuals were selected based on visibility, and we followed a rotation through age-sex classes.

**Statistical Analyses.** After exploring several error distributions, we found that our data best complied with the assumptions of a linear mixed model (LMM). We used LMMs to analyze the effect of plant-level and primate-level variables on intake rate (fruits consumed per minute of foraging behavior). Because a lognormal distribution best characterized our intake rate data, we performed a log-transformation before analysis. The models were fit in R version 3.3.2 (57), using the `lmer` function from the package `lme4` (58). Significance was estimated using a Wald  $\chi^2$  test conducted using the `Anova` function from the package `car` (59). Because of the X-linked nature of color vision variation, it was not possible to include both sex and color vision phenotype simultaneously in the model. We therefore initially tested for an effect of sex by including only dichromatic females and males in the analysis (“Sex model,” Table 1). We set as fixed effects categorical variables representing the sex, the age class, and the fruit color conspicuity category, an ordinal variable representing the ripe fruit index, and an interaction between sex and age class. We allowed intercepts in the sex model to vary across random effects of categorical variables representing animal identity, tree species, and a categorical variable representing the fruit patch visit identity of the food tree (i.e., a snapshot of phenological condition of a given tree during a visit by one or more monkeys). All reported *P* values are based on two-tailed tests.

Sex did not have a significant main effect on fruit intake rate, and was not involved in a significant interaction with age (Table 1); therefore, our “Main model” included color vision type as a fixed effect, and we included data from males and females in the analysis. The main model also included age class, fruit conspicuity, and ripe fruit index as fixed effects, along with relevant interaction terms (Table 1). For the main model, we allowed the slope of the main effect of color vision phenotype to vary across the same random effects as described for the “Sex model,” along with all intercepts. To test for an effect of dominance rank, we ran a LMM of intake rates for all mature individuals, including rank class as a fixed effect along with color vision type, fruit conspicuity, ripe fruit index, and relevant interaction terms (Table 1). Intercepts and the slope of color vision phenotype were again set to vary across random effects of animal identity, tree species, and fruit patch visit identity. Because male and female ranks were assessed relative to other members of the same sex only, we also ran a LMM to test for a dominance effect for males and females separately. We allowed for rank changes across years as necessary for some individuals, reflecting changes in group membership or dominance status (Dataset S1).

To test whether fruits of colors we modeled to be more conspicuous to trichromatic monkeys (“conspicuous fruits,” Dataset S2) were eaten more quickly by trichromats, we conducted planned comparisons of the least-squares means by color vision type for conspicuous fruits, cryptic fruits, and dark fruits. We used the Holm–Bonferroni method to adjust *P* values for multiple comparisons. All code for LMM models written for this project is available on GitHub ([https://github.com/kchiou/capuchin\\_color\\_vision](https://github.com/kchiou/capuchin_color_vision)).

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