Color Vision Variation and Foraging Behavior in Wild Neotropical Titi Monkeys (*Callicebus brunneus*): Possible Mediating Roles for Spatial Memory and Reproductive Status

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Abstract The selective advantages to primates of trichromatic color vision, allowing discrimination among the colors green, yellow, orange, and red, remain poorly understood. We test the hypothesis that, for primates, an advantage of trichromacy over dichromacy, in which such colors are apt to be confused, lies in the detection of yellow, orange, or red (YOR) food patches at a distance, while controlling for the potentially confounding influences of reproductive status and memory of food patch locations. We employ socially monogamous titi monkeys (*Callicebus brunneus*) which, like most platyrrhine primates, have polymorphic color vision resulting in populations containing both dichromatic and trichromatic individuals. Wild *Callicebus brunneus* spent most foraging time in YOR food patches, the locations of most of which were likely to have been memorable for the subjects. Overall, both dichromatic and trichromatic females had significantly higher encounter rates than their dichromatic male pair mates for low-yield ephemeral YOR food patches whose locations were less likely to have been remembered. We detected no difference in the encounter rates of dichromatic and trichromatic females for such patches. However, the data suggest that such a difference may be detectable with a larger sample of groups of *Callicebus brunneus*, a larger sample of foraging observations per group, or both. We propose that a trichromatic advantage for foraging primates may be realized only when individuals' energy requirements warrant searching for nonmemorable YOR food patches, a context for selection considerably more limited than is often assumed in explanations of the evolution of primate color vision.

Keywords Foraging · Lactation · Primates · Spatial memory · Trichromacy

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Introduction

It is an unresolved evolutionary puzzle why some primates are unique among placental mammals (Eutheria) in having acquired trichromatic color vision, allowing consistent discrimination among colors that appear to humans as green, yellow, orange, and red (Jacobs 2009). Trichromacy is the norm in humans, apes, and Old World monkeys (Catarrhini). However, most other diurnal placental mammals have dichromatic vision, in which those colors may be difficult to distinguish from each other under natural lighting conditions (Jacobs 2009; Sharpe *et al.* 1999). Interestingly, most Neotropical monkeys (Platyrrhini) and some Malagasy lemurs (Strepsirrhini, Lemuroidea) have polymorphic color vision, such that a single population can include a rich mixture of both dichromatic and trichromatic individuals (Jacobs 2007; Jacobs *et al.* 2002; Tan and Li 1999; Veilleux and Bolnick 2009).

In the retinas of most diurnal primates, short-wavelength sensitive (S) cone cells contain a photopigment, specified by an autosomal opsin gene, that absorbs light maximally at *ca.* 430 nm (Jacobs 2008). The retinas of catarrhines also contain middle-wavelength sensitive (M) and long-wavelength sensitive (L) cones containing photopigments with peak light absorbance at *ca.* 535 nm and 562 nm, respectively. M and L photopigments are specified by separate X-chromosome opsin genes, and it is the interactions between signals generated by S, M, and L cones that facilitate trichromacy (Jacobs 2008). In contrast, primates with polymorphic color vision have only a single X-chromosome opsin gene, with (usually) 2 or 3 alleles specifying functionally distinct M/L photopigments having peak light absorbances between *ca.* 530 nm and 565 nm. Heterozygous females produce 2 variants of M/L opsin that are each expressed in different M/L cone cells in the retina and, in conjunction with S cones, support trichromatic color vision. However, hemizygous males and homozygous females have dichromatic vision as a result of producing, in conjunction with the S opsin, only a single M/L opsin variant. This system potentially results in large numbers of both dichromatic and trichromatic individuals being born into the same population of animals (Jacobs 2007; Surridge *et al.* 2003).

The fact that trichromacy has been conservatively maintained in all catarrhines examined to date (Jacobs 2008) suggests that it confers a selective advantage (Surridge *et al.* 2003). Similarly, in platyrrhines, the similarity and conservative maintenance of the M/L gene polymorphism in nearly all extant genera suggest that it originated at least 20 million yr ago in an early platyrrhine (Boissinot *et al.* 1998; Hunt *et al.* 1998) and is under balancing selection (Hiwatashi *et al.* 2010; Surridge and Mundy 2002).

Selective Advantage of Trichromacy

Color vision in terrestrial animals may have coevolved with colorful fruits and flowers, making such food resources more easily detectable to animals against green leaves and thereby facilitating pollination and seed dispersal (Allen 1879; Lomáscolo and Schaefer 2010). For primates, this hypothesis has expanded to predict a trichromatic advantage in the detection (Mollon 1989) and recognition (Liebe *et al.* 2009) of young edible leaves (Dominy and Lucas 2001; Lucas *et al.*

2003), conspecifics (Changizi *et al.* 2006; Fernandez and Morris 2007; Sumner and Mollon 2003a), and predators (Caine 2002; Smith *et al.* 2005), in addition to fruits (Mollon 1989; Sumner and Mollon 2003b).

Given the wide range of suggested selective advantages, it would be beneficial to identify the contexts in which extant primates use trichromatic color vision in the wild. Foraging is one such context that may be broadly applicable to the many trichromatic species across the primate order that rely on colorful fruits, flowers, and leaves for food. Sumner and Mollon (2000a, b) distinguished 2 foraging tasks for which forest-dwelling primates may employ color vision: detection and discrimination. Search time during foraging may decrease if food patches can be easily detected from a distance, in which case, from a primate's perspective, the coloration of food items, e.g., fruits or young leaves, should contrast with the dappled background of mature leaves and branches. On arriving in a food patch, an animal's average rate of energy intake may increase if it can easily discriminate between the colors of calorie-rich foods, e.g., ripe or riper fruits, and those of less desirable foods, e.g., unripe or less ripe fruits.

For the task of within patches discrimination between ripe and unripe, or less ripe, fruit within patches, theoretical models predict a modest trichromatic advantage (Sumner and Mollon 2000b), and a naturalistic foraging task with captive *Saguinus* (tamarins) has demonstrated such an advantage (Smith *et al.* 2003b). However, definitive evidence of a trichromatic advantage during foraging within patches is currently lacking from wild populations (Hiramatsu *et al.* 2008; Melin *et al.* 2008; Vogel *et al.* 2007). Recent work by Melin *et al.* (2009) suggests a trichromatic advantage in food item selection during foraging on conspicuously colored ripe figs (*Ficus* sp.) by capuchins (*Cebus capucinus*). However, this did not translate into a detectable advantage in feeding rate. Trichromacy may in fact provide little advantage during foraging within patches because both dichromats and trichromats can use smell, touch, luminance, size, shape, and position cues when selecting food items at close range (Dominy 2004; Dominy *et al.* 2001; Hiramatsu *et al.* 2008, 2009; Melin *et al.* 2009).

Evidence of a selective advantage for trichromats in long-distance detection of colorful foods is also somewhat equivocal. Several modeling studies have suggested that the trichromatic vision of both catarrhines and heterozygous platyrrhines is superior to that of dichromats for detecting both fruits (de Araujo *et al.* 2006; Osorio *et al.* 2004; Regan *et al.* 2001; Riba-Hernandez *et al.* 2004; Stoner *et al.* 2005; Sumner and Mollon 2000a) and young leaves (Dominy and Lucas 2001; Lucas *et al.* 2003; Sumner and Mollon 2000a) against a background of mature green leaves. In accord with these predictions, in a study of captive marmosets (*Callithrix*), designed to mimic natural detection tasks at maximum distances of 6 m, Caine and Mundy (2000) found a modest trichromatic advantage over dichromats in distinguishing orange targets against a green/brown background. However, there is currently no behavioral evidence to support a trichromatic advantage in the long-distance detection of colorful food patches by wild primates. Dominy *et al.* (2003a) found no evidence that presumably trichromatic female tamarins (*Saguinus*) were more likely than dichromatic males to find yellow fruit patches. Similarly, Smith *et al.* (2003a) concluded that trichromacy was no better than sex and individual characteristics other than color vision as a determinant of leadership during foraging in groups of *Saguinus*.

Controlling for Possible Confounds

One reason for the discord between captive and modeling studies of color vision on one hand, and field studies on the other, may be that we have not yet identified and adequately controlled for aspects of primate ecology that are relevant for the individuals' use of color vision in the wild. For primates, tropical forests are neither temporally nor spatially uniform in resource availability (Terborgh 1983), nor do individuals, e.g., reproductive females, have the same energy requirements year-round (Dewey 1997). If there is a selective advantage to trichromacy, we may be able to detect it only when individuals are most energetically constrained.

In addition, there is growing evidence that primates can remember the locations of many foods, potentially reducing variance in foraging success resulting from different capacities for long-distance food-patch detection. Several field studies have demonstrated the use of spatial memory in large-area food patch exploitation by forest-living primates such as *Cebus* (Janson 1998), *Pithecia* (sakis: Cunningham and Janson 2007), and *Cercocebus* and *Lophocebus* (mangabeys: Janmaat *et al.* 2006), and there is highly suggestive evidence from *Saguinus* (Garber 1989). In all of these studies, the subjects appeared to remember both the locations and the states of renewal of dispersed, temporally predictable fruit resources, in accord with expectations of efficient fruit foragers (Milton 2000). Thus, studies investigating potential foraging advantages among trichromatic primates in the wild may first need to control for variation in resource availability, energetic requirements, and the use of spatial memory.

Hypotheses of the Present Study

We hypothesize that trichromacy provides an advantage over dichromacy to primates in the long-distance detection of colorful food patches whose locations are not stored in the individuals' memories. An enhanced ability to detect previously unknown food patches may have important fitness consequences, particularly during periods of energy stress. When nutritional requirements exceed the availability and productivity of noncolorful food patches and colorful food patches whose locations are remembered, then the importance of discovering supplemental colorful food patches may increase. In this context, selection may favor traits such as trichromacy that increase the rate at which these supplemental patches are detected. In the case of primates with polymorphic trichromacy, this would result in heterozygote advantage and balancing selection at the polymorphic M/L opsin gene locus.

We address this hypothesis using a wild population of titi monkeys (*Callicebus brunneus*). First, we test the prediction that the exploitation of food patches containing yellow, orange, or red (YOR) coloration is an important part of the foraging behavior of these monkeys. We then test the prediction that trichromats detect more nonmemorable YOR food patches than dichromats per unit time searching, particularly during periods of energy stress. This should manifest in observable dichromat/trichromat differences in YOR patch encounter rate. We control for differences in food availability, e.g., due to variation in home range quality and seasonal fruit production (Dominy *et al.* 2003b; Jacobs 1997; Lucas *et al.* 2003), by accounting for the grouping of individuals within territories, and by

observing the same individuals across seasons. We control for differential nutritional requirements, e.g., due to lactation, by comparing the same individuals in different reproductive conditions. Finally, we control for the potential use of spatial memory by excluding all food patches that were known to have been exploited by the subjects in the past.

Methods

Study Site and Subjects

The Estación Biológica de Cocha Cashu in Manu National Park, Madre de Dios, Peru (11°53′S, 71°24′W), comprises both mature high-ground tropical forest and seasonally flooded successional forest (Terborgh 1983). Overall forest fruit production increases markedly during the wet season of October–April (Terborgh 1983).

Callicebus brunneus (brown titi monkeys: Hershkovitz 1990) are small (*ca.* 1 kg), socially monogamous, arboreal omnivores with slight sexual dimorphism, generally conservative morphology, and polymorphic color vision (Hershkovitz 1990; Jacobs and Deegan 2005; Kinzey 1981; Wright 1984). *Callicebus brunneus* devote most foraging time to fruit, but also eat leaves and insects (Kinzey 1981; Wright 1985). The social unit consists of an adult female and male and their undispersed offspring (Wright 1984), which together defend exclusive territories of 5–12 ha at this field site (Bunce 2009). An infant is carried almost entirely by the adult male during 4–7 mo until it can travel independently (Wright 1984). During the study period, ≤2 offspring were present in any group at one time.

Behavioral Sampling

We followed 5 habituated groups of *Callicebus brunneus* (1, 2, 3, S, and W) for 107 d from January 23 to June 3 and June 29 to October 6, 2006. This period spans the entire dry season (May–September) and approximately half of the wet season. Three groups included trichromatic adult females and 2 groups included dichromatic adult females. We followed each group for 18–23 weekdays on a randomly ordered schedule. A 2-observer team conducted continuous focal animal sampling (Altmann 1974) simultaneously on the adult female and male in each group. Each day we randomly assigned observers to a focal individual. *Callicebus brunneus* are active for *ca.* 10–12 h/d (Kinzey 1981). We observed both adults simultaneously for a mean (±SD) of 7.7 (±2.7) h/d, with a range of 1.1–11.6 h. This resulted in a range of 128–207 total observation hours per focal group. We located 3 groups (2, 3, and W) at the start of each day with a TR-4 VHF receiver and RA-14 antenna (Telonics, Mesa, AZ) coupled with 25 g MI-2 radio transmitter collars (Holohil Systems, Carp, Ontario, Canada) custom modified with no external antennas on adult females. We located 2 groups (1 and S) using recorded vocalization playbacks. Bunce (2009) details animal habituation, capture, and collaring methods.

We assigned behavior to one of five exclusively defined categories: foraging; socializing, e.g., grooming; resting; traveling; and other behavior. We recorded time

at all behavioral category transitions using Axim X30 handheld computers (Dell, Round Rock, TX) running a custom data collection program. For the present analysis we focus on foraging, which we define as ingesting, manipulating (with the hands or mouth), carrying (in the mouth), searching for (within a food patch), or usurping (from another group member) a food item. Because of the density of the forest, we did not always have an unobstructed view of a foraging focal individual. We scored such an individual as foraging if we could hear or see falling food items originating from its location.

We conducted a 35- to 90-min interobserver reliability trial once/mo (8 total trials), wherein 2 observers recorded the behavior of a single focal individual simultaneously and independently from a similar vantage point. We used intraclass correlation coefficients (ICCs) to assess interobserver agreement on the amount of time the focal individual spent in each observed behavioral category during a trial. We calculated an ICC for each trial using 2-way analysis of variance models with absolute agreement measures (McGraw and Wong 1996; Shrout and Fleiss 1979) using the irr package (Gamer *et al.* 2007) of R (R Development Core Team 2008). ICCs for the 8 trials ranged between 0.96 and 1.00. The proximity of these coefficient values to 1 indicates that the variance in the records contributed by the 2 observers was very small compared to the total variance in the data.

Food Patch Classification

We defined a single food patch as a physical location, e.g., a tree, of a certain food type, e.g., a fruit species, exploited by an individual or individuals and visited for a continuous time period (regardless of length), even if temporally separated foraging events occurred during the visit. According to this definition, we considered a solitary insect to be a food patch. We attempted to identify and mark the locations of all food patches exploited by the focal individuals. We identified food items dropped by the subjects or collected from the same patch and we classified food species as YOR (yellow, orange, or red) if a normal human trichromat (J. A. Bunce) had described the original food patch as containing yellow, orange, red, or pink elements at the time of collection. Where possible, we matched collected food items to the same or closely related plant species whose detectability for dichromats and trichromats has been modeled by Regan *et al.* (2001), Osorio *et al.* (2004 and D. Osorio, *pers. comm.*), or Hiramatsu *et al.* (2008). This served as a partial check on the ability of the YOR system to classify food patches accurately according to the potential for a detection advantage by trichromatic *Callicebus brunneus*. Relying even partially on human color classifications to represent animal vision can be inappropriate, especially when an animal's visual perception is known to be very different from that of humans (Bennett *et al.* 1994). However, with few exceptions (Regan *et al.* 2001), the set of colored food items that a normal human trichromat can distinguish from background leaves should match or encompass the set distinguishable by any polymorphic platyrrhine phenotype (de Araujo *et al.* 2006; Osorio *et al.* 2004; Riba-Hernandez *et al.* 2004; Stoner *et al.* 2005). We classified food patches containing brightly colored immature fruits, e.g., *Stylogyne cauliflora* (Myrsinaceae: Bunce 2009, Fig. 3.1) or peduncles, e.g., *Huertea glandulosa* (Staphyleaceae: Bunce 2009, Fig. 3.2) as YOR patches even if, by themselves, we

would not have classified the patch elements actually consumed by the monkeys, e.g., ripe fruits, as YOR. We classified patches containing food items that we could not collect and for which we could not record a color classification in the field as non-YOR. The vast majority of such patches probably consisted of cryptic solitary insects that are unlikely to be characterized by YOR coloration.

Memorable and Discovered Patches

We define "memorable" patches as patches we observed to be exploited on multiple occasions by any number of group individuals or those exploited simultaneously by >1 individual, but only once during the observation period. Most patches in this latter class were species that tended to produce fruit in at least moderate quantities over several days or weeks (J. A. Bunce, *pers. obs*.), and therefore seem likely to have been revisited on days when the group was not observed. We assume that productive food sources exploited on multiple occasions are reasonable candidates for location by spatial memory for primates living in small territories (Cunningham and Janson 2007).

In contrast, we define "discovered" patches as patches we observed to be exploited only once during the entire study period by an individual foraging alone. We assume that such patches, exploited by lone individuals, approximate the set of patches found opportunistically, e.g., without social facilitation, and are less likely to represent predetermined destinations located in relation to memorable landmarks using spatial memory. It is impossible to be certain that the discovered category does not include some patches whose locations the subjects remembered, although we assume that such exceptions are few. We classified individual patches, e.g., fruit trees, of the same species as memorable or discovered depending on how the monkeys exploited each particular patch. We included patches exploited by lone individuals, whose locations and coloration we could not record, in the discovered category. This usually occurred because the focal individual ate a food item, presumably an insect, so quickly while traveling that we could not mark its location. We assume such foraging was also indicative of visual discovery instead of spatial memory. When comparing the foraging behavior of dichromatic and trichromatic *Callicebus brunneus*, we focus on discovered patches to reduce the effects of spatial memory, which is likely to be comparable in dichromatic and trichromatic animals.

Reproductive Status

We recorded births, nursing bouts, and adult male infant-carrying behavior. It was difficult to quantify the frequency and duration of nursing bouts because nursing often occurred in hidden areas of dense vegetation. Consequently, we judged a female to be lactating heavily from the day of birth of her infant to the last observed day of male infant-carrying behavior, and we designated this the infant dependency period (IDP). The IDP lasted for *ca*. 5–7 mo (slightly longer than the 4 mo observed by Wright 1984) and corresponds to a period of rapid weight gain for infant *Callicebus* in captivity (Garber and Leigh 1997). We assumed that the majority of wild infants' nutrition during the IDP came from milk, as we observed little independent foraging during most of this period. Consequently, we expected an adult female's daily energy

requirements and energy intake rate to be highest during the IDP, as reported for wild *Cebus* (McCabe and Fedigan 2007) and captive *Callithrix* (Nievergelt and Martin 1999) during early lactation. Once traveling independently of the adult male, young *Callicebus brunneus* engaged in much exploratory foraging, although they returned to the female to nurse until the age of *ca.* 10 mo (slightly longer than the 8 mo observed by Wright 1984). This latter period of infant locomotor independence roughly corresponds to a gradual slowing in weight gain of captive infant *Callicebus* (Garber and Leigh 1997), and we assumed that female milk production and daily energy requirements were reduced, as suggested for wild *Cebus* (McCabe and Fedigan 2007). We classified all behavioral observations outside of the IDP as non-IDP, even if we still observed limited nursing. During the study period, the proportion of observation days falling within the IDP ranged between 0.28 and 0.39 for the 5 focal groups.

Color Vision Determination

We completed behavioral data collection and color classification of food patches in the field (January–October 2006) before the color vision genotypes of the focal individuals were determined (February 2007–January 2010). Bunce *et al.* (2011) details the genotyping methods and genotypes of all focal individuals in this study, with the exception of 1 adult male from group 3 that disappeared in March 2006 and was replaced by a new male whose genotype was determined. The adult females of groups 1, 3, and W were trichromats, having allele combinations of 535/550 nm, 550/562 nm, and 550/562 nm, respectively, while the adult females from groups 2 and S were both dichromats, having the 550 nm allele. Color vision genotypes generally correspond well with cone light absorbance measures and dichromatic or trichromatic color perception in platyrrhines (Jacobs 2007; Saito *et al.* 2005).

Statistical Methods

To determine the overall importance to *Callicebus brunneus* of particular types of food patches, we divided the observed patch encounters into categories, e.g., fruit, leaf, YOR, non-YOR, memorable, discovered, etc. For a given patch category, we calculated the proportion of daily patch encounters and the proportion of total daily foraging time, i.e., time per day that ≥ 1 adult was observed to be foraging, for each observation day and then calculated the mean across all focal individuals and all observation days in the study period (Fig. 1).

To address the hypothesis of a foraging difference between dichromats and trichromats, we used the number of food patches we observed a focal individual to exploit (patch encounters) as an approximation of the number of food patches that the individual detected and recognized as food. We modeled the number of patch encounters by individual *Callicebus brunneus* using Poisson regression with fixed and random effects, i.e., varying-intercept multilevel models (Gelman and Hill 2007, p. 237). The Poisson distribution is a standard model for randomly varying numbers of events, e.g., encounters, per interval, e.g., unit time. We interpreted the encounter rate as the number of food patches each individual encountered per day divided by the amount of time per day the individual spent searching for food patches. We estimated the amount of time spent searching for patches by the amount of time
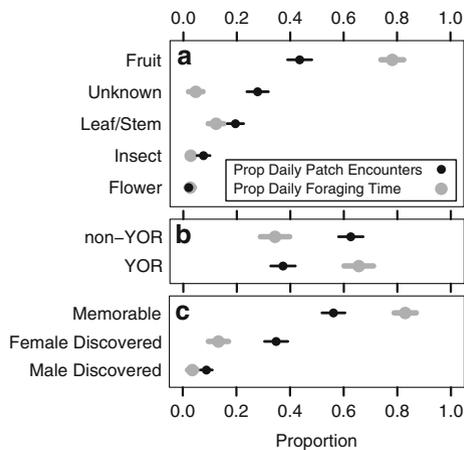
Fig. 1 Proportions of daily food patch encounters (black circles) and daily foraging time (gray circles) of *Callicebus brunneus* by (**a**) food class; (**b**) food patches with no yellow, orange, or red (YOR) characteristics vs. YOR patches; (**c**) memorable food patches that were potentially located by means of spatial memory vs. discovered food patches for which spatial memory was probably not employed. We present data from 1430 patch encounters over 105 observation days on which we observed foraging. Bars represent 95% confidence intervals about the daily proportions. Unknown patches represent food items that were ingested too quickly to be identified and were most likely small solitary cryptic insects.

per day that we observed an individual to be traveling. Thus we included daily travel time as the exposure time in the Poisson model. We related the expected encounter rate to a set of binary predictor variables including Sex, Vision (dichromacy or trichromacy), Season (wet or dry), and IDP (independent or dependent), through the natural logarithm link function. Although trichromacy can occur only in females, the algebraic structure of the predictors Sex and Vision permits their inclusion together in a regression model as main effects. However, we cannot include the interaction Sex*Vision, as it produces a redundancy in the design matrix. We modeled a group-level random effect by a Gaussian distribution with a variance estimated from the data. This random effect used the data from each adult pair to control for variation in territory quality.

We fitted multilevel Poisson regression models to the patch encounter data using the lme4 package (Bates *et al.* 2008) in R (R Development Core Team 2008). We reduced a full model with all predictors, pairwise interactions (excluding the interaction Sex*Vision), and the group-level random effect by sequentially eliminating predictors and interactions on the basis of lowering values for the Akaike information criterion (AIC), with such reductions informed by coefficient significance level ($p < 0.05$) in the model and hypothesized sign and magnitude of the coefficients. We then examined the sequence of reductions by comparing the reduced nested models using likelihood ratios. We monitored dispersion, a measure of Poisson model fit, via the sum of the squared standardized residuals (Gelman and Hill 2007, p. 114), also known as the Pearson statistic (Wang *et al.* 2002). Once we chose a final model, we plotted residuals to check for systematic errors in fit.

To examine the possibility of a foraging advantage for heavily lactating trichromatic females, while controlling for differences in food availability among home ranges, we first estimated population-wide discovered YOR patch encounter

rates from the best fitting Poisson regression model. We then constructed confidence intervals on the natural log scale, i.e., where the linear model operates, for simple contrasts of these rate estimates (Bickel and Doksum 1977, pp. 177–178; Schenker and Gentleman 2001). This facilitated an appropriate statistical comparison of the population-wide encounter rates for YOR patches discovered by dichromatic and trichromatic individuals inside and outside of the IDP.

Results

Food Patch Classification

We recorded a total of 1430 food patch encounters (including YOR, non-YOR, memorable, and discovered patches) during the study period, with a mean of 286 patch encounters (range 136–508) for each of the 5 focal groups of *Callicebus brunneus*. Within this set of food patches, we could distinguish 137 plant and insect types (we identified some plants and insects only to family, to genus, or as morphospecies). We matched 16 fruit species to the same or closely related species whose detectability to dichromatic and trichromatic platyrrhines has been modeled (Hiramatsu *et al.* 2008; Osorio *et al.* 2004, D. Osorio, *pers. comm.*; Regan *et al.* 2001). In all but 1 case, the YOR categorization assigned by the trichromatic human collector coincided with model predictions of better detectability to trichromats than to dichromats. The exception involved ripe fruits of the epiphyte *Monstera obliqua* (Araceae), and may be attributable to regional variation in fruit coloration (Bunce 2009). In this study, we classified *Monstera obliqua* fruit as YOR. The good correspondence between the YOR classification and the model results in most instances gives us confidence that the YOR classification is a reasonable approximation of the food species better detected by trichromats than by dichromats from a distance. In total, we classified 73 of the 137 food types (53%) as YOR. These are listed, along with other food species observed outside of the present study period, in Bunce (2009, Appendices C, D). We did not classify any of the 115 identified insect food patches in the YOR category.

Foraging Overview

We observed *Callicebus brunneus* to exploit a range of different food classes, although they spent a mean of 78% (95% CI: 74–82%) of daily foraging time in fruit patches (Fig. 1a). Of all food patches encountered over the course of a day, a mean of only 37% (95% CI: 33– 42%) were YOR (Fig. 1b). However, the monkeys devoted a mean of 66% (95% CI: 60–71%) of daily foraging time to these YOR patches, indicating their importance in the diet of *Callicebus brunneus*, their large quantity of food items per patch, their long food-item processing time, or all of the above.

Of all daily patch encounters, a mean of 56% (95% CI: 52–61%) were memorable (Fig. 1c). Such patches accounted for a mean of 83% (95% CI: 79–87%) of the subjects' daily foraging time, and we observed the focal individuals to visit these patches a mean total of 3 times (range 1–10) over the course of the study. In contrast, a mean of 35% (95% CI: 31–39%) and 9% (95% CI: 7–11%) of all daily patch

encounters by the adult female or male, respectively, were discovered (Fig. 1c). In general, such patches likely contained insufficient food items to make simultaneous exploitation by multiple individuals energetically profitable. This is in accord with the short foraging time per discovered patch [a mean of 1.4 min/patch (95% CI: 1.1–1.7)] vs. per memorable patch [a mean of 8.6 min/patch (95% CI: 7.2–10.0)].

Among all daily discovered patches, a mean of only 16% (95% CI: 11–20%) were YOR. We limit all subsequent analyses to these 93 discovered YOR patches (range 5–36 patches/group), representing 44 different plant types (Bunce 2009, Appendix C). Discovered YOR patches constituted a mean of only 8% (95% CI: 5–10%) of total daily patch encounters by *Callicebus brunneus*, and the monkeys devoted a mean of only 6% (95% CI: 3–8%) of total daily foraging time to these patches.

Comparison of Dichromats and Trichromats

The final multilevel Poisson regression model for discovered YOR patch encounters contained the significant predictors Sex, IDP, and the interaction of Vision and IDP (Table I). We eliminated the predictor Season, whose coefficient was not significantly different from 0. However, the conclusions are unchanged if Season is included in the model.

Females, in general, had higher estimated patch encounter rates (encounters/h travel) than their male pair mates, both inside the IDP [trichromatic females: 0.77 (95% CI: 0.42–1.43), dichromatic females: 0.34 (95% CI: 0.13–0.86), males: 0.10 (95% CI: 0.04–0.23)] and outside the IDP [trichromatic females: 0.45 (95% CI: 0.26–0.81), dichromatic females: 0.77 (95% CI: 0.37–1.59), males: 0.22 (95% CI: 0.12–0.41)] (Fig. 2). Analysis of the encounter rate differences (Table II) further supports this trend. Although we could not statistically distinguish between the encounter rates of dichromatic and trichromatic females either inside or outside of the IDP (Table II), there was a nonsignificant trend for trichromatic females to have higher rates during the IDP, while dichromatic females had higher rates when the infant was independently mobile (Fig. 2).

Discussion

YOR Patch Detection and Memory

Here we have shown that food items occurring in YOR patches, likely to be more visually detectable to trichromats than to dichromats from a distance, composed approximately half of the food species in the diet of *Callicebus brunneus* and accounted for the majority (66%) of daily foraging time. These results accord well with reflectance and modeling studies investigating the detectability of naturally occurring food items to dichromatic and trichromatic primates (de Araujo *et al.* 2006; Dominy and Lucas 2001; Hiramatsu *et al.* 2008; Lucas *et al.* 2003; Osorio *et al.* 2004; Regan *et al.* 2001; Riba-Hernandez *et al.* 2004; Snodderly 1979; Stoner *et al.* 2005; Sumner and Mollon 2000a), most of which report that trichromats may be better able to detect many, if not most, ingested fruits and leaves, or exploited fruit and leaf species, against a mature leaf background. Importantly, however, our results

Table I Multilevel Poisson regression model for YOR food patches discovered by adult *Callicebus brunneus*

Model component or characteristic	Coefficient or model summary	*p*-value
Fixed effect predictors[a]:		
Intercept	−1.089 (0.48)	0.023
Sex = male	−1.233 (0.399)	0.002
Vision = trichromacy	0.83 (0.55)	0.131
IDP = independent infant[b]	0.83 (0.4)	0.037
Trichromacy and independent infant	−1.358 (0.486)	0.005
Random effect variance:		
Group of *C. brunneus*	0.185	
Model characteristics:		
Log likelihood	−93.297	
Deviance	186.593	
n (animal-days)[c]	214	
Pearson statistic[d]	206.86	

Because we expect the number of patch encounters to scale linearly with the amount of time per day that an individual spends searching, we included the natural logarithm of the exposure time (daily travel time) in this model as an offset, i.e., we fixed its coefficient at one (Gelman and Hill 2007, p. 112)

[a] Coefficients appear with standard errors in parentheses

[b] We parameterized the model so that the coefficient of IDP indicates foraging outside of the period of infant locomotor dependence

[c] The unit of analysis is the animal-day, which we defined as the observed behavior of 1 individual on 1 d. Simultaneous observations of both adults in each socially monogamous pair of *Callicebus brunneus* yield an *n* of 214 animal-days

[d] A dispersion ratio of 0.99, i.e., very close to 1, indicates good model fit. We calculated this by dividing the Pearson statistic by $(n − k)$ degrees of freedom, where we estimated *k* at 6 regression coefficients, i.e., intercept, predictors, and random effect variance (Gelman and Hill 2007, pp. 114–115, 525). Plots of the binned residuals (Gelman and Hill 2007, pp. 558–559) revealed no systematic errors in model prediction

suggest that such observations may lead to overestimates of the number of instances in which trichromacy would provide an advantage over dichromacy to a foraging primate. In spite of the importance of YOR food items in the diet of *Callicebus brunneus*, we argue that spatial memory is likely to mitigate any trichromatic advantage over dichromats in long-distance patch detection during most daily foraging.

Both dichromatic and trichromatic *Callicebus brunneus* are likely to be adept at using spatial memory to locate food patches that are profitably revisited, such as large trees producing fruit over several days or weeks. *Callicebus brunneus* use traditional travel routes through their small territories and often use the same feeding and resting trees over consecutive years (Wright 1985), and even across generations (Bunce 2009). A network of such fixed travel routes may be indicative of a system of spatial memory in which an animal conceptualizes well-known local sites in the home range (e.g., important feeding, resting, or sleeping areas) as being spatially
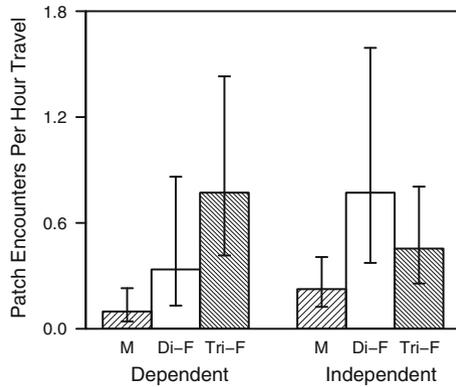
Fig. 2 Encounter rate estimates for YOR patches discovered by adult male (M), dichromatic female (Di-F), and trichromatic female (Tri-F) *Callicebus brunneus* per hour of observed travel during the infant dependency period (Dependent) and during periods when the infant was traveling independently (Independent). We calculated rate estimates and 95% confidence intervals (bars) from a multilevel Poisson regression model (Table I) fit to data collected over 214 animal-days from 7 males (including 2 that replaced resident males), 2 dichromatic females, and 3 trichromatic females. See Table II for significance tests of encounter rates among color vision classes.

related through a network of routes and landmarks (Garber 2000; Poucet 1993). An individual's memory may record and store metric relations within well known local sites more precisely than it stores the metric characteristics of routes themselves, and the areas through which they pass (Poucet 1993). Recent studies of *Ateles* and *Lagothrix* (spider and woolly monkeys, respectively: Di Fiore and Suarez 2007) and *Saguinus* (Garber 2000) report data consistent with this theory of spatial memory. For *Callicebus brunneus*, most YOR patches are large, dispersed, and temporally reliable, i.e., exploited multiple times or by multiple individuals or both, and probably constitute well known (and remembered) local sites connected by routes in the cognitive spatial representations of both dichromats and trichromats. In contrast, discovered YOR patches constitute only *ca*. 8% of the total daily patches exploited by *Callicebus brunneus*, and our results suggest these patches are likely to be low-

Table II 95% confidence limits for the differences (contrasts) in log daily encounter rates of discovered YOR food patches

	M	Di-F	Tri-F
M	–	0.31, 2.16*	1.01, 3.11*
Di-F	0.31, 2.16*	–	−0.45, 2.11
Tri-F	0.01, 1.40*	−1.55, 0.49	–

We estimated log encounter rates for males (M, all dichromatic), dichromatic females (Di-F), and trichromatic females (Tri-F) from the multilevel Poisson regression model in Table I. Confidence limits (CLs) for log encounter rate differences (column – row) during periods of infant locomotor dependence (i.e., during the IDP) appear above the diagonal, while CLs for differences (row – column) during periods of infant independence appear below the diagonal. We calculated all CLs using the Bonferroni correction (Shaffer 1995, p. 569) for 5 comparisons. Although there are 6 contrasts in question, only 5 of these are unique, as the Di-F – M contrasts inside and outside of the IDP are algebraically redundant

*95% confidence intervals that do not contain 0, indicating a significant difference in log encounter rates

yield, i.e., requiring only short in-patch foraging times, and ephemeral, i.e., having long/indefinite regeneration times, thus rendering multiple visits unrewarding. *Callicebus brunneus* may encounter such patches opportunistically in areas represented cognitively in less detail, such as alongside routes during travel between well known local sites. We suggest that trichromacy is most advantageous for the detection of this less frequently exploited class of YOR food patch.

Lactation and Dichromat/Trichromat Foraging Differences

In this study, all females, regardless of color vision and lactational state, had higher encounter rate estimates for discovered YOR patches than did their dichromatic male pair mates. This finding suggests consistent year-round sex differences in foraging behavior of *Callicebus brunneus* and may indicate that such patches are important to females even though they compose a relatively minor part of the overall diet. It remains to be determined whether these sex differences in foraging are due to different nutritional requirements (Tirado Herrera and Heymann 2004) or to other constraints, e.g., impeded mobility of males that carry or maintain proximity to less mobile offspring (Wright 1984).

We hypothesized that a trichromatic advantage in the detection of nonmemorable YOR food patches would be particularly important during periods of energy stress. We report a nonsignificant trend for a trichromatic foraging advantage during the IDP (Fig. 2), when females were lactating heavily and energy intake requirements were likely to be highest. This trend appears to be reversed outside of the IDP. However, a larger sample of *Callicebus brunneus* groups, a larger sample of discovered YOR patch foraging observations per group, or both, is needed to more conclusively address the issue of whether lactational state differentially affects the foraging behavior of dichromatic and trichromatic females.

If the observed nonsignificant trends are robust in the face of future data, they may lend some support to the aforementioned hypothesis of a trichromatic foraging advantage. In particular, the apparent similarity of dichromatic female encounter rates outside the IDP and trichromatic encounter rates during the IDP is not inconsistent with this hypothesis. Higher energetic requirements during the IDP may motivate all females to actively seek out additional nonmemorable YOR food patches. Such additional patches may be difficult to find, requiring substantially more search time per encounter, and thereby decreasing the patch encounter rates of all females relative to rates outside of the IDP. We expect any decrease in encounter rate during the IDP to be less pronounced for trichromats, as they should be more efficient at detecting such patches. Thus, trichromatic encounter rates during the IDP, when all encounter rates are expected to be lower, need not be higher than dichromatic encounter rates outside the IDP. However, by itself, this explanation cannot account for the trend for low trichromatic encounter rates outside the IDP. The resolution of these issues and validation of the observed trends require further investigation.

For many primates, an advantage of trichromacy over dichromacy in long-distance food patch detection is likely to be most important, and observable, when individuals forage on nonmemorable YOR patches. Our results suggest that, for *Callicebus brunneus*, this type of foraging occurs much less frequently than might be assumed based on the importance of YOR food items in the diet. We suggest that

periods of energy stress, such as early lactation, may motivate heavier reliance on nonmemorable YOR patches. This may explain why field studies have yet to identify a trichromatic advantage in long-distance food patch detection in the wild (Dominy *et al.* 2003a; Smith *et al.* 2003a), but captive studies can elicit such an advantage under experimental conditions in which spatial memory is intentionally uninformative and variation in foraging motivation, e.g., hunger, may be minimal (Caine and Mundy 2000). A more limited context for a trichromatic foraging advantage, as suggested by our data, highlights the need for future investigation into whether selection by this means is sufficient to explain the evolution and maintenance of trichromatic color vision in primates.

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