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Does colour vision type drive dietary and nutritional niche differentiation in wild capuchins (*Cebus imitator*)?

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The polymorphic colour vision system of platyrrhine monkeys is a remarkable example of balancing selection. Yet, the underlying mechanism of natural selection remains debated. Here we test the potential for dietary niche differentiation between sensory phenotypes. Monkeys with dichromacy (red-green ‘colourblindness’) are predicted to eat more camouflaged foods while trichromatic monkeys (‘typical’ human-like colour vision) are predicted to eat more reddish foods. We studied a population of wild Costa Rican capuchins (*Cebus imitator*), comparing the diet and nutrition of adult female dichromats and trichromats. We classified the conspicuity of diet items in capuchin visual space and calculated dietary intake, nutritional intake and niche overlap during periods of high and low habitat-wide fruit abundance. Dichromats and trichromats had similar nutritional profiles, but we found evidence of niche differentiation in the invertebrate prey consumed. In support for our prediction regarding cryptic invertebrate prey, dichromats ate more camouflaged surface-dwelling invertebrates, while trichromats ate more extracted ants. Contrary to our prediction regarding reddish foods, dichromats consumed more dark reddish figs than did trichromats. However, these fruits were likely to be conspicuous to both dichromats and trichromats in luminance contrast. Overall, our results suggest that monkeys with different colour vision types achieve similar nutritional intakes in slightly different ways. Behavioural flexibility driven by sensory differences may decrease intragroup feeding competition while meeting species-specific nutritional needs. Our research sheds light on the extent of foraging niche differentiation in a population of wild mammals and its potential contribution to maintaining colour vision polymorphism.

Balancing selection promotes diversity within populations by maintaining multiple phenotypes (Key et al., 2014; Llaurens et al., 2017). The study of stable polymorphisms offers exciting opportunities to understand the processes that maintain genetic and phenotypic diversity (Herdegen et al., 2014; Kadri et al., 2014; van Oosterhout et al., 2006). One classic example is the polymorphic colour vision system of most diurnal monkeys in the Americas (infraorder: Platyrrhini), which displays clear genetic signatures of balancing selection on the opsin genes underlying retinal cone light sensitivity (Hiwatashi et al., 2010). Dichromatic monkeys, which possess two cone types and are red-green colourblind, coexist with trichromats, which possess three cone types and exhibit ‘typical’ colour vision relative to humans. This variation is due to multiple alleles of a single X-linked medium to long wavelength-sensitive (M/LWS; *OPN1LW*) opsin gene (Mollon, 1984). Coupled with an autosomal short wavelength-sensitive (SWS, *OPN1SW*) opsin gene that is present in both sexes, the result is polymorphic trichromacy: heterozygous females are trichromats, while all males and homozygous females are dichromats (Hunt et al., 1998; Jacobs, 1998). The genotype–phenotype relationship is straightforward, and this system presents a unique opportunity to investigate sensory

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variation and its behavioural consequences (Bergman & Beehner, 2023; Bradley & Lawler, 2011; Brent & Melin, 2014). While this colour vision polymorphism has been well characterized since its discovery nearly 40 years ago, the prevailing hypothesis for the maintenance of colour vision variation within populations remains subject to ongoing debate (Jacobs, 1998; Kawamura & Melin, 2017; Mollon et al., 1984; Moreira et al., 2019; Veilleux et al., 2016).

For decades the prevailing hypothesis for colour vision variation invoked heterozygous advantage, which posits that trichromatic females are universally better adapted to their environment overall than are their dichromatic groupmates (Mollon et al., 1984; Surridge et al., 2003; Vogel et al., 2007). However, field research largely fails to support this hypothesis (Fedigan et al., 2014; Melin et al., 2007; Vogel et al., 2007; but see Green, 2014). Alternative mechanisms have been suggested and include negative frequency-dependent selection, mutual benefit of association and niche differentiation (Hartl & Clark, 1997; Mollon et al., 1984). These mechanisms involve dichromatic and trichromatic individuals being better suited to different tasks and may generate nonmutually exclusive predictions. Each hypothesis predicts advantages to individuals living in polymorphic groups. Negative frequency dependence suggests that the fitness of one phenotype is inversely related to its frequency in the population, such that the less common forms have some form of advantage, for example in evading predators or mate attraction (Olendorf et al., 2006). In the case of platyrrhine primates, if the least common phenotype benefits from less competition for food or other resources, then this could lead to negative frequency-dependent selection (Mollon et al., 1984). Mutual benefit of association suggests that individuals benefit from coexisting in mixed phenotype groups because they are alerted to resources or predators by groupmates who are better suited to detect them (Veilleux et al., 2016). There is some evidence that trichromats are better than dichromats at detecting yellowish mammalian predators against a forest background (de Moraes et al., 2021; Pessoa et al., 2014), while dichromats may be better at detecting cryptic snakes due to an enhanced ability to break camouflage (Caine, 2002; Isbell, 2006; Saito et al., 2005). Lastly, the niche differentiation hypothesis posits that dichromat and trichromat individuals occupy distinct ecological niches. Unlike under negative frequency dependence, the fitness of each phenotype is predicted to be impacted by the carrying capacity of each ecological niche and not directly by how rare their phenotype is per se.

Foraging niche differentiation, in which the coexistence of intraspecific morphs is facilitated by each morph specializing on a different resource, would decrease feeding competition between individuals of the same cohesive group. The occurrence of foraging niche differentiation could lend support for the niche differentiation hypothesis, although it could also occur under other evolutionary mechanisms. The occurrence of foraging niche differentiation is reported in various polymorphic systems, including African seedcrackers (Smith, 1987), threespine stickleback, *Gasterosteus aculeatus* (Svanbäck & Bolnick, 2007), and spadefoot toads (Martin & Pfennig, 2010). Given the diverse nature of primate diets (Hogan & Melin, 2018; Vasey, 2002), niche differentiation may be a viable mechanism for the persistence of intraspecific colour vision variation in platyrrhines. Under this scenario, dichromatic and trichromatic individuals would each specialize on resources for which they are best suited to exploit.

Evidence of task-specific foraging advantages to different colour vision phenotypes has been found in both wild and captive settings. Trichromatic marmosets and tamarins forage more efficiently than dichromats for conspicuous ‘reddish’ foods in a naturalistic environment (Caine & Mundy, 2000; Smith et al., 2003). In a study of wild, white-faced capuchins, *Cebus imitator*, trichromats had higher intake rates of ripe fruit that were modelled to be chromatically conspicuous to trichromats (typically ‘reddish’ ripe fruits), but not to dichromats (Melin et al., 2017). Conversely, dichromatic monkeys have higher intake rates for camouflaged foods in captivity (cereal balls; Caine et al., 2010) and in the wild (surface-dwelling invertebrates: Melin et al., 2007, 2010; Smith et al., 2012). This dichromat advantage has been attributed to a heightened ability of red-green colourblind individuals to detect patterns and shapes and break invertebrate camouflage (Morgan et al., 1992; Saito et al., 2005). Importantly, hypotheses of niche differentiation predict that foraging niche differentiation is particularly strong in highly seasonal environments, where food abundance and feeding competition oscillate (Baker & Baker, 1973; Lister, 1981; Schoener, 1982). In such environments, periods of food scarcity may select for increased foraging niche differentiation due to increased feeding competition, wherein individuals benefit more strongly by diversifying their diets to meet nutritional needs. Heightened foraging niche differentiation during periods of food scarcity has been documented in predatory shorebirds (Baker & Baker, 1973), rainforest anoles (Lister, 1981) and four species of South American primates (Stevenson et al., 2000), where dietary overlap decreases during periods of food shortage. In the context of intraspecific niche differentiation, foraging niche differentiation may allow different morphs to avoid direct competition with other members of the population by specializing on different resources (Marshall & Wrangham, 2007; McKnight & Hepp, 1998; van Woerden et al., 2014).

Foraging niche differentiation can also have consequences for nutrient intake (Bergstrom et al., 2018; Lambert & Rothman, 2015; Raubenheimer & Rothman, 2013, 2015). Invertebrates, for example, consist primarily of protein and lipids (Rothman et al., 2014), whereas fruits consist primarily of water-soluble carbohydrates, i.e. sugars such as fructose and glucose (Bergstrom et al., 2018; Levey & del Rio, 2001; Razeng & Watson, 2015; Smith et al., 2007). Previous research into nutritional outcomes using nutritional geometry has revealed species-specific macronutritional regulation in taxa ranging from slime moulds to mountain gorillas, *Gorilla beringei beringei*, such that species appear to have a specific nutrient intake range that they remain within (Felton et al., 2009; Kohl et al., 2015; Köhler et al., 2012; Rothman et al., 2011; Simpson & Raubenheimer, 1995; Takahashi et al., 2019). Niche differentiation between colour vision phenotypes, if sufficiently pronounced, could lead to divergent macronutrient intake profiles, with important downstream consequences for postingestive processes such as digestive efficiency (Behmer & Joern, 2008; Simpson & Raubenheimer, 2012). To date, two studies have explicitly evaluated the potential for colour-vision based niche differentiation by examining activity budgets (DePasquale et al., 2021; Melin et al., 2008). Both studies found no difference in how dichromats and trichromats allocate their time budgets. However, these analyses were coarse in scale and membership in a cohesive social group likely constrains the opportunity for large differences in time allocation. Opportunities for fine-scale niche divergence in diet have yet to be assessed, a gap we begin to fill with this study.

Here we combine a behavioural study of food intake with existing visual models of food conspicuity in species-specific colour space to investigate whether fine-scale foraging niche differentiation occurs between colour vision phenotypes in a population of wild, white-faced capuchins in Costa Rica. We additionally leveraged an ongoing ecological assessment of fruit abundance from transects and phenology surveys to document periods of fruit scarcity and unite this with analysis of food nutritional composition and models of nutritional intake. Specifically, we tested key predictions of the niche differentiation hypothesis with the following three research questions. (1) Do dichromats and trichromats differ in food intake patterns? We predicted that they would differentially consume food types to which they were well suited (i.e. chromatically conspicuous reddish fruit for trichromats versus gleaned invertebrates for dichromats). (2) Do dichromats and trichromats differ in nutritional intake? We predicted elevated water-soluble carbohydrate intake in trichromats and elevated protein intake in dichromats. (3) Does dietary and nutritional niche overlap vary seasonally? We predicted decreases in overlap when habitat-wide fruit abundance is low, when feeding competition is likely to be highest. Our overarching goal was to determine the extent to which dichromats and trichromats occupy distinct foraging niches and how this may vary with fruit availability, a key first step towards evaluating niche differentiation as a potential mechanism contributing to the maintenance of polymorphic colour vision.

METHODS

Study Site and Species

Sector Santa Rosa (SSR), located within the Área de Conservación Guanacaste in northwestern Costa Rica, comprises a ~100 km^2 mosaic of primary and regenerating tropical dry forest and is a UNESCO World Heritage Site. This region of Costa Rica is highly seasonal, experiencing a cool, wet season typically from mid-May until mid-November, and a hot, dry season from mid-November to mid-May in which widespread defoliation occurs (Janzen & Hallwachs, 2020; Montalvo et al., 2019; Woodworth et al., 2018). Fruit availability in SSR is subject to significant seasonal fluctuation; ripe fruit availability typically reaches its lowest at the beginning and end of the wet season, although there is considerable interannual variation (Bergstrom, 2015; Campos et al., 2020; Hogan & Melin, 2018; Melin, Hiramatsu, et al., 2014; Orkin et al., 2019). The Santa Rosa Primate Field Project has been collecting longitudinal data on the wild white-faced capuchins within Santa Rosa since 1983; all study individuals are thus well habituated and individually recognizable (Fedigan & Jack, 2012; Melin et al., 2020). The forest canopy in SSR is relatively low (6–15 m; Kalacska et al., 2004). This is conducive to detailed behavioural observation of diet, making Santa Rosa one of very few wild systems where observation conditions allow for rigorous testing of the niche differentiation hypothesis.

Capuchins prefer ripe fruit when available, which can account for up to 80% of their diet seasonally, but they are inventive and extractive foragers, characterized by a high degree of omnivory (Fragaszy et al., 2004; Melin, Young, et al., 2014). Invertebrates comprise 20–50% of the capuchin diet, which includes a wide variety of both surface-dwelling and embedded invertebrates (McCabe & Fedigan, 2007; Melin et al., 2008; Perry et al., 2012). Capuchins at SSR have been genotyped to determine colour vision status (Hiramatsu et al., 2005; Melin, Hiramatsu, et al., 2014). Like most other platyrrhine primates, white-faced capuchins have multiple alleles of the medium to long wavelength-sensitive (M/LWS) opsin gene located on the X chromosome, which underlies the polymorphic colour vision system (Jacobs, 2009; Kawamura, 2016). In our study population, three M/LWS alleles are present: 561 (red-sensitive), 543 (yellow-sensitive) and 532 (green-sensitive), in addition to the blue-sensitive 426 cone that is present on an autosome in both dichromats and trichromats (Hiramatsu et al., 2005; Jacobs & Deegan, 2003). Females with two of the same M/LWS alleles (homozygous) are dichromats, while those having two different M/LWS alleles (heterozygous) are trichromats (Jacobs, 1998). All males are hemizygous (possess a single M/LWS allele on their single X chromosome) and are dichromatic.

Behavioural Data Collection

We collected behavioural data between 14 June and 19 November 2019. We studied only adult females to avoid the well-documented impact of age and sex on primate diets, including at SSR (Harrison, 1983; Liu et al., 2016; Rose, 1994; Rothman et al., 2008). To further control, in so far as possible, for variation driven by the physical and social environment, we used paired, 2 h continuous focal follows ($N = 154$) to simultaneously observe the behaviour of a dichromatic adult female and a trichromatic adult female (Altmann, 1974; Melin et al., 2018) in the same social group at the same time. We observed 11 dichromat–trichromat pairs, totaling 22 individual females, from four social groups (Appendix Table A1). The same two individuals were always followed together. Pairs were of similar dominance rank and chosen in advance by A.D.M. Observers were kept blind to each focal female's colour vision phenotype to prevent unconscious bias. We recorded the duration of foraging and other behaviours (Appendix Table A2), as well as the taxonomy of food items when possible. For fruit, we also recorded the ripeness. To document intake rates, we counted bites of individual items ingested. We additionally calculated nutrient intake rates per bite, described below. If one of the two focal animals was out of sight for more than 10 min, we would pause both focal follows and resume when the animal was relocated and both subjects were once again in sight.

Food Classification

To objectively classify fruit colour, we leveraged existing fruit colour data based on fruit and foliage reflectance spectra and cone catch models of capuchin visual space generated by Melin, Hiramatsu, et al. (2014). There are two components of colour: chromaticity and luminance. Chromaticity describes the colour itself (i.e. hue, saturation), while luminance is a measure of brightness (i.e. light versus dark) and is independent of chromaticity. Both chromaticity and luminance can be used in foraging, with chromaticity potentially more important in long-distance fruit detection and luminance more important in short-range foraging (Hiramatsu et al., 2005, 2008; Melin, Hiramatsu, et al., 2014). Based on Table 2 from Melin, Hiramatsu, et al. (2014), in which fruit species were classified using a machine-learning algorithm as either chromatically discriminable, or not, to the six phenotypes in SSR, we divided fruit into four categories (Appendix Table A3): (1) chromatically conspicuous to trichromats only (these fruits are generally yellowish to reddish in hue), (2) similarly chromatically conspicuous to trichromatic and dichromatic phenotypes, (3) chromatically cryptic to trichromatic and dichromatic phenotypes (usually greenish) and (4) conspicuous in luminance to trichromatic and dichromatic phenotypes (dark in colour). When fruit fell into more than one category, e.g. conspicuous in both chroma and luminance, we prioritized chromatic conspicuity in our classification. All dichromatic monkeys in our sample possessed the red-shifted (561) allele, which is the most frequent in our population (Melin, Hiramatsu, et al., 2014), and we categorized fruit conspicuity for this dichromatic phenotype specifically, in addition to the three trichromatic phenotypes present (Melin, Hiramatsu, et al., 2014; Osorio et al., 2004; Smith et al., 2003). We used these categorizations to generate a priori hypotheses regarding which fruit taxa we would expect to confer a trichromat advantage. Details on the methods used by Melin, Hiramatsu, et al. (2014) to generate the colour data leveraged here are presented in the Appendix following best practices suggested by White et al. (2015).

Treatment of Invertebrates

We classified the types of invertebrates consumed in our study according to the way the monkeys find and consume them (Appendix Table A3). Some invertebrates can be gleaned off the surface of leaves, tree trunks and branches; these tend to be camouflaged with their substrate (Cuthill et al., 2019). Other invertebrates are embedded in dead branches, dead leaves and rotting wood and thus must be extracted from their substrate. These invertebrates are hidden and typically do not use mimicry or colour camouflage.

Nutritional Data Collection

We analysed macronutritional data for 57 plant and invertebrate taxa consumed by capuchins in our study; most of these data were generated by Bergstrom (2015). For specific invertebrates not measured by Bergstrom (2015), we used macronutrient concentrations from Rumpold and Schlüter (2013). For invertebrates, chitin values (based on those reported in Rothman et al., 2014) were included in lieu of neutral detergent fibre, to account for the chitinous exoskeleton characteristic of many invertebrate prey (Finke, 2007). When we observed the capuchins eating fruits for which nutritional data was previously unavailable, we collected samples from the same tree the capuchins were seen eating, or from nearby trees of the same species and phenophase. Samples were collected within a week of the observation (Rothman et al., 2012). Following Bergstrom (2015), we processed the foods in the same manner as the capuchins (for example, isolating pulp). We then weighed and dried the samples at 60 °C using a Nesco Gardenmaster food dehydrator. Samples were weighed again post-drying and analysed for macronutrient content (crude protein, crude fat, water-soluble carbohydrates, neutral detergent fibre) at the same laboratory used by Bergstrom (2015), Dairy One Laboratories in Ithaca, New York, U.S.A. We were unable to collect some food items (~3% of the diet) and could not find their nutritional data in the literature; for these items, we substituted the average macronutrient composition of the most similar food type (e.g. fruit, caterpillar) and used the dry mass of similarly sized foods of the same type. Nutritional composition of capuchin dietary items are provided in the Appendix Table A4.

On average, fruits from our study period ($N = 32$) consisted of 7.2% crude protein (range 2.2–19.3%), 6.7% crude fat (range 0.3–38.3%), 31.3% water-soluble carbohydrates (range 3.2–68.4%) and 35.2% neutral detergent fibre (range 7–75.6%) on a dry matter basis. Conversely, the invertebrates ($N = 22$) from our study period consisted of 64.5% crude protein (range 35.3–86.7%), 16.9% crude fat (range 6.5–51.4%), 6.2% water-soluble carbohydrates (range 0.8–23.7) and 10.6% chitin (range 3–18.5%) on a dry matter basis. Surface-dwelling and embedded invertebrates had similar nutritional profiles.

Estimating Nutrition Per Bite

We chose to use bite counts rather than entire unit counts to account for the ‘wasteful foraging’ habits of white-faced capuchins, who often drop large portions of fruit uneaten (Melin et al., 2018). While advantageous as a more accurate measure of intake in this species, it requires an estimation of dry mass per bite. To do so, three observers independently estimated the maximum and minimum number of bites required to complete the foods observed in our study period ($N = 57$ foods) based on field experience observing capuchin foraging behaviour. These estimates were then averaged to reach a species level approximation. A limitation of this estimation is that it assumes bite sizes are the same across foods, which may introduce noise into our analyses. We then calculated the average number of bites to complete each food item and divided the average dry mass of that food by the average number of bites to obtain an estimation of dry mass per bite. To obtain nutrition per bite, we then multiplied the dry mass per bite of each food by that food's macronutrient percentage, reported on a dry matter basis.

Defining Periods of High and Low Fruit Abundance

To assess whether seasonality in ripe fruit availability impacts niche differentiation, we calculated monthly fruit abundance in kg/ha based on monthly phenological data combined with habitat-wide transects of the size and density of food trees (e.g. Bergstrom et al., 2018; Campos et al., 2020; Carnegie et al., 2011; Hogan & Melin, 2018; Orkin et al., 2019). The ripe fruit biomass in June, July and August (mean ± SD = 11.67 ± 2.33 kg/ha; range 8.76–14.47) was distinctly lower than in September, October, and November (49.26 ± 16.95 kg/ha; range 29.12–70.57; Fig. 1). We included low and high fruit season as a categorical value in our models to facilitate comparisons of the strength of niche differentiation in relation to overall patterns in food abundance.

Other Host Level Variables

Dominance rank has been shown to influence foraging patterns in adult female capuchins (Vogel, 2005). To minimize the influence of dominance in our analyses, we included dominance rank (low, mid, high) as a fixed effect. Rankings were based on frequency and direction of dominance–submission and agonistic dyadic interactions collected collaboratively year-round by members of the Santa Rosa Primate Field Project (Bergstrom & Fedigan, 2010). We scaled ranks between 1 and 0 to account for differences in group size, and we converted these to an ordinal variable (Levy et al., 2020). We then ranked females as having low (scaled rank ≤ 0.33), mid (scaled rank between 0.34 and 0.66) or high (scaled rank >0.66) rank. Rank varied among dichromats and trichromats and was not biased in any one direction. While reproductive status is known to affect food and nutrient intake rates in white-faced capuchins (Bergstrom et al., 2018; McCabe & Fedigan, 2007), our sample lacked sufficient variation in reproductive states to be able to control for this effect explicitly. However, we controlled for individual identity (ID) and pair ID in all our models.

Data Analysis

We ran generalized linear mixed-effects models (GLMMs) to examine whether colour vision phenotype predicted (1) bite counts taken of different food types or (2) nutrient intake (g). To account for possible influences of habitat-wide fruit abundance on diet and nutrition, we included habitat-wide fruit abundance as a categorical variable (high, low) and an interaction term between colour vision and fruit abundance in our models. Our unit of analysis for every model was each paired focal follow ($N = 154$ paired 2 h focal follows) and we included log focal duration (s) as an offset in each of our models to account for stochastic differences in observational effort.

To examine whether dichromats and trichromats differ in food intake patterns (Research Question 1), we used a negative binomial GLMM with total number of bites (bite count) per food taxon in each 2 h focal follow as the response variable and a three-way interaction between colour vision phenotype, food taxon (e.g. fruit species or invertebrate classification) and fruit biomass category as a fixed effect (model formula: Bite count ~ Colour vision phenotype × Food taxon × Fruit biomass category + Dominance category + offset(log(FocalDuration) + (1 | Animal ID) + (1 | Pair ID)). Negative binomial models are commonly used for count data and were chosen for our analysis to account for data overdispersion (Richards, 2008; Ver Hoef & Boveng, 2007). We also included the dominance category (high, mid, low) for each monkey as a fixed

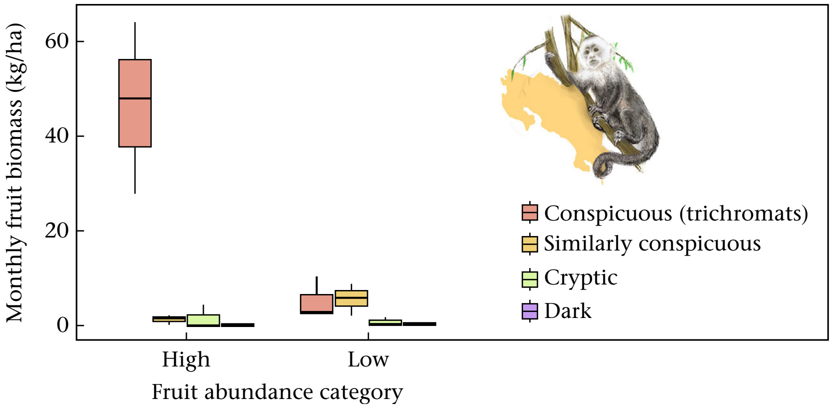

Figure 1. Box plots displaying fruit biomass in kg/ha in high and low fruit months, coded by colour conspicuity. Illustration by Alejandra Tejada Martinez.

effect. To account for individual variation and spatiotemporal predictability of dyads foraging simultaneously, we also included random effects of animal ID and pair ID. We did not include social group ID as a random effect because it lowered model fit; we relied on the assumption that controlling for pair and animal ID is likely to capture much of the stochastic variation not due to variables of interest. We limited our analysis to the 15 most consumed food taxa; these top 15 food taxa include six arthropod categories and nine fruit species and made up >80% of the food consumed during our study. To test our predictions based on colour vision type, we generated estimated marginal means of bite counts in high and low fruit periods. Rather than interpreting full model results, our approach was to conduct planned Tukey-adjusted pairwise comparisons of these estimated marginal means to test our a priori hypotheses (Kaltenbach, 2021).

To answer whether dichromats and trichromats differ in nutritional intake (Research Question 2), we built three GLMMs with a gamma distribution, each with different response variables corresponding to the intake (g) of the three nutrients: crude protein, water-soluble carbohydrates and neutral detergent fibre (Model formula: Nutrient intake (g) ~ Colour vision phenotype × Fruit biomass category + Dominance category + offset(log(FocalDuration) + (1 | Animal ID) + (1 | Pair ID)). For each of these models, we included two fixed effects: a two-way interaction between colour vision phenotype and fruit biomass category as well as dominance category. As in our bite count model, we also included random effects of animal ID and pair ID to account for individual variation and spatiotemporal predictability of dyads foraging simultaneously. From the results of these models, we calculated estimated marginal means for water-soluble carbohydrates, protein and fibre and conducted Tukey-adjusted pairwise comparisons to compare dichromats and trichromats for the different nutrients in high and low fruit periods. In addition, we constructed right-angle mixture triangles (RMTs), a tool from nutritional geometry that can be used to visualize nutritional niche space (Machovsky-Capuska et al., 2016; Raubenheimer, 2011). RMTs can help reveal whether individuals get relatively more of their energy from proteins, fat or water-soluble carbohydrates. We generated three RMTs: one showing how the energy of food items was proportioned in terms of macronutrient content and two showing nutritional intake between dichromats and trichromats in the high and low fruit period. We also constructed RMTs including neutral detergent fibre to visualize how the presence of fibre, typically a feeding deterrent for smaller primates, might impact intake (Wrangham et al., 1998; Appendix Fig. A1). We visually inspected the RMTs generated for dichromatic and trichromatic monkeys and noted obvious differences in how individuals of different phenotypes occupied the space in the triangle, which represents how dichromats and trichromats proportioned their macronutrient intake.

We assessed whether dietary and nutritional niche overlap varies seasonally (Research Question 3), specifically whether dietary and nutritional niche overlap decreases when food abundance is low, by calculating Pianka's index in different periods of food abundance and using our RMTs. Pianka's index is a measure of dietary niche overlap that calculates the proportion of resource use between two groups. This measure ranges from 0 to 1: 0 indicates complete niche differentiation, while 1 indicates complete niche overlap; this can be interpreted as a percentage of dietary overlap. We used the estimated marginal means of different food taxa in high and low fruit months (calculated in Research Question 1) as our resource categories for calculating Pianka's index. Using the R package ‘EcoSimR’ (Gotelli et al., 2015), we generated two Pianka's indices: one for the high fruit period and one for the low fruit period. While Pianka's index has seldom been applied to questions of intraspecific niche differentiation, which complicates the interpretation of its biological significance, it is a straightforward metric that is well suited to our bite count data. We thus leveraged this metric to quantify overlap in bite counts. To determine how nutritional niche overlap changes with fruit abundance, we compared the RMTs for dichromat and trichromat intake in high and low fruit abundance. Detailed methods for both Pianka's index and RMTs can be found in the Appendix. All analyses were performed with R statistical software v4 using the packages ‘lme4’, ‘emmeans’ and ‘EcoSimR’ (Bates et al., 2015; Gotelli et al., 2015; Lenth et al., 2020; R Core Team, 2022).

Ethical Note

This research adhered to the laws of Costa Rica and Canada and complied with protocols approved by the Área de Conservación Guanacaste and by the Canada Research Council for Animal Care through the University of Calgary's Life and Environmental Care Committee (No. AC15-0161).

RESULTS

Do Dichromats and Trichromats Differ in Food Intake Patterns?

We first investigated differences in bites of food taxa to determine whether trichromats consume more conspicuous fruit taxa and whether dichromats consume more cryptic invertebrates. To examine the effect of colour vision, we compared estimated marginal means generated by our full model (Appendix Table A5). In the high fruit abundance period, we found that trichromats had higher bite counts of extracted ants and dichromats had higher bite counts of gleaned invertebrates (extracted ants: odds ratio ± SE = 0.407 ± 0.128, *z* ratio = −2.850, *P* = 0.0044; gleaned invertebrates: odds ratio ± SE = 1.722 ± 0.384, *z* ratio = 2.439, *P* = 0.0147; Fig. 2, lower left panel). In the low fruit period, pairwise comparisons revealed that dichromats took significantly more bites of the fig *Ficus cotinifolia* (odds ratio ± SE = 4.283 ± 2.628, *z*

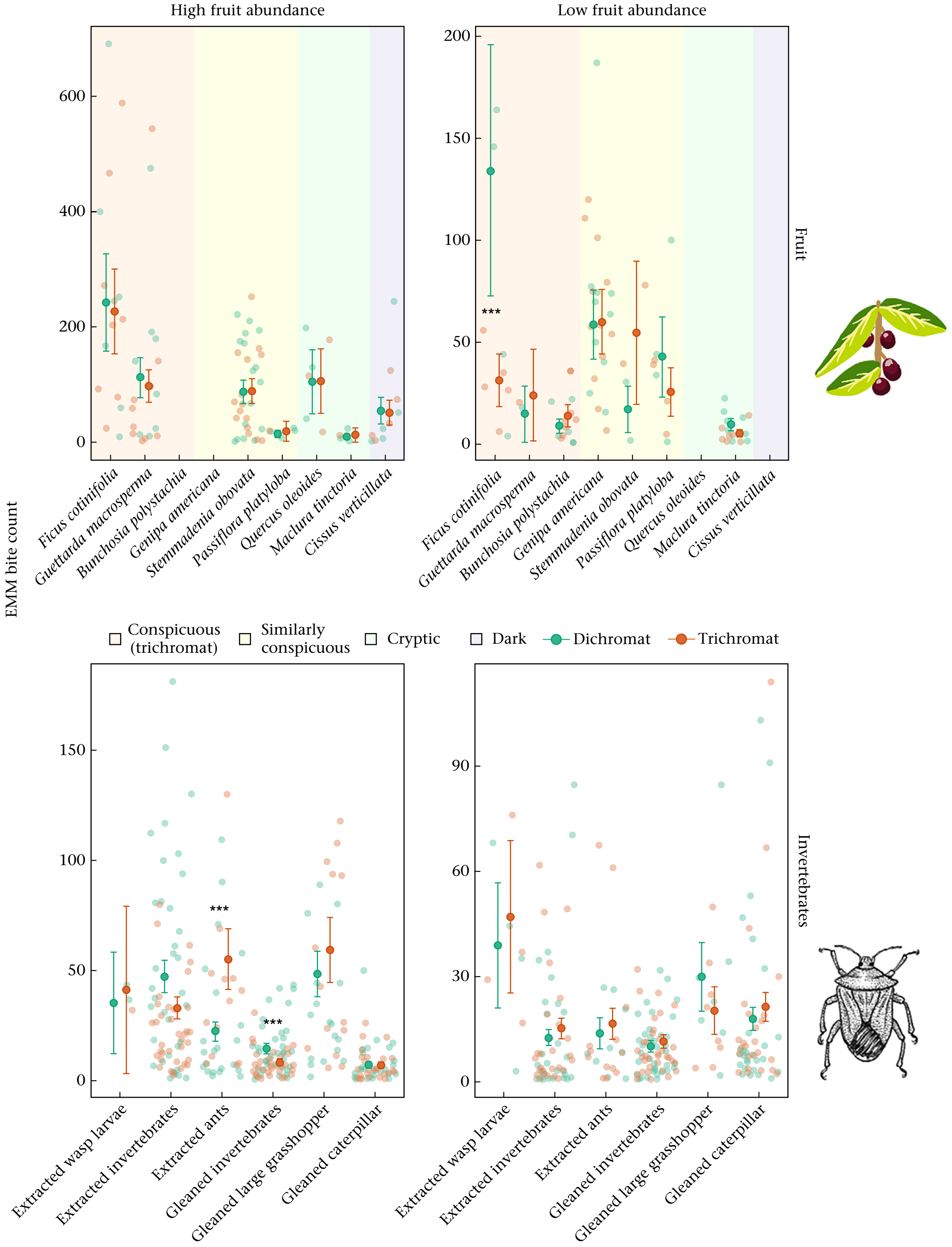

Figure 2. Estimated marginal means (EMMs) of fruit and invertebrate bite counts during high and low fruit periods according to colour vision phenotype and fruit conspicuity. EMMs account for variation in dominance, individual identity, focal pair and focal duration, and so may not be centred on raw data. Note that the scales differ between plots due to variation in bite counts between different food items/fruit periods. Asterisks indicate statistically significant ($P < 0.05$) pairwise contrasts. Image credit: Alyssa Bohart (fruit); Pearson Scott Foresman (shield bug).

ratio = 2.370, $P = 0.0178$; Fig. 2, upper right panel), which was predicted to be more conspicuous to trichromats. There were otherwise no differences between dichromats and trichromats in bite counts of fruits in any conspicuity category. Lastly, social dominance was a statistically significant predictor of bite count, with mid-ranking females exhibiting higher bite counts than low- or high-ranking females (Appendix Table A5). In terms of overall foraging, capuchins consumed more fruit when habitat-wide fruit abundance was high than when it was low. Conversely, capuchins consumed more invertebrates when fruit abundance was low (Fig. 2, Appendix Fig. A2).

Do Dichromats and Trichromats Differ in Nutritional Intake?

To test the prediction of nutritional divergence, we examined intake of (1) crude protein, (2) water-soluble carbohydrates and (3) fibre by examining the estimated marginal means (EMMs) of dichromats and trichromats generated by our full model (Appendix Table A6). Pairwise comparisons of EMMs for protein, carbohydrates and fibre revealed no significant differences in nutrient intake between colour vision phenotypes (Fig. 3). In line with these results, our RMTs show that dichromats and trichromats do not visibly differ in the relative composition of metabolizable energy intake in either the high or low fruit abundant months (Fig. 4b).

Does Dietary and Nutritional Niche Overlap Vary Seasonally?

Differences in overall nutritional intake between high and low fruit months were pronounced, with more nutrients consumed in high fruit months (Fig. 3). We compared measures of niche overlap in high and low fruit abundance to determine whether dietary and nutritional niche overlap decreased during periods of low fruit abundance. The Pianka's index comparing resource use, as measured by bites of different food taxa, between dichromats and trichromats was 0.99 in high fruit months and 0.73 in low fruit months, indicating an overall high degree of dietary overlap, but a reduction by ca. 26% in the low fruit period. Overall, dichromats and trichromats appeared to overlap heavily in the proportional intake of crude fat, crude protein and water-soluble carbohydrates during both high and low fruit abundance. However, our RMTs showed that the overall breadth of nutritional space occupied by dichromats and trichromats decreased in the low fruit period, indicating increased nutritional niche overlap and nutritional constraint when fruit abundance was low (Fig. 4b). Taking Pianka's index and our RMTs together, dichromats and trichromats overlapped less in bite counts but more in nutritional intake when fruit abundance was low.

DISCUSSION

We studied the foraging behaviour and food intake rates of wild adult female capuchin monkeys with differing colour vision phenotypes. Our main findings were two-fold: we found differences in the types of invertebrates eaten by dichromats and trichromats during the high fruit period and a difference in *Ficus cotinifolia* intake during the low fruit period. These results suggest subtle dietary differences. While we found some support for our prediction that dichromats consume more surface-dwelling invertebrates, we failed to find sweeping support for our prediction regarding differences in conspicuous fruit intake. In addition, we found that dichromats and trichromats had highly similar nutritional profiles. This suggests dichromats and trichromats achieve similar nutritional profiles through subtle diet differences. Finally, our results show that habitat-wide fruit abundance shaped the diet and nutrition of all study individuals. We discuss these results in detail below.

Do Dichromats and Trichromats Differ in Food Intake Patterns?

In times of high fruit abundance, dichromats consumed significantly more small invertebrates gleaned from plant surfaces and trichromats consumed significantly more embedded ants that they extracted from dead wood. These results indicate subtle dietary differences due to colour vision type and are consistent with prior research. Melin et al. (2007, 2010) found that dichromats are more efficient than trichromats at gleaning camouflaged invertebrates, which they attributed to an enhanced ability of dichromats to break camouflage, and that trichromats are more efficient than dichromats at extracting invertebrates, a task for which colour vision is presumably unimportant. The authors posited that dichromats and trichromats may specialize on these different invertebrate types. Our results support this hypothesis and indicate that niche differentiation may be taking place in the context of invertebrate foraging. Williamson et al. (2021) examined age−sex variation in primate diets in the same forest and found that invertebrate foraging presents more opportunity for niche differentiation than does fruit foraging, a result consistent with our data. This could be related to the fact that fruit resources are generally more shareable

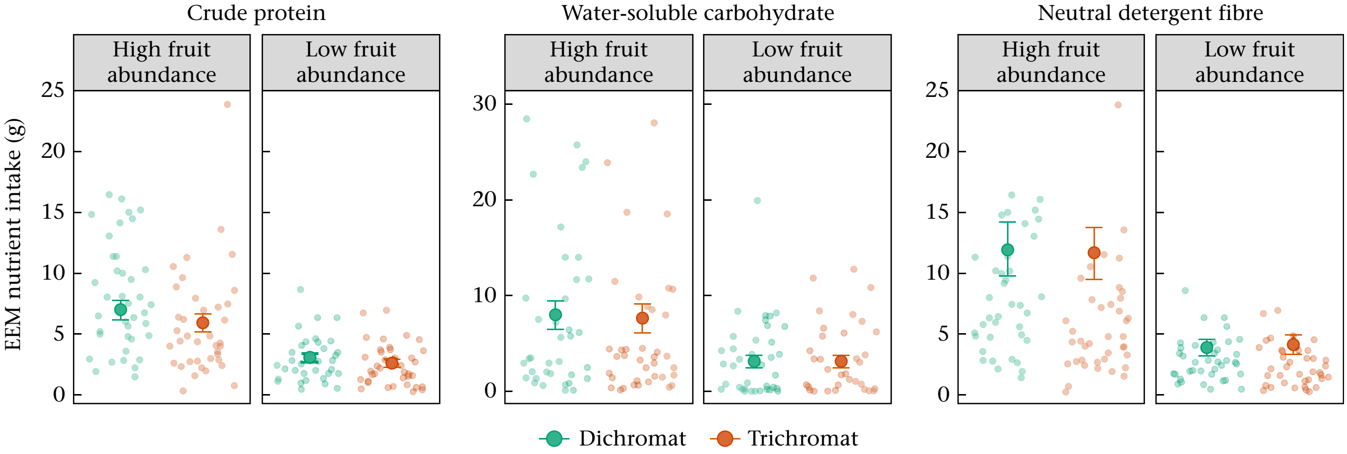

Figure 3. Estimated marginal means (EMMs) of nutrient intake (g) for dichromats and trichromats during high and low fruit abundance. EMMs account for variation in dominance, individual identity, focal pair and focal duration, and so may not be centred on raw data.

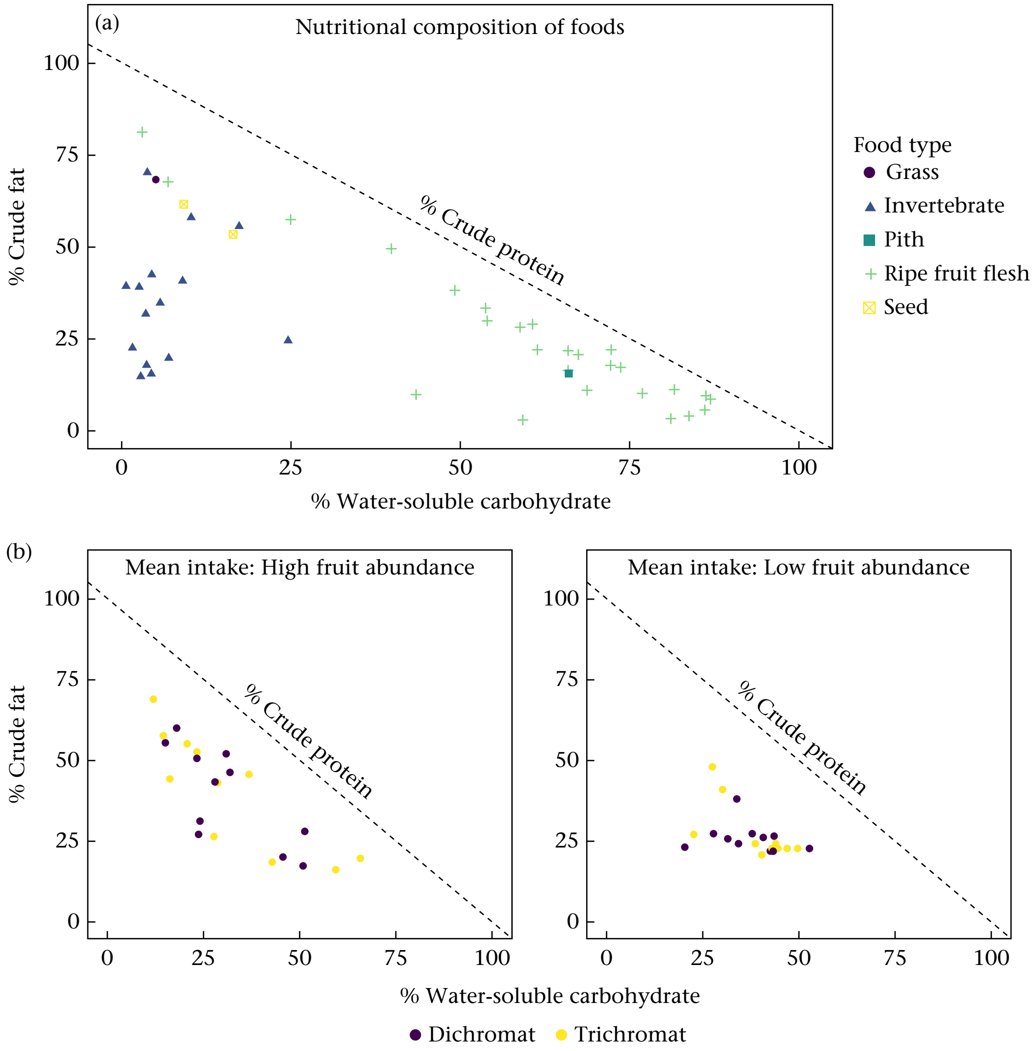

Figure 4. Right-angled mixture triangle (RMT) depicting the relative contributions of water-soluble carbohydrates, crude fat and protein to (a) metabolizable energy of different capuchin food types and (b) each focal female's average metabolizable energy intake in months of high and low fruit abundance.

than invertebrate resources, which may contribute to a mutual benefit of association between individuals of different colour vision phenotypes. Such an argument for mutual benefit of association was made in the context of fruit foraging by Verreaux's sifakas, *Propithecus verreauxi verreauxi*, with polymorphic colour vision (Veilleux et al., 2016). Individuals in mixed-phenotype groups spent more time feeding on fruit than individuals in dichromat-only groups.

Within fruit foraging, fruit bite counts were largely comparable between dichromats and trichromats regardless of modelled conspicuity to the different phenotypes. However, we found that dichromats took significantly more bites of the dark red fig *Ficus cotinifolia* when fruit abundance was low. Fig trees are large-crowned, productive and memorable; they are a key resource to capuchins in Santa Rosa and provide a food source for many days when fruiting (Parr et al., 2011). Although trichromats are modelled to be better able to perceive the reddish hue of this species in chromatic space (Melin, Hiramatsu, et al., 2014), these figs also exhibit a strong achromatic contrast with background foliage (Hiramatsu et al., 2008). Achromatic contrast has been argued to be more important than chroma over short foraging distances (Hiramatsu et al., 2008). Dichromats have long been suggested to rely on achromatic cues, such as luminance, to assess the ripeness of dark fruits, and dichromatic capuchins and spider monkeys are very efficient at feeding on the figs of *Ficus cotinifolia* (Hiramatsu et al., 2008; Melin et al., 2009). Dichromats have also been reported to use nonvisual senses more often than trichromats when feeding, and often use their sense of smell to assess fruits (Melin et al., 2009, 2022). These *F. cotinifolia* figs change in odour profile with ripeness, another cue available to dichromats (Melin et al., 2009, 2019). Overall, *F. cotinifolia* is likely to be a relatively ‘easy’ source of fruit for dichromats, especially in comparison to small patches of ephemeral reddish food sources, which have been shown to carry a trichromat advantage (Hogan et al., 2018).

Do Dichromats and Trichromats Exhibit Nutritional Differences?

Contrary to our second prediction, trichromats and dichromats did not differ in nutritional intake. Rather, both absolute and proportional nutritional intake by dichromats and trichromats largely overlapped during months of high and low fruit abundance. This result is perhaps not surprising, given that most of the significant bite differences we found were within invertebrate categories, which have largely comparable nutritional profiles, i.e. high protein, low carbohydrates (Fig. 4a). Given that they belong to the same species, dichromats and trichromats may be constrained in how much they can differentiate their nutritional profile. Protein is a particularly important macronutrient for these small-bodied primates (Bergstrom et al., 2019). To consume similar levels of protein, dichromats and trichromats appear to differ in their invertebrate foraging strategies, which likely results in differing energetic costs. By targeting embedded prey, which involves ripping and chewing into branches and under bark, trichromats likely exert more effort per unit time to achieve comparable protein intake as dichromats, who gleaned more surface-dwelling invertebrates from surfaces. Future studies testing energetic investment in diet acquisition may provide further insight.

Does Dietary and Nutritional Niche Overlap Vary Seasonally?

We predicted that the largest separation in diet and nutrition between colour vision types would be during months of low fruit abundance due to increased ecological pressures to avoid intraspecific competition. We found that Pianka's index, a measure of diet overlap, decreased by ca. 26%, from 0.99 to 0.73, when fruit was scarce, indicating a marginally lower degree of niche overlap. This was consistent with our prediction. Such a decrease in overlap by about 25% seems likely to be impactful and worthy of follow-up investigation. In terms of nutritional niche differentiation, our results indicate that dichromats and trichromats continued to overlap strongly in relative composition of nutrient intake during both high and low fruit periods. Despite the overall drop in total grams of nutrient intake, which reflects the poorer nutritional landscape when fruit was scarce, dichromats and trichromats consumed similar levels of protein, fat and carbohydrates. Taken together we found no evidence of nutritional niche divergence due to sensory phenotype at the scale examined here.

Seasonal Drivers of Diet and Nutrition

We join others in highlighting the impact of seasonality on diet and nutrition of frugivores in tropical ecosystems (Bergstrom et al., 2018; Conklin-Brittain et al., 1998; Knott, 1998; Koch et al., 2017; Marshall et al., 2014; Worman & Chapman, 2005). In capuchins, fruit abundance appears to drive foraging and nutritional patterns: when fruit abundance is high, individuals consume more fruit and more grams of nutrients overall, including more grams of protein, carbohydrates and fibre. As habitat-wide fruit abundance drops, so does overall food consumption, and invertebrates increase in relative proportion of the diet (Bergstrom et al., 2018; Mosdossy et al., 2015). Beyond influencing dietary strategies in frugivorous primates, the cyclical nature of fruit abundance in tropical ecosystems has implications for other ecological processes, including migratory patterns in frugivorous birds and bats (Boyle et al., 2011; Levey, 1988; Richter & Cumming, 2006) as well as plant–frugivore network dynamics (Ramos-Robles et al., 2018).

Conclusions and Future Directions

Here we tested the extent to which fine-scale dietary and nutritional niche differentiation may be occurring between individuals with different sensory phenotypes in a wild platyrrhine primate. We found limited support for this idea: colour vision type appears to explain some seasonal diet variation in sources of invertebrate types and fruits, although this variation is somewhat different than we had predicted, especially in the context of fruit foraging. We found no support for the directional prediction that trichromats consume more chromatically conspicuous ripe fruit. Differences in patterns of invertebrate consumption between dichromats and trichromats that we observed are consistent with previous findings that dichromats specialize on more camouflaged prey, while trichromats focus time on extracting difficult, embedded prey (Melin et al., 2007). This opens new future questions regarding the ontogeny of this behavioural difference, especially given the importance of social learning in this large-brained species (Eadie, 2015; Perry, 2020; Perry, 2011). Our study focused on adult females, which had likely already achieved foraging competency; we would expect greater differences in juveniles as they learn to navigate a complex foraging landscape. Paired studies of juvenile capuchins would help illuminate this. Despite small dietary differences, adult female dichromats and trichromats achieved remarkably similar nutritional intake profiles. The capacity for nutritional variation may be relatively constrained: capuchins are large-brained, highly active primates and unlike some other primates, maintain a relatively high-energy diet year-round (Bergstrom et al., 2018; Fragaszy et al., 2004; McCabe & Fedigan, 2007). Taken together, this suggests a limited ability for adult female capuchins to significantly separate their nutrient intake according to colour vision phenotype.

Although our study included a relatively large sample for wild primates, a limitation of our study was the small number of individuals. Future efforts following more groups and individuals simultaneously would be labour-intensive but likely generate additional analytical power. Furthermore, social factors of group-living species may have led to nonindependence of foraging patterns, such that the behaviour of one pair member influences the other. While we attempted to control for this by including pair ID as a random factor (and the paired focal follow method allows for excellent control of environmental and group variation), it remains a limitation of the study system. In addition, limitations imposed by our assumption that bite sizes are constant across foods as well as our use of existing nutritional data, which may not reflect the exact quality of the items consumed by subjects in our study, may have introduced noise into our analysis.

Our study joins a growing body of work that seeks to shed light on the mechanisms behind balancing selection and the persistence of intraspecific variation. Future studies of other colour-vision polymorphic populations and species would allow conclusions about the likelihood of niche differentiation as a force influencing the balancing selection acting on colour vision phenotype and underlying opsin genes more generally. To this end, it would be exciting to determine whether animals expressing visual pigments more sensitive to longer wavelengths differ in diet from animals expressing visual pigments more sensitive to medium wavelengths, as proposed nearly 20 years ago by Osorio et al. (2004). Additional research should also seek to investigate other niche dimensions (i.e. temporal and microhabitat use; Caine et al., 2010; Yamashita et al., 2005) as well as to examine other possible nonmutually exclusive mechanisms of balancing selection, including mutual benefit of association and negative frequency dependence. Senses form a key interface between organisms and their social and physical environments. Research into polymorphic sensory variation will continue to benefit evolutionary biologists, ecologists and geneticists who seek to better understand the mechanisms and function of phenotypic variation in populations.

Author Contributions

Allegra N. DePasquale: Conceptualization, Methodology, Formal analysis, Investigation, Data curation, Writing – Original draft, Writing – Review & editing, Visualization, Project administration, Funding acquisition. **Jeremy D. Hogan:** Formal analysis, Writing – Review & editing. **Cinthia Villalobos-Suarez**: Investigation, Data curation, Writing – Review & editing. **Megan A. Mah**: Investigation, Data curation, Writing – Review & editing. **Jean-Christophe Martin**: Investigation, Data curation, Writing – Review

& editing. **Linda M. Fedigan**: Conceptualization, Resources, Writing – Review & editing, Supervision, Funding acquisition. **Jessica M. Rothman**: Investigation, Resources, Writing – Review & editing. **Amanda D. Melin**: Conceptualization, Methodology, Resources, Writing – Original draft, Writing – Review & editing, Supervision, Project administration, Funding acquisition.

Data Availability

The data and code supporting this manuscript can be located at the following link: https://github.com/allegradepasquale/focal_niche_divergence_analysis.git.

Declaration of Interest

None.

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at https://doi.org/10.1016/j.anbehav.2023.08.016.

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Appendix

Colour Categorizations

We categorized the fruit species analysed here into colour categories to generate a priori predictions based on Table 2 from Melin, Hiramatsu, et al. (2014). Melin et al. measured the reflectance spectra of ripe dietary fruits alongside the upper and lower surface of mature leaves of the same species relative to a white reflectance standard (WS-1-SL) using a USB 4000 portable spectrometer and LS-1 light source (Ocean Optics, Inc., Dunedin, FL, U.S.A.) in situ in SSR. The dark reference was stored by turning off the light source and covering the probe with a dark cloth, held in a black bag. When recording reflectance spectra, five measurements/item per surface were performed to achieve an adequate representation of each item. For each measurement the 'scans to average' was set to 5 and the boxcar width was set to '3' in the Ocean Optics software. The measurements were taken with the probe held in a customized holder at a distance of 0.5–1 cm from the surface of the fruit (adjusted as needed to bring the white reflectance standard fully within the measurement range of the instrument) at a 45-degree angle. The mean reflectance was computed for all ripe fruits, as well as upper and lower leaves, for each species. Quantum catch for each photoreceptor was calculated according to the following formula that represents the quantum catch of photoreceptor i over the primate visual spectrum (400–700 nm)

$$Qi = \int_{400}^{700} R(\lambda)I(\lambda)Si(\lambda)\mathrm{d}\lambda$$

where $R(\lambda)$ represents the reflectance spectrum, $I(\lambda)$ represents the irradiance spectrum ('forest shade' measured in SSR), $Si(\lambda)$ is the spectral sensitivity function of the ith photoreceptor containing S or M/L photopigments. Chromaticity for each item was modelled as a ratio of the quantum catches by the S, L and M cone types found in SSR. The peak spectral sensitivities of the M/L opsin were set to 532 nm (M), 543 nm (ML) and 561 nm (L). The S pigment peak sensitivity was set to 426 nm.

The chromaticity of each species was modelled following the methodology of Hiramatsu et al. (2008): red-green chromaticity (trichromats only) = QL/(QL + QM); blue-yellow chromaticity for trichromats = QS/(QL + QM) and for dichromats = QS/(2QL or 2QM). We normalized the modelled sensitivity at the cornea for the S, M and L cones such that the quantum catch of a 100% reflective surface under flat illumination was 1, and we used these values in the chromaticity calculation. Accordingly, the resultant chromaticity values are not based on estimates of cone proportions (Sumner & Mollon, 2000).

To model the conspicuity of fruits against background foliage for each phenotype, Melin, Hiramatsu, et al. (2014) implemented a support vector machine (SVM) algorithm using LIBSVM (Chang & Lin, 2011) in MATLAB. This supervised machine-learning algorithm analyses training data to construct a hyperplane, which is then used to objectively classify fruits as chromatically discriminable from background foliage, or not, separately for each trichromatic and dichromatic phenotype. Trichromatic SVMs implement both red-green and blue-yellow chromaticities while dichromatic SVMs implement only blue-yellow chromaticities. Fruits were classified as chromatically discriminable to a given phenotype if the SVM could correctly discriminate fruit chroma from leaf chroma. If fruit chroma and leaf chroma overlapped and the SVM could not correctly identify a fruit, then the fruit was considered to be cryptic to that phenotype. Table 2 in Melin, Hiramatsu, et al. (2014) summarizes the conspicuity results for each plant species.

Our categories were defined as follows, based on the chromatic discrimination data in Table 2 of Melin, Hiramatsu, et al. (2014).

Chromatically conspicuous to trichromats only

The fruit is chromatically conspicuous (i.e. a 'yes' in Table 2 of Melin, Hiramatsu, et al., 2014) to at least two out of three trichromatic phenotypes and chromatically inconspicuous (i.e. a 'no') to the 561 dichromatic phenotype.

Similarly chromatically conspicuous to trichromatic and dichromatic phenotypes

The fruit is chromatically conspicuous to at least two trichromatic phenotypes as well as the 561 dichromatic phenotype.

Chromatically cryptic to trichromatic and dichromatic phenotypes

The fruit is chromatically inconspicuous (i.e. a 'no') to at least two trichromatic phenotypes as well as the 561 dichromatic phenotype. Data for the acorn *Quercus oleoides* are missing from Melin, Hiramatsu, et al. (2014). We categorized this fruit as cryptic due to its greenish hue and lack of conspicuous colour change.

Conspicuous in luminance to trichromatic and dichromatic phenotypes (dark)

Fruits that are dark purple-black. The only fruit species in our top 15 taxa that we analysed that fell into this category was *Cissus verticillata*, which are black when ripe.

Right-Angled Mixture Triangles (RMTs)

Nutritional geometry refers to a set of state-based modelling techniques that allow for visualization of patterns in nutritional intake, either in absolute amounts or proportions. We applied Raubenheimer's (2011) right-angled mixture triangle (RMT), a tool from proportion-based nutritional geometry, to both our food nutritional composition data and focal intake data. This allowed us to visualize how capuchins mix food resources to achieve their nutritional intake by comparing the relative contributions of different macronutrients to the metabolizable energy of the food items themselves and capuchin nutrient intake. We used this approach to then estimate whether dichromats and trichromats differ in the balance of nutrients that comprises their metabolizable energy intake during periods of low and high fruit abundance. This approach can be used to visualize nutritional niche separation, i.e. whether dichromats get relatively more of their energy from proteins and fat and whether trichromats get relatively more of their energy from water-soluble carbohydrates. Three axes, x, y and z, are present in an RMT, forming a right-angle triangle with the z axis (also called the 'implicit' axis) as the hypotenuse. Each axis represents a macronutrient (protein, sugar, fat) scaled from 0 to 100, indicating 0–100% contribution to metabolizable energy. Thus, adding the x and y value for any point and subtracting by 100 will produce the z value.

To determine the relative macronutrient contributions to metabolizable energy, we converted the macronutrient value to its equivalent in kilocalories using Atwater conversion factors (crude protein × 4, water-soluble carbohydrates × 4, crude fat × 9; Merrill & Watt, 1955). We then summed these to obtain metabolizable energy from macronutrients and divided each macronutrient by metabolizable energy to determine its percentage of contribution to metabolizable energy. In our calculation of metabolizable energy, we included only crude protein, water-soluble carbohydrates and crude fat. Other components of nonstructural carbohydrates, including pectin and starch, were excluded due to limitations of available data but may be present (Rothman et al., 2012). We constructed three RMTs: one depicting macronutrient contributions to metabolizable energy of dietary food items and two depicting macronutrient contribution to metabolizable energy for each focal animal's average intake, separated by high and low fruit months.

Pianka's Index of Niche Overlap

Pianka's index measures the relative amount of overlap in resource use between two groups by calculating resource use as a proportion of total resources. This index is typically used for measuring overlap between pairs of species, but we adopted it for measuring overlap in food intake between two phenotypes within a single species. Pianka's index ranges from 0 to 1; a value of 0 indicates complete niche separation (i.e. 0% overlap), while a value of 1 indicates complete niche overlap (i.e. 100% overlap). Thus, values closer to 1 indicate greater overlap (MacArthur & Levins, 1967; Pianka, 1973, 1974). We used the R package 'EcoSimR' to calculate the observed Pianka's index (Gotelli et al., 2015). The resource categories used to calculate Pianka's index were the estimated marginal means generated for Research Question 1: bites taken by dichromats and trichromats of each food taxon in times of high and low fruit abundance. Since they were generated from our bite count GLMM, our resulting Pianka's indices thus control for the effects of dominance, animal ID and pair ID.

Table A1
Dichromat–trichromat pairs of adult female white-faced capuchins

Dichromat	Trichromat	Group	Pair ID
KI (red)	FT (green-red)	RM	1
SH (red)	MA (green-red)	RM	2
SI (red)	PR (green-red)	RM	3
ED (red)	LA (green-red)	RM	4
SJ (red)	SS (green-yellow)	LV	5
CT (red)	OR (green-red)	LV	6
VN (red)	CH (red-yellow)	LV	7
CE (red)	TH (red-yellow)	LV	8
QD (red)	PD (green-yellow)	GN	9
RS (red)	MW (green-red)	BR	10
SP (red)	WK (green-red)	BR	11

For each individual, we also list their colour vision type. All dichromats in our study had a red-shifted phenotype, corresponding to a peak light sensitivity of their long wavelength-sensitive cone opsin of ca. 561 nm. The trichromats have two long wavelength-sensitive cone opsins, composed of red (561 nm) and/or yellow (ca. 543 nm) and/or green-shifted (ca. 532 nm) cone opsins.

Table A2
The Santa Rosa Primate Field Project standardized behavioural ethogram

Behaviour	Description
Forage fruit- extractive (EFF)	Pounding, scrubbing, breaking open (etc.) fruit
Forage insect- extractive (EFI)	Tearing or breaking branches, ripping bark
Forage flower (FFL)	Feeding on flowers
Forage fruit (FFR)	Feeding on fruit
Forage insects (FIN)	Feeding on insects
Forage other (FOT)	Feeding on bromeliad leaves, pith, vertebrates
Drink (DRI)	Drinking
Intergroup encounter (IGE)	Intergroup encounter with another monkey group
Mobbing (MOB)	Mobbing a predator
Play (PLA)	Playing: biting, chasing, bouncing, pushing, etc.
Solitary rest (RES)	Resting away from conspecifics
Social active (SAC)	Acting affiliatively (i.e. allogrooming)
Social aggressive (SAG)	Aggressive towards conspecifics: biting, chasing, etc.
Self-directed (SDI)	Autogrooming
Social rest (SRE)	Resting in contact with conspecifics
Travel (TRA)	Travelling; not foraging or socializing
Visual forage (VFO)	Looking for food (includes gleaning insects while moving)
Vigilant (VIG)	Scanning intently at long range (not for food)
Other (OTH)	Any other behaviour not covered
Out of sight (OOS)	Individual is out of sight

Table A3
Food categorizations for the top 15 foods included in this study

Food type	Classification
Invertebrate	
Wasp larvae	Embedded
Unknown extracted invertebrate	Embedded
Ants	Embedded
Unknown gleaned invertebrate	Gleaned
Large grasshopper	Gleaned
Caterpillar	Gleaned
Fruit	
Ficus cotinifolia	Conspicuous (trichromat)
Guettarda macrosperma	Conspicuous (trichromat)
Bunchosia polystachia	Conspicuous (trichromat)
Genipa americana	Similarly conspicuous
Stemmadenia obovata	Similarly conspicuous
Passiflora platyloba	Similarly conspicuous
Quercus oleoides	Cryptic
Maclura tinctoria	Cryptic
Cissus verticillata	Dark

Fruit conspicuity categorizations are based on fruit reflectance and chromatic discrimination modelling for each dichromatic and trichromatic phenotype, from Melin, Hiramatsu, et al. (2014). Invertebrates are classified according to substrate.

Table A4
Nutritional composition data for foods ($N = 57$) included in this study

Taxon	Food type	WM (g)	DM (g)	%H_2O	%DM	%CP	%CF	%WSC	%NDF	Sources and Comments
Spondias mombin	Ripe fruit flesh	4.69	0.64	86.4	13.6	3.7	6.6	48.3	19.1	Bergstrom (2015)
Byrsonima crassifolia	Ripe fruit flesh	1.4	0.22	84.4	15.6	4.8	10	18.1	40.2	Bergstrom (2015)
Passiflora platyloba	Ripe fruit flesh	13.7	2.16	84.2	15.8	2.2	0.7	23.4	34.9	Using average fruit NDF, using *Genipa americana* weight and *Passiflora platyloba* water content to calculate dry mass
Ficus hondurensis	Ripe fruit flesh	0.82	0.14	83.2	16.8	6.4	5.1	46.3	32.2	Bergstrom (2015)
Maclura tinctoria	Ripe fruit flesh	3.99	0.7	82.5	17.5	11.2	15	43.5	24	Bergstrom (2015)
Bromelia plumieri	Ripe fruit flesh	9.23	1.62	82.4	17.6	4.6	0.7	31.8	7.3	Bergstrom (2015), using all fruit WSC average
Caterpillar	Invertebrate	0.26	0.05	80.2	19.8	60.2	21.9	10.8	6.1[a]	Using 'medium' caterpillar; Bergstrom (2015)
Eugenia salamensis	Ripe fruit flesh	2.82	0.58	79.5	20.6	3.2	2.8	62.7	14.1	Bergstrom (2015)
Ficus ovalis	Ripe fruit flesh	0.77	0.17	78.2	21.8	3.3	3.4	68.4	19.9	Bergstrom (2015)
Guettarda macrosperma	Ripe fruit flesh	2.98	0.65	78.1	21.9	3.6	2.5	40.8	41.4	Bergstrom (2015)
Margaritaria nobilis	Ripe fruit flesh	0.41	0.09	76.9	23.1	6	8.8	8.6	67.5	Bergstrom (2015)
Allophylus occidentalis	Ripe fruit flesh	0.29	0.07	76.8	23.2	19.3	22.9	5.2	37.6	Bergstrom (2015)
Sciadodendron excelsum	Ripe fruit flesh	0.41	0.09	76.7	23.3	7.6	8.8	31.8	33.4	Bergstrom (2015); average fruit WSC
Large insect	Invertebrate	2.37	0.59	74.9	25.1	70.5	20.7	0.8	7.4[a]	Using large grasshopper: Bergstrom (2015), Rothman et al. (2014)
Katydid	Invertebrate	2.37	0.59	74.9	25.1	70.5	20.7	0.8	7.4[a]	Bergstrom (2015), Rothman et al. (2014)
Large grasshopper	Invertebrate	2.37	0.59	74.9	25.1	70.5	20.7	0.8	7.4[a]	Bergstrom (2015), Rothman et al. (2014)
Cecropia peltata	Ripe fruit flesh	0.84	0.3	73.7	26.3	6.9	5.4	39.4	29.2	Bergstrom (2015)
Various insect	Invertebrate	0.3	0.08	73	27	60.9	8.1	1.3	10.6[a]	Substituting 'various invertebrates': Bergstrom (2015), Rothman et al. (2014)
Cricket	Invertebrate	0.67	0.18	72.7	27.3	74.5	6.5	4	7.4[a]	Rothman et al. (2014)
Cordia panamensis	Ripe fruit flesh	0.44	0.13	69.6	30.4	7.3	9.2	43.2	49.8	Bergstrom (2015)
Ficus cotinifolia	Ripe fruit flesh	0.52	0.16	68.8	31.2	7.4	6.1	24.8	41.2	Bergstrom (2015)
Cockroach	Invertebrate	7.29	2.29	68.5	31.5	86.7	8.9	4.1	9.8[a]	Bergstrom (2015), Rothman et al. (2014)
Chomelia spinosa	Ripe fruit flesh	0.58	0.19	67.7	32.3	3.4	2.7	18.3	60.2	Bergstrom (2015)
Small grasshopper	Invertebrate	0.85	0.28	67.4	32.6	74.5	6.5	4	7.4[a]	Bergstrom (2015), Rothman et al. (2014)
Cicada	Invertebrate	2.62	0.86	67.1	32.9	81.6	6.6	2.8	12.2[a]	Bergstrom (2015), Rothman et al. (2014)
Wasp larvae	Invertebrate	0.1	0.03	66.7	33.3	48.9	10.6	23.7	3.0[a]	Bergstrom (2015), Rothman et al. (2014)
Ants	Invertebrate	0.02	0.0068	66.2	33.8	51.8	15.6	2.3	17.9[a]	Bergstrom (2015)
Diospyros salicifolia	Ripe fruit flesh	1.53	0.55	63.9	36.1	5.7	1.4	19.5	75.6	Bergstrom (2015)
Small crunchy insect	Invertebrate	0.16	0.06	62.9	37.1	81.6	6.6	2.8	12.2[a]	Using shield bug: Bergstrom (2015), Rothman et al. (2014)
Stinkbug	Invertebrate	0.16	0.06	62.9	37.1	81.6	6.6	2.8	12.2[a]	Bergstrom (2015), Rothman et al. (2014)
Scorpion	Invertebrate	1.45	0.57	60.9	39.2	72.3	16	4	10.6[a]	Bergstrom (2015), Rothman et al. (2014)
Genipa americana	Ripe fruit flesh	13.7	5.6	59.1	40.9	8.6	5.1	31.8	37.4	Bergstrom (2015) Average fruit WSC
Stemmadenia obovata	Ripe fruit flesh	9.73	4.06	58.3	41.7	16.6	38.3	3.2	38	Bergstrom (2015)
Jacquinia nervosa	Ripe fruit flesh	2.29	1.05	53.9	46.1	6.7	2.4	40.2	38.3	Bergstrom (2015)
Quercus oleioides	Ripe fruit flesh	0.9	0.42	53.4	46.6	6.1	2.6	23	16.5	Bergstrom (2015)
Bunchosia polystachia	Ripe fruit flesh	0.71	0.36	50.2	49.8	9.4	0.3	14.7	38	Using *Bunchosia ocellata*; Bergstrom (2015)
Vachellia collinsi	Ripe fruit flesh	0.2	0.12	40	60	6.1	0.6	31.8	7	Average fruit WSC
Luehea candida	Seed	0.03	0.02	38.6	61.4	19.6	15.6	10.8	25.3	Bergstrom (2015)
Lasiacis sorghoidea	Grass	0.01	0.01	30.9	69.1	12.8	14.7	2.4	55.9	Bergstrom (2015)
Luehea speciosa	Seed	0.02	0.02	0	100	17.8	16.8	5.6	42.3	Bergstrom (2015)
Unknown *Ficus*	Ripe fruit flesh	0.7033	0.1567	77.7	22.3	5.7	4.9	46.5	31.1	Bergstrom (2015)
Gonolobus barbatus	Ripe fruit flesh	12.69	2.87	77.4	22.6	7	6.8	31.8	34.9	Using *Matalea quirosii* weight and average fruit values
Matalea quirosii	Ripe fruit flesh	12.69	2.87	77.4	22.6	7	6.8	31.8	34.9	Fruit average
Solanum hazenii	Ripe fruit flesh	0.51	0.26	49	51	7	6.8	31.8	34.9	Fruit average, estimated weight
Cissus verticillata	Ripe fruit flesh	0.25	0.16	36	64	7	6.8	31.8	34.9	Fruit average, estimated weight
Cordia guanacastensis	Ripe fruit flesh	0.03	0.02	33.3	66.7	7	6.8	31.8	34.9	Fruit average, estimated weight
Paullinea cururu	Ripe fruit flesh	0.02	0.01	50	50	7	6.8	31.8	34.9	Fruit average, estimated weight
Psychotria horizontalis	Ripe fruit flesh	0.02	0.01	50	50	7	6.8	31.8	34.9	Fruit average, estimated weight
Bursera simaruba	Pith	0.09	0.01	88.9	11.1	4.7	1.8	17	45.6	Estimated dry weight
Inga vera	Ripe fruit flesh	10.17	1.73	83	17	15.7	1.5	14.7	47.7	Eadie (2013); using free simple sugars instead of WSC; wet mass calculated from H_2O (83%) from Lim (2012)
Beetle	Invertebrate	0.85	0.28	67.1	32.9	40.7	33.4	13.2	8.7[a]	Rumpold and Schlüter (2013), Rothman et al. (2014), using small grasshopper weight
Snail	Invertebrate	1.3	0.53	59.2	40.8	64.4	16.9	6.2	10.6[a]	Average invertebrate value, average invertebrate weight
Spider	Invertebrate	0.67	0.18	73.1	26.9	65.2	7.9	6.2	13.1[a]	Rothman et al. (2014), using cricket weight and average invertebrate WSC value
Moth	Invertebrate	1.3	0.59	54.6	45.4	42.5	51.4	6.2	17.8[a]	Rothman et al. (2014), average invertebrate WSC, estimated weight
Dragonfly	Invertebrate	0.67	0.18	73.1	26.9	55.2	19.8	4.6	11.8[a]	Rumpold and Schlüter (2013), using cricket weight
Cocoon	Invertebrate	0.1	0.03	70	30	64.4	16.9	6.2	10.6[a]	Average invertebrate value, using wasp larvae weight
Termite	Invertebrate	0.02	0.0068	66	34	35.3	32.7	22.8	18.5[a]	Rumpold and Schlüter (2013)

WM: wet mass; DM: dry mass; CP: crude protein; CF: crude fat; WSC: water-soluble carbohydrates; NDF: neutral detergent fibre. For food items without published data, values are estimated based on foods of the same class (invertebrate or fruit) and similar size with details provided in the Sources and Comment column.

[a] Values from Rothman et al. (2014).

Table A5

Results of the full negative binomial generalized linear mixed model for bite counts in response to colour vision phenotype, food taxon, fruit abundance and the interaction of these variables

Fixed effect	Estimate	SE	*z*	Pr(>|*z*|)
(Intercept)	−5.19783	0.65503	−7.935	2.10E-15
Phenotype	0.1567	1.12872	0.139	0.88958
Extracted ants	−0.45252	0.68285	−0.663	0.50753
Gleaned invertebrates	−0.88418	0.67536	−1.309	0.19047
Gleaned large grasshopper	0.31677	0.691	0.458	0.64665
Gleaned caterpillar	−1.61187	0.67789	−2.378	0.01742*
Extracted invertebrates	0.29277	0.67408	0.434	0.66405
Ficus cotinifolia	1.92765	0.73383	2.627	0.00862*
Guettarda macrosperma	1.15774	0.71968	1.609	0.10769
Bunchosia polystachia	−1.47349	0.60577	−2.432	0.015*
Genipa americana	0.41146	0.53994	0.762	0.44604
Stemmadenia obovata	0.90755	0.68851	1.318	0.18746
Passiflora platyloba	−0.86991	0.80135	−1.086	0.27768
Quercus oleiodes	1.08919	0.84515	1.289	0.19748
Maclura tinctoria	−1.26768	0.7942	−1.596	0.11045
Cissus verticillata	0.43531	0.76427	0.57	0.56896
FruitBiomassCategoryLow	0.09703	0.79999	0.121	0.90347
DominanceCategoryLow	0.01054	0.11123	0.095	0.92449
DominanceCategoryMid	0.26444	0.10401	2.543	0.01101*
Phenotype: Extracted ants	0.74256	1.17428	0.632	0.52715
Phenotype: Gleaned invertebrates	−0.70032	1.14986	−0.609	0.54249
Phenotype: Gleaned large grasshopper	0.04586	1.17248	0.039	0.9688
Phenotype: Gleaned caterpillar	−0.16607	1.15691	−0.144	0.88586
Phenotype: Extracted invertebrates	−0.51793	1.15151	−0.45	0.65286
Phenotype: *Ficus cotinifolia*	−0.22337	1.22029	−0.183	0.85476
Phenotype: *Guettarda macrosperma*	−0.29826	1.20186	−0.248	0.804
Phenotype: *Bunchosia polystachia*	0.26267	0.85112	0.309	0.75761
Phenotype: *Genipa americana*	−0.16846	0.75849	−0.222	0.82424
Phenotype: *Stemmadenia obovata*	−0.14325	1.17201	−0.122	0.90272
Phenotype: *Passiflora platyloba*	0.08744	1.53453	0.057	0.95456
Phenotype: *Quercus oleiodes*	−0.14278	1.35005	−0.106	0.91577
Phenotype: *Maclura tinctoria*	0.07944	1.5403	0.052	0.95887
Phenotype: *Cissus verticillata*	−0.2107	1.26403	−0.167	0.86762
Phenotype: FruitBiomassCategoryLow	0.03394	1.30807	0.026	0.9793
Extracted ants: FruitBiomassCategoryLow	−0.58288	0.88752	−0.657	0.51134
Gleaned invertebrates: FruitBiomassCategoryLow	−0.46033	0.83284	−0.553	0.58045
Gleaned large grasshopper: FruitBiomassCategoryLow	−0.579	0.88894	−0.651	0.51483
Gleaned caterpillar: FruitBiomassCategoryLow	0.83886	0.84084	0.998	0.31845
Extracted invertebrates: FruitBiomassCategoryLow	−1.41534	0.83636	−1.692	0.0906
Ficus cotinifolia: FruitBiomassCategoryLow	−0.68836	0.97729	−0.704	0.48122
Guettarda macrosperma: FruitBiomassCategoryLow	−2.13003	1.264	−1.685	0.09196
Stemmadenia obovata: FruitBiomassCategoryLow	−1.73503	1.06352	−1.631	0.1028
Passiflora platyloba: FruitBiomassCategoryLow	0.96662	1.03293	0.936	0.34938
Maclura tinctoria: FruitBiomassCategoryLow	−0.12923	0.97221	−0.133	0.89425
Phenotype: Extracted ants: FruitBiomassCategoryLow	−0.75082	1.40971	−0.533	0.59431
Phenotype: Gleaned invertebrates: FruitBiomassCategoryLow	0.63492	1.34686	0.471	0.63735
Phenotype: Gleaned large grasshopper: FruitBiomassCategoryLow	−0.62515	1.42845	−0.438	0.66165
Phenotype: Gleaned caterpillar: FruitBiomassCategoryLow	0.15011	1.36026	0.11	0.91213
Phenotype: Extracted invertebrates: FruitBiomassCategoryLow	0.51001	1.35425	0.377	0.70647
Phenotype: *Ficus cotinifolia*: FruitBiomassCategoryLow	−1.42193	1.51588	−0.938	0.34823
Phenotype: *Guettarda macrosperma*: FruitBiomassCategoryLow	0.60211	1.89411	0.318	0.75057
Phenotype: *Stemmadenia obovata*: FruitBiomassCategoryLow	1.11884	1.63663	0.684	0.49421
Phenotype: *Passiflora platyloba*: FruitBiomassCategoryLow	−0.79573	1.79203	−0.444	0.65702
Phenotype: *Maclura tinctoria*: FruitBiomassCategoryLow	−0.87295	1.74186	−0.501	0.61626

Phenotype values are calculated with dichromat as the reference. Dominance rank is included to control for variation arising from social dominance hierarchies in capuchins. Asterisks indicate statistical significance ($P < 0.05$).

Table A6
Results of the gamma generalized linear mixed models for nutrient intake in response to colour vision phenotype, fruit abundance and the interaction of these variables

Fixed effect	Estimate	SE	*t*	*P*
Protein intake model				
(Intercept)	−6.875646	0.148274	−46.371	< 2e-16
PhenotypeT	−0.164183	0.144245	−1.138	0.255
FruitBiomassCategoryLow	−0.825428	0.127309	−6.484	0.0000000000895*
DominanceCategorylow	0.119728	0.175641	0.682	0.4955
DominanceCategorymid	0.382711	0.152052	2.517	0.0118*
PhenotypeT: FruitBiomassCategoryLow	0.004262	0.181088	0.024	0.9812
WSC intake model				
(Intercept)	−6.83017	0.22423	−30.461	< 2e-16
PhenotypeT	−0.05078	0.27507	−0.185	0.853528
FruitBiomassCategoryLow	−0.93498	0.27326	−3.422	0.000623*
DominanceCategorylow	0.32509	0.23507	1.383	0.166672
DominanceCategorymid	0.43422	0.23999	1.809	0.0704
PhenotypeT: FruitBiomassCategoryLow	0.04039	0.38407	0.105	0.916243
NDF intake model				
(Intercept)	−6.49647	0.22277	−29.162	< 2e-16
PhenotypeT	−0.02513	0.2456	−0.102	0.9185
FruitBiomassCategoryLow	−1.11577	0.24374	−4.578	0.0000047*
DominanceCategorylow	0.47002	0.21613	2.175	0.0297*
DominanceCategorymid	0.52211	0.22469	2.324	0.0201*
PhenotypeT: FruitBiomassCategoryLow	0.07825	0.33646	0.233	0.8161

WSC: water-soluble carbohydrates; NDF: neutral detergent fibre. Phenotype values are calculated with dichromat as the reference level. Dominance rank is included to control for variation arising from social dominance hierarchies in capuchins. Asterisks indicate statistical significance ($P < 0.05$).

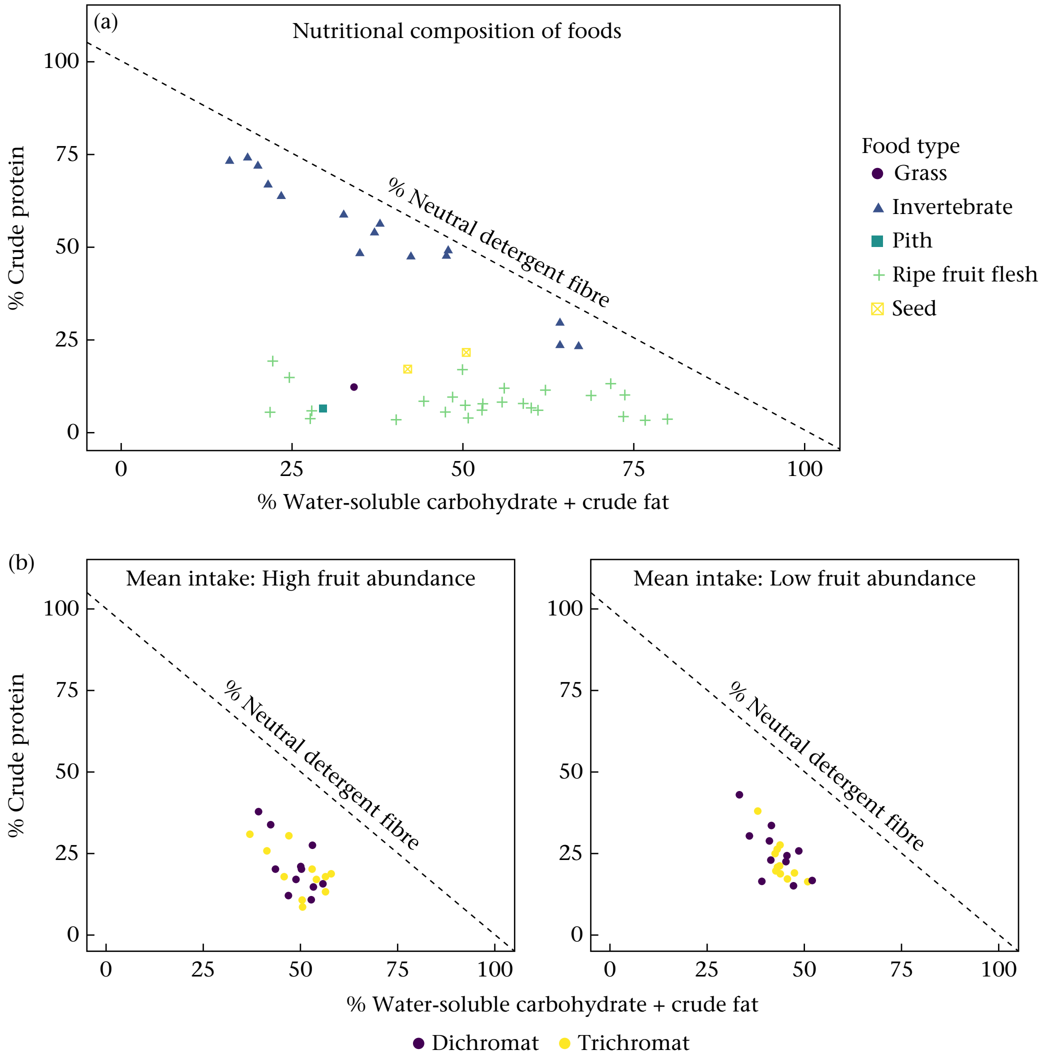

Figure A1. Right-angled mixture triangle (RMT) depicting the relative contributions of water-soluble carbohydrates + crude fat, crude protein and neutral detergent fibre to (a) total metabolizable energy of different capuchin food types and (b) each focal female's average metabolizable energy intake in months of high and low fruit abundance.

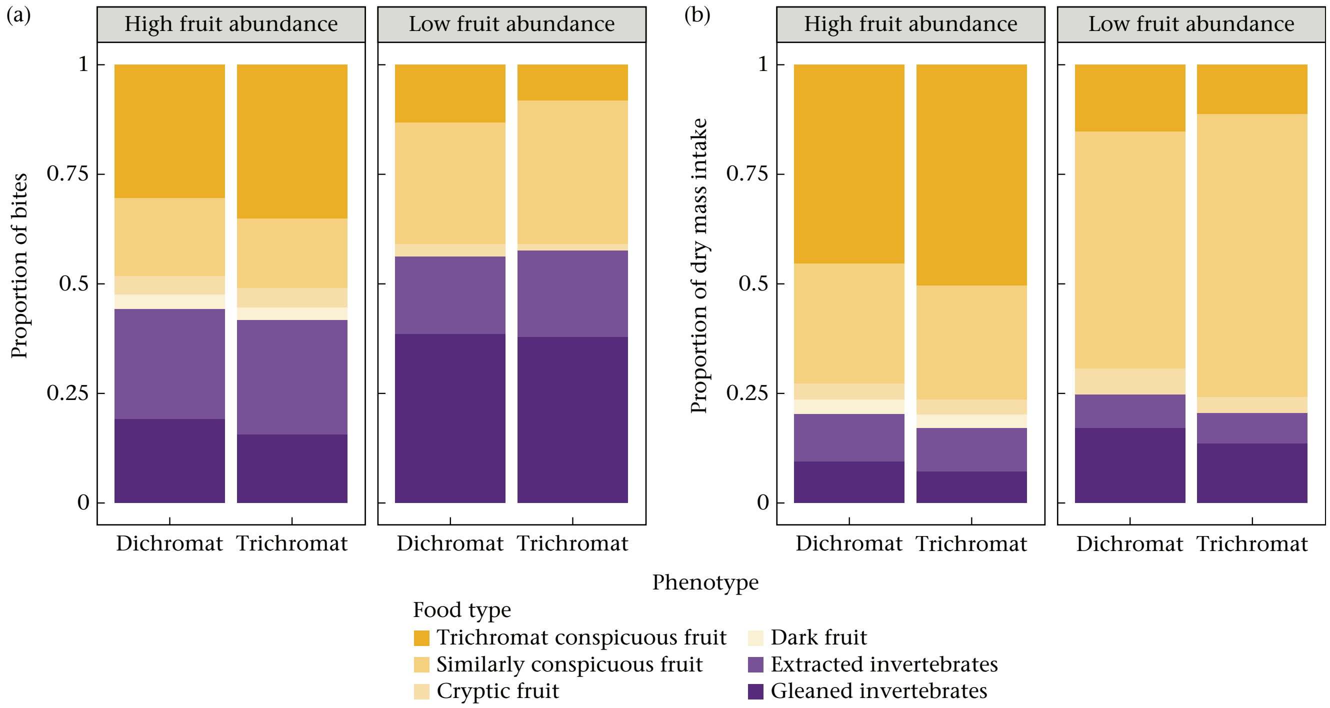

Figure A2. (a) Proportion of bites for fruit and invertebrate resources in times of high and low fruit abundance. (b) Proportion of dry matter intake in times of high and low fruit abundance.