Behavioral Ecology

The official journal of the ISBE
International Society for Behavioral Ecology

Behavioral Ecology (2021), 32(4), 599–608. doi:10.1093/beheco/arab001

Original Article

Testing the niche differentiation hypothesis in wild capuchin monkeys with polymorphic color vision

Allegra N. DePasquale,[a] Shasta E. Webb,[a] Rachel E. Williamson,[a] Linda M. Fedigan,[a] and Amanda D. Melin[a,b]

[a]Department of Anthropology and Archaeology, University of Calgary, 2500 University Dr NW, Calgary, AB T2N 1N4, Canada and [b]Department of Medical Genetics, Cumming School of Medicine, University of Calgary, 3330 Hospital Dr NW, Calgary, AB T2N 4N1, Canada

Received 2 July 2020; revised 15 November 2020; editorial decision 6 January 2021; accepted 12 January 2021; Advance Access publication 22 March 2021.

The polymorphic color vision system present in most North, Central, and South American monkeys is a textbook case of balancing selection, yet the mechanism behind it remains poorly understood. Previous work has established task-specific foraging advantages to different color vision phenotypes: dichromats (red-green colorblind) are more efficient foraging for invertebrates, while trichromats (color "normal" relative to humans) are more efficient foraging for "reddish" ripe fruit, suggesting that niche differentiation may underlie the maintenance of color vision variation. We explore a prediction of the niche differentiation hypothesis by asking whether dichromatic and trichromatic capuchin monkeys (*Cebus imitator*) diverge in their foraging activity budget, specifically testing whether dichromats forage more frequently for invertebrates and trichromats forage more frequently for "reddish" ripe fruit. To assess this, we analyze a large data set of behavioral scan samples ($n = 21\,984$) from 48 wild adult female capuchins of known color vision genotype, dominance rank, and reproductive status, together with models of food conspicuity. We find no significant differences between dichromats and trichromats in the frequency of scans spent foraging for different food types but do find that nursing females forage less overall than cycling females. Our results suggest that the potential for color-vision-based niche differentiation in foraging time may be curtailed by the energetic requirements of reproduction, behavioral synchrony caused by group living, and/or individual preferences. While niche differentiation in activity budgets by color vision type is not apparent, fine-scale niche differentiation may be occurring. This research enhances our understanding of the evolutionary processes maintaining sensory polymorphisms.

Key words: **activity budgets, balanced polymorphism, balancing selection, foraging ecology, opsin gene, sensory ecology**

INTRODUCTION

Balancing selection plays an important role in preserving phenotypic diversity within populations, which can lead to the persistence of genetic polymorphisms over long stretches of time. Examples span a wide variety of taxa and include the major histocompatibility complex in vertebrates (Hedrick 1998) and complementary sex determinism in hymenopterans (Cho et al. 2006). These polymorphisms can be maintained through at least four major processes: 1) heterozygote advantage, in which heterozygotes have higher fitness than homozygotes; 2) frequency dependence, in which the fitness of a phenotype is linked to its prevalence in a population; 3) mutual benefit of association, in which different phenotypes benefit from associating with one another; and 4) niche differentiation, in which each phenotype occupies a distinct ecological niche, thereby increasing the fitness of distinct phenotypes by decreasing competition (Hartl and Clark 1997; Hedrick 2006; Llaurens et al. 2017). Understanding the processes of balancing selection contributes to our understanding of adaptive variation—a major goal common to biological subfields. However, our understanding as to how these mechanisms function to maintain genetic polymorphisms in wild animal populations remains limited.

We can improve our understanding of balancing selection by investigating systems where the variation is straightforward and well characterized. The polymorphic color vision system of monkeys in the Americas (Infraorder Platyrrhini) meets both criteria and is a well-suited system in which to investigate how balancing selection operates (Kawamura et al. 2012; Brent and Melin 2014). Multiple variants of the gene underlying red-green color vision are widespread in platyrrhines (Mollon et al. 1984; Jacobs 1998, 2009; Vorobyev 2004). In this system, individuals within the same species

---

Address correspondence to A. N. DePasquale. E-mail: allegra.depasquale@ucalgary.ca; A. D. Melin. E-mail: amanda.melin@ucalgary.ca

and social group may differ in color vision due to the presence of a single, polymorphic, middle–long-wave sensitive (M/LWS) opsin gene located on the X chromosome. When combined with the autosomal short-wave sensitive (S) opsin (Jacobs 2008), the result is partially sex-linked trichromacy: heterozygous females are trichromats, while homozygous females and all males are dichromats—effectively red-green colorblind. This system has persisted over deep evolutionary time in most platyrrhine genera. The longstanding persistence of this opsin variation, its existence in diverse branches of the platyrrhines, and genetic evidence of balancing selection on opsin genes (Hiwatashi et al. 2010) suggest that it is adaptive and actively maintained by natural selection. The exact mechanism, however, has been the subject of considerable debate.

For years, the heterozygote advantage hypothesis was considered the most likely mechanism maintaining color vision polymorphism in platyrrhines. It posits that opsin variation persists due to overdominance by heterozygote (trichromatic) females, that is, that trichromats are better suited to their environment than are dichromats (Mollon et al. 1984). Direct tests of this hypothesis, however, have yielded mostly equivocal or unsupportive results (Vogel et al. 2007; Melin et al. 2009; Fedigan et al. 2014; but see Green 2014), highlighting the need to investigate other hypotheses. The niche differentiation hypothesis posits that each color vision phenotype occupies a distinct foraging niche in their shared environment; niche differentiation would allow for higher fitness of all phenotypes by reducing intragroup feeding competition, ultimately leading to the persistence of allelic variation as each color vision phenotype occupies a distinct fitness peak according to their visual ecology. The possibility of niche differentiation as a mechanism maintaining polymorphic color vision was suggested first by Mollon et al. (1984), who hypothesized that niche specialization may occur via habitat partitioning. In later iterations of this hypothesis, research groups, including Jacobs (1994), Regan et al. (2001), and Osorio et al. (2004), among others, have suggested that dichromats and trichromats may specialize on different food resources due to phenotype-specific differences in foraging efficiency, which may lead to frequency-dependent selection or niche differentiation. Such polymorphic resource specialization, in which different morphs within the same species utilize different resources, can be found in diverse vertebrate taxa, including African finches (Smith 1987), Cocos finches (Werner and Sherry 1987), Arctic charr (Snorrason et al. 1994), and tiger salamanders (Whiteman et al. 1996). Intriguingly, evidence of task-specific foraging advantages in wild platyrrhines based on color vision type (Melin et al. 2007, 2017) may set the stage for niche differentiation in activity budget if time allocation to different food types follows detection or selection advantages.

Previous work in both wild and captive settings has shown that dichromatic and trichromatic platyrrhines have task-specific advantages in foraging efficiency. Trichromatic monkeys have higher efficiency for reddish (conspicuous) food items, including many red, orange and yellow fruit and flowers (Smith et al. 2003; Melin et al. 2017; Hogan et al. 2018), while dichromats have higher efficiency in capturing surface-dwelling invertebrates (Melin et al. 2007; Caine et al. 2010; Smith et al. 2012), likely due to an advantage of red-green colorblindness in breaking camouflage (Morgan et al. 1992). Expanding on this, an analysis of capuchin dietary fruit color finds 70–80% of the frugivorous diet is modeled to be discriminable to trichromats, while less than a third is discriminable to dichromats (Melin, Hiramatsu, et al. 2014). Such task-specific foraging advantages could enable color vision polymorphism to be maintained via niche differentiation if, for example, if dichromats and trichromats forage predominantely on disparate food items. The only study to date to investigate color-vision-based niche differentiation found no evidence of niche differentiation in gross-scale foraging time, though small sample size and subjective fruit classification may have limited the results (Melin et al. 2008). Given recent evidence of fine-scale niche differentiation in a diverse array of other animal taxa, including Arctic charr (Hawley et al. 2016), tree lizards (Lattanzio and Miles 2016), and African cichlids (Ford et al. 2016), this hypothesis warrants further attention.

Here, we use a large, multiyear data set of behavioral scan data from wild, adult female white-faced capuchins, combined with the quantitative classification of fruit conspicuity to assess the influence of color vision phenotype on foraging activity budgets. Differences in activity budgets may emerge from differences in foraging efficiency in at least two ways. First, individuals may spend more time on tasks for which they are less efficient in order to achieve sufficient intake of this resource type (resource limitation). Second, individuals may spend more time engaging in tasks for which they are more efficient in order to maximize energy and/or nutrient gain (niche specialization). A third option is that activity budgets do not vary by color vision type, perhaps due to constraints associated with movement, group cohesion, social dominance, or physiological demands. For example, reproductive status and social dominance have been shown to influence primate foraging patterns (Hemingway 1999; Vogel 2005; McCabe and Fedigan 2007). We predict that monkeys with different color vision phenotypes will engage more frequently in the foraging activities for which they are more efficient (niche specialization hypothesis). Specifically, we predict that dichromats will forage more frequently for surface-dwelling, camouflaged invertebrates (P1) and trichromats will forage more frequently for conspicuous fruits (P2), reflecting their higher efficiencies for these food types.

MATERIALS AND METHODS

Study site

We conducted research in Sector Santa Rosa (SSR), Área de Conservación Guanacaste, Costa Rica. SSR is a UNESCO World Heritage Site (10°45’ to 11°00’ N and 85°30’ to 85° 45’ W). This site is in the northwestern part of the country, near the Nicaraguan border and the city of Liberia, the capital of Guanacaste province. SSR consists of highly seasonal tropical dry forest. Most annual rain (800–2600 mm) falls during a cool, wet season lasting from May until December. This is followed by a hot, dry season with widespread defoliation from January until April. Temperatures peak around 34 °C during the late dry season. Fruit abundance is also highly seasonal at this site, reaching its lowest from October to March (Carnegie, Fedigan, and Melin 2011).

Study animals

White-faced capuchins (*Cebus imitator)* are medium (3–5 kg), omnivorous primates that live in multimale, multifemale groups of 12–35 individuals (Fedigan and Jack 2001; Fedigan and Jack 2011; Perry et al. 2012; Melin et al. 2020). Capuchin diets are highly diverse and consist of anywhere from 20% to 85% fruits and 25% to 60% invertebrates, including caterpillars, grasshoppers, and cockroaches (Young 2005; Melin et al. 2008). White-faced capuchins are known for their complex foraging techniques and relatively large brains

(Melin, Young, et al. 2014). The Santa Rosa capuchins have been studied for >35 years and are well habituated and individually recognizable (Fedigan and Jack 2012; Melin, et al. 2020). Like most other platyrrhine primates, white-faced capuchins have allelic trichromacy. In this species, three opsin alleles with different peak sensitivities are present at the M/LWS locus: 532 (green sensitive), 543 (yellow sensitive), and 561 (red sensitive; Hiramatsu et al. 2005). All individuals in this study population have been genotyped, and all observers were unaware of individual color vision phenotypes at the time of data collection (Melin, Hiramatsu, et al. 2014). Of our 152 genotyped individuals, 109 are dichromats and 43 are trichromats. To remove confounding variation due to age and sex, we analyze data from the 48 genotyped adult females: 17 dichromats and 31 trichromats. Color vision phenotype and genotype breakdowns for adult females by group are shown in Table 1; we have only one dichromatic phenotype in our adult female population—the red-shifted (561) phenotype.

Behavioral data collection

Data for this project were collected during by four researchers over 11 years: 2007–2008 (A.D.M.), 2016 (S.E.W.), 2017 (R.E.W.), and 2018 (S.E.W.) during all-day (dawn to dusk) follows. Our data set spans wet and dry seasons approximately equally. Data were collected from four social groups in 2007–2008 (Guanacaste [GN], Los Valles [LV], Exclosure [EX], and Cerco de Piedro [CP]) and four social groups in 2016–2018 (GN, LV, AD, and RM). AD and RM resulted from a fission event of CP group in 2013. We report data for all adult females across these groups (n = 48). We used instantaneous scan sampling to record the behavior of all visible individuals every 30 min within a 10-min window. Foraging behaviors include both feeding and searching; invertebrate foraging is distinguished from fruit foraging by the context of the behavior (i.e., in a fruiting tree or not) as well as by the behaviors themselves: investigating leaves and bark while moving through the environment at a moderate pace is indicative of invertebrate foraging, while scanning the nearby branches in a fruit patch is indicative of fruit foraging (Supplementary Table 1). For feeding, we also recorded the relevant taxon and part being consumed (Altmann 1974; Melin et al. 2018). To examine possible confounds of reproductive status and dominance, we classified all adult females as pregnant, nursing, or cycling by back calculating from known births, assuming a 158-day gestation period and a year of lactation, following Carnegie, Fedigan, and Ziegler (2011). Lactation records were cross-validated by notes on infant suckling behavior. If an infant disappeared within the first year of life, we assumed the cessation of lactation and resumption of cycling. We calculated dominance using rankings of mature individuals (≥6 years old) collected collaboratively by the Santa Rosa Primate Field Project year-round. Rankings are based on the frequency and direction of agonistic interactions between dyads in the same group; males and females are ranked separately (Bergstrom and Fedigan 2010). Ranks were scaled between 1 and 0 to account for group size differences, and these were converted to an ordinal variable (Levy et al. 2020) with the levels low (scaled rank ≤0.33), mid (scaled rank between 0.34 and 0.66), and high (scaled rank >0.66) to account for the relatively relaxe dominance hierarchies characteristic of this species (Bergstrom and Fedigan 2010).

To classify color conspicuity of different fruits (n = 64 species) as conspicuous only to trichromats, conspicuous to both trichromats and the red-shifted dichromatic phenotype, cryptic to all phenotypes, or dark, we used fruit reflectance data and capuchin visual space color models (Melin, Hiramatsu, et al. 2014; Melin et al. 2017). We use reflectance spectrometry methods and capuchin-specific color space models that allow us to objectively classify fruits as cryptic or conspicuous to color vision phenotypes of *Cebus imitator* rather than subjective classifications based on the human visual system. A fourth category, "dark," consists of fruits that are similarly visible to both dichromat and trichromat phenotypes due to strong luminance contrasts. Detailed methods are provided in Melin, Hiramatsu, et al. (2014) and Melin et al. (2017). In brief, we measured reflectance spectra of five ripe fruits of each fruit species, as well as surrounding upper and lower leaves, using a portable spectrometer, together with irradiance spectra collected in the forest. Reflectance spectra across individual fruits were averaged before calculating species chromaticity values. Variation around the species mean for fruits and for leaves was low (standard deviation ranged from 0.0004 to 0.11 across fruits) and did not affect conspicuity categorization, that is, each individual fruit of a given species would have been assigned the same chromaticity category. These spectra were used to calculate chromaticity values—modeled as the ratio of quantum catches for the different L, M, and S alleles found in our study population. Chromaticity values were assessed under a "forest shade" illuminant. Given the phenomenon of color constancy in vertebrate visual systems and consistency of the color contrast of fruits and leaves across different illuminants (e.g., open, shaded, and closed canopy) in Santa Rosa, we do not anticipate the diurnal illuminant used to strongly affect our results (Neumeyer 1998; Ebner 2007; Melin, Hiramatsu, et al. 2014; Melin et al. 2017). A machine-learning approach was then used to determine if simulated trichromat and dichromat phenotypes could accurately discriminate between fruits and leaves, thus eliminating any human bias or a priori cutoff values. For two species, *Cissus verticillata* and *Paullinia cururu*, reflectance data were not available.

Table 1

Frequency of each genotype and phenotype by social group of adult female white-faced capuchins in SSR, Costa Rica. λ_{max} refers to the peak wavelength sensitivities of each M/LWS cone. Because this analysis only includes females, two *M/LWS* alleles are present. Only one dichromatic genotype (red shifted, RR) is found in our adult female study population. Due to a group fission event that occurred after the 2007–2008 season, three individuals from CP group occur in multiple study groups: two in RM, and one in AD

			Frequency per group				
Peak sensitivity (λ_{max}) of cone photopigment(s)	Genotype	Phenotype	AD	CP	EX	GN	LV	RM
532–561 (Widest separation)	GR	Trichromat	5	0	1	6	2	4
532–543 (Green shifted)	GY	Trichromat	0	0	1	3	2	0
543–561 (Red shifted)	RY	Trichromat	0	0	1	2	4	0
561–561 (Red shifted)	RR	Dichromat	2	6	0	5	3	4

Table 2

Fruit conspicuity categorizations for 64 dietary fruits included in this study. Categorizations are based on fruit reflectance and subsequent chromatic discrimination modeling for each color vision phenotype from Melin et al. (2014)

Fruit taxon	Family	Color category
Sciadodendron excelsum	Araliaceae	Dark
Spondias mombin	Anacardiaceae	Conspicuous (tri only)
Sapranthus palanga	Annonaceae	Cryptic
Annona reticulata	Annonaceae	Conspicuous (tri only)
Stemmadenia obovata	Apocynaceae	Conspicuous (both)
Acrocomia aculeata	Areacaceae	Conspicuous (tri only)
Cordia guanacastensis	Boraginaceae	Conspicuous (tri only)
Cordia panamensis	Boraginaceae	Cryptic
Bromelia pinguin	Bromeliaceae	Conspicuous (both)
Bromelia plumieri	Bromeliaceae	Conspicuous (tri only)
Bursera simaruba	Burseraceae	Conspicuous (tri only)
Holocereus costaricensis	Cactaceae	Conspicuous (tri only)
Hirtella racemosa	Chrysobalanaceae	Cryptic
Curatella americana	Dilleniaceae	Conspicuous (tri only)
Doliocarpus dentatus	Dilleniaceae	Conspicuous (tri only)
Davilla kunthii	Dilleniaceae	Conspicuous (tri only)
Diospyros salicifolia	Ebenaceae	Conspicuous (tri only)
Sloanea terniflora	Elaeocarpaceae	Conspicuous (both)
Erythroxylum havanense	Erythroxylaceae	Conspicuous (tri only)
Sapium glandulosum	Euphorbiaceae	Conspicuous (tri only)
Margaritaria nobilis	Euphorbiaceae	Cryptic
Sebastiana pavoniana	Euphorbiaceae	Conspicuous (both)
Hymanea coubaril	Fabaceae	Conspicuous (tri only)
Vachellia collinsi	Fabaceae	Conspicuous (tri only)
Quercus oleoides	Fagaceae	Cryptic
Zuelania guidonia	Flacourtiaceae	Conspicuous (both)
Casearia arguta	Flacourtiaceae	Conspicuous (both)
Muntingia calabura	Flacourtiaceae	Conspicuous (tri only)
Casearia sylvestris	Flacourtiaceae	Conspicuous (tri only)
Byrsonima crassifolia	Malpighiaceae	Conspicuous (both)
Bunchosia ocellata	Malpighiaceae	Conspicuous (tri only)
Malvaviscus arboreus	Malvaceae	Conspicuous (tri only)
Miconia argentea	Melastomataceae	Conspicuous (tri only)
Mouriri myrtilloides	Melastomataceae	Dark
Trichilia martiana	Meliaceae	Conspicuous (tri only)
Trichilia glabra	Meliaceae	Conspicuous (both)
Ficus cotinifolia	Moraceae	Conspicuous (tri only)
Ficus hondurensis	Moraceae	Conspicuous (tri only)
Ficus ovalis	Moraceae	Conspicuous (both)
Maclura tinctoria	Moraceae	Cryptic
Ficus goldmanii	Moraceae	Cryptic
Trophis racemosa	Moraceae	Conspicuous (tri only)
Ficus obtusifolia	Moraceae	Cryptic
Castilla elastica	Moraceae	Conspicuous (tri only)
Ficus morazaniana	Moraceae	Cryptic
Psidium guajava	Myrtaceae	Conspicuous (tri only)
Karwinskia calderoni	Rhamnaceae	Dark
Krugiodendron ferreum	Rhamnaceae	Conspicuous (tri only)
Genipa americana	Rubiaceae	Conspicuous (both)
Randia monantha	Rubiaceae	Conspicuous (tri only)
Guettarda macrosperma	Rubiaceae	Conspicuous (tri only)
Alibertia edulis	Rubiaceae	Conspicuous (tri only)
Dipterodendron costaricense	Sapindaceae	Conspicuous (tri only)
Allophylus occidentalis	Sapindaceae	Conspicuous (tri only)
Paullinia cururu	Sapindaceae	Conspicuous (tri only)
Manilkara chicle	Sapotaceae	Conspicuous (tri only)
Simarouba glauca	Simaroubaceae	Dark
Guazuma ulmifolia	Sterculiaceae	Dark
Jacquinia nervosa	Theophrastaceae	Conspicuous (both)
Luehea candida	Tiliaceae	Conspicuous (tri only)
Luehea speciosa	Tiliaceae	Conspicuous (tri only)
Apeiba tibourbou	Tiliaceae	Conspicuous (tri only)
Cecropia peltata	Urticaceae	Conspicuous (tri only)
Cissus verticillata	Vitaceae	Dark

We classified these species with fruits that appear visually similar to human trichromacy and for which we do have data (Table 2).

Unfortunately, methods of estimating color conspicuity and crypsis are not readily transferable from fruits to invertebrates. While some exceptions may exist, we take advantage of the fact that almost all of the palatable invertebrates eaten by primates and gleaned from surfaces are well camouflaged as a defense mechanism (Stevens and Merilaita 2011; Ruxton et al. 2019; Goodman 2020), and we classify all gleaned prey as camouflaged.

Data analysis

We grouped the data by rotation (n = 147), consisting of 2–5 consecutive days of data collection on the same social group. Animals were excluded from the analysis if they had less than three scan records per rotation. We analyzed all data using R statistical software (R Core Team 2020; RStudio Team 2019) and the package lme4 (Bates et al. 2015). We fit a series of generalized linear mixed models with a Poisson distribution to determine the significant predictors, if any, of different foraging activities. In all models, color vision phenotype, social dominance rank, and reproductive status were designated as fixed effects, while monkey ID nested within social group was included as a random effect. In all models, we also included average maximum temperature (degree Celsius), average minimum temperature, and average rainfall (centimeters) as fixed effects to control for the pronounced seasonality characteristic of SSR, which is known to affect the behavior of all individuals (Campos and Fedigan 2009). Finally, we used log-transformed total behavioral scans per monkey per rotation as an offset variable to control for differences in observational effort per individual per rotation, that is, variation in how often any one animal was sampled during the scan data collection for each group rotation.

Our first model tested for differences in total foraging scans (including scans recorded as visually foraging, extractive invertebrate foraging, fruit foraging, surface-dwelling invertebrate foraging, and "other" foraging) by fitting a model with total scans in any foraging behavior (Supplementary Table 1) as the response variable and all behavioral scans recorded as the offset. We then tested for differences in the frequency of fruit and invertebrate foraging behavior between color vision phenotypes. First, we tested for differences in total fruit foraging by designating total scans fruit foraging as the response variable and all behavioral scans as the offset. To evaluate whether there were differences in scans devoted to gleaning surface-dwelling invertebrates, we modeled number of scans invertebrate foraging as the response variable with all behavioral scans as the offset. Finally, we ran a model to test for differences in the number of scans devoted to conspicuous fruit foraging, with all behavioral scans as the offset. In this model, we used scans foraging for fruits that are conspicuous to *trichromats only* as the response variable. To ascertain the strength of each fixed effect, we ran chi-square tests for each model using the drop1 function in the R package lme4 (Bates et al. 2015). We also computed estimated marginal means for each model using the emmeans function in the R package emmeans (Lenth et al. 2020). We conducted pairwise comparisons between trichromats and dichromats and included a Tukey honest significant difference adjustment to account for running multiple tests on the same data and used this to visualize model results. Model results are summarized in Table 3. All code for these analyses can be found at https://github.com/allegradepasquale/scan_niche_divergence_analysis.

Table 3

Summary of generalized linear mixed models predicting four variables: number of scans spent in all foraging states, number of scans spent fruit foraging, number of scans spent surface-dwelling invertebrate foraging, and number of scans spent conspicuous fruit foraging. Asterisks denote statistical significance ($P < 0.05$)

Model name	Fixed effect	χ^2	df	P value
Total foraging model	Color vision phenotype	1.217	1	0.270
	Dominance	1.860	2	0.395
	Reproductive status	7.789	2	0.020*
	Max temperature (°C)	23.465	1	<0.001*
	Min temperature (°C)	6.166	1	0.013*
	Rainfall (cm)	3.124	1	0.077
Total fruit foraging model	Color vision phenotype	1.759	1	0.185
	Dominance	2.203	2	0.332
	Reproductive status	4.120	2	0.127
	Max temperature (°C)	7.579	1	0.006*
	Min temperature (°C)	42.779	1	<0.001*
	Rainfall (cm)	0.416		0.519
Surface-dwelling invertebrate foraging model	Color vision phenotype	0.484	1	0.487
	Dominance	3.102	2	0.212
	Reproduction	3.879	2	0.144
	Max temperature (°C)	0.071	1	0.790
	Min temperature (°C)	30.063	1	<0.001*
	Rainfall (cm)	0.203	1	0.653
Conspicuous fruit foraging model	Color vision phenotype	1.596	1	0.206
	Dominance	12.300	2	0.002*
	Reproductive status	1.872	2	0.392
	Max temperature (°C)	1.526	1	0.217
	Min temperature (°C)	40.364	1	<0.001*
	Rainfall (cm)	1.636	1	0.201

RESULTS

In total, we analyzed 21 984 individual scans for 48 adult females. Color vision phenotype was not a significant predictor of the proportion of the activity budget devoted to foraging behavior, that is, the total number of foraging scans ($\chi^2 = 1.217$, degrees of freedom [df] = 1, $P = 0.270$), or of the total scans spent foraging for fruit, controlling for all scans they were observed ($\chi^2 = 1.759$, df = 1, $P = 0.185$). Contrary to our prediction, color vision phenotype was not a significant variable in explaining the variation in foraging activity budget for surface-dwelling invertebrates ($\chi^2 = 0.484$, df = 1, $P = 0.487$) or conspicuous fruit ($\chi^2 = 1.596$, df = 1, $P = 0.206$). Dichromats did not forage more frequently for surface-dwelling invertebrates (Figure 1c) and trichromats did not forage more frequently for conspicuous fruits (Figure 1d). We computed estimated marginal means for color vision phenotype, including a Tukey honest significant difference test, and compared them using *z*-tests. (Figure 1a–d).

Reproductive status was a significant predictor of total overall foraging scans ($\chi^2 = 7.789$, df = 2, $P = 0.020$) but not of scans recorded in specific foraging activities: surface-dwelling invertebrate foraging ($\chi^2 = 3.879$, df = 2, $P = 0.144$), general fruit foraging ($\chi^2 = 4.120$, df = 2, $P = 0.127$), or conspicuous fruit foraging ($\chi^2 = 1.872$, df = 2, $P = 0.392$). Estimated marginal means for each reproductive state are shown in Figure 1e–h. Nursing females foraged significantly less than cycling females (cycling–nursing: estimate = 0.091, standard error [SE] = 0.037, $P = 0.034$; nursing–pregnant: estimate = −0.087, SE = 0.040, $P = 0.081$; pregnant–cycling: estimate = 0.00515, SE = 0.0424, $P = 0.9919$). Social dominance was not a significant predictor for three of the four variables considered here: total foraging ($\chi^2 = 1.860$, df = 2, $P = 0.395$); total fruit foraging ($\chi^2 = 2.203$, df = 2, $P = 0.332$); and surface-dwelling invertebrate foraging ($\chi^2 = 3.102$, df = 2, $P = 0.212$). However, dominance category was a significant predictor of conspicuous fruit foraging ($\chi^2 = 12.300$, df = 2, $P = 0.002$). There was no difference between high-, mid-, and low-ranking individuals in total foraging scans, total fruit foraging, or invertebrate foraging, but high-ranking individuals foraged less frequently for conspicuous fruits (high–low: estimate = −0.158, SE = 0.071, $P = 0.069$; high–mid: −0.270, SE = 0.084, $P = 0.004$; low–mid: estimate = −0.112, SE = 0.087, $P = 0.405$; Supplementary Figure 1). When we ran the conspicuous fruit foraging model with an interaction between dominance category and color vision phenotype to determine if color vision and dominance could be influencing one another, this interaction was not significant ($\chi^2 = 1.960$, df = 2, $P = 0.375$). We similarly ran the conspicuous fruit foraging model with an interaction between reproductive status and color vision phenotype, which also was not significant ($\chi^2 = 0.395$, df = 2, $P = 0.821$).

DISCUSSION

We predicted task-specific differences in foraging activity budgets based on color vision phenotype—specifically that dichromats would forage more frequently for cryptic invertebrates and trichromats would forage more frequently for conspicuous resources due to previous findings indicating a trichromat advantage when foraging for conspicuous fruits and flowers, and a dichromat advantage when foraging for camouflaged invertebrates (Caine and Mundy 2000; Smith et al. 2003, 2012; Melin et al. 2007, 2017; Caine et al. 2010). Contrary to our predictions, we found that dichromats and trichromats did not differ in either of these variables. These findings are consistent with past research using a far more limited data set that found no broad-scale differences in capuchin foraging according to color vision type (Melin et al. 2008). This indicates that, despite the discrete differences in invertebrate and fruit-foraging

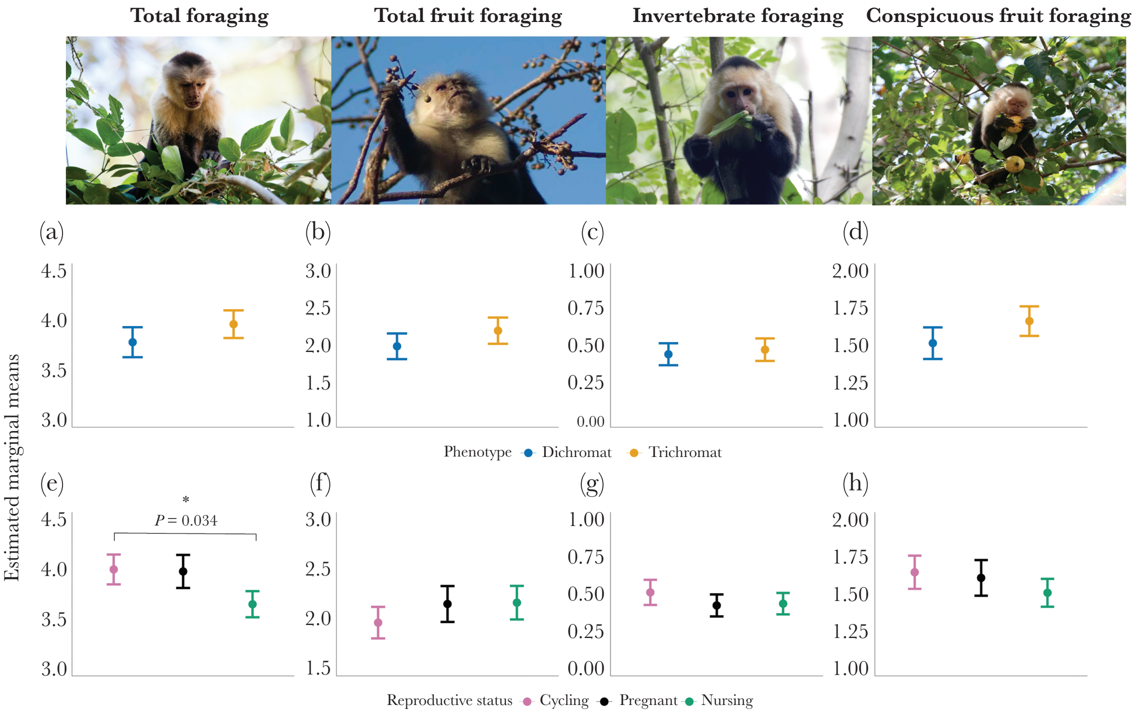

Figure 1

Foraging activity budget of white-faced capuchin monkeys by color vision phenotype and reproductive status. We present estimated marginal means of number of scans per rotation spent in all foraging states (A/E; includes visual foraging, extractive invertebrate foraging, surface-dwelling invertebrate foraging, fruit foraging, and foraging "other"), total fruit foraging (B/F), surface-dwelling invertebrate foraging (C/G), and fruit foraging only for conspicuously colored fruits (D/F). Estimated marginal means are generated from models including dominance, reproductive status, maximum and minimum daily temperature, and rainfall to isolate the effect of color vision phenotype. Asterisks denote statistical significance.

efficiency previously reported between dichromats and trichromats in our study population (Melin et al. 2007, 2010, 2017), the hypothesis that this results in divergent activity budgets can be robustly rejected. Dichromats and trichromats do not appear to have distinct foraging activity budgets. This may reflect constraints on time allocation due to living in a cohesive social group or to individual-level differences that shape diet and behavior.

Our finding that reproductive status is a significant predictor of overall foraging scans is consistent with previous evidence that pregnant and nursing females of some species spend less time in foraging states, and more time resting, than cycling conspecifics (Rose 1994; Hemingway 1999; Vasey 2002; McCabe and Fedigan 2007). Given the high energetic costs of reproduction in primates, particularly during lactation, this finding is unsurprising. Sexually mature female mammals are predicted to face the greatest pressure to avoid feeding competition and separate their niches from other group members as their reproductive success hinges most directly on food resources (Wrangham 1980; Ruckstuhl and Neuhaus 2002; Watts 2005; Breed et al. 2006; Hierlihy et al. 2013). Rather than switching food resources to avoid competition, our results indicate that females engage in an energy-minimizing strategy to cope with reproductive costs. This strategy likely outweighs any potential effect of color vision on foraging time. Thus, the potential for niche differentiation in activity budget due to color vision type is likely constrained in part by reproductive costs.

We find that social dominance significantly impacts conspicuous fruit foraging and that this pattern is primarily driven by high-ranking individuals foraging less frequently for conspicuous fruit. This finding was unexpected, and we hypothesize that it could be an artifact of faster patch processing time in small food patches by dominant monkeys. Through dominance-biased priority of access, high-ranking individuals are often able to monopolize small, high-value resources, such as ripe fruit patches (Tilson and Hamilton 1984; Janson 1985; van Schaik and van Noordwijk 1988; Stockley and Bro-Jørgensen 2011; Dorning and Harris 2017). In white-faced capuchins, high-ranking females have been shown to have higher efficiency in ripe fruit patches (Vogel 2005). While it is puzzling that a dominance effect is not found in our overall fruit foraging model, it is likely related to the fact that most of the "conspicuous" fruit species in this analysis are smaller tree species (Supplementary Figure 2); these "small patch" species are the most likely to be monopolizable by dominant individuals (Vogel 2005). Our results suggest that an efficiency advantage of being high-ranking translates into fewer scans observed foraging on small, conspicuous resources than that of mid- or low-ranking individuals, likely because these lower-ranking individuals need more time to locate fruit in a slightly depleted food patch, making these lower-ranking individuals more likely to be observed while foraging for conspicuous fruits.

Constraints on niche differentiation in foraging activity budget

Our results highlight possible constraints of living in small, cohesive, and socially hierarchical groups where the ability to search for disparate resources is likely curtailed by the need for frequent and cohesive group movement in search of food, as well as by vigilance behaviors (Isbell and Young 1993; Molvar and Bowyer 1994; Osorio et al. 2004; Majolo et al. 2008; Aivaz and

Ruckstuhl 2011; Olson et al. 2015). The costs of group living are well recognized, though most studies to date have examined the effect of group size on intragroup feeding competition, with larger groups exhibiting greater competition and greater daily travel length (Janson and Goldsmith 1995; Chapman and Chapman 2000a, 2000b). Rather than offsetting the costs of group living by fissioning into smaller subgroups, as is characteristic of African elephants and spotted hyenas, as well as the primate genera *Pan* and *Ateles* (members of which inhabit the same habitats as *Cebus*), capuchin groups remain cohesive year-round, regardless of seasonal fluctuations in habitat-wide fruit availability (Chapman 1990). This may limit their ability to diverge significantly in activity budgets due to pressures of maintaining group coordination, ultimately leading to a large degree of behavioral synchrony (Kavanagh 1978; Harrison 1985; Agetsuma 1995; King and Cowlishaw 2009). Our results additionally highlight individual-level constraints due to reproduction, as seen in the depressed foraging activity of nursing capuchins, as well as to other aspects of biology, including thermoregulation. Temperature, a significant variable in all of our models, impacts foraging activity budgets (Campos and Fedigan 2009; Bergstrom 2015). Given the intense seasonality characteristic of our field site, monkeys spend much time resting in the hot, dry season as a means of thermoregulating. Half of our data points each year are from the hot dry season in SSR. Combining this impact with increased resting time due to reproduction, as well as the need to achieve a nutritionally balanced diet, likely constrains the potential for color vision phenotype to significantly affect activity budget (Felton et al. 2009).

Comments on hypotheses of balancing selection

While niche differentiation is not evident in the variables analyzed here, we cannot rule out the possibility that finer-scale diet differentiation is occurring at the level of net food intake. For example, research in wild montane ungulates (Hobbs 1983), generalist grasshoppers (Behmer and Joern 2008), and sympatric mule and white-tailed deer populations (Berry et al. 2019) all suggest that differentiation in nutritional intake may underlie such phenomena as species coexistence and ecological invasion. Dichromats and trichromats may occupy distinct nutritional niches due to differences in intake rates of different food types (Melin et al. 2007, 2010, 2017), and their constituent nutrients, even though the results of this study indicate that foraging activity budgets may not differ. Furthermore, it should be noted that diet is only a single axis of the ecological niche; differentiation in habitat use due to lighting conditions that facilitate foraging efficiency is another axis that should be considered (Yamashita et al. 2005; Caine et al. 2010; Freitag and Pessoa 2012).

It also remains plausible that niche differentiation is not a mechanism favoring the maintenance of color vision polymorphism. Future studies should address the possibility of mutual benefit of association in platyrrhines, which posits that dichromats and trichromats have equal fitness by living in mixed color vision phenotype groups, likely due to both resource and predator detection benefits (Caine 2002; Pessoa et al. 2014). The mutual benefit of association hypothesis has been previously supported in sifakas with polymorphic color vision (Veilleux et al. 2016), where it was found that individuals in mixed-phenotype, dichromat–trichromat groups had higher body mass and longer fruit foraging times than dichromat-only groups. It may be fruitful to examine foraging outcomes and vigilance behaviors between dichromat-only and dichromat–trichromat groups. Lastly, Green (2014) reports results in support of the heterozygote advantage hypothesis in tufted capuchin monkeys (genus *Sapajus*), suggesting that this mechanism may also require further attention.

CONCLUDING REMARKS

The hypotheses for balancing selection that emphasize foraging differences are inherently confounded by the complex interactions between multimodal foraging and social learning. Monkeys with different color vision types may achieve similar foraging activity budgets through various mechanisms of behavioral compensation. For example, dichromats have been suggested to compensate for the lack of visual information by using olfactory information: they sniff fruits significantly more than trichromats (Melin et al. 2019). Capuchins are highly intelligent, social animals and learn many of their foraging behaviors from observing conspecifics. Dichromats may learn from an early age how to locate fruit without red-green color vision, and trichromats may learn how to glean invertebrates despite an impeded ability to break visual camouflage.

Despite decades of research, the adaptive value of polymorphic color vision continues to invite future study. While it is clear at this point that broad-scope differentiation in foraging activity budgets likely does not underlie the maintenance of this variation, fine-scale niche differentiation and mutual benefit of association both warrant further investigation. Understanding color vision polymorphism and its behavioral correlates will help us understand the fundamental evolutionary processes of balancing selection and adaptation. Due to this widespread applicability, researchers from overlapping fields such as behavioral ecology, evolutionary biology, and animal behavior all stand to benefit from future investigations into this fascinating system.

SUPPLEMENTARY MATERIAL

Supplementary data are available at *Behavioral Ecology* online.

FUNDING

This work was supported by the Wenner-Gren Foundation, the Leakey Foundation (A.D.M.), the National Sciences and Engineering Council of Canada Discovery Grant, the Canada Research Chairs Program (A.D.M. and L.M.F.), the Vanier Canada Graduate Scholarship, the American Society of Primatologists General Small Grant, and the Alberta Children's Hospital Research Institute (S.E.W.).

We thank R. Blanco Segura and M. M. Chavarria and staff from the Área de Conservación Guanacaste and Ministerio de Ambiente y Energía. Warmest thanks also to A. Guadamuz, A. Blauel, S. Chevez, R. Lopez, J. Hogan, U. Kalbitzer, B. Klug, M. Lemmon, M. Myers, N. Parr, L. Weckman, K. Kries, N. Carrethers, N.Ferrero, and N. Beeby. Photos belong to F. Campos, E. Sargeant, and A. Melin. This research adhered to the laws of Costa Rica, the United States, 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.

Data availability: Analyses reported in this article can be reproduced using the data provided by DePasquale et al. (2021). All code for these analyses can be found at https://github.com/allegradepasquale/scan_niche_divergence_analysis.

Handling editor: Marie Herberstein

REFERENCES

Agetsuma N. 1995. Foraging synchrony in a group of Yakushima macaques (*Macaca fuscata yakui*). Folia Primatol. 64(4):167–179. doi: 10.1159/000156850.

Aivaz AN, Ruckstuhl KE. 2011. Costs of behavioral synchrony as a potential driver behind size-assorted grouping. Behav Ecol. 22(6):1353–1363. doi: 10.1093/beheco/arr141.

Altmann J. 1974. Observational study of behavior: sampling methods. Behaviour. 49:227–267.

Bates D, Maechler M, Bolker B, Walker S. 2015. Fitting linear mixed-effects models using lme4. J Stat Softw. 67(1):1–48. doi: 10.18637/jss.v067.i01.

Behmer ST, Joern A. 2008. Coexisting generalist herbivores occupy unique nutritional feeding niches. Proc Natl Acad Sci USA. 105:1977–1982.

Bergstrom ML. 2015. Seasonal effects on the nutrition and energetic condition of female white-faced capuchin monkeys [PhD thesis]. [Calgary (Canada)]: University of Calgary. doi: 10.11575/PRISM/27720.

Bergstrom ML, Fedigan LM. 2010. Dominance among female white-faced capuchin monkeys (*Cebus capucinus*): hierarchical linearity, nepotism, strength and stability. Behaviour. 147(7):899–931.

Berry SL, Shipley LA, Long RA, Loggers C. 2019. Differences in dietary niche and foraging behavior of sympatric mule and white-tailed deer. Ecosphere, 10(7):e02815. doi: 10.1002/ecs2.2815.

Breed GA, Bowen WD, McMillan JI, Leonard ML. 2006. Sexual segregation of seasonal foraging habitats in a non-migratory marine mammal. Proc Biol Sci. 273:2319–2326.

Brent LJ, Melin AD. 2014. The genetic basis of primate behavior: genetics and genomics in field-based primatology. Int J Primatol. 35:1–10.

Caine NG. 2002. Seeing red: consequence of individual differences in color vision in callitrichid primates. In: Miller, LE, editor. Eat or be eaten: predator sensitive foraging among primates. Cambridge: Cambridge University Press. p. 58–73. doi: 10.1017/CBO9780511610233.005.

Caine NG, Mundy NI. 2000. Demonstration of a foraging advantage for trichromatic marmosets (*Callithrix geoffroyi*) dependent on food colour. Proc Biol Sci. 267:439–444.

Caine NG, Osorio D, Mundy NI. 2010. A foraging advantage for dichromatic marmosets (*Callithrix geoffroyi*) at low light intensity. Biol Lett. 6:36–38.

Campos FA, Fedigan LM. 2009. Behavioral adaptations to heat stress and water scarcity in white-faced capuchins (*Cebus capucinus*) in Santa Rosa National Park, Costa Rica. Am J Phys Anthropol. 138:101–111.

Carnegie SD, Fedigan LM, Melin AD. 2011. Reproductive seasonality in female capuchins (*Cebus capucinus*) in Santa Rosa (Area de Conservación Guanacaste), Costa Rica. Int J Primatol. 32(5):1076–1090. doi: 10.1007/s10764-011-9523-x.

Carnegie SD, Fedigan LM, Ziegler TE. 2011. Social and environmental factors affecting fecal glucocorticoids in wild, female white-faced capuchins (*Cebus capucinus*). Am J Primatol. 73:861–869.

Chapman CA. 1990. Ecological constraints on group size in three species of neotropical primates. Folia Primatol (Basel). 55:1–9.

Chapman CA, Chapman LJ. 2000a. Constraints on group size in red colobus and red-tailed guenons: examining the generality of the ecological constraints model. Int J Primatol. 21(4):565–585. doi: 10.1023/A:1005557002854.

Chapman CA, Chapman LJ. 2000b. Determinants of group size in primates: the importance of travel costs. In: Boinski S, Garber PA, editors. On the move: how and why animals travel in groups. Chicago (IL): University of Chicago Press. p. 24–41.

Cho S, Huang ZY, Green DR, Smith DR, Zhang J. 2006. Evolution of the complementary sex-determination gene of honey bees: balancing selection and trans-species polymorphisms. Genome Res. 16:1366–1375.

DePasquale AN, Webb SE. 2021. Testing the niche differentiation hypothesis in wild capuchin monkeys with polymorphic color vision. Behav Ecol. doi: 10.5061/dryad.g1jwstqq4.

Dorning J, Harris S. 2017. Dominance, gender, and season influence food patch use in a group-living, solitary foraging canid. Behav Ecol. 28(5):1302–1313. doi: 10.1093/beheco/arx092.

Ebner M. 2007. Color constancy. Hoboken, NJ: John Wiley & Sons.

Fedigan LM, Jack K. 2001. Neotropical primates in a regenerating Costa Rican dry forest: a comparison of howler and capuchin population patterns. Int J Primatol. 22(5):689–713.

Fedigan LM, Jack KM. 2011. Two girls for every boy: The effects of group size and composition on the reproductive success of male and female white-faced capuchins. Am J Phys Anthropol. 144:317–326.

Fedigan LM, Jack KM. 2012. Tracking neotropical monkeys in Santa Rosa: lessons from a regenerating Costa Rican dry forest. In: Kappeler PM, Watts DP, editors. Long-term field studies of primates. New York: Springer. p. 165–184. doi: 10.1007/978-3-642-22514-7_8.

Fedigan LM, Melin AD, Addicott JF, Kawamura S. 2014. The heterozygote superiority hypothesis for polymorphic color vision is not supported by long-term fitness data from wild neotropical monkeys. PLoS One. 9:e84872.

Felton AM, Felton A, Lindenmayer DB, Foley WJ. 2009. Nutritional goals of wild primates. Funct Ecol. 23(1):70–78. doi: 10.1111/j.1365-2435.2008.01526.x.

Ford AGP, Rüber L, Newton J, Dasmahapatra KK, Balarin JD, Bruun K, Day JJ. 2016. Niche differentiation facilitated by fine-scale ecological partitioning in a recent cichlid fish adaptive radiation. Evolution. 70(12):2718–2735.

Freitag FB, Pessoa DM. 2012. Effect of luminosity on color discrimination of dichromatic marmosets (*Callithrix jacchus*). J Opt Soc Am A Opt Image Sci Vis. 29:A216–A222.

Goodman A. 2020. Correlation between substrate selection and body color of neotropical katydids (Orthoptera: Tettigoniidae). Ecol Entomol. doi: 10.1111/een.12942

Green AT. 2014. Consequences of color vision variation on performance and fitness in capuchin monkeys [Unpublished PhD thesis]. [Missoula (MT)]: University of Montana.

Harrison MJS. 1985. Time budget of the green monkey, *Cercopithecus sabaeus*: some optimal strategies. Int J Primatol. 6(4):351–376. doi: 10.1007/BF02736383.

Hartl DL, Clark GC. 1997. Principles of population genetics. Sunderland (MA): Sinauer Associates.

Hawley KL, Rosten CM, Christensen G, Lucas MC. 2016. Fine-scale behavioural differences distinguish resource use by ecomorphs in a closed ecosystem. Sci Rep. 6:24369.

Hedrick PW. 1998. Balancing selection and MHC. Genetica. 104:207–214.

Hedrick PW. 2006. Genetic polymorphism in heterogeneous environments: the age of genomics. Annu Rev Ecol Evol Syst. 37(1):67–93. doi: 10.1146/annurev.ecolsys.37.091305.110132.

Hemingway CA. 1999. Time budgets and foraging in a Malagasy primate: do sex differences reflect reproductive condition and female dominance? Behav Ecol Sociobiol. 45(3):311–322. doi: 10.1007/s002650050566.

Hierlihy CA, Carcía-Collazo R, Chavez Tapia CB, Mallory FF. 2013. Sexual dimorphism in the lizard *Sceloporus siniferus* support for the intraspecific niche differentiation and sexual selection hypotheses. Salamandra 49:1–6.

Hiramatsu C, Tsutsui T, Matsumoto Y, Aureli F, Fedigan LM, Kawamura S. 2005. Color-vision polymorphism in wild capuchins (*Cebus capucinus*) and spider monkeys (*Ateles geoffroyi*) in Costa Rica. Am J Primatol. 67:447–461.

Hiwatashi T, Okabe Y, Tsutsui T, Hiramatsu C, Melin AD, Oota H, Schaffner CM, Aureli F, Fedigan LM, Innan H, et al. 2010. An explicit signature of balancing selection for color-vision variation in new world monkeys. Mol Biol Evol. 27:453–464.

Hobbs NT, Baker DL, Gill RB. 1983. Comparative nutritional ecology of montane ungulates during winter. J Wildl Manag. 47(1):1–16. doi: 10.2307/3808046.

Hogan JD, Fedigan LM, Hiramatsu C, Kawamura S, Melin AD. 2018. Trichromatic perception of flower colour improves resource detection among New World monkeys. Sci Rep. 8:10883.

Isbell LA, Young TP. 1993. Social and ecological influences on activity budgets of vervet monkeys, and their implications for group living. Behav Ecol Sociobiol. 32(6):377–385. doi: 10.1007/BF00168821.

Jacobs GH. 1994. Variations in primate color vision: mechanisms and utility. Evol Anthropol. 3(6):196–205. doi: 10.1002/evan.1360030606.

Jacobs GH. 1998. A perspective on color vision in platyrrhine monkeys. Vision Res. 38:3307–3313.

Jacobs GH. 2008. Primate color vision: a comparative perspective. Vis Neurosci. 25:619–633.

Jacobs GH. 2009. Evolution of color vision in mammals. Philos Trans R Soc B Biol Sci. 364(1531):2957–2967. doi: 10.1098/rstb.2009.0039.

Janson C. 1985. Aggressive competition and individual food consumption in wild brown capuchin monkeys (*Cebus apella*). Behav Ecol Sociobiol. 18(2):125–138. doi: 10.1007/BF00299041.

Janson CH, Goldsmith ML. 1995. Predicting group size in primates: foraging costs and predation risks. Behav Ecol. 6(3):326–336. doi: 10.1093/beheco/6.3.326.

Kavanagh M. 1978. The diet and feeding behavior of *Cercopithecus aethiops tantalus*. Folia Primatol. 30(1):30–63. doi: 10.1159/000155854.

Kawamura S, Hiramatsu C, Melin AD, Schaffner CM, Aureli F, Fedigan LM. 2012. Polymorphic color vision in primates: evolutionary considerations. In: Hirai H, Imai H, Go Y, editors. Post-genome biology of primates. Tokyo (Japan): Springer. p. 93–120. doi: 10.1007/978-4-431-54011-3_7.

King AJ, Cowlishaw G. 2009. All together now: behavioural synchrony in baboons. Anim Behav. 78(6):1381–1387. doi: 10.1016/j.anbehav.2009.09.009.

Lattanzio MS, Miles DB. 2016. Trophic niche differentiation among color morphs that exhibit alternative mating tactics. R Soc Open Sci. 3(4):150531. doi: 10.1098/rsos.150531.

Lenth R, Singmann H, Love J, Buerkner P, Herve M. 2020. emmeans: estimated marginal means, aka least-squares means (Version 1.4.7) [Computer software]. Available from: https://CRAN.R-project.org/package=emmeans. Accessed 4 June 2020.

Levy EJ, Zipple MN, McLean E, Campos FA, Dasari M, Fogel AS, Franz M, Gesquiere LR, Gordon JB, Grieneisen L, et al. 2020. A comparison of dominance rank metrics reveals multiple competitive landscapes in an animal society. Proc Royal Soc. 287(1934):20201013.

Llaurens V, Whibley A, Joron M. 2017. Genetic architecture and balancing selection: the life and death of differentiated variants. Mol Ecol. 26:2430–2448.

Majolo B, de Bortoli Vizioli A, Schino G. 2008. Costs and benefits of group living in primates: group size effects on behaviour and demography. Anim Behav. 76(4):1235–1247. doi: 10.1016/j.anbehav.2008.06.008.

McCabe GM, Fedigan LM. 2007. Effects of reproductive status on energy intake, ingestion rates, and dietary composition of female *Cebus capucinus* at Santa Rosa, Costa Rica. Int J Primatol. 28(4):837–851. doi: 10.1007/s10764-007-9159-z.

Melin AD, Chiou KL, Walco ER, Bergstrom ML, Kawamura S, Fedigan LM. 2017. Trichromacy increases fruit intake rates of wild capuchins (*Cebus capucinus* imitator). Proc Natl Acad Sci USA. 114:10402–10407.

Melin AD, Fedigan LM, Hiramatsu C, Hiwatashi T, Parr N, Kawamura S. 2009. Fig foraging by dichromatic and trichromatic *Cebus capucinus* in a tropical dry forest. Int J Primatol. 30(6):753–775. doi: 10.1007/s10764-009-9383-9.

Melin AD, Fedigan LM, Hiramatsu C, Kawamura S. 2008. Polymorphic color vision in white-faced capuchins (*Cebus capucinus*): is there foraging niche differentiation among phenotypes? Behav Ecol Sociobiol. 62(5):659–670. doi: 10.1007/s00265-007-0490-3.

Melin AD, Fedigan LM, Hiramatsu C, Sendall CL, Kawamura S. 2007. Effects of color vision phenotype on insect capture by a free-ranging population of white-faced capuchins, *Cebus capucinus*. Anim Behav. 73(1):205–214. doi: 10.1016/j.anbehav.2006.07.003.

Melin AD, Fedigan LM, Young HC, Kawamura S. 2010. Can color vision variation explain sex differences in invertebrate foraging by capuchin monkeys? Curr Zool. 56(3):300–312.

Melin AD, Hiramatsu C, Parr NA, Matsushita Y, Kawamura S, Fedigan LM. 2014. The behavioral ecology of color vision: considering fruit conspicuity, detection distance and dietary importance. Int J Primatol. 35(1):258–287. doi: 10.1007/s10764-013-9730-8.

Melin AD, Hogan JD, Campos FA, Wikberg E, King-Bailey G, Webb S, Kalbitzer U, Asensio N, Murillo-Chacon E, Hernandez SC, et al. 2020. Primate life history, social dynamics, ecology, and conservation: contributions from long-term research in Área de Conservación Guanacaste, Costa Rica. Biotropica. doi: 10.1111/btp.12867.

Melin AD, Nevo O, Shirasu M, Williamson RE, Garrett EC, Endo M, Sakurai K, Matsushita Y, Touhara K, Kawamura S. 2019. Fruit scent and observer colour vision shape food-selection strategies in wild capuchin monkeys. Nat Commun. 10:2407.

Melin AD, Webb SE, Williamson RE, Chiou KL. 2018. Data collection in field primatology: a renewed look at measuring foraging behavior. In: Kalbitzer U, Jack KM, editors. Primate life histories, sex roles, and adaptability: essays in honour of Linda M. Fedigan. New York: Springer International Publishing. p. 161–192. doi: 10.1007/978-3-319-98285-4_9.

Melin AD, Young HC, Mosdossy KN, Fedigan LM. 2014. Seasonality, extractive foraging and the evolution of primate sensorimotor intelligence. J Hum Evol. 71:77–86.

Mollon JD, Bowmaker JK, Jacobs GH. 1984. Variations of colour vision in a New World primate can be explained by polymorphism of retinal photopigments. Proc R Soc Lond B Biol Sci. 222:373–399.

Molvar EM, Bowyer RT. 1994. Costs and benefits of group living in a recently social ungulate: the Alaskan moose. J Mammal. 75(3):621–630. doi: 10.2307/1382509.

Morgan MJ, Adam A, Mollon JD. 1992. Dichromats detect colorcamouflaged objects that are not detected by trichromats. Proc Biol Sci. 248(1323):291–295.

Neumeyer C. 1998. Comparative aspects of color constancy. In Walsh V, Kulikowski J, editors. Perceptual constancy: why things look as they do. Cambridge (UK): Cambridge University Press. p. 323–351.

Olson RS, Haley PB, Dyer FC, Adami C. 2015. Exploring the evolution of a trade-off between vigilance and foraging in group-living organisms. R Soc Open Sci. 2:150135.

Osorio D., Smith AC., Vorobyev M., Buchanan-Smith HM.2004. Detection of Fruit and the Selection of Primate Visual Pigments for Color Vision. The American Naturalist, 164(6), 696–708.

Perry S, Godoy I, Lammers W. 2012. The Lomas Barbudal Monkey Project: two decades of research on *Cebus capucinus*. In: Kappeler PM, Watts DP, editors. Long-term field studies of primatesSpringer. p. 141–163. doi: 10.1007/978-3-642-22514-7_7.

Pessoa DM, Maia R, de Albuquerque Ajuz RC, De Moraes PZ, Spyrides MH, Pessoa VF. 2014. The adaptive value of primate color vision for predator detection. Am J Primatol. 76:721–729.

R Core Team. 2020. R: a language and environment for statistical computing. Vienna (Austria): R Foundation for Statistical Computing. Available from: https://www.R-project.org/. Accessed 1 June 2020.

Regan BC, Julliot C, Simmen B, Viénot F, Charles-Dominique P, Mollon JD. 2001. Fruits, foliage and the evolution of primate colour vision. Philos Trans R Soc Lond B Biol Sci. 356:229–283.

Rose LM. 1994. Sex differences in diet and foraging behavior in white-faced capuchins (*Cebus capucinus*). Int J Primatol. 15(1):95–114. doi: 10.1007/BF02735236.

RStudio Team. 2019. RStudio: integrated development for R. Boston: RStudio, Inc. Available from: http://www.rstudio.com/. Accessed Jun 1 2020.

Ruckstuhl KE, Neuhaus P. 2002. Sexual segregation in ungulates: a comparative test of three hypotheses. Biol Rev Camb Philos Soc. 77:77–96.

Ruxton GD, Allen WL, Sherratt TN, Speed MP. 2019. Avoiding attack: the evolutionary ecology of crypsis, aposematism, and mimicry. Oxford: Oxford University Press.

Smith TB. 1987. Bill size polymorphism and intraspecific niche utilization in an African finch. Nature. 329(6141):717–719. doi: 10.1038/329717a0.

Smith AC, Buchanan-Smith HM, Surridge AK, Osorio D, Mundy NI. 2003. The effect of color vision status on the detection and selection of fruits by tamarins (*Saguinus* spp.). J Exp Biol. 206(18):3159–3165. doi: 10.1242/jeb.00536.

Smith AC, Surridge AK, Prescott MJ, Osorio D, Mundy NI, Buchanan-Smith HM. 2012. Effect of color vision status on insect prey capture efficiency of captive and wild tamarins (*Saguinus* spp.). Anim Behav, 83(2):479–486. doi: 10.1016/j.anbehav.2011.11.023.

Snorrason SS, Skúlason S, Jonsson B, Malmquist HJ, Jónasson PM, Sandlund OT, Lindem T. 1994. Trophic specialization in Arctic charr *Salvelinus alpinus* (Pisces; Salmonidae): morphological differentiation and ontogenetic niche shifts. Biol J Linn Soc. 52(1):1–18. doi: 10.1111/j.1095–8312.1994.tb00975.x.

Stevens M, Merilaita S. 2011. Animal camouflage: mechanisms and function. Cambridge: Cambridge University Press.

Stockley P, Bro-Jørgensen J. 2011. Female competition and its evolutionary consequences in mammals. Biol Rev Camb Philos Soc. 86:341–366.

Tilson RL, Hamilton WJ. 1984. Social dominance and feeding patterns of spotted hyaenas. Anim Behav. 32(3):715–724. doi: 10.1016/S0003-3472(84)80147-5.

van Schaik CP, van Noordwijk MA. 1988. Scramble and contest in feeding competition among female long-tailed macaques (*Macaca fascicularis*). Behaviour. 105(1/2):77–98.

Vasey N. 2002. Niche separation in *Varecia variegata rubra* and *Eulemur fulvus albifrons*: II. Intraspecific patterns. Am J Phys Anthropol. 118:169–183.

Veilleux CC, Scarry CJ, Di Fiore A, Kirk EC, Bolnick DA, Lewis RJ. 2016. Group benefit associated with polymorphic trichromacy in a Malagasy primate (*Propithecus verreauxi*). Sci Rep. 6:38418.

Vogel ER. 2005. Rank differences in energy intake rates in white-faced capuchin monkeys, *Cebus capucinus*: the effects of contest competition. Behav Ecol Sociobiol. 58(4):333–344. doi: 10.1007/s00265-005-0960-4.

Vogel ER, Neitz M, Dominy NJ. 2007. Effect of color vision phenotype on the foraging of wild white-faced capuchins, *Cebus capucinus*. Behav Ecol. 18(2):292–297. doi: 10.1093/beheco/arl082.

Vorobyev M. 2004. Ecology and evolution of primate color vision. Clin Exp Optom. 87(4–5):230–238. doi: 10.1111/j.1444-0938.2004.tb05053.x.

Watts DP. 2005. Sexual segregation in nonhuman primates. In: Rukstuhl K, Neuhaus P, editors. Sexual segregation in vertebrates: ecology of the two sexes. Cambridge (UK): Cambridge University Press.

Werner TK, Sherry TW. 1987. Behavioral feeding specialization in *Pinaroloxias inornata*, the “Darwin’s Finch” of Cocos Island, Costa Rica. Proc Natl Acad Sci USA. 84:5506–5510.

Whiteman HH, Wissinger SA, Brown WS. 1996. Growth and foraging consequences of facultative paedomorphosis in the tiger salamander,*Ambystoma tigrinum nebulosum*. Evol Ecol. 10(4):433–446. doi: 10.1007/BF01237728.

Wrangham RW. 1980. An ecological model of female-bonded primate groups. Behaviour. 75(3–4):262–300.

Yamashita N, Stoner KE, Riba-Hernández P, Dominy NJ, Lucas PW. 2005. Light levels used during feeding by primate species with different color vision phenotypes. Behav Ecol Sociobiol. 58(6):618–629. doi: 10.1007/s00265-005-0936-4.

Young HC. 2005. Sharp spines and toxic stings: how white-faced capuchins (*Cebus capucinus*) overcome the defence mechanisms of invertebrates in Costa Rica [MA thesis]. [Calgary (Canada)]: University of Calgary.