

## **Monkey see... what? Evidence for Ecological and Social Selection in the Evolution of Primate Color Vision**

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### **Evolution of Color Vision**

Vision allows us to perceive our world and gain information on our surroundings. It is an ancient trait that has evolved many times in the animal kingdom and has taken many shapes and forms in different organisms - from simple light detection in single-celled organisms to the extensive multi-chromatic vision of mantis shrimp which detects 16 spectral types, 12 of which are linked to color perception (Vorobyev 2004). The term 'chromatic vision' refers to the ability to perceive colors due to varying peak sensitivities of photopigments in the eye to certain spectral wavelengths of light, thus determining which colors are perceived and differentiated between.

Many vertebrates, such as reptiles and birds, are tetrachromatic, meaning that they have four photopigments in their retina which allow them to detect four distinct spectral wavelength peaks (Melin et al. 2017b; Jacobs & Rowe 2004). Evidence suggests that tetrachromatic vision is the ancestral, or plesiomorphic, state in vertebrates, having evolved in an early ancestor more than 540 million years ago as an adaptation to detect variance in lighting in shallow aquatic habitats (Vorobyev 2004). Around 250-230 million years ago, early mammals transitioned to and maintained an exclusively nocturnal activity pattern. During this period of evolutionary time, two photoreceptors were lost in these mammalian ancestors, perhaps through drift or selection, producing a fixed dichromatic state which has been widely retained in mammals today (Melin et al 2017b; Vorobyev 2004; Jacobs & Rowe 2004). Among the placental mammals, primates are the only clade to have re-gained a photoreceptor in their evolution to achieve a trichromatic state (Hiramatsu et al. 2008; Vorobyev 2004; Osorio & Vorobyev 1996), thus producing heightened visual acuity and an increased reliance on vision as the dominant sense (Moreira et al 2019; Melin et al. 2017b).

There are three opsin photopigments which produce chromatic vision in primates. The short-wavelength sensitive autosomal opsin gene (s opsin; SWS) detects blue pigments at the 440-nm spectral peak (Melin et al. 2017b; Osorio & Vorobyev 1996). Coupled with a mid-wavelength-sensitive opsin gene (Mopsin; MWS) which detects green pigments at the 533-nm spectral peak in primates, a blue-yellow spectral channel is produced which allows dichromats to differentiate luminance in their surroundings. Trichromatic primates, in addition to SWL and MWL photopigments, have a long-wavelength-sensitive opsin gene (Lopsin; LWS) which detects red pigments at the 565-nm spectral peak, thus allowing them to differentiate between red-green spectral channels and see colors in the red/orange/yellow color

range (Melin et al. 2017b; Heesy & Ross 2001; Osorio & Vorobyev 1996). MWS and LWS opsin genes are located on the X chromosome, thus are sex-linked in some primates. Variation in the presence and peak sensitivities of these three photopigments produce extensive variation in the allelic and phenotypic diversity of photopigments, thus producing multiple chromatic states and types of color vision in primates. Playing a key role in how organisms perceive and react to their environment, color vision directly contributes to individual fitness, thus it is likely to be under strong evolutionary selective pressures. Observed patterns of chromacy across the primate clade reveal frequent losses and gains of chromatic state within lineages, offering support for this idea (Jacobs et al. 2019) and begging further investigation of the fundamental evolutionary pressures selecting for different chromatic states.

### **Seeing Red: The Rise of Trichromatic Vision in Old World Monkeys, Apes, and Humans**

Old World monkeys, apes, and humans (parvorder: Catarrhini; here on "Catarrhines") are routine trichromats, meaning both sexes can uniformly differentiate between red-green spectral channels. This ability is the result of an ancestral duplication of the OPN1LW opsin gene and subsequent divergence towards and fixation at different wavelength sensitivities (Moreira et al. 2019; Melin et al. 2017b). This mutation is estimated to have occurred about 40 million years ago, proceeding the phylogenetic divergence from primates in the New World (Vorobyev 2004). There remains much debate in the literature over the evolutionary pressures selecting for Catarrhine trichromacy. The leading hypothesis predicts an adaptive advantage for trichromats in foraging for reddish ripe fruit and young leaves (Matsumoto et al. 2014; Regan et al. 2001; Osorio & Vorobyev 1996). Other proposed hypotheses include a superior ability of trichromats to perform visual tasks which include spatial perception or reference, an improved ability to recognize objects or predators under patchy or variable lighting (Jacobs et al. 2019), and an adaptive role in social signaling via modulations in skin color which may reveal information on emotion, health, female ovulatory state, and dominance (ex. Hiramatsu et al 2017).

### **Polymorphic Chromacy: The Case of the New World Monkeys**

New World monkeys (parvorder: Platyrrhini; here on "Platyrrhines") did not experience the same opsin gene duplication and fixation as the Catarrhines, thus each X chromosome possesses only one opsin photopigment gene at a locus, resulting in a sex-linked LWS/MWS polymorphism (Moreira et al. 2019; Fedigan et al. 2014). Hemizygous males (having one X chromosome), and females homozygous for a photopigment allele, are thus dichromatic and functionally red-green colorblind. However, females heterozygous for the LWS/MWS opsin allele produce both photopigments, detect both spectral peaks, and are thus functionally trichromatic and able to perceive red hues (Jacobs et al. 2019; Melin et al. 2017b; Valenta et al. 2016; Fedigan et al. 2014; Heesy & Ross 2001). The retention and maintenance of this chromatic polymorphism suggests selective pressures at work, as evolutionary theory otherwise predicts its loss through drift and a shift towards the fixation of the more advantageous allele (Jacobs et al. 2019). The leading hypotheses to explain the selection for this polymorphism include the heterozygote superiority hypothesis, which predicts an adaptive advantage based on the ability to differentiate between red-green color channels, as is the case in foraging (Fedigan et al. 2014), the idea that different genotypes are better suited for different tasks (Fedigan et al. 2014), and the idea of polymorphism maintenance through balancing selection, perhaps via niche divergence,

frequency dependent selection, or mutual benefit of association (Jacobs 2019; Melin et al. 2017a; Fedigan et al. 2014).

Interestingly, two genera amongst the Platyrrhines diverged from the allelic polymorphism to the fixation of a single chromatic state, thereby suggesting either a loss of allelic diversity through drift or, more likely, active directional selection. Howler monkeys (genus: *Alouatta*) evolved routine trichromacy independent of Catarrhines through an analogous duplication of the opsin genes (Hiramatsu et al. 2008; Heesy & Ross 2001). It has been suggested that, being the most folivorous species of the Platyrrhines, Howlers may have evolved this trait in convergence with Catarrhines due to the similar foraging advantage red-green differentiation would confer in the search for young, nutrient-rich leaves common on both continents (Melin et al. 2017b).

Likewise, evidence suggests that Owl monkeys (genus: *Aotus*) have diverged away from the polymorphic chromatic vision common in Platyrrhines to grey-scale MWS monochromatic vision through loss of S opsin function (Vorobyev 2004). A similar shift towards monochromacy has been reported to have occurred in the Old-World bush babies (genus: *Galago*), possibly as a result of drift due to relaxed selection by nocturnal activity patterns (Hiramatsu et al. 2008; Vorobyev 2004).

### **Strepsirrhines: Dichromatic, with Exceptions**

Lemurs and lorises (order: Strepsirrhini; here on "Strepsirrhines") are generally dichromatic, possessing two functional photopigments, mostly commonly the SWS and MWS opsins. Interestingly, considerable variation has been reported in multiple lemur genera (*Eulemur*, *Varecia*, *Propithecus*), with trichromatic, polymorphic, and seemingly derived, or re-evolved, dichromatic vision being variably present across lineages (Melin et al 2017b; Kawamura et al. 2012; Changizi et al. 2006; Vorobyev 2004). It has been suggested that this variation may be explained by varying luminance and cryptic coloration in fruits, or as an adaptation to improve object recognition in lowly-lit rainforests (Jacobs et al. 2019).

### **Selection Pressures and Synthesis**

Primates have undergone extensive niche specialization in the Old and New Worlds, producing extensive variation in life histories relating to diet, activity pattern, sociality, and mating systems adapted to specific environments and socio-sexual and ecological contexts (Moreira et al. 2019). Therefore, it is not surprising that adaptive selection would favor considerable variation in chromacy across the order. Yet, there remains much work to be done in identifying the social and ecological factors which are most closely associated with patterns of chromacy.

A trichromatic advantage in foraging for red, ripe fruits from a green leafy background, and young red pigmented leaves from older, tougher, less nutritious leaves, is widely hypothesized to be the primary evolutionary pressure selecting for routine trichromacy in Catharrhines and aiding in the maintenance of the Platyrrhine opsin polymorphism. However, evidence for the adaptive foraging hypothesis remains mixed. For example, some studies on Platyrrhines have reported a higher foraging efficiency in captive callitrichid trichromats

(*Callithrix*, *Saguinus*) compared to dichromats (Smith et al. 2003), and greater intake rates and a higher accuracy of trichromats white faced capuchins (*Cebus*) in selecting ripe fruits compared to dichromats in the same population (Melin et al. 2017a; Melin et al. 2013). In contrast, other studies have found no significant differences in foraging efficiency (Hiramatsu et al. 2008) or energy acquisition rates (Vogel et al. 2007) between trichromatic and dichromatic individuals in populations of spider monkeys (*Ateles*) and capuchins (*Cebus*), respectively.

A second hypothesis which has been gaining increased attention and support in recent years proposes a social signaling advantage of trichromats in perceiving red modulations in skin color, which may serve as honest or dishonest signals in revealing emotional state (for ex. blushing, flushing and blanching in humans), socio-sexual signals, health, and threat displays (Rigaill et al. 2019; Moreira et al. 2019; Changizi et al 2006; Vorobyev 2004). It is well documented that many Catarrhines, Platyrrhines, and the two genera of polymorphic chromatic Strepsirrhines (*Varecia*, *Propithecus*) have convergently developed large patches of bare skin on their faces, ano-genital area, chest and hindquarters (Rigaill et al 2019, Moreira et al. 2019; Changizi et al. 2006) and that changes in red-tone skin color occur due to variable concentrations of oxygenated hemoglobin in the blood which alters perceivable red color saturation and reflectance (Rigaill et al. 2019; Changizi et al 2006). Furthermore, estrogen receptors in the skin of primates modulates blood flow, producing perceptible changes in skin color in association with the female reproductive cycle and social status (Moreira et al 2019; Rigaill et al 2019). A study by Hiramatsu et al. (2017) offers support that trichromatic humans can successfully detect variation in red skin color. Overall, evidence for this hypothesis is building, but remains anecdotal and isolated to behavioral studies on a small number of species (see Moreira et al. 2019 for review). To assess the role modulations in skin color may play in the selection of trichromatic vision in different species, it is important to understand the social contexts in which they would function for each species in accordance to dominance hierarchies, social systems, and mating systems (Moreira et al. 2019).

Through this meta-analysis, I aim to take the first steps in filling this knowledge gap by synthesizing relationships between explanatory variables for the two leading hypotheses proposed to explain the role of and selection for primate color vision: the adaptive foraging hypothesis and the social signaling hypothesis. Specifically, by combining data on variables related to foraging behavior (diet, activity patterns) and social factors (dominance hierarchies, mating systems, skin exposure, skin color, and social system), I aim to identify variables which best correlate with and explain the most meaningful variation in primate color vision. By doing so, I aim to advance the field by adding to the growing body of literature on the evolutionary pressures selecting for different vision types, with the ultimate goal of elucidating how specific social and ecological factors shape foraging efficiency and communication amongst primates.

## **Methods**

### *Data Collection*

Data on skin color, skin exposure, and chromacy were gathered from a review of primary literature and further supplemented with information on diet percent composition, mating system, social system, and dominance hierarchies from a comprehensive encyclopedia on living

primate species (Rowe et al. 2016). Species were selected for analyses based on the availability of data categorizing facial skin color and skin exposure of primates, available in Moreira et al. (2019). Skin exposure was assigned by Moreira et al. (2019) to five categorical levels based on 2-5 forward-facing images: 1) predominantly covered face, with exposed skin around the nostrils; 2) mostly covered face, with exposed skin around the eyes; 3) mostly exposed face, with skin around the nose and eyes exposed, or around the nose and mouth exposed; 4) predominantly exposed face, with exposed skin around the eyes, nose, and mouth; and 5) completely exposed face, which includes cheeks, nose, eyes, and forehead. Skin color was assigned, using the same images, to four categorical levels: 1) hyperpigmented (dark) skin; 2) mottled skin, which is mostly depigmented with small pigmented patches; 3) depigmented skin; and 4) hypervascularized (red) skin. Data on phenotypic chromacy were then gathered for each species from a phylogenetic model reporting trends in primate chromacy created by Heesy & Ross (2001), then expanded to include monochromacy as a fourth chromatic category based on later reports documenting its discovery (Vorobyev 2004). Species were then cross referenced using an encyclopedia on primates (Rowe et al. 2016) to assign life-history information on rank dominance (presence/absence), mating system (four levels: polygynous, polyandrous, polygynandrous, monogamous), social system (seven levels: one male-one female pairings (1M-1F), one male-multifemale groups (1M-MF), multimale-one female groups (MM-1F), multimale-multifemale groups (MM-MF), all-male bands, solitary, and fission-fusion groups), and diet (percent composition and presence/absence; 9 levels: ripe fruits, unripe fruits, seeds, leaves, exudates, flowers, nectar/flowers, vertebrates, and invertebrates; average calculated if percent-range given). Combined, the complete data set includes 106 primate species of 49 genera and 20 sub families, representing 4 major groupings within the primate order: Platyrrhines (n=70), Catarrhines (n=28), Strepsirrhines (n=7) and Tarsiiformes (n=1) (Supplementary Material Table A). Selected species included in the study were dependent on available data. A limitation of this study is the uneven distribution of species included in this study from each order.

### *Data Analyses*

Data analyses were performed using RStudio v. 1.1.456. The 'rda' function in the 'vegan' R package v. 2.5.3 was used to construct a principal components analysis ordination based on presence/absence data for foraging and social factors (Figure 1). Correlations between variables were assessed with Spearman's Rho tests using a 0.95 confidence interval, performed using the 'cor.test' function in the 'stats' R package v. 3.5.1 for foraging (Table 1) and social variables (Table 2).

### *Results*

A strong positive correlation exists between trichromatic vision and a highly folivorous diet ( $p < 0.001$ ) and a strong negative correlation between polymorphic chromacy and a folivorous diet ( $p < 0.001$ ; Table 1). No other dietary component significantly correlated with chromatic vision.

Both monochromatic and dichromatic vision were found to have strong negative correlations with diurnal activity patterns ( $p < 0.001$ ), and strong positive correlations with a

nocturnal activity pattern ( $p < 0.001$ ; Table 1). Trichromacy and polymorphic chromacy did not significantly correlate with activity pattern ( $p > 0.05$ ). Correlations between diet and activity patterns were assessed but were highly insignificant so were excluded from further analysis.

Trichromatic vision was found to have a strong positive correlation with skin exposure, polygyny, the presence of dominance hierarchies, 1M-MF social groups, a solitary social structure ( $p < 0.001$ ), and all-male-groups ( $p < 0.05$ ). Both monochromatic and dichromatic vision were found to have a strong negative correlation with skin exposure ( $p < 0.001$ ). In addition, monochromatic vision was found to negatively correlate with the presence of dominance hierarchies, MM-MF social groups ( $p < 0.001$ ), and 1M-MF social groups ( $p < 0.05$ ), and strongly positively correlate with monogamy and 1M-1F social groups ( $p < 0.001$ ). Polymorphic chromacy was found to have a strong negative correlation with polygyny, 1M-MF social groups ( $p < 0.001$ ), and a solitary social structure ( $p < 0.01$ ), and to have a strong positive correlation with polyandry and polygynandry ( $p < 0.05$ ). Skin color did not significantly correlate with chromatic vision ( $p > 0.05$ ; Table 2).

Table 1. Spearman's Rho Correlations between foraging variables and chromatic vision type for 103 primate species. Numbers indicate rho correlation values (-1,1). Significance levels are denoted with asterisks.

Foraging Variables		Vision Type			
		Monochromatic	Dichromatic	Trichromatic	Polymorphic
Diet	Fruits (Unripe)	-0.024	-0.034	0.022	-0.003
	Fruits (Ripe)	0.207	-0.113	-0.195	0.181
	Seeds	-0.105	-0.150	-0.021	0.101
	Leaves	-0.174	0.127	<b>0.620***</b>	<b>-0.615***</b>
	Exudates	-0.051	0.177	-0.138	0.086
	Nectar/Flowers	0.194	-0.144	0.226	-0.222
	Vertebrates	-0.030	-0.043	0.103	-0.079
	Invertebrates	-0.099	0.110	-0.081	0.066
Activity Pattern	Diurnal	<b>-0.567***</b>	<b>-0.809***</b>	0.201	0.237
	Cathemeral	-0.017	<b>0.701***</b>	-0.114	-0.135
	Nocturnal	<b>0.701***</b>	<b>0.483***</b>	-0.162	-0.192

N=103

Significance Values: \* $P \leq 0.05$ ; \*\* $P \leq 0.01$ ; \*\*\* $P \leq 0.001$ ; ^AS  $0.05 < P \leq 0.07$ ; NS  $P > 0.05$

Table 2. Spearman's Rho Correlations between social variables and chromatic vision type for 106 primate species. Numbers indicate rho correlation values (-1,1]. Significance levels are denoted with asterisks.

Social Variables		Vision Type			
		Monochromatic	Dichromatic	Trichromatic	Polymorphic
Facial Skin	Skin Exposure	<b>-0.371***</b>	<b>-0.337**</b>	<b>0.370***</b>	-0.010
	Skin Color	-0.166	0.197	-0.119	0.137
Dominance Structure	Hierarchical	<b>-0.405***</b>	0.022	<b>0.421***</b>	-0.171
Mating System	Polygyny	-0.190	0.178	<b>0.481***</b>	<b>-0.412***</b>
	Polyandry	-0.089	-0.053	-0.198 <sup>^</sup>	<b>0.260*</b>
	Polygynandry	<b>-0.226*</b>	0.002	-0.135	<b>0.260*</b>
	Monogamy	<b>0.448***</b>	-0.138	-0.204 <sup>^</sup>	-0.018
Social System	1M- 1F Groups	<b>0.367***</b>	0.089	-0.081	-0.171
	1M-MF Groups	<b>-0.220*</b>	0.006	<b>0.575***</b>	<b>-0.420***</b>
	MM-1F Groups	-0.131	0.106	-0.078	0.111
	MM-MF Groups	<b>-0.385***</b>	0.030	0.0979	0.121
	All Male Bands	-0.062	-0.037	<b>0.266*</b>	-0.203 <sup>^</sup>
	Fission Fusion	-0.202 <sup>^</sup>	0.0217	0.045	0.0678
	Solitary	-0.16707	-0.099	<b>0.477***</b>	<b>-0.319**</b>

N=106

Significance Values: \*P≤0.05; \*\*P≤0.01; \*\*\*P≤0.001; <sup>^</sup>AS 0.05<P≤0.07; NS P>0.05

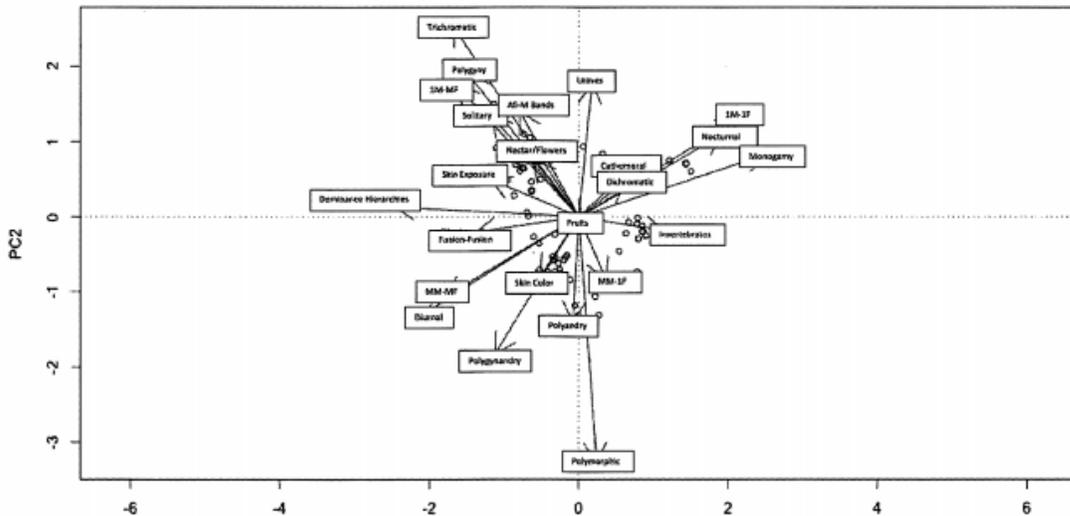


Figure 1. Principal components analysis mapping associations between chromacy, diet, skin exposure, skin color, mating system, social system, presence of dominance hierarchies, and activity pattern for 106 primate species. Closely grouped variables along a linear axis in the same direction indicate a positive correlation between the variables (for ex. "monogamy", "nocturnal" and "IM-1F"). If variables are opposite one another along a linear axis, a negative correlation between the variable exist (ex. "Polymorphic" (chromacy) and "Leaves"). Variables at a 90-degree angle to one another are unassociated or have very weak associations (ex. "Dominance Hierarchies" and "Polymorphic". The longer the arrow, the farther out the variable separated when plotted in 3-dimension. Shorter arrows/central placement (ex. "Fruits") indicates ubiquitous association with multiple variables widely separated on the ordination axes.

## Discussion

### *Adaptive Foraging*

Increased foraging efficiency between red-green spectra for species whose diet is composed largely of reddish foods would offer support for the selection of routine trichromacy in Catarrhines and Alouatta through directional selection towards adaptive spectral peaks, and maintenance of the Platyrrhine chromatic polymorphism via the heterozygote superiority hypothesis (Fedigan et al. 2014). Here, as expected by the adaptive foraging hypothesis, a highly folivorous diet was found to significantly positively correlate with trichromatic vision (Table 1), presumably because red-green differentiation aids trichromats in foraging by improving their ability and efficiency at locating young, red-pigmented leaves which provide more energy and nutrients than older leaves (Jacobs et al. 2011; Melin et al. 2017b; Lucas et al. 2003; Regan et al. 2001). Mirroring these results, a number of previous studies have reported greater fruit foraging efficiency (Smith et al. 2003), fruit intake rates (Melin et al. 2017a), and greater accuracy in ripe fruit selection of trichromatic Platyrrhines compared to their dichromatic counterparts (Melin et al. 2013). Hogen et al. (2018) reports a similar trend for conspicuously colored flowers, with trichromatic individuals (Cebus) being found to visit flower patches more frequently than dichromats. However, in opposition to the adaptive foraging hypothesis, no significant correlations were found in this analysis between trichromatic vision and fruit and nectar/flower consumption, both of which are often conspicuously colored in the red/orange/yellow color range.

Few primates would turn down the opportunity to forage on fruits if encountered given their high nutrient and caloric density. Hence, it is possible the insignificant correlation between color vision and the percent composition fruit makes up of the diet could be a relic of the ubiquitous presence of a base level of frugivory in the majority of primates included in this analysis. Figure 1 appears to offer support for this explanation, as the "fruits" category fails to separate within the ordination space. Instead, its central location in the ordination suggests an equal association with other variables grouped along the ordination axes, and thus an insignificant correlation with any individual variables within the sample space.

Furthermore, it is important to note that the "fruit" diet category is fully inclusive of all fruits eaten, with no further breakdown of categories based on important characters impacting their conspicuity - such as fruit color, fruit luminance, and fruit size. For example, there may be a fruit produced by a given plant species which cryptically ripens, remaining green/brown rather than turning reddish, thus making it less perceptible to trichromats. Couple this trait with heightened fruit luminance, and it would become increasingly more conspicuous to a dichromat and increasingly less to a trichromat. This idea is supported in a study by Hiramatsu et al. (2008) through their finding that luminance contrasts have the greatest effect on the foraging efficiencies of dichromatic vs trichromatic spider monkeys (*Ateles*). Incorporating measures on fruit hue and luminance contrast, along with having a larger sample size, would increase statistical power and would help provide the material required to tease apart the characteristics which may account for this variation.

Variation in ability between dichromatic and trichromatic individuals in detecting food sources in a given area offers support for a few of the hypotheses proposed to maintain chromatic

polymorphism in Platyrrhines (review in Fedigan et al. 2014). For example, if different genotypes, and thus phenotypes, are better suited to detect different foods, niche differentiation may be encouraged through differential foraging behaviors between phenotypes, thereby decreasing competition and increasing carrying capacity. Similarly, stabilizing selection may maintain the polymorphism as a result of frequency-dependent selection, during which the foraging success of a phenotype depends on its relative abundance in the population. For example, being a dichromat in a group of trichromats would provide an adaptive advantage to finding cryptic fruit due to relaxed intra-group competition. But, if the entire population were to be dichromatic and could equally see the cryptic fruit, competition for it would be expected to increase, thus decreasing the adaptive advantage at high abundance. An additional mechanism of balancing selection which may be actively selecting for patterns in chromacy within Platyrrhines is the idea of mutual benefit of association (Jacobs 2019; Melin et al. 2017a; Fedigan et al. 2014). This is the idea that dichromats and trichromats in a population would mutually benefit one another through social foraging, where for example, one individual's detection of a fruit tree leads the whole group there to benefit.

Environmental variables such as light levels and habitat structure, through variance in forest density and canopy cover for instance, may further exert pressure on chromacy through effects on luminance. For example, Melin et al. (2013) and Vorobyev (2004) suggest that luminance may be more important in forests with patchy, variable lighting. Since there is evidence that variation in luminance may substantially impact visual detection of contours and spatial depth (Hiramatsu et al. 2008), a dimly lit forest with a dense canopy and patchy lighting may indeed be expected to drive the co-evolution of fruit luminance for heightened conspicuity to dichromatic seed dispersers while maintaining selection on dichromacy to detect these differences. This may be what happened with *Eulemur rubriventer*, one of the aforementioned Strepsirrhines which had re-evolved dichromacy from a polymorphic ancestor. Similar to Hiramatsu et al. (2008), Jacobs et al. 2019, found high luminance contrasts and more cryptic coloration of the fruits found in the forests of Madagascar in which *E. rubriventer* lives, thus increasing selection for dichromacy and potentially explaining the re-derivation of the dichromatic state.

Although not significant, it was found that dichromatic vision is positively associated with an invertebrate heavy diet (insects, arthropods, spiders; Table 1), as would be expected by the adaptive foraging hypothesis. This idea is supported by previous evidence that dichromats are more efficient at gleaning insects than trichromats (in *Cebus*), likely due to a superior ability in vision to break camouflage and detect invertebrate contours against substrates (Melin et al. 2017a). A larger sample size may improve statistical power and allow for stronger detection of these associations.

Lastly, it is important to consider in light of the previous discussion that using diet percentage as a proxy for the relative importance of each food for a species as done in this analysis may not be the best indicator of selection for chromacy because hold-over foods during times of year when food abundance is low may have a disproportionately large effect on individual fitness and selection than would be expected by its given abundance or portion of the diet during other times of year.

### *Activity Patterns*

Detection of luminance in low light may act as an important selective pressure for dichromatic vision (Melin et al. 2013). Thus, it would be expected that dichromatic vision would be more common in nocturnal and cathemeral primates, while trichromacy would be more closely associated with a diurnal activity pattern. Analyses here provide support for this concept (Table 1), with dichromatic vision being found to significantly negatively correlate with a diurnal lifestyle, and significantly positively correlate with cathemeral and nocturnal activity patterns. Trichromacy positively correlated with a diurnal activity patterns, however this result was not significant. Overall, activity patterns do not appear to be a reliable predictor of chromacy based on the considerable variation in chromacy observed in diurnal primates.

### *Social Signaling*

In order for skin to provide a canvas on which social signaling information can be displayed through red modulations in skin color, two conditions must first be met: 1) there must be exposed skin; and 2) species must have trichromatic vision to detect changes in red coloration. Given these conditions are met, it is predicted that skin color modulations may reveal information on female reproductive cycling, emotional state, health, and dominance (Rigaill et al. 2019; Moreira et al. 2019; Changizi et al 2006; Vorobyev 2004). Thus, in the same vein of thought, it would be expected that factors such as skin color, skin exposure, and trichromatic vision would positively correlate with more complex social contexts such as in the presence dominance hierarchies, MM-MF groups, and polygamous mating systems. This hypothesis is well-supported by the results of this study. Strong positive correlations were found between trichromacy and skin exposure, polygyny, the presence of dominance hierarchies, 1M-MF groups, solitary individuals, and all male bands (Table 2). In these contexts, and specifically in large 1M-MF social groups, one could imagine that having trichromatic vision that aids males in their assertion of dominance, and helps to assess mate quality of females, and gauge female receptivity to maximize chances of siring offspring, would be beneficial due to its direct selection on reproductive fitness. Solitary individuals and individuals in all-male bands would similarly be trying to maximize reproductive success. Thus, being able to know when solitary females or females in other groups are fertile may similarly be select for in all-male bands and for solitary males as a means of timing courtship advances or sneak copulations. As expected by the social signaling hypothesis, negative correlations between trichromatic vision and monogamy were found. When monogamous, reproductive success is more assured for the individuals involved, thus receiving social information through modulations in skin color would not be expected to be under strong evolutionary selection. Interestingly, polyandry was significantly negatively associated with trichromatic vision. Future studies should be aimed at further teasing apart whether the social information being shared through skin modulations of these species are more closely linked to dominance hierarchies and indicative of rank status, or to female reproductive status. Changizi et al. (2006) confirms the observed pattern that many trichromatic primate species tend to have bare faces, likely to perceive these signals. In addition, evidence on spectral peak sensitivity has placed the optimal wavelength for primates to detect red modulations in skin color via blood oxygen saturation at 550-nm, seemingly perfectly centered at the trichromatic maxima of 535-562-nm (Osorio et al. 2004), Dichromatic individuals would not be able to perceive this saturation (Osorio et al. 2004). Taken together, this is strong evidence

that social evolutionary pressures have spectrally tuned photoreceptors for trichromatic vision (Hiramatsu et al. 2017), thus suggesting strong selection for its function in socio-sexual communication and offering strong support for the evolution of trichromacy being linked to the social signaling hypothesis. Anecdotal evidence from the literature supports that red modulations in skin color have been linked in behavioral studies to sexual solicitations, social rank, assessment of dominance, competitive ability, willingness to engage in fights, multimale social systems, and quantitatively assessed male androgen status (See full review in Moreira et al. 2019). Interestingly, beyond color alone, Rigai et al. (2019) found that skin color (face and hindquarters) in Japanese Macaques did not closely track female fertility phase. However, luminance values in the same skin patches did reveal differences between pre- and post-ovulatory time frames. Furthermore, Rigai et al. (2019) found that hindquarters tended to be redder in non-conceptive females, and that higher-ranking females tended to have darker hindquarters. In contrast, other species of Catarrhines may develop reddening of sexual skin around ovulation, as well documented in the chimpanzees (*Pan*), further offering support that skin color modulations and trichromacy are linked to social signaling (Vorobyev 2004).

In line with this theory, results from this analysis find that monochromatic and dichromatic vision are strongly negatively correlated with skin exposure, meaning that they have more fur covering their faces. Without skin exposure, any social signals conveyed through skin color modulations would not be perceived, and therefore should not be selected for and should not be closely associated with the complex group structures characteristic of trichromatic Catarrhines. In support of this theory, monochromacy was found to strongly positively correlate with monogamy and 1M-1F groups, and strongly negatively correlated with polygyny, dominance hierarchies, 1M MF groups, and MM-MF groups. Dichromatic vision did not significantly correlate with any of these social factors, possibly due to small sample size (Table 2).

It was found that there is a negative correlation between polymorphic chromacy and skin exposure, similarly, indicating that they have more fur around their faces. Given that the Platyrrhines vary extensively in this trait - from close to zero skin exposure (ex. *Saguinus mystax*) to entirely exposed faces and heads (ex. *Cacajao calvus*; Moreira et al. 2019)- the extensive variation and mix of correlations for this group may be expected, specifically since social signaling via modulations in skin color would only be socially relevant for the few species which have the phenotypic skin patches to display red saturation (see Table 2 for correlations). Moreira et al. (2019) reports that skin exposure seems to be an evolutionary plastic trait which is frequently gained and lost in evolutionary lines, specifically in Platyrrhines. Therefore, although social signaling may be actively occurring in the few bare-faced polymorphic chromats on a case-by-case basis, evidence suggests that overarching factors other than social signaling would better explain the extensive variation of skin exposure in Platyrrhines. A review of the literature suggests that balancing selection and heterozygote advantage hypotheses may better support the maintenance of polymorphic chromacy in these species (see full review in Fedigan et al. 2014).

Insignificant correlations were found in this analysis between skin color and all vision types (Table 2), likely because the categories created for this variable (hypervascularated, unpigmented, mottled, hyperpigmented) function as proxies to indicate how well modulations in

skin color could be detected (for example, a red flush in hyperpigmented skin would not be as conspicuous as a red flush in unpigmented skin), but do not themselves directly reflect modulations in red saturation.

It is important to note that categorizations of skin exposure in this analysis only included facial skin based on data availability. Future studies should consider skin luminance and skin exposure of the chest, hindquarters, and anogenital region to further assess evidence for the social signaling hypothesis (Moreira et al. 2019). It is important too to note that while significant correlations may suggest a role in social signaling, changes in color could alternatively be consequences of physiology and may not be involved in the signaling and receiving of social information (Changizi et al. 2006).

## **Conclusion**

The two leading hypotheses proposed to explain patterns in chromatic color vision across the primate clade include the foraging advantage hypothesis and the social signaling hypothesis. Under the foraging advantage hypothesis, trichromatic individuals would be expected to better detect conspicuous reddish fruits and young leaves in the red-green color channel, meanwhile dichromatic individuals would be expected to better detect cryptically colored fruit based on luminance in the blue-yellow color channel and be more efficient in foraging for invertebrates through their heightened ability to break camouflage. This may lead to cases of balancing selection and heterozygote superiority amongst species with polymorphic color vision. Results of this meta-analysis offer some support for the adaptive foraging hypothesis through trichromatic advantage in foraging for young leaves. Other dietary correlations were found to be insignificant, however a review of literature provides support of this hypothesis when context-specific information on environment and luminance are considered. Under the social signaling hypothesis, trichromatic vision would be expected to allow for the detection of modulations in skin color due to differences in blood oxygen concentrations which create red saturation, which may reveal information on dominance, fertility, emotion, and health. Results of this meta-analysis provide strong support for the social signaling hypothesis in trichromatic primates. Future studies should focus on further examining interactions and co-variance between explanatory variables of each hypothesis, with the aim being to investigate whether evidence supports the idea of chromatic vision being an exaptation, or a trait that has been co-opted for another function different than that it was initially selected for.

Supplementary Materials

Table A. List of species including in data analyses, organized by order, sub-family, and genus (n=106 species total).

Genus	Sub-family	Parvorder/Order	Species ID
<i>Allenopithecus</i>	Cercopitheciinae	Catarrhini	<i>A. nigroviridis</i>
<i>Cercocebus</i>	Cercopitheciinae	Catarrhini	<i>C. chrysogaster</i>
<i>Cercopithecus</i>	Cercopitheciinae	Catarrhini	<i>C. diana</i>
<i>Chlorocebus</i>	Cercopitheciinae	Catarrhini	<i>C. pygerythrus</i>
<i>Erythrocebus</i>	Cercopitheciinae	Catarrhini	<i>E. patas</i>
<i>Lophocebus</i>	Cercopitheciinae	Catarrhini	<i>L. albigena</i>
<i>Mococa</i>	Cercopitheciinae	Catarrhini	<i>M. mulatta</i>
<i>Mandrillus</i>	Cercopitheciinae	Catarrhini	<i>M. sphinx</i>
<i>Miopithecus</i>	Cercopitheciinae	Catarrhini	<i>M. talapoin</i>
<i>Papio</i>	Cercopitheciinae	Catarrhini	<i>P. papio</i>
<i>Rungwecebus</i>	Cercopitheciinae	Catarrhini	<i>R. kipunji</i>
<i>Theropithecus</i>	Cercopitheciinae	Catarrhini	<i>T. gelada</i>
<i>Colobus</i>	Colobinae	Catarrhini	<i>C. guereza</i>
<i>Nasalis</i>	Colobinae	Catarrhini	<i>N. larvatus</i>
<i>Ptilocolobus</i>	Colobinae	Catarrhini	<i>P. rufomitratus</i>
<i>Presbytis</i>	Colobinae	Catarrhini	<i>P. potenziani</i>
<i>Procolobus</i>	Colobinae	Catarrhini	<i>P. verus</i>
<i>Pygathrix</i>	Colobinae	Catarrhini	<i>P. nigripes</i>
<i>Rhinopithecus</i>	Colobinae	Catarrhini	<i>R. bieti</i>
<i>Semnopithecus</i>	Colobinae	Catarrhini	<i>S. entellus</i>
<i>Simias</i>	Colobinae	Catarrhini	<i>S. concolor</i>
<i>Gorilla</i>	Homininae	Catarrhini	<i>G. gorilla</i>
<i>Pan</i>	Homininae	Catarrhini	<i>P. troglodytes</i>
<i>Hooleck</i>	Hylotidae	Catarrhini	<i>H. hooleck</i>
<i>Hylobates</i>	Hylotidae	Catarrhini	<i>H. pileatus</i>
<i>Nomascus</i>	Hylotidae	Catarrhini	<i>N. leucogenys</i>
<i>Symphalangus</i>	Hylotidae	Catarrhini	<i>S. syndactylus</i>
<i>Pongo</i>	Ponginae	Catarrhini	<i>P. abelii</i>
<i>Alouatta</i>	Alouattinae	Platyrrhini	<i>A. belzebul</i> , <i>A. caraya</i> , <i>A. guariba</i> , <i>A. macconnelli</i> , <i>A. palliata</i> , <i>A. pigra</i> , <i>A. sensiculus</i>
<i>Aotus</i>	Aotinae	Platyrrhini	<i>A. azarae</i> , <i>A. griseimembra</i> , <i>A. infuatus</i> , <i>A. lemurinus</i> , <i>A. nancymaeae</i> , <i>A. nigricaps</i> , <i>A. trivirgatus</i> , <i>A. vociferans</i>
<i>Ateles</i>	Atelinae	Platyrrhini	<i>A. belzebuth</i> , <i>A. chamek</i> , <i>A. geoffroyi</i> , <i>A. hybridus</i> , <i>A. marginatus</i> , <i>A. paniscus</i> <i>A. fusciceps</i>
<i>Brachyteles</i>	Atelinae	Platyrrhini	<i>B. arachnoides</i> , <i>B. hypoxanthus</i>
<i>Lagothrix</i>	Atelinae	Platyrrhini	<i>L. lagothricha</i>
<i>Callitchebus</i>	Callitchebinae	Platyrrhini	<i>C. colmbrai</i> , <i>C. cupreus</i> , <i>C. donacophilus</i> , <i>C. hoffmannsi</i> , <i>C. lugens</i> , <i>C. moloch</i> , <i>C. nigritrans</i> , <i>C. personatus</i> , <i>C. torquatus</i>
<i>Callimico</i>	Callitrichinae	Platyrrhini	<i>C. goeldii</i>
<i>Callithrix</i>	Callitrichinae	Platyrrhini	<i>C. aurita</i> , <i>C. geoffroyi</i> , <i>C. jacchus</i> , <i>C. kuhlii</i> , <i>C. penicillata</i>
<i>Sagulnus</i>	Callitrichinae	Platyrrhini	<i>S. bicolor</i> , <i>S. geoffroyi</i> , <i>S. imperator</i> , <i>S. labiatus</i> , <i>S. leucopus</i> , <i>S. midas</i> , <i>S. mystax</i> , <i>S. niger</i> , <i>S. nigricollis</i> , <i>S. oedipus</i> , <i>S. tripartitus</i>
<i>Cebus</i>	Cebinae	Platyrrhini	<i>C. albifrons</i> , <i>C. capucinus</i> , <i>C. kaapor</i> , <i>C. olivaceus</i>
<i>Sapajus</i>	Cebinae	Platyrrhini	<i>S. apella</i> , <i>S. libidinosus</i> , <i>S. robustus</i> , <i>S. xanthosternus</i>
<i>Cacajao</i>	Pitheciinae	Platyrrhini	<i>C. calvus</i> , <i>C. hosomi</i> , <i>C. melanocephalus</i>
<i>Chiropates</i>	Pitheciinae	Platyrrhini	<i>C. albinasus</i> , <i>C. chiropates</i> , <i>C. utahicki</i>
<i>Pithecia</i>	Pitheciinae	Platyrrhini	<i>P. irrorata</i> , <i>P. monachus</i> , <i>P. pithecia</i>
<i>Saimiri</i>	Saimiriinae	Platyrrhini	<i>S. oerstedii</i> , <i>S. sclureus</i>
<i>Microcebus</i>	Cheirogaleidae	Strepsirrhini	<i>M. rufus</i>
<i>Daubentonia</i>	Daubentonidae	Strepsirrhini	<i>D. madagascariensis</i>
<i>Galago</i>	Galagidae	Strepsirrhini	<i>G. gallarum</i>
<i>Propithecus</i>	Indridae	Strepsirrhini	<i>P. coquereli</i> , <i>P. perrieri</i>
<i>Eulemur</i>	Leumuroidea	Strepsirrhini	<i>E. rufus</i>
<i>Loris</i>	Loridae	Strepsirrhini	<i>L. lydekkerianus</i>
<i>Tarsius</i>	Tarsiidae	Tarsiiformes	<i>T. dentatus</i>

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