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RESEARCH ARTICLE

The Adaptive Value of Primate Color Vision for Predator Detection

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The complex evolution of primate color vision has puzzled biologists for decades. Primates are the only eutherian mammals that evolved an enhanced capacity for discriminating colors in the green–red part of the spectrum (trichromatism). However, while Old World primates present three types of cone pigments and are routinely trichromatic, most New World primates exhibit a color vision polymorphism, characterized by the occurrence of trichromatic and dichromatic females and obligatory dichromatic males. Even though this has stimulated a prolific line of inquiry, the selective forces and relative benefits influencing color vision evolution in primates are still under debate, with current explanations focusing almost exclusively at the advantages in finding food and detecting socio-sexual signals. Here, we evaluate a previously untested possibility, the adaptive value of primate color vision for predator detection. By combining color vision modeling data on New World and Old World primates, as well as behavioral information from human subjects, we demonstrate that primates exhibiting better color discrimination (trichromats) excel those displaying poorer color visions (dichromats) at detecting carnivoran predators against the green foliage background. The distribution of color vision found in extant anthropoid primates agrees with our results, and may be explained by the advantages of trichromats and dichromats in detecting predators and insects, respectively. Am. J. Primatol.

Key words: trichromatic advantage; visual polymorphism; color vision modeling; behavioral approach; trichromatism

INTRODUCTION

Trichromatic color vision, characterized by an enhanced capacity for discriminating colors in the green–red part of the spectrum, has evolved exclusively in one group within eutherian mammals, the primates [Jacobs, 2010]. While Catarrhini (Old World monkeys and apes) and one genus (*Alouatta*) of Platyrrhini (New World monkeys) present three types of cone pigments and are routinely trichromatic [Jacobs et al., 1996], most New World monkeys exhibit a color vision polymorphism [Jacobs, 2007], characterized by the occurrence of trichromatic and dichromatic females and obligatory dichromatic males in the same species. The maintenance of such polymorphism in New World monkeys has been primarily attributed to balancing selection, acting through the differential adaptive benefits of dichromatism (roughly equivalent to human red–green color blindness) and trichromatism (roughly equivalent to human normal color vision) [Hiwatashi et al., 2010].

Primate dichromatism is believed to be maintained due to its advantage in camouflage breaking

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and the identification of cryptic food [Mollon, 1989]. Evidence from psychophysical studies in humans [Morgan et al., 1992; Saito et al., 2006], behavioral experiments in captive primates [Caine et al., 2010; Saito et al., 2005; Smith et al., 2012], and field observations [Melin et al., 2007, 2010; Smith et al., 2012] supports this hypothesis, suggesting that dichromats can indeed break camouflage and outperform trichromats in capturing surface-dwelling insects. On the other hand, trichromatism has been suggested to be advantageous in the detection of conspicuous food [Mollon, 1989] (e.g., fruits [Sumner & Mollon, 2000] and "young" leaves [Dominy & Lucas, 2001]) against a green foliage background, and socio-sexual signaling [Changizi et al., 2006]. However, a trichromatic advantage has not yet been clearly confirmed by field observations [Dominy et al., 2003; Melin et al., 2008; Smith et al., 2003a], despite the predictions from modeling studies [De Araujo et al., 2006; Dominy & Lucas, 2001; Osorio & Vorobyev, 1996; Perini et al., 2009; Sumner & Mollon, 2000] and behavioral evidence [Caine & Mundy, 2000; Melin et al., 2013; Smith et al., 2003b]. In fact, a few studies combining visual modeling and behavioral data suggest that color may not in fact play an essential role in short distance fruit detection [Hiramatsu et al., 2008, 2009] or mate choice [Higham et al., 2010].

Predation risk is a major ecological factor driving primate evolution [Isbell, 1994; Stanford, 2002]; however, its relevance to color vision evolution and polymorphism maintenance has been untested. Indeed, no study has yet assessed the value of predator detection for the evolution of primate color vision. Two hypotheses could be drawn: first, that trichromatism should be advantageous in identifying conspicuous predators against a green foliage background, as it happens for primates of conspicuous colorations (e.g., golden lion tamarins) [Sumner & Mollon, 2003]; second, that dichromatic primates should use achromatic information (e.g., shapes, outlines, and textures) more effectively to break predator camouflage and outperform trichromats, in the same way they might do when foraging for insects [Melin et al., 2007; Smith et al., 2012]. However, given that the great majority of mammals are dichromatic [Jacobs, 2010], it is likely that mammal-eating predators have evolved a camouflaged pelage most effective in deceiving dichromatic preys. Therefore, trichromatic color vision may confer an advantage if predator pelage is russet or yellowish in color, supporting the former hypothesis.

Quantifying color information alone is not sufficient to disregard a dichromatic advantage in camouflage breaking. As might be the case for cryptic insect detection [Melin et al., 2007; Smith et al., 2012], the dichromatic visual system may benefit from the processing of achromatic cues, which is disturbed by color [Morgan et al., 1992]. Therefore, besides measuring the chromatic contrast between predator coats and foliage background, trichromats and dichromats also need to be tested in their ability to detect predators under natural (visually complex) scenarios, where both chromatic and achromatic cues are available. Since carnivorans have been the principal group of predaceous mammals throughout much of the Cenozoic Era [Meloro & Elton, 2012; Rose, 2006], here we quantify the color contrast from the coats of different New World primate carnivoran predators against the green foliage background, as well as the time required by dichromats and trichromats to identify some of these predators hidden in natural vegetation.

METHODS

Visual Modeling

Reflectance spectra measurement

Using a portable spectrometry system (Ocean Optics, Dunedin, FL, USA) to characterize the predator and natural background colors, we measured 184 reflectance spectra (29 different patches for each specimen, with exception of *Eira barbara* that had only 10 different body areas measured) from the coat of seven taxidermized carnivoran primate predators (*Leopardus colocolo*, *Leopardus pardalis*, *Leopardus tigrinus*, *Puma concolor*, *Puma yagouarundi*, *Panthera onca*, and *E. barbara*) [Calleia et al., 2009] and 100 reflectance spectra from 20 trees (five spectra from each tree: one from upper young leaf surface, one from lower young leaf surface, one from upper mature leaf surface, one from lower mature leaf surface, and one from the bark) in a gallery forest of the Gama Environmental Protection Area (15°55′S/44°53′W), Brazil. Our carnivoran specimens were taxidermized and properly stored (had not been exposed to ambient light as part of a public display) for no more than 5 years, preserving their original coloration, since time of storage is not a factor that should preclude color-based data collection on research skins [Kamilar et al., 2012]. During data acquisition, the specimens were briefly moved to a place where they could be illuminated by diffuse natural light. The spectrometer (USB2000 VIS-NIR Fibre Optic Spectrometer, Ocean Optics, Inc.) was connected to an optical fiber (R400-7-UV-VIS, Ocean Optics, Inc.) and was calibrated based on the reflection of a standard white surface (WS-1, Ocean Optics, Inc.) and by obstructing the fiber (black standard). After calibration, reflectance spectra were measured by positioning the optical fiber at 45° and 1 cm from the surface of the stimuli.

Color contrast calculation

Platyrrhini and Catarrhini color vision were modeled [Osorio & Vorobyev, 1996] based on collected reflectance spectra, yielding 18,400 pairwise color contrast comparisons (in units of just noticeable difference—JND) of the predator and background spectra for each different phenotype. Calculations also took into account the illuminant spectrum from the gallery forest, as a general descriptor of illumination conditions, and the cone sensitivity curves of 21 different primate phenotypes (Table I). The spectral peak values used for generating the cone sensitivity curves were approximations, since in literature we can find slightly different spectral peaks estimations for the same photopigments [Gegenfurtner & Sharpe, 1999; Jacobs, 2007]. Visual modeling, including derivation of cone sensitivity curves, was conducted using the R [R Development Core Team, 2013] package "pavo" [Maia et al., 2013]. In order to maintain consistency with the modeling methods of past studies [e.g., De Araujo et al., 2006; Osorio et al., 2004], and since this information is only available for a few species of non-human primates, the effects of cone optical density and filtering by macular pigment and lens [Sumner & Mollon, 2000; Wyszecki & Stiles, 2000] were disregarded. Either including or leaving these variables out of the analysis did not change the pattern of the results or the conclusions drawn.

Statistical analyses

When the color contrast between two objects (target against background) produces a value that exceeds the threshold of 1 JND (just noticeable difference), the target is to be considered detectable against the background [Sperling & Harwerth, 1971]. Furthermore, when one color contrast exceeds another in at least 1 JND unit, it can be considered perceptually higher (more contrasting) [Osorio et al., 2004]. Additionally to this qualitative interpretation of the data, we also used linear mixed models (LMM) and generalized linear mixed models (GLMM, binomial with logit link function) to test, respectively, for the differences in chromatic contrast (in log-transformed JNDs) and detectability (odds of detecting a predator against the background given its contrast, with a detection success considered when pairwise JND >1) between dichromats and trichromats accounting for the sources of non-independence (described below).

First, we compared color contrasts (in JND units) of the predator and background spectra in a model with log-transformed JND values as the response variable, and visual phenotype (dichromat or trichromat) as the predictor variable. Due to the pairwise nature of measurements, individual measurements of chromatic distance cannot be considered independent observations. Therefore, the body part of the predator was included as a random effect nested within predator species, and the background sample was included as crossed random term. In addition, since multiple dichromat and trichromat phenotypes were considered, visual phenotype was also added as a random effect, with separate levels for dichromats and trichromats. We considered a total of 21 phenotypes, 8 dichromat and 13 trichromat,

TABLE I. Phenotypes Included in Our Modeling, in the Same Order of Appearance as in Figure 3, and the Respective Taxonomic Groups in Which They Occur [According to Gegenfurtner & Sharpe, 1999; Jacobs, 2007]

Phenotype		Taxon
420/530	Dichromat	Homo
420/565	Dichromat	Homo
420/530/565	Trichromat	Homo
430/530	Dichromat	Brachyteles, Callicebus
430/536	Dichromat	Cebus/Sapajus, Callicebus, Pithecia, Samiri
430/543	Dichromat	Brachyteles, Callicebus, Callimico, Callithrix, Leontopithecus, Saguinus
430/550	Dichromat	Ateles, Cebus, Callicebus, Lagothrix, Pithecia, Saimiri
430/556	Dichromat	Callimico, Callithrix, Cebuella, Leontopithecus, Saguinus
430/562	Dichromat	Ateles, Cebus/Sapajus, Callicebus, Callimico, Callithrix, Cebuella, Lagothrix, Leontopithecus, Saguinus, Samiri, Pithecia
430/530/536	Trichromat	Cebus/Sapajus, Callicebus, Saimiri
430/536/543	Trichromat	Callicebus
430/530/543	Trichromat	Brachyteles, Callicebus
430/543/550	Trichromat	Callicebus
430/536/550	Trichromat	Cebus/Sapajus, Callicebus, Pithecia, Samiri
430/530/550	Trichromat	Callicebus
430/543/556	Trichromat	Callimico, Callithrix, Leontopithecus, Saguinus
430/556/562	Trichromat	Callimico, Callithrix, Cebuella, Leontopithecus, Saguinus
430/550/562	Trichromat	Ateles, Cebus/Sapajus, Callicebus, Lagothrix, Pithecia, Samiri
430/543/562	Trichromat	Callicebus, Callimico, Callithrix, Leontopithecus, Saguinus
430/536/562	Trichromat	Cebus/Sapajus, Callicebus, Pithecia, Samiri
430/530/562	Trichromat	Callicebus, Alouatta

representing the major phenotypes observed in humans and in New World primates (Table I).

To compare the detectability of predators we calculated the number of pairwise comparisons in which predators' color would be discernible from the background color (i.e., number of color contrasts yielding JND scores >1), which were included in a GLMM with binomial family and logit link function. The model structure was as described above, with the exception that the crossed random effect was not included, since values were grouped in successes and failures and levels were balanced within predator species.

The fixed effect was tested by dropping from the model and comparing the two nested models through Likelihood Ratio Tests. For LMMs, we computed maximum likelihood estimates to compare models, and then calculated the effect estimates from the best model using restricted maximum likelihood. For both LMM and GLMM, we also calculated marginal and conditional R^2 values of the final model [Nakagawa & Schielzeth, 2012], where the marginal R^2 corresponds to the variance explained by the fixed effect in the model (visual phenotype class—dichromat and trichromat), and the conditional R^2 corresponds to the variance explained by the full model (i.e., also accounting for the random effects of phenotypes, predator species and body patch).

Behavioral Testing

Subjects

Forty human subjects, 20 presenting normal color vision and 20 presenting severe red–green color vision deficiencies (for practical reasons, hereafter called trichromats and dichromats, respectively) were selected and diagnosed, under diffuse natural light, by the Ishihara (24 Plate edition) and the HRR (4th edition) tests, since giving both tests can be useful to provide accurate identification of red–green color deficiency [Birch, 2010]. All subjects were 18–30 years old college students that had normal or corrected visual acuity. The research adhered to the American Society of Primatologists principles for the ethical treatment of primates and complied with protocols approved by the human research ethics committee (CEP/UFRN: proc. 026/11). Informed consents were obtained from all subjects, adhering to the legal requirements of Brazilian law.

Stimuli capture and manipulation

Our stimuli were digital photographs of natural scenarios of the Gama Environmental Protection Area, in Brasilia, DF (15°55′S/44°53′W), and Dunas State Park, in Natal, RN (5°49′S/35°11′W), some of them containing a hidden artistically taxidermized carnivoran (*Leopardus* spp., *P. concolor*, or *Galictis cuja*) that were borrowed from public displays of the University of Brasilia and the Federal University of Rio Grande do Norte. We used a digital SRL camera (Canon T2i a.k.a. Canon 550D/Canon Kiss X4; Canon, Tokyo, Japan) and a Pantone ColorChecker Passport (Pantone LLC, Carlstadt, NJ, USA) to capture pictures in RAW format and standardize camera's color rendering [e.g., Bergman & Beehner, 2008; Stevens et al., 2007]. While attached to a tripod (Deluxe Tripod 200; Canon, Inc.), the camera had its temporizer set to 2 sec in order to minimize blurring caused by tremors. Pictures were captured between 9 a.m. and 3 p.m., with plenty daylight available. The camera was set to work under AV mode (automatic shutter speed) with an ISO of 100 or 200, according to light availability. We used the EF-S 18–55 mm lens (Canon, Inc.) set at 55 mm focal length (88 mm equivalent). Aperture was set to f/36 to obtain the maximum depth of field. Decrease in sharpness, due to the small aperture, was not considered critical. Using the ColorChecker Passport Camera Calibration Software (Pantone LLC, Inc.) custom DNG profiles were created. Through Adobe Camera RAW, these DNG profiles were applied to the RAW files for color adjustments. RAW adjusted photos were subsequently converted to TIFF and edited in Adobe Photoshop in order to produce final stimuli in which the predator's largest dimension would occupy <5 cm of a 22″ touch-screen monitor's surface.

Experimental procedure

Nine different sets of vegetation background photographs were presented to the subjects. Each set consisted of four photographs, one of them depicting a carnivoran in a background scenario, while the other three exhibiting the background without the carnivoran (Fig. 1). Each set was displayed twice, yielding a total of 18 trials per subject, with each photograph appearing randomly in a different position on a TouchSmart IQ510br 22″ touch-screen monitor (Hewlett-Packard Company, Palo Alto, CA, USA), color-calibrated by using a Pantone hueyPRO colorimeter (Pantone LLC, Inc.). A chin and forehead rest kept the monitor at a constant viewing distance of 40 cm from the subject. On the beginning of each trial, in order to assure that the subjects' were fixating their gaze at the center of the monitor, a gray screen with a black cross in its center was displayed, followed by a set of pictures as soon as the black cross was directly touched by the subject (Fig. 1). Subjects were asked to point, immediately upon detection, which photograph displayed a hidden animal, and had 1 min to decide before another trial started with the presentation of another gray screen. A custom software developed for the experiment controlled picture presentation and recorded subjects' responses, calculating their reaction times.

Statistical analyses

LMM for repeated measures were used to compare trichromats and dichromats with respect

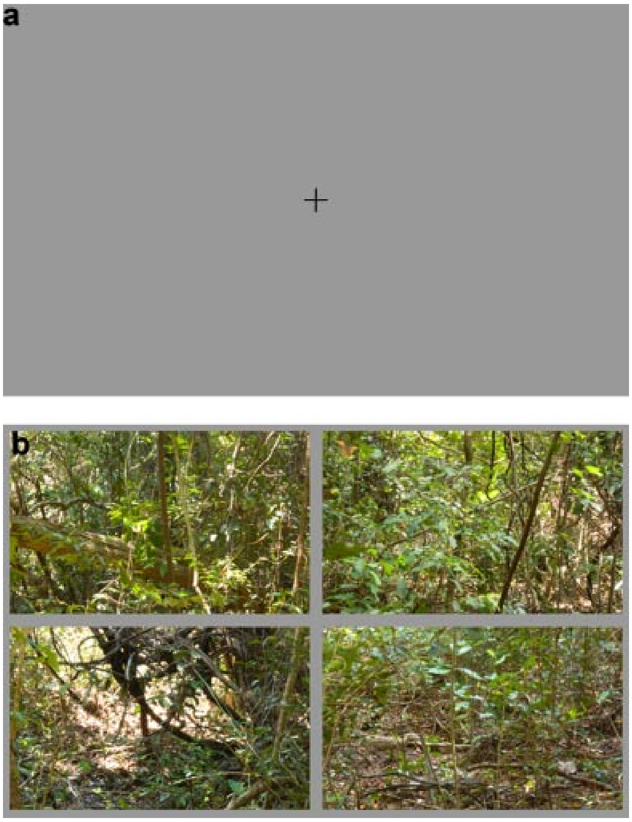

Fig. 1. Each behavioral trial began with a gray screen and was followed by a set of pictures. **a**: Gray screen with a black cross, used to assure that the subjects were fixating their gaze at the center of the monitor at the beginning of each trial. **b**: One set of picture quadruplets, in which one photograph displays a hidden animal (lower right panel) while three others exhibit only the vegetation background.

to mean log-transformed reaction times in seconds for predator detection. We considered a significance level of 5% for all tests, and all analyses were conducted using R software [R Development Core Team, 2013].

RESULTS

As predicted by our first hypothesis, human trichromats identified predators hidden in photographs of natural vegetation significantly faster (LMM: $F = 9.10$, $\mathrm{df} = 1$, $P = 0.002$) than dichromats (Fig. 2).

Using visual models to infer primate color perception, we found that predators could be contrasted from the background with respect to their coat color, so that trichromats, presenting chromatic contrast values around five units of JND, perceptually outperformed dichromats, exhibiting chromatic contrasts that fluctuated around the detection threshold of 1 JND (Fig. 3). The overall score for dichromat color contrast was statistically lower ($\chi^2 = 43.91$, $\mathrm{df} = 1$, $P < 0.001$; marginal $R^2 = 27.15\%$, conditional $R^2 = 79.94\%$) than that displayed by trichromats (Fig. 4).

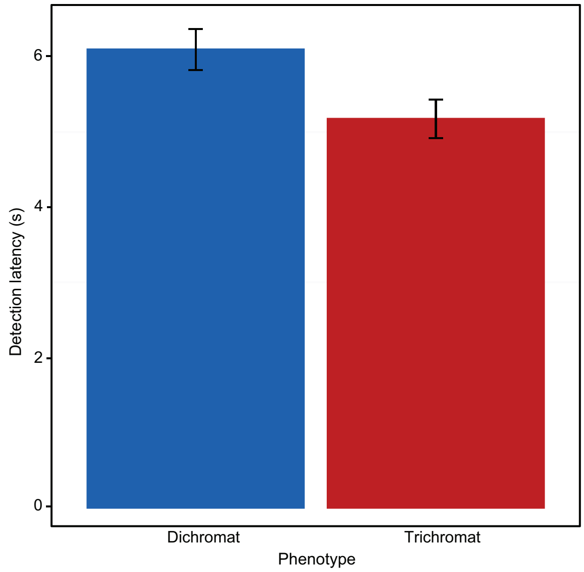

Fig. 2. Behavioral evidence supports the trichromatic advantage in predator detection. Mean reaction time (latency) in seconds for carnivoran detection is lower for human trichromats than for dichromats. Error bars indicate the standard error of the mean.

As a consequence, the odds of detecting predator coats against a natural background were 21.71 times greater for trichromats than dichromats (odds ratio; GLMM: $\chi^2 = 40.12$, $\mathrm{df} = 1$, $P < 0.001$, marginal

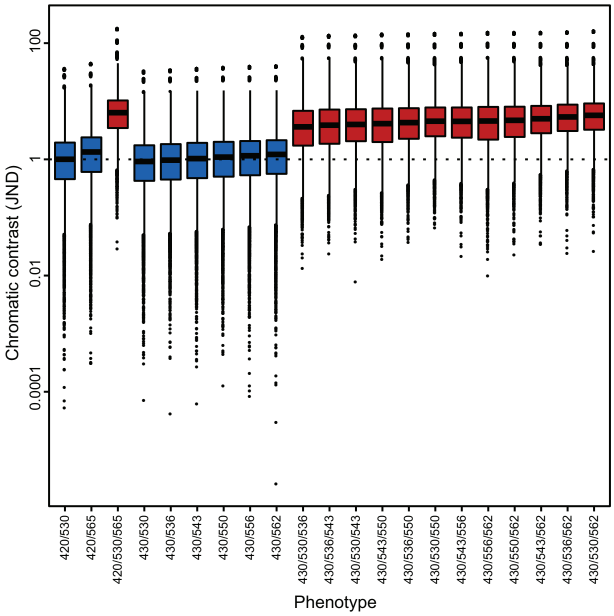

Fig. 3. Modeled chromatic contrasts between the coats of carnivoran predators and foliage background show a trichromatic perceptual advantage. Dichromatic and trichromatic phenotypes are represented in blue and red, respectively. Dotted line indicates the perceptual threshold of 1 JND (just noticeable difference). *Y*-axis is presented in log-scale; black dots denote values that fall outside the 75% central range.

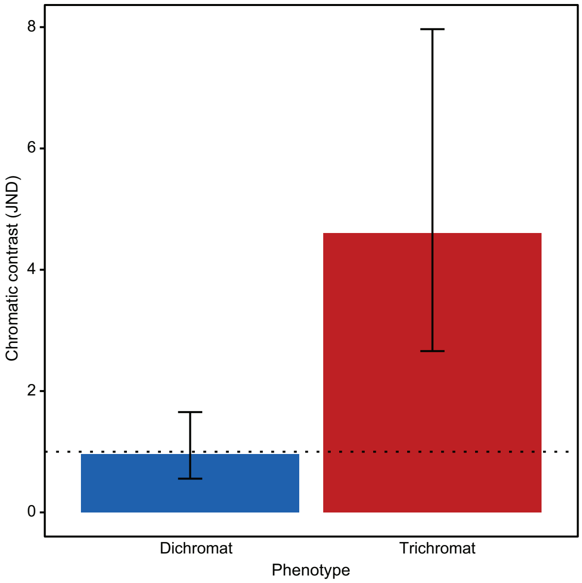

Fig. 4. Dichromatic general scores for color contrast are statistically lower than trichromatic scores. Dotted line indicates the perceptual threshold of 1 JND (just noticeable difference). Error bars represent 95% confidence intervals.

$R^2 = 29.35\%$, conditional $R^2 = 57.07\%$). While trichromats had a near absolute probability of detecting a predator based on color contrast (odds: 0.96; 95% confidence intervals—CI: 0.90–0.99), dichromats faired much worse, with detection chances of around 50% (odds: 0.54; 95% CI: 0.30–0.76) (Fig. 5).

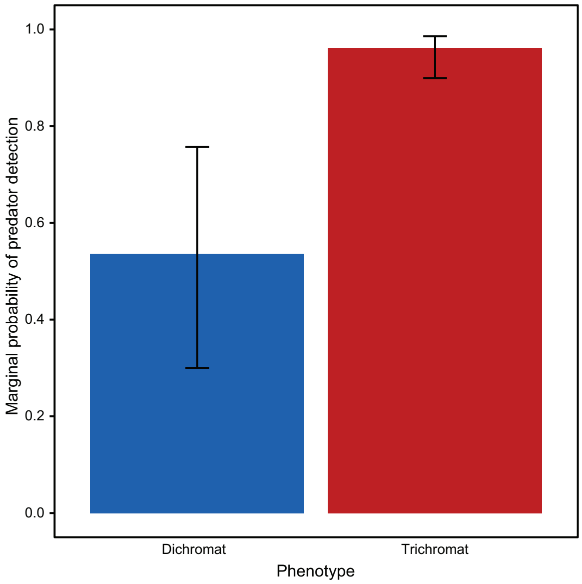

Fig. 5. Trichromats show a higher predator detectability, based on the number of pairwise comparisons in which predators' color would be discernible from the background' color (i.e., number of color contrasts yielding JND scores >1). Error bars represent 95% confidence intervals.

DISCUSSION

Our conclusion that trichromats were better suited than dichromats in identifying carnivoran predators against background vegetation was replicated for the visual system of humans, an Old World primate (Catarrhini), and all New World primates (Platyrrhini) that were already scrutinized with respect to their color vision, which is a strong indication that our finding stands as a general trend for anthropoid color vision. The fact that the chromatic contrast between the predators' yellowish coats and the greenish background were statistically and perceptually higher for trichromats gives support to the hypothesis that trichromatism should be advantageous in identifying conspicuous predators. Our behavioral evidence, on the other hand, does not support the hypothesis that dichromatic primates should be advantageous in using achromatic information to break predator camouflage.

In primatological literature, predation risk and diet are often associated with body size [Fleagle, 1998; Stanford, 2002; Terborgh, 1983], since smaller primates include more insects and less leaves into their diets and suffer a higher predation pressure [Fleagle, 1998; Isbell, 1994; Stanford, 2002]. Here, we argue that these two selective pressures will likely interact to explain the distribution of color vision among anthropoid primates, which would benefit from both the trichromatic advantages for predator detection, as supported by our results, and the dichromatic advantages for cryptic insect foraging, suggested by other studies [Melin et al., 2007; Smith et al., 2012].

For instance, dichromatism would not have been strongly selected in Catarrhini, since insects may have never comprised an important food source for the more heavily bodied and terrestrial Old World primate ancestors from the Miocene [Fleagle, 1998]. In addition, since the early radiation of felids (the most important mammalian taxa of primate predators [Calleia et al., 2009; Meloro & Elton, 2012]) took place in the Old World and did not reach North America until well into the Miocene [Meloro & Elton, 2012; Rose, 2006], catarrines may have been consistently exposed to a considerable predation risk [Isbell, 1994; Meloro & Elton, 2012; Stanford, 2002] favoring the maintenance of the large body sizes and trichromatism found in extant species.

The picture for platyrrhines is considerably more variable and complex. In the New World, 10 genera of small-sized primates (weighting less than 4 kg) rely on fruits and insects [Fleagle, 1998] and, with exception of genus *Aotus* (which are monocromats and thus cannot see colors), all present polymorphic color vision [Jacobs, 2007]. *Aotus* monochromatism may be explained by a reduced benefit of color vision related to a decrease in predation risk owing to its nocturnal niche [Stanford, 2002; Wright, 1989]. In contrast, heavier platyrrhines (weighting more than 5 kg) are unable to include substantial amounts of insects in their diets [Fleagle, 1998; Terborgh, 1983] and, consequently, would not be selected for dichromatism. Thus, these medium- and large-sized primates should be expected to carry a routine trichromatism, similar to that found in catarrhines. Indeed, *Alouatta* (howler monkeys), which are medium-sized sluggish vegetarian atelids [Terborgh, 1983] and thus subjected to considerable predation risk [Calleia et al., 2009; Terborgh, 1983], is known to be routinely trichromatic [Jacobs et al., 1996]. However, contrary to predicted, larger atelids [*Ateles* (spider monkeys), *Brachyteles* (woolly spider monkeys), and *Lagothrix* (woolly monkeys)] are polymorphic, presenting dichromatic individuals in their populations [Jacobs, 2007]. Only a few large-sized felids (e.g., *Panthera* and *Puma*), whose populations tend to be highly dispersed [Terborgh, 1983], may, eventually, capture these heavier primates [Calleia et al., 2009; Terborgh, 1983]. Therefore, we suggest that a relatively low predation risk and a constraint in exploiting insects as a main food source, found in larger platyrrhines, may have weaken the selective pressures for trichromatism and dichromatism, respectively. As a result, the visual polymorphism of larger atelids could simply reflect the maintenance of a primitive state found in ancestral platyrrhines [Heesy & Ross, 2001], which were small bodied and relied mostly on insects and fruits [Fleagle, 1998].

If our suggestions are correct, it would be reasonable to predict that, owing to different degrees in predation risk, *Callicebus* (titi monkeys) and larger atelids should show a, respectively, higher and lower tendency in having trichromatic individuals in their populations, when compared to most New World primates. *Callicebus* are small neotropical primates that do not use any of the three major strategies employed by other primates to thwart predation (development of large bodies, crypticity and formation of large groups) [Terborgh, 1983]. For this reason, *Callicebus* predation risk must be disproportionally high, compelling them to spend much of their time sitting beneath umbrella-like canopies of vines or inside densely foliated trees [Terborgh, 1983] and to make use of a very complex alarm call system [Cäsar et al., 2013] in order to avoid predators. Remarkably, while *Callicebus* has five different alleles that express photopigments with maximum sensitivity on the green–red spectral range [Jacobs, 2007], allowing them to increase the proportion of trichromatic females in their populations to 80%, each species of *Ateles*, *Brachyteles*, and *Lagothrix* has been found to have only two alleles [Jacobs, 2007; Talebi et al., 2006], which could reduce the frequency of trichromatic females to 50%. Thus, the variation of color vision found in anthropoid primates seems to be in consonance with our results, and may be explained by the selective advantages of trichromats and dichromats in detecting predators and insects, respectively.

To our knowledge, this is the first work to examine the adaptive value of primate color vision for predator detection. We found strong evidence supporting that trichromatism should be advantageous in identifying conspicuous mammalian predators against a green foliage background, while rejecting the hypothesis that dichromatism should break predator camouflage more effectively and outperform trichromats. Given that carnivoran predators have likely been selected for camouflage specialized in deceiving dichromatic preys, such as most mammals [Jacobs, 2010], it is thus intuitive that trichromatism may have provided primate species a selective advantage in predator avoidance. Future work exploring the differential benefits of primate color vision phenotypes in detecting other predators, such as snakes and raptors, should reveal if the adaptive value presented here applies to all classes of predators. Additionally, since primate hair color diversity might also be related to camouflage [Kamilar et al., 2012], visual modeling studies, examining how predators would detect primates against their natural background, should be also encouraged, especially in species in which infants have a more conspicuous coat than adults [Sumner & Mollon, 2003]. Given that predation events and predator encounters are rare and challenging to observe in the field, further naturalistic experiments, as well as comparative studies, should provide promising alternatives to elucidate the origin and maintenance of trichromatism in primates.

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