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Visual detection and fruit selection by the mantled howler monkey (*Alouatta palliata*)

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Abstract

Howler monkeys (platyrrhini) have evolved routine trichromatic color vision independently from catarrhines, which presents an opportunity to test hypotheses concerning the adaptive value of distinguishing reddish from greenish hues. A longstanding hypothesis posits that trichromacy aids in the efficient detection of reddish-ripe fruits, which could be an advantage for the detection of the nutritional content of the fruit, such as sugars. In the present study, we assessed fruit visual conspicuity and selection based on color and sucrose content by wild mantled howler monkeys (*Alouatta palliata*) on Agaltepec Island, Mexico. We used colorimetry to classify dietary fruits as cryptic (greenish) or conspicuous (reddish) against their background leaves. Species-specific color models indicate that trichromatic howler monkeys should be more efficient in discriminating the conspicuous ripe fruits from leaves compared to detecting cryptic ripe fruits from leaves. We found howler monkeys consume more cryptic fruits compared to conspicuous fruits, and that they consume more unripe fruits than ripe fruits. The consumption (acceptance) of fruit was independent of sucrose content, and thus this disaccharide may not play an essential role in mantled howler food selection. Our findings suggest that routine trichromatic color vision may aid in the detection and discrimination of conspicuously colored fruits, but that the final decision whether to accept or reject a fruit probably involves the use of other senses in addition to vision.

KEYWORDS

Alouatta, food selection, frugivory, sucrose, trichromacy

1 | INTRODUCTION

Primate visual systems are unique among mammals and the selective pressures underlying the emergence of red-green color vision have been subject to intense debate and study (Dominy & Lucas, 2004; Kawamura et al., 2012; Melin et al., 2017; Pessoa et al., 2014; Sumner & Mollon, 2000a, 2000b). Inter- and intraspecific variation in opsin genes underlies the diversity of primate color vision within and between species (Hunt, Carvalho, Cowing, & Davies, 2009; Jacobs, 2008; Kaas, 2010). Remarkably, platyrrhines and lemurs possess a polymorphic visual system due to allelic variation of a single opsin gene sensitive to medium-wavelength (MWS) to long-wavelength (LWS), such that all males and some homozygous females are dichromatic whereas heterozygous females have a trichromatic vision (Jacobs, 2007; Jacobs et al., 2017; Kawamura et al., 2012; Surridge, Osorio, & Mundy, 2003).

In contrast, African and Asian monkeys and apes, as well as humans (catarrhines), display routine trichromacy, which is due to duplication of the opsin gene sensitive to LWS. This duplication occurred in the ancestor of the catarrhines and resulted in two types of opsin genes L (red) and M (green), which are adjacent to each other on the X chromosome (Bowmaker, Astell, Hurst, & Mollon, 1991;

Jacobs & Deegan, 1999; Surridge et al., 2003). Duplication of the LWS opsin gene evolved independently in *Alouatta*, the only genus of platyrrhine monkey to possess uniform trichromacy (Hunt et al., 2009; Jacobs, 1996; Silveria et al., 2014; Surridge et al., 2003). In each of the major radiations of primates, a third short-wavelength sensitive (SWS) autosomal opsin gene facilitates the perception of blue light. As a consequence, trichromatic primates can distinguish shades in the red-green (RG) range of the visible spectrum, in addition to shades through the yellow-blue ancestral axis (YB; Hiwatashi et al., 2010; Jacobs, 1996).

The debate surrounding selective pressures favoring routine and polymorphic trichromacy has received much attention and has centered on foraging-related challenges (Melin et al., 2009; Melin et al., 2016; Smith, Buchanan-Smith, Surridge, Osorio, & Mundy, 2003; Veilleux et al., 2016). Trichromatic vision is hypothesized to provide an advantage in the detection of foods such as young red leaves (Dominy & Lucas, 2004; Lucas, Darvell, Lee, Yuen, & Choong, 1998) and ripe fruits (Regan et al., 2001; Riba-Hernández, Stoner, & Lucas, 2005). In many fruits, the color changes are an indicator of maturation (Osorio & Fernie, 2013; Reid, 2002); however, some fruits are chromatically similar to the greenish background provided by leaves throughout their ripening process (Regan et al., 2001). Consequently, one of the challenges for primates is the detection and selection of nonconspicuous fruits in an arboreal environment of brown and green tones, where the ambient luminosity varies widely (Regan et al., 1998), in addition to efficient discrimination of the ripe from the unripe fruits. Trichromatic color vision is posited to have been favored for these challenges (Smith et al., 2003).

Studies on fruit selection in non-human primates suggest that trichromatic primates are more efficient in the detection of conspicuous foods compared to dichromatic primates (Dominy & Lucas, 2004; Regan et al., 2001, 1998; Sumner & Mollon, 2000a, 2000b). For example, trichromatic individuals of the genera *Callithrix* and *Saguinus* were more efficient in locating conspicuous orange, ripe fruits against a greenish background compared to dichromatic individuals (Caine & Mundy, 2000; Smith et al., 2003). However, it has been proposed that trichromatic primates are less efficient in the detection of cryptic fruit colors (green, brown) compared to conspicuous fruit colors (yellow, orange, or red) against a greenish background (Caine & Mundy, 2000; Dominy & Lucas, 2001; Smith et al., 2003). Similarly, both trichromatic and dichromatic primates have been reported to prefer conspicuous fruits over cryptic fruits (Gautier-Hion et al., 1985; Julliot, 1996; Melin et al., 2009; Regan et al., 1998; Sumner & Mollon, 2000a).

Finally, recent studies reported that routinely trichromatic mantled howler monkeys (*Alouatta palliata*) should have an advantage in the detection of reddish young leaves, which are important in their diets, against a green background. Advantages for both fruits and leaves may have led to stronger selection and routine trichromacy in *Alouatta* (Melin et al., 2017) relative to other platyrrhine monkeys. There is a lack of information about whether the trichromacy of howler monkeys is also efficient in the detection of conspicuous fruits compared to cryptic fruits (Regan et al., 1998). However, in the few studies to date, Julliot (1996) and Martins (2008) found that red howler monkeys (*A. seniculus*) and brown howlers (*A. guariba*) selected red, orange, and yellow fruits at higher percentages relative to greenish ones.

Color changes that occur with ripening are likely to be related to internal changes such as the nutritional and energy content (Dominy, 2004a; Gautier-Hion et al., 1985; Willson & Whelan, 1990). Sugar is an important nutrient for primates and thought to be a key reward from fruits (Felton, Felton, Raubenheimer, & Foley, 2009). For example, in fruits selected by the spider monkey (*Ateles geoffroyi*), there is an increase in sucrose in those plant species that have fruit with one or more color changes during the ripening process, so that the color may be a potential indicator of sugar content (Pablo-Rodríguez, Hernández-Salazar, Aureli, & Schaffner, 2015). However, for howler monkeys, less is known. Though howlers can subsist on a leaf-based diet and are the most folivorous platyrrhine primates, they also eat ripe fruit when it is available and gain energy from sugars. Interestingly, large quantities of simple sugars might be unhealthy for howler monkeys due to a decrease in digesta retention times (Espinosa-Gómez, Gómez-Rosales, Wallis, Canales-Espinosa, & Hernández-Salazar, 2013; Milton, 1980) and potentially affect the acquisition of other nutrients. There is a shortage of information on howler monkey fruit selection and the role of sugars. It has been reported that fruits that change to conspicuous colors have higher sugar content compared to cryptic fruits (Pablo-Rodríguez et al., 2015; Sourd & Gautier-Hion, 1986), but data are very sparse.

The detection and selection of fruit by howler monkeys is poorly known overall, but important for assessing competing hypotheses of color vision evolution. We, therefore, ask the following questions: (a) Are the cryptic and conspicuous ripe fruits distinct from background leaves in wavelengths that are visible to mantled howler monkeys? Because the trichromacy hypothesis supports the efficiency in detecting reddish colorations, we suggest that conspicuously colored fruits would be visible for the trichromatic howler monkey compared to cryptic fruits, which are similar in color to background leaves; (b) Does the visual performance of mantled howler monkey color vision, as estimated through visual models, differ between predicted cryptic and conspicuous ripe fruits compared to unripe fruits? We expected that trichromacy in mantled howler monkeys would be more efficient in the detection of conspicuous ripe fruits compared to cryptic ripe fruits; (c) Is the acceptance, versus rejection, of conspicuous and cryptic ripe fruits associated with their sucrose content? We predicted that the sucrose content of the fruits would be correlated with their rate of acceptance (consumption).

2 | METHODS

2.1 | Ethics statement

Our study was noninvasive, and field observations adhered to the American Society of Primatologists' Principles for the Ethical

Treatment of Non-Human Primates and to the Code for the Best Practices in Field Primatology. The research protocol was approved by the Mexican Secretaría de Medio Ambiente y Recursos Naturales (No. 09/GS-2132/05/10) and the NOM-059-SEMARNAT-2010.

2.2 | Study site and subjects

Fieldwork was carried out on Agaltepec Island (18°27′–18°28′N and 95°02′–95°03′W) located in Lake Catemaco, Veracruz, Mexico. The island has an area of 8.3 ha and includes flora of four types of vegetation: Medium subdeciduous forest, riparian vegetation, secondary vegetation, and grassland area (López-Galindo & Acosta-Pérez, 1998; Rodríguez-Luna, Domínguez-Domínguez, Morales-Mávil, & Martínez-Morales, 2003). The climate of the region is warm-humid, with an annual rainfall of 1,980 mm. The dry season covers the months of March to May and the wet season June to February (Soto & Gama, 1997). Nine female and 11 male adult mantled howler monkeys (*A. palliata*) were observed ($N = 20$). We identified all monkeys individually through fur spots and scars.

2.3 | Behavioral data collection

We collected data on fruit-feeding behavior between March 2017 and January 2018. We performed observations 4 days/week for 5 hr a day, adopting an alternating schedule (07:00 a.m.–12.00 noon or 12.00 noon–05:00 p.m.). We used a rotating focal-animal sampling of 10 min (Altmann, 1974). In total, we collected behavioral data during 135.8 hr, with a mean of 6.79 ± 0.7 hr per individual. When an animal selected a fruit, we recorded the acceptance (consumption) or rejection of the food item and the corresponding plant species. We distinguished between ripe and unripe for each of the fruits consumed by the focal monkey based on observations through binoculars of fruit color and size. For the fruits that did not noticeably change color with ripening, we used only fruit size to distinguish between ripe and unripe fruits. We made these categorizations subjectively and verified them with spectral reflectance data and sucrose content on representative subsets of fruits observed.

We defined acceptance as an animal consuming at least 75% of a given fruit (Pablo-Rodríguez et al., 2015). We categorized fruits as *cryptic*, those that showed no noticeable color changes during their maturation, and were chromatically similar to the leaves. *Conspicuous* fruits were classified as those that presented yellow, red, or orange shades when ripe (Dominy, 2004a; Gautier-Hion et al., 1985; Melin et al., 2009; Pablo-Rodríguez et al., 2015; Regan et al., 2001; Riba-Hernández et al., 2005).

2.4 | Collection of fruits

Once per week, after having completed the behavioral observations, we collected five ripe and five unripe fruits from each of the six plant species that howlers consumed during our study (Table 1). We chose fruits with similar characteristics to those recorded during behavioral sampling. To validate our categorization as cryptic or conspicuous and as ripe or unripe, we measured the color (reflectance spectra) of fruits using a spectrometer (USB Ocean Optics®) and their sucrose content using a refractometer (Atago®, Automatic Brix 0.0–33.0%; Kitamura, Yumoto, Poonswad, Chuailua, & Plongmai, 2004; Pablo-Rodríguez et al., 2015). We used sucrose as the carbohydrate that might offer a cue about the ripeness and value of the fruit, as it is simple to measure in the field and this sugar has been proposed a criterion for the selection of food in other primate

TABLE 1 Description of fruit species consumed by mantled howler monkeys in Agaltepec Island

Species	Description	Category
Sideroxylon capiri	Medium to large tree, which reaches 35 m in height, the fruits are 3–4-cm long, smooth-looking berries that contain a 2.0–2.5-cm brown seed (García & Di Stefano, 2005).	Cryptic; coloration of green to greenish-yellow in its state of maturity.
Spondias mombin	A medium-sized tree, which reaches 20 m in height, fleshy drupe-like fruit 3–4-cm long, contains a 2.5-cm long nugget with multiple seeds. Fruit from July to October (Penningtón & Sarukhán, 2005).	Conspicuous; it changes from green to yellow-green, going through yellow and finally orange when ripe.
Ficus insipida	Evergreen tree, 4–20-m tall, spherical cones with a diameter of 15–25 mm and 15–30-mm long (Durán-Ramírez, Fonseca-Juarez, & Ibarra-Manríquez, 2010).	Cryptic; green in its mature stage.
Ficus maxima	Evergreen tree, 7–18-m tall, with spherical cones of 10–30 mm. Fruits from March to November (Durán-Ramírez, Fonseca-Juarez, & Ibarra-Manríquez, 2010).	Cryptic; green in its mature stage.
Chlorophora tinctoria	Tree, 10–30-m tall, with a wide and dense canopy. Irregularly shaped fruit, 1.2–1.8 cm in diameter, with fleshy and edible pulp. Fruits between May and September (Niembro, 1983).	Cryptic; greenish-yellow in its mature stage.
Ficus lundelli	Tree, 20-m tall and evergreen, with cones 6–15 mm in diameter (Durán-Ramírez et al., 2010).	Conspicuous; it changes from green to red when ripe.

species (Laska, 1996; Laska, Carrera-Sánchez, Rodríguez-Rivera, & Rodríguez-Luna, 1996; Laska, Scheuber, Carrera-Sánchez, & Rodríguez-Luna, 1999). We individually packed fruits in airtight bags and carried inside coolers with freezer gel packs and transported to the laboratory (INBIOTECA) of the Universidad Veracruzana for color analysis, described below. Five extra samples of fruits were selected for each species to determine their sucrose content fruits.

2.5 | Spectral reflectance data

We measured the reflectance spectra of fruits from the six dietary plant species in ripe and unripe stages (Table 1). We additionally measured the reflectance spectra of the upper surfaces of five mature leaves from each plant species to quantify the background color and color contrast against the fruit. We used a spectrometer with illumination provided by a pulsed xenon lamp (PX-2), which illuminates across a wavelength range of 200–850 nm (Ocean Optics®). To calibrate the spectrometer before each session of measurements, we used a white reflectance standard (WS-1 Ocean Optics®) and we recorded a dark spectrum with each session (Software SpectraSuite 2.0.162; Hiramatsu et al., 2008; Lucas et al., 2001; Riba-Hernández, Stoner, & Osorio, 2004). All color measurements were made in a dark room to minimize external light interference.

2.6 | Fruit chromaticity plots

We calculated the average reflectance of the cryptic and the conspicuous fruits (both in ripe and unripe states) and of the leaves as the substrate, delimiting the values obtained in the ranges of 400–700 nm. The chromaticity diagrams represent the mean and standard deviation of the peak reflectance values of the surfaces of each item (ripe fruit, unripe fruit, and leaf). The peak sensitivity values ($\lambda_{\max}$) used for the MWS (532 nm) and LWS (564 nm) photopigments were based on sensitivity curves for the opsins of mantled howler monkeys (Matsushita, Oota, Welker, Pavelka, & Kawamura, 2014). For the SWS photopigment of mantled howler monkeys, we used the value of 435 nm, which is intermediate to the estimated values for *Ateles* (432 nm) and *Lagothrix* (437 nm), which are the most closely related taxa (Jacobs & Deegan, 2001).

To evaluate the chromaticity of ripe fruits (target) against unripe fruits and against leaves, respectively, we calculated the chromatic distance between the target and the background along the RG (L/[M+L]) and YB (S/[M+L]) chromatic axes, displayed in two-dimensional chromaticity graphs. We calculated luminance to take into account the achromatic aspects of color (log [M+L]). In our models, we used a representative external illumination (irradiance) value measured in the dry tropical forest of the Santa Rosa Sector “Guanacaste Conservation Area”, in northwest Costa Rica (10°45′–11°00′N y 85°30′–85°45′W). The measurement was performed on a cloudy day using a spectrophotometer (USB 2000) with a cosine corrector (Melin et al., 2017). This area is home to three species of primates, including mantled howler monkey populations (*A. palliata*).

We predicted the discrimination of ripe fruits (target) against unripe fruits and leaves, respectively, using “just noticeable difference” (JND) units, where 1 JND is the minimum predicted threshold at which a viewer can detect a target against a background. When the difference between the spectrum of ripe fruits exceeds 1 JND the fruit is considered to be detectable from leaves and unripe fruits. Discriminability is predicted to increase with increasing JND. This model offers a clear criterion to measure the performance of color vision near the threshold (Osorio & Vorobyev, 1996; Osorio, Smith, Vorobyev, & Buchanan-Smith, 2004; Wyszecki & Stiles, 1982). We based our value of 1 JND on data from humans tested under laboratory conditions (Sperling & Harwerth, 1971), and the assumption is that the value is also significant for other primates with trichromatic color vision, such as mantled howler monkeys (Jacobs, 2007; Muniz, de Athaide, Gomes, Finlay, & Silveira, 2014).

2.7 | Statistical analysis

We used a mixed generalized linear model (GLMM) with binomial distribution to analyze the acceptance or rejection of dietary fruits. We run a separate model for each fruit species, and we included the identity of the monkey as a random factor (Zuur, Ieno, Walker, Saveliev & Smith, 2009). We included fixed effects as (a) the concentration of sucrose, (b) the maturity of the fruit (ripe and unripe), and (c) gender of the individual. GLMMs were performed in the R software Version 3.6.0 using the package lme4 (R Core Team, 2019; Bates, Maechler, Bolker, & Walker, 2015).

We used a Student's *t* test for comparing sucrose concentrations between (a) ripe and unripe cryptic fruits and (b) ripe and unripe conspicuous fruits. For data that were not normally distributed according to a Kolmogorov–Smirnov Test, we performed a Mann–Whitney *U* test. For species (*Ficus maxima*, *Ficus insipida*, *Chlorophora tinctoria*, and *Sideroxylon capiri*) fruits not changed color—green. One species (*Ficus lundelli*) changed color from green to red and finally, one species (*Spondias mombin*) changed color twice: Green to yellow to orange. We used analysis of variance for *S. mombin*, which fruits changed color twice. We used Tukey's test to differences between the green-, yellow-, and orange-colored fruits.

3 | RESULTS

3.1 | Are the cryptic and conspicuous ripe fruits distinct from background leaves?

Cryptic fruits (*S. capiri*, *C. tinctoria*, *F. maxima*, and *F. insipida*) showed reflectance peaks around 550 nm for both ripe and unripe fruits, which is similar to the peak reflectance of leaves (Figure 1a–d). However, in both ripe and unripe stages, cryptic fruits reflected a broader range of longer wavelengths (wider breadth of the

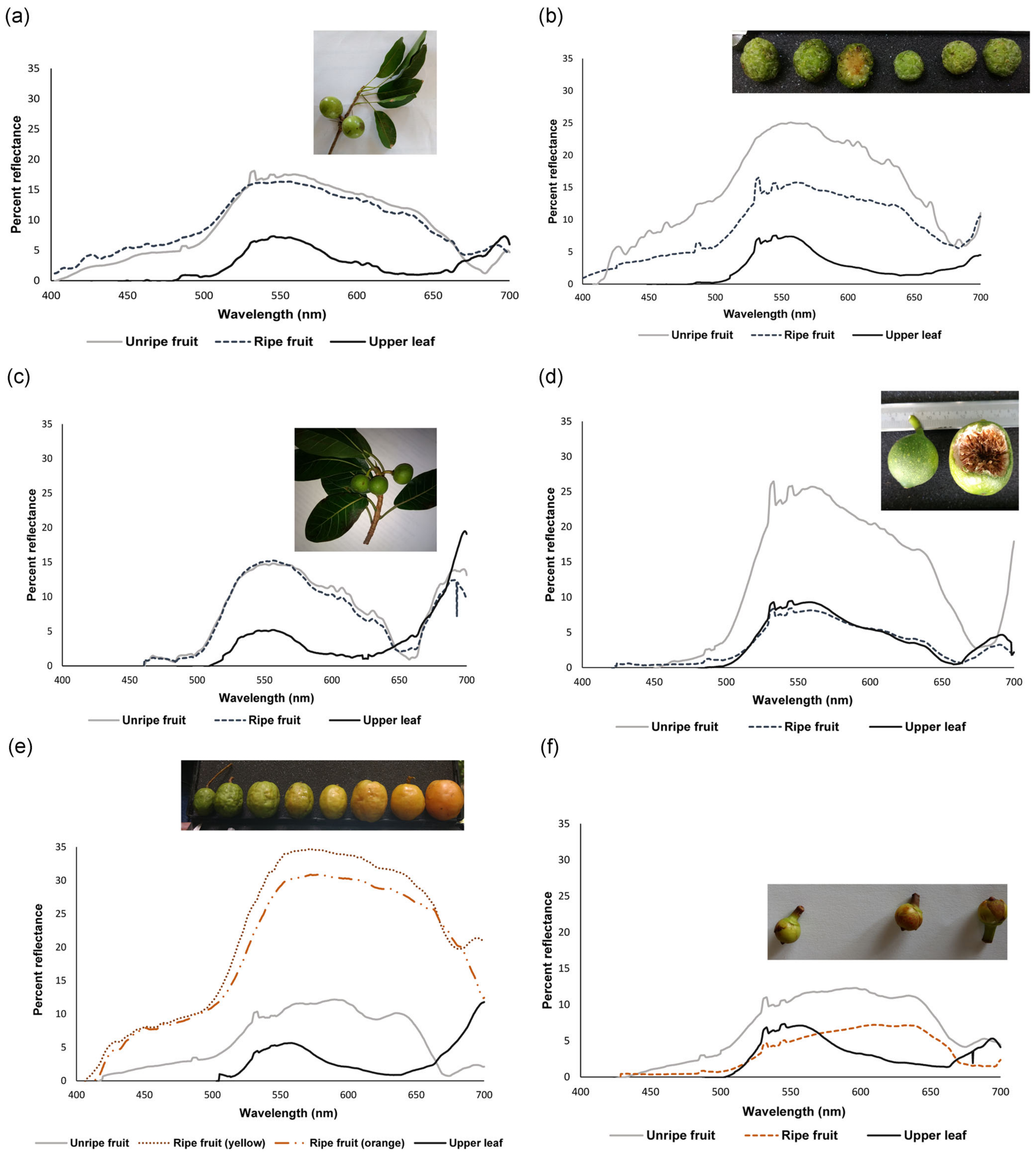

FIGURE 1 Mean reflectance spectra of ripe fruits, unripe fruits and leaves (background) along the visible spectrum (400–700 nm) of (a) *Sideroxylon capiri*, (b) *Chlorophora tinctoria*, (c) *Ficus maxima*, (d) *Ficus insipida*, (e) *Spondias mombin*, and (f) *Ficus lundelli*. *N* = 5 per species

reflectance spectra) compared to leaves. The peak reflectance of conspicuous fruits was clearly long-wavelength-shifted compared to unripe fruits and leaves, typically between 550 and 650 nm (Figure 1e,f). The ripe fruits that changed color with ripening to be more yellowish/orangish compared to the unripe fruits and leaves to the human eyes showed a λ_{max} value at about 570 nm. Ripe fruits that change in color from green to red (i.e., *F. lundelli*) had λ_{max} values around 640 nm (Figure 1f).

We present the reflectance values of the surfaces of the fruits of each plant species, as well as of the surface of the leaves using the

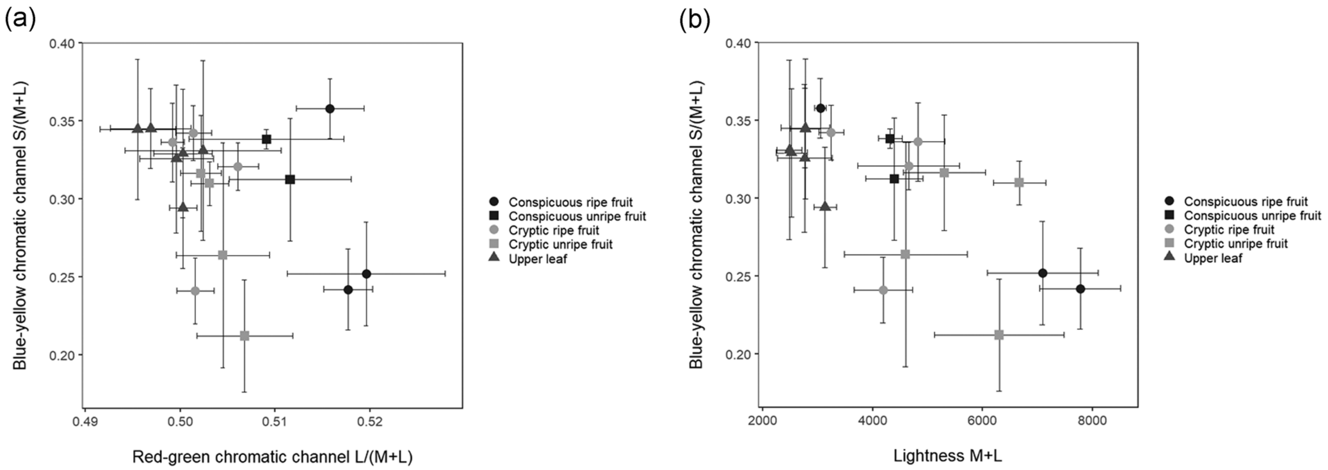

FIGURE 2 Chromaticity of the surfaces of fruits and leaves (greenish background) of six fruits species consumed by the mantled howler monkeys. (a) The *X*-axis represents the green-red chromatic channel (L/[M+L]) and the *Y*-axis represents the yellow-blue chromatic channel (YB; S/[M+L]) for howler monkeys trichromacy. Higher values on the green-red chromatic axis indicate redder colorations. Higher values on the YB chromatic axis indicate blue colorations; (b) luminance values (*X*-axis; log [L+M]) as a function of the YB chromatic axis (*Y*-axis). Each point represents the average of five fruits (ripe and unripe) of conspicuous species *(Spondias mombin* and *Ficus lundelli)*, and cryptic species *(Sideroxylon capiri*, *Chlorophora tinctoria*, *Ficus maxima*, and *Ficus insipida*), as well as the leaf surfaces (greenish background)

chromaticity plots (Figure 2a,b). The distance between two points across the *X*-axis represents the extent to which they differ from each other through the RG chromatic channel. The distance between points along the *Y*-axis represents the variation in the YB color channel. We found that ripe fruits of the conspicuous *S. mombin* and *F. lundelli* species were chromatically distant from the unripe fruits and the leaves along the RG axis. The ripe and unripe fruits of the cryptic fruits (*S. capiri*, *C. tinctoria*, *F. maxima*, and *F. insipida*) were chromatically similar to leaves (greenish background; Figure 2a). In the YB axis, all the cryptic and the conspicuous fruit species were not chromatically separated from leaves or along the luminance axis (Figure 2b).

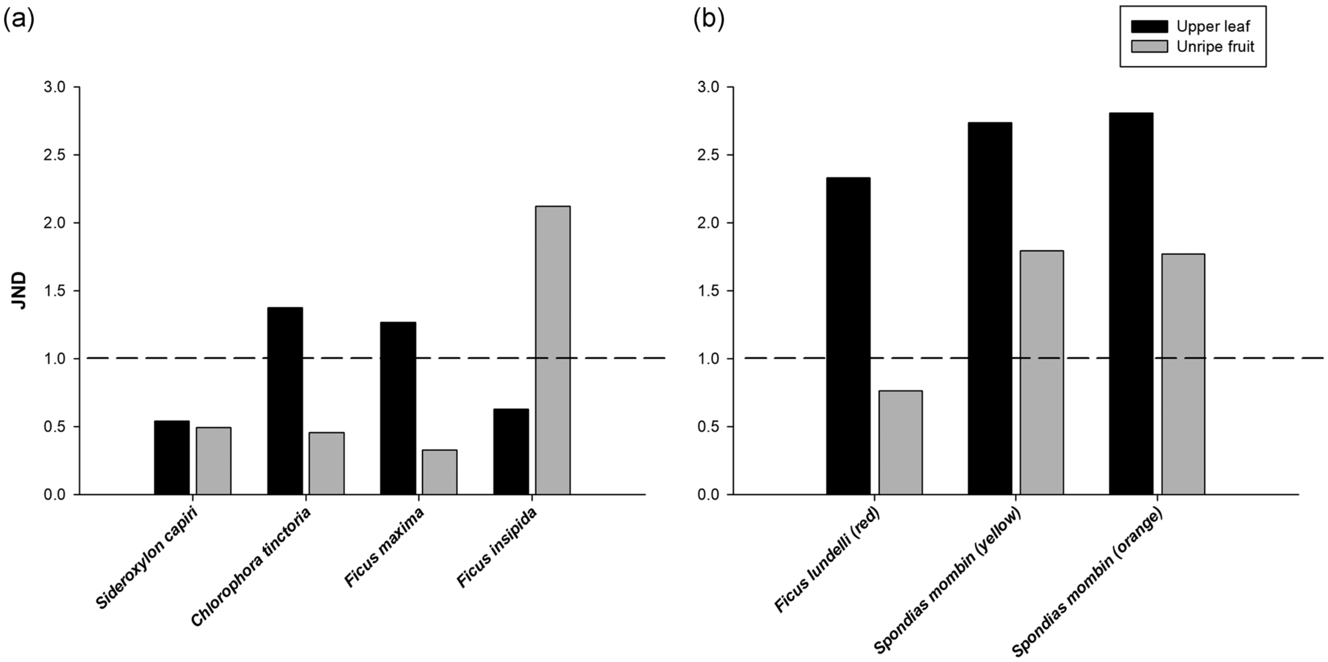

FIGURE 3 Just noticeable difference (JND) analysis for ripe fruits observed against the greenish background (black bar) and unripe fruits (gray bar) in (a) cryptic species and (b) conspicuous species. Ripe fruits of species with <1 JND value (represented by a dotted line in both figures) are not predicted to be chromatically distinguishable from the background to howlers

3.2 | Does the visual performance of mantled howler monkeys, estimated through visual models, differ between cryptic and conspicuous ripe fruits compared to unripe fruits?

Our analysis of chromatic differences between the ripe fruits and unripe fruits and leaves, respectively, showed that the cryptic fruits of the species *C. tinctoria* and *F. maxima*, had values >1 JND with respect to the greenish background. Ripe fruits are detectable against the leaves, although they are not modeled to be chromatically distinguishable from unripe fruits. In the case of *F. insipida*, we recorded a value >1 JND for the unripe fruit, whereas the species *S. capiri*, was the only one that showed values <1 JND for the greenish background and the unripe fruit (Figure 3a).

For conspicuous fruits (yellow and orange colors), the species *S. mombin* presented values >1 JND. For ripe fruits of the *F. lundelli* (red color) a value >1 JND was found for the greenish background, whereas there was a value <1 JND for unripe fruits (Figure 3b).

3.3 | Is the acceptance, versus rejection, of conspicuous and cryptic ripe fruits associated with their sucrose content?

Sucrose content was significantly higher in ripe fruits compared to unripe fruits, except for the *F. insipida* species. We obtained for *S. mombin*, which showed color changes from green (unripe fruits), to yellow and orange (ripe fruits), significant differences in sucrose content between all the color stages. The post hoc Tukey's test showed significant differences between green and yellow, green and orange, and yellow and orange fruits (Table 2).

We found a significantly higher consumption (acceptance) of cryptic fruits (mean percentage of acceptance 86.7% ± standard deviation 0.8%) compared to the acceptance of conspicuous fruits (mean percentage of acceptance 73.3% ± 1.2%; $\chi^2 = 4.29$, $df = 1$, $p < .05$). We also found that unripe fruits acceptance was significantly higher (mean percentage of acceptance 85.4% ± 0.33%) compared to ripe fruits (mean percentage of acceptance 72.5% ± 0.86%; $\chi^2 = 31.01$, $df = 1$, $p < .001$).

3.3.1 | Fruit acceptance in cryptic species

We found a significantly higher fruit acceptance in unripe fruits compared to ripe fruits for the species: *C. tinctoria* (mean percentage of ripe fruit acceptance 75.55% ± 4.56%; mean percentage of unripe fruit acceptance 92.79% ± 4.5%; $\chi^2 = 8.05$, $df = 1$, $p = .004$); *F. maxima* (mean percentage of ripe fruit acceptance 75.5% ± 5.2%; mean percentage of unripe fruit acceptance 94.5 ± 0.96%; $\chi^2 = 29.76$, $df = 1$, $p < .001$); and *S. capiri* (mean percentage of ripe fruit acceptance 70.35% ± 3.04%; mean percentage of unripe fruit acceptance 90.54% ± 1.18%; $\chi^2 = 11.84$, $df = 1$, $p < .001$). However, the acceptance of ripe fruits was significantly higher with respect to the acceptance of unripe fruits in *F. insipida* (mean percentage of ripe fruit acceptance 74.28% ± 3.63%; mean percentage of unripe fruit acceptance 35.82% ± 5.7%; $\chi^2 = 26.41$, $df = 1$, $p < .001$).

We found that when sucrose content increased, the acceptance of ripe fruits significantly decreased (as an inverse U-shape curve). This effect was true for *C. tinctoria* ($\chi^2 = 7.96$, $df = 1$, $p = .004$); *F. maxima* ($\chi^2 = 35.53$, $df = 1$, $p < .001$); and *S. capiri* ($\chi^2 = 8.18$, $df = 1$, $p = .004$). In contrast, the acceptance of fruits in *F. insipida* was significantly higher when sucrose content was higher ($\chi^2 = 26.56$, $df = 1$, $p < .001$).

3.3.2 | Fruit acceptance in conspicuous species

No significant differences in acceptance were found between ripe and unripe fruits for *F. lundelli* (mean percentage of ripe fruit acceptance 89.95% ± 2.15%; mean percentage of unripe fruit acceptance 98.20% ± 1.06%; $\chi^2 = 3.56$, $df = 1$, $p = .059$); and *S. mombin* (mean percentage of ripe fruit acceptance 65.29% ± 1.93%; mean percentage of unripe fruit acceptance 65.94% ± 2.30%; $\chi^2 = 0.21$, $df = 1$, $p = .64$). Furthermore, we did not find an effect of sucrose

TABLE 2 Mean ± standard deviation and sucrose concentration (g/L) in ripe and unripe fruits of cryptic and conspicuous fruit species consumed by howler monkeys

Species	Category	Unripe fruits	*N* fruits	Ripe fruits	*N* fruits	*t* (*df*)	*U*	*F*	*P* value
Sideroxylon capiri	Cryptic	12.5.±1.7	40	14.8 ± 1.6	20	–	111.5	–	<.001
Ficus maxima	Cryptic	6.5 ± 1.7	15	11.6 ± 2.2	10	−5.7 (23)	–	–	<.001
Ficus insipida	Cryptic	5.9 ± 0.9	14	6.5 ± 1.0	6	−1.1 (18)	–	–	.25
Ficus lundelli	Conspicuous	8.4 ± 1.1	10	12.2 ± 2.4	10	–	46.5	–	.009
Chlorophora tinctoria	Cryptic	8.8 ± 1.7	10	13.4 ± 0.8	10	–	25	–	.008
Spondias mombin	Conspicuous	10.13 ± 1.7	55	12.3 ± 1.02 (yellow)	35	–	–	173.2	<.001
				14.8 ± 0.9 (orange)	20				

content on acceptance in fruit species: *S. mombin* ($\chi^2 = 0.01$, $df = 1$, $p = .89$) and *F. lundelli* ($\chi^2 = 1.14$, $df = 1$, $p = .28$).

Male and female howler monkeys did not significantly differ in their acceptance of fruits. This was true both for cryptic fruits (mean percentage of acceptance by males: 87% ± 1.11%; mean percentage of acceptance by females: 85.9% ± 1.23%; $\chi^2 = 0.17$, $df = 1$, $p = .67$) and for conspicuous fruits (mean percentage of acceptance by males: 74.7% ± 1.61%; mean percentage of acceptance by females: 71.6% ± 1.82%; $\chi^2 = 0.36$, $df = 1$, $p = .54$).

4 | DISCUSSION

The results of the present study support our prediction and indicate that mantled howler monkeys should be able to detect conspicuously colored fruits against a background of leaves more efficiently than they detect cryptic fruits. Studies in other platyrrhines suggest that conspicuous fruits are more detectable for trichromats compared to dichromats (Melin et al., 2017, 2019; Regan et al., 2001; Riba-Hernández et al., 2005; Sumner & Mollon, 2000a). Our results indicate that the trichromacy in mantled howler monkeys could be beneficial to detect conspicuous colorations and thus adaptative to these primates when feeding on fruit.

Although howler monkeys should be less efficient in the discrimination of cryptic fruits due to their similarity to leaves and lack of color change with ripeness, it is evident that they can detect them and select them. The results of our JND analysis showed that mantled howler monkeys should be able to detect ripe cryptic fruits from the greenish background and they even preferred them over conspicuous ones. There are two hypotheses about the evolutionary role of trichromatic vision, one supporting the adaptation to folivory (Dominy & Lucas, 2001; Lucas et al., 1998) and the other supporting the adaptation to frugivory (Osorio et al., 2004; Sumner & Mollon, 2003). It has also been described in the genus that they select cryptically colored (brown or green) ripe fruits (Guillotin, Dubost, & Sabatier, 1994; Julliot, 1996; Martins, 2008; Stoner, Riba-Hernández, & Lucas, 2005). We suggest that trichromatic vision in *Alouatta* allows them to access a broad feeding niche and both types of resources, leaves and fruits. As they seemed to prefer unripe, cryptic fruits for some plant species, trichromacy may help them avoid the sugary, colorful ripe fruit of some species.

Selection of cryptic fruits—that is, those that do not change color during maturation—may be based on other physical or chemical properties that allow their assessment through the use of senses other than vision (Dominy, 2004b). Softening of the fruit, an increase in size and an increased production of volatile compounds during maturation allow an animal to assess a fruit's degree of ripeness, and thus its nutritive value, using the senses of touch, smell, and taste (Brady, 1987; Cipollini & Levey, 1991; Kays, 2004; Kinzey & Norconk, 1990; Willson & Whelan, 1990). In another study conducted during our observation period with the same troop of mantled howler monkeys, the animals used their sense of touch more frequently during the inspection of mature cryptic fruits than during the inspection of immature cryptic fruits and conspicuous fruits (of both ripe and unripe state). Thus, vision is not the only sense that mantled howler monkeys may employ for assessing the quality of fruit, especially with fruits that do not change color. Intense use of such nonvisual sensory cues for assessing the quality of fruits has also been reported in spider monkeys (*A. geoffroyi*; Hiramatsu et al., 2009), capuchin monkeys (*Cebus capucinus*; Melin et al., 2009, 2019) and chimpanzees (*Pan troglodytes*; Dominy et al., 2016).

We additionally assessed if the sucrose content correlated positively with the acceptance of conspicuous and cryptic fruits. We found that mantled howler monkeys accepted cryptic fruits to a higher degree compared to conspicuous fruits. Further, we found no significant correlation between the degree of acceptance of cryptic and conspicuous fruits and their sucrose content. Although some studies suggest that conspicuous colorations are associated with higher sucrose content in fruits (Pablo-Rodríguez et al., 2015; Riba-Hernández et al., 2005; Stoner et al., 2005) this is a phenomenon that is not present in all fruits (i.e., *S. capiri*, *F. maxima*, and *C. tinctoria* in our study). We found that the sucrose content of the fruits selected by mantled howler monkeys were on a similar range 6–12 g/L), suggesting that both cryptic and conspicuous fruits are potentially offering the same sucrose reward to the mantled howler monkeys. Interestingly, we found that the howlers consumed significantly more unripe fruits compared to ripe fruits. A possible explanation of why howlers preferred to accept unripe fruits may be related to their digestive physiology; although soluble carbohydrates such as sucrose are readily absorbed, howler monkeys are hindgut fermenters, and high sugar consumption might affect the food passage time, affecting the effectiveness of food fermentation, because their food passage and digestion is slower compared to highly frugivorous primates such as spider monkey (Espinosa-Gómez et al., 2013; Milton, 1998). Further, howler monkeys can obtain more net energy from gastrointestinal fermentation of leaves than from metabolizing soluble carbohydrates from fruits (Milton, 1980). Thus, sucrose as a nutrient may play a discrete role in food selection strategies of mantled howler monkeys. Recently, it has been proposed that the Mesoamerican howler monkey adopts the strategy that aims to balance the diet in terms of the amount of fruit and leaves consumed (Garber, Righini, & Kowalewski, 2015) which may explain the ability of *A. palliata* to exploit a wide range of food items including both leaves and fruits.

Anatomical studies have shown that mantled howler monkeys which are described as mainly folivorous have markedly fewer fungiform papillae, which are responsible for the detection of sweet stimuli, compared to frugivorous species such as *A. geoffroyi* (Alport, 2007). This difference in the number of fungiform papillae may be responsible for between-species differences in taste sensitivity for sweet stimuli (Hernández-Salazar, Dominy, & Laska, 2015). However, physiological studies are needed to determine the taste threshold for different sugars in howler monkeys to corroborate this notion.

The results of the present support the prediction that mantled howler monkeys should be able to detect conspicuous ripe fruits more efficiently than cryptic fruits against a greenish background, suggesting that trichromatic color vision contributes to the detection of reddish fruits in howler monkeys. In howler monkeys, the trichromacy may, therefore, be related to the selective pressure of having to detect both young red leaves, as highlighted in other studies, and conspicuous reddish fruits. Further, we conclude that neither color nor sucrose content had a significant effect on fruit acceptance. Future studies should include other nonstructural carbohydrates such as fructose, glucose, starch, pectins, and an assessment of the use of senses other than vision to assess possible correlations with fruit acceptance in mantled howler monkeys.

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CONFLICT OF INTERESTS

The authors declare that there are no conflict of interests.

DATA AVAILABILITY STATEMENT

The data that supports the findings of this study are available in the Supporting Information Material of this article.

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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