

Why are fruits colorful? The relative importance of achromatic and chromatic contrasts for detection by birds

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Abstract The colors of fruits and flowers are traditionally viewed as an adaptation to increase the detectability of plant organs to animal vectors. The detectability of visual signals increases with increasing contrasts between target and background. Contrasts consist of a chromatic aspect (color) and an achromatic aspect (light intensity), which are perceived separately by animals. To evaluate the relative importance of fruits' chromatic and achromatic contrasts for the detection by avian fruit consumers we conducted an experiment with artificial fruits of four different colors in a tropical forest. We displayed the fruits against two different backgrounds, an artificial background and a natural one, because they differed in achromatic properties. We found no effect of the type of background on fruit detection rates. Detection rates differed for the four fruit colors. The probability of detection was explained by the chromatic contrast between fruits and their background, not by the achromatic contrasts. We suggest that birds attend primarily to chromatic contrast probably because these are more reliably detected under variable light conditions. Consistent with this hypothesis, we found habitat-specific differences in the conspicuousness of natural fruit colors in the study area. Fruits of understory species that are subjected to the variable light conditions within a forest displayed higher chromatic contrasts than species growing in the open restinga forest with constant bright illumination. There was no such difference for achromatic contrasts. In sum, we suggest that fruit colors differ between habitats because fruit colors that have strong chromatic contrasts against background can increase plants' reproductive success, particularly under variable light conditions.

Keywords Atlantic forest · Eye model · Frugivory · Plant–animal interaction · Signal

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Introduction

Plants that rely on color-sensitive animals to pollinate their flowers and disperse their seeds are expected to increase their reproductive success with conspicuous colors that facilitate detection and attract animal vectors (Kerner 1895; Schaefer et al. 2004). The colors of their reproductive organs therefore meet the criteria of classical signals, which are defined as structures that increase the fitness of the sender by altering the behavior of other organisms such as seed dispersers as receivers (Maynard-Smith and Harper 1995). Although fruit colors are traditionally viewed as an adaptation to seed dispersers, the selective pressures on fruit coloration are not well understood (Willson and Whelan 1990; Schmidt et al. 2004). During the 1980s and early 1990s, the most influential hypothesis aimed to explain how seed dispersers might influence the evolution of plant coloration assumed that they have strong preferences for certain colors. Although some studies reported color preferences of fruit consumers (Puckey et al. 1996; Siitari et al. 1999; Whitney 2005), most bird species exhibit inconsistent and transient color choices with high variability within and between individuals (Willson et al. 1990; Willson and Comet 1993; Traveset and Willson 1998; Schmidt et al. 2004).

In general, the detectability of a visual signal is determined by its contrast against background, the visual conditions during signaling and by the visual perception of the animal receiving the signal (Endler 1990). In recent years, eye models that account for the spectral sensitivities of animals (Vorobyev and Osorio 1998) are increasingly used to predict the optimal design of signals in evolutionary ecology (Endler and Mielke 2005). Animals can use different aspects of a signal to detect and discriminate objects (Giurfa et al. 1997). Under constant conditions in the laboratory, birds and insects use chromatic aspects of color for the detection of large targets and achromatic aspects (that are based solely on differences in the intensity of reflected light), for the detection of small objects and pattern (Osorio et al. 1999; Spaethe et al. 2001). However, eye models make no predictions on the relative importance of chromatic and achromatic aspects of a signal and they do not predict detectability if the intensity of illuminating light varies or the target differs in distance to the receiver (Vorobyev and Osorio 1998). To assess optimal signal design, it is therefore important to test detection rates of differently colored fruits under natural conditions with variable illumination.

We conducted an experiment with artificial fruits in the understory of a tropical lowland forest and determined fruit detection by birds. To study which aspects of a signal influence fruit detection, we designed four differently colored artificial fruits and displayed them against two different backgrounds in a 4×2 design. We used an avian eye model (Vorobyev and Osorio 1998) to determine chromatic and achromatic contrasts between fruits and their background as seen by birds. Because the backgrounds sported very different achromatic properties, the experiment allowed us to evaluate the relative importance of chromatic and achromatic contrasts for fruit detection. We also analyzed the fruit-foliage contrasts of natural fruit species that grow in two different forest types, the lowland forest characterized by drastic changes in illumination between sun spots and dark forest shade and the open restinga forest (shrubland) by relatively constant ambient light. We expected that species growing under different light conditions differ in their fruit-foliage contrasts with higher contrasting fruits in the forest with lower light intensity and more variability in ambient light.

Materials and methods

Study site

Fieldwork was carried out from July to August 2004 on Ilha do Cardoso State Park, a subtropical island, in São Paulo state, southeastern Brazil (25°05' S; 47°53' W). The vegetation of the island is composed exclusively of Atlantic rain forest and is constituted by five different types: mangroves, dune vegetation, restinga forest (shrubland), lowland tropical rainforest and highland tropical rainforest (Noffs and Baptista Noffs 1982). The present study was conducted in the lowland tropical rainforest, which is characterized by an understory level and a relatively continuous and dense canopy level that can reach 20 m with a large amount of epiphytes and vines. The adjacent restinga forest resides on sandy soils and is characterized by an open canopy that can reach 4–5 m (Bernardi et al. 2005). The most important frugivorous birds in the forest understory are *Chyroxiphia caudata* (Pipridae), *Turdus rufiventris*, *Turdus albicollis* (Turdidae) and tanagers (Thraupidae), such as *Tangara* and *Tachyphonus* (Marsden et al. 2003).

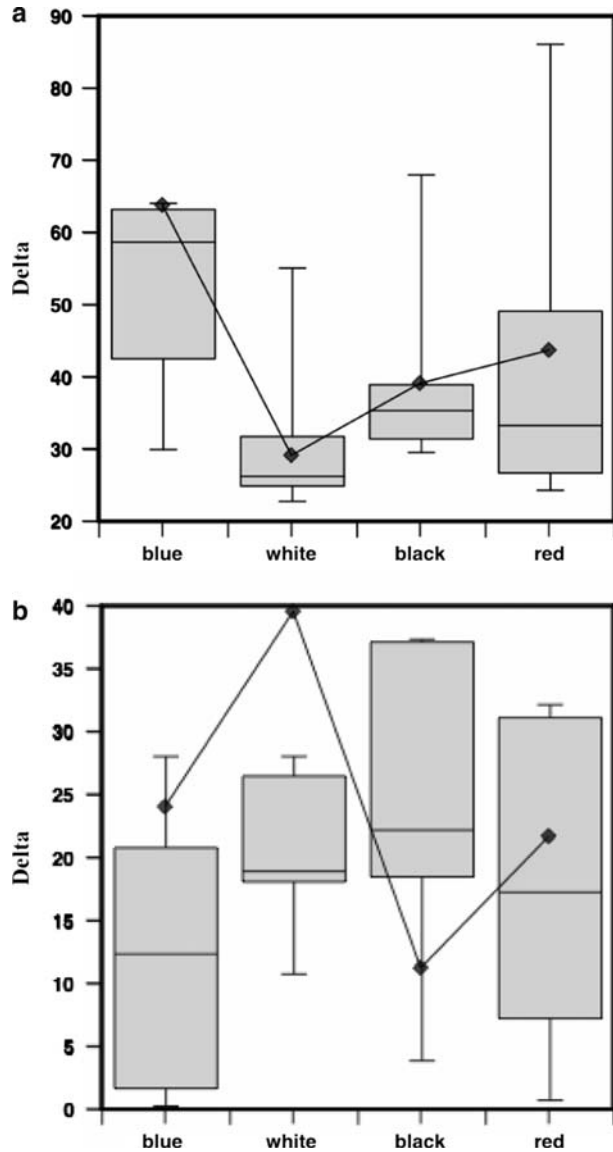
The climate is generally warm and wet throughout the year but may be divided into two seasons: a cold and drier period from April to August when temperature may drop to nearly 13°C and rainfall is ~500 mm, and a warm and rainier period from September to March when temperature may reach 32°C and rainfall 1800 mm (Oliveira-Filho and Fontes 2000).

Experimental design

We used modeling clay (plasticine) to shape spherical artificial fruits of 14 mm diameter that have been used in previous studies on fruit detection by birds (see Alves-Costa and Lopes 2001; Galetti et al. 2003). In the lowland forest, we placed fruits in 240 shrubs (60 for each different color) at 50 m distance from each other. In each shrub we attached to branches 20 single fruits of the same color with a string. Only shrubs between 1 and 2 m height without fruits or flowers were selected for the experiment. Previous experiments on captive frugivorous birds showed that they promptly accepted the artificial fruits (M.G. unpublished data).

We selected four different fruit colors: UV-blue, red, black and white. We chose these colors because their chromatic and achromatic contrasts closely matched those of natural fruits (Fig. 1), except for the achromatic contrasts of white fruits. Our artificial fruits are thus a good representation of natural variation in fruit contrasts at our study site. We used two types of backgrounds, one artificial background consisting of 50 mm circles of yellow cardboard that were attached with the fruits. A slit and central hole allowed the artificial background to be placed with the same string of the artificial fruit and this close association between fruit and background permitted birds to view and detect fruits consistently against this background even if seen from different angles. This background was considerably larger than fruits and larger than conspicuously colored secondary structures that are associated with fruit displays (e.g., bracts; Burns and Dalen 2002). The artificial background was selected because it differed strongly from natural backgrounds in achromatic contrasts but yielded similar chromatic contrast (see below). Every second shrub that we used for the experiments featured these artificial backgrounds. The remaining displays (50%) had no artificial background and hung in front of natural backgrounds i.e. the leaves. We used a random design in our experiment so that color and presence or absence of background were randomly selected. Fruits were checked after 96 h, by counting the

Fig. 1 Mean and standard deviation of natural (a) chromatic and (b) achromatic contrasts (jnds values) of blue, red, black and white fruits in the study site. The line illustrates the contrasts of artificial fruits



number of pecked or removed fruits. Different animals leave different marks in the artificial fruits, which made it possible to distinguish between mammals (teeth mark), insects (dots or stripes) and birds (beak mark) (Alves-Costa and Lopes 2001). Marks of mammals and insects were ignored. Because teeth marks were recorded in very few cases (two fruits), we assumed that birds removed all missing fruits.

Color measurements and contrast calculation

We measured the reflectance spectra of 15 artificial fruits of each color, 15 artificial backgrounds and leaves of the 16 most common shrubs in the study site as an

approximation of natural foliage background. In order to account for variability in leaf coloration within species, we measured 10 leaves of these 16 shrubs and calculated the mean reflectance of each species. We computed the mean of the 16 species as an approximation of overall natural background reflectance (Fig. 2). We also measured the reflectance of 20 natural fruits and 10 leaves of 16 common shrubs in the lowland forest and of 20 fruits and 10 leaves of 34 species of the restinga forest. We performed all measurements with Ocean optics USB2000 spectrometer and a Top Sensor System Deuterium-Halogen DH-2000 (both Ocean Optics, Duiven, The Netherlands) as a standardized light source. Reflectance was measured as the proportion of a standard white reference tile (Top Sensor Systems WS-2).

Chromatic and achromatic contrasts between the mean reflectance of fruits and artificial background or leaves were calculated according to the model of avian vision, which assumes that receptor noise limits discrimination (Vorobyev and Osorio 1998). Because passerine birds are the most important frugivorous birds in the understory of our study site (see above) and of neotropical forests in general (Loiselle and Blake 1991), we used an eye model based on the spectral sensitivities of the blue tit (*Cyanistes caeruleus*) with a UVS cone (Hart et al. 2000). Based on analytical approximation of cone visual pigments and oil droplet spectra, we calculated the quantum catch of each class of single cones (LWS, MWS, SWS, UVS), denoted by the subscript i , as the integrated product of the receptor sensitivity spectrum (R_i), reflectance spectrum (S), and illumination spectrum (I):

$$Q_i = R_i(\lambda)S(\lambda)I(\lambda)d\lambda \quad (1)$$

The quantum catches are used to find relative contrasts against fruits and background as the log of the quotient of quantum catches from both spectra. The result of this calculation is the contrast Δf for each receptor type i :

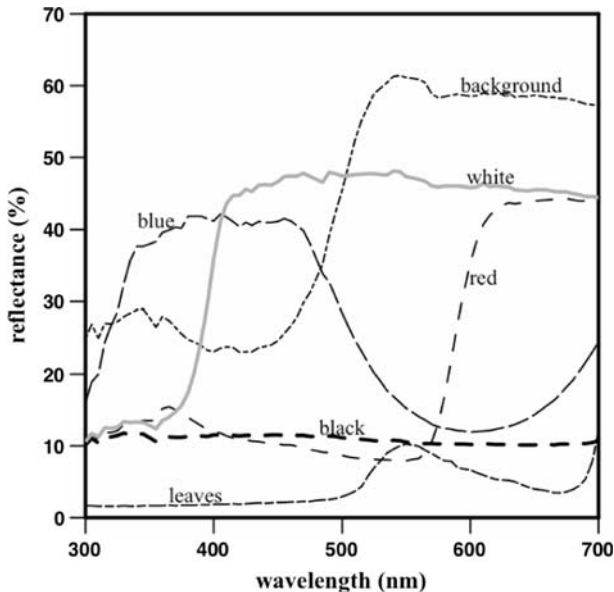


Fig. 2 Mean reflectance spectra of blue, red, black, white artificial fruits, artificial background and leaves of the understory

$$\Delta f_i = \ln(Q_i \text{ fruit}) - \ln(Q_i \text{ background}) = \ln(Q_i \text{ fruit}/Q_i \text{ background}) \quad (2)$$

To quantify discrimination using all receptor types in a given visual system, each receptor class is first assigned a noise value ω based on its individual Weber fraction (v) and on the receptor proportion (n) (Vorobyev et al. 2001):

$$\omega_i = v_i/n_i \quad (3)$$

Then we calculated discrimination values for tetrachromatic visual system. The subscript number of each variable in Eq. 4 is the value given for a particular receptor class:

$$\begin{aligned} \Delta S^2 = & [(\omega_1\omega_2)^2(\Delta f_4 - \Delta f_3)^2 + (\omega_1\omega_3)^2(\Delta f_4 - \Delta f_2)^2 \\ & + (\omega_1\omega_4)^2(\Delta f_3 - \Delta f_2)^2 + (\omega_2\omega_3)^2(\Delta_4 - \Delta f_1)^2 \\ & + (\omega_2\omega_4)^2(\Delta f_3\Delta f_1)^2 + (\omega_3\omega_4)^2(\Delta_2 - \Delta f_1)^2] / [(\omega_1\omega_2\omega_3)^2 \\ & + (\omega_1\omega_2\omega_4)^2 + (\omega_1\omega_3\omega_4)^2 + (\omega_2\omega_3\omega_4)^2] \end{aligned} \quad (4)$$

Results of the calculation using Eq. 4 provide the chromatic distance (ΔS) separating the perceptual values of two spectra in receptor space. The units for ΔS are jnds (just noticeable differences), where 1 jnd is at the threshold of discrimination, values less than 1 jnd indicate that two colors are indistinguishable and values above 1 can be discriminated (Osorio and Vorobyev 1996).

The achromatic (brightness contrast) analysis is similar to the chromatic one, where comparisons are based on brightness differences alone:

$$\Delta S = |\Delta f_i/\omega|$$

Fruit colors differed in their chromatic contrasts against natural and artificial background (one-way ANOVA, $F = 11.61$, $df = 3$, $P < 0.0001$; $F = 738.91$, $df = 3$, $P < 0.0001$, respectively). UV-blue fruits had higher contrasts than black and white fruits, and red fruits had higher contrasts than white fruits against leaves. Against artificial background, all fruits differed in their contrasts (UV-blue > red > black > white) (Table 1, 2). Fruits also differed in their achromatic contrasts against leaves and the artificial background (one-way ANOVA, $F = 21.64$, $df = 3$, $P < 0.0001$, $F = 4.42$, $df = 3$, $P = 0.01$, respectively). Against leaves, black fruits had smaller contrasts than blue and white fruits. Against artificial background, all fruits differed in their contrasts, excepted for blue and red (Tables 1, 2). Fruits were darker than the artificial background and brighter than leaves (see signs in Table 1).

In statistical analyses we used detection as a binary response variable. In other words, we analyzed whether or not a shrub with artificial fruits was detected after 96 h. When a shrub had at least one pecked or removed fruit we consider that birds detected it, otherwise it counted as not detected. We used detection as the dependent variable and chromatic and achromatic contrast (values of jnd) as independent variables and the presence or absence of the artificial background as a fixed factor in Logistic Regression.

Results

After 96 h, 68.3% of all shrubs were detected by birds. Nearly half (48.8%) of all detected shrubs had artificial backgrounds and 51.2% of shrubs had no background. Thus, although the artificial background contrasted against the leaves (chromatic contrasts 17 jnds,

Table 1 Chromatic and achromatic contrasts (mean values of jnds) of fruit color against natural and artificial background

Color	Chromatic		Achromatic	
	Artificial	Natural	Artificial	Natural
Blue	50.11	63.72	(-)18.82	(+) 24.01
Red	30.77	43.64	(-)21.19	(+) 21.64
Black	23.83	39.04	(-)31.64	(+) 11.19
White	17.02	29.09	(-)3.29	(+) 39.54

For achromatic contrasts, positive and negative values indicate whether fruit is darker or brighter than the background

Table 2 Results of the post hoc test (*P*-values) following ANOVA, from multiple comparisons between fruit colors against both backgrounds (natural and artificial) in relation to chromatic and achromatic contrasts

Multiple comparisons		Chromatic		Achromatic	
		Natural	Artificial	Natural	Artificial
Blue	Red	0.5	0.003	0.9	0.9
	Black	0.001	<0.001	<0.001	0.03
	White	<0.001	0.002	0.01	0.9
Red	Black	0.05	<0.001	<0.001	0.1
	White	<0.001	<0.001	0.002	0.7
Black	White	0.4	<0.001	<0.001	0.01

The mean difference is significant at the 0.05 level

achromatic contrasts 12 jnds), its presence did not influence the likelihood of detection by frugivorous birds ($\chi^2 = 0.02$, $P = 0.87$). Supporting the observation that the artificial background did not influence detection rate, we found no difference between the total number of pecked fruits per shrub between shrubs with and without artificial background (one-way ANOVA, $F = 0.004$, $df = 1$, $P = 0.94$).

Detection rates of the four fruit colors differed. The probability of detection was explained by the chromatic contrast between fruits and their artificial background ($\chi^2 = 4.72$, $df = 1$, $P = 0.02$) and natural background ($\chi^2 = 33.22$, $df = 1$, $P < 0.0001$). Fruits with higher chromatic contrasts had higher rates of detection with a strong correlation between the percentage of detected shrubs and their chromatic contrasts ($r_s = 1.0$, $P < 0.001$) (Fig. 3).

Although the results was also significant for achromatic contrasts against artificial and natural background ($\chi^2 = 4.69$, $df = 1$, $P = 0.03$; $\chi^2 = 11.75$, $df = 1$, $P < 0.001$, respectively), there was no correlation between the percentage of detected shrubs and their achromatic contrasts ($r_s = -0.2$, $P = 0.8$) (Fig. 3). The result predicted an unrealistic inverse relationship between achromatic contrast and detection that did not provide a close match of the variation in detection rates (see Fig. 3).

Chromatic contrasts of natural fruits against leaves from common understory species of the lowland forest differed from those of the restinga forest. Higher values of contrasts were found in the lowland forest (45 jnds \pm 3.3 (mean \pm SE) in comparison with restinga

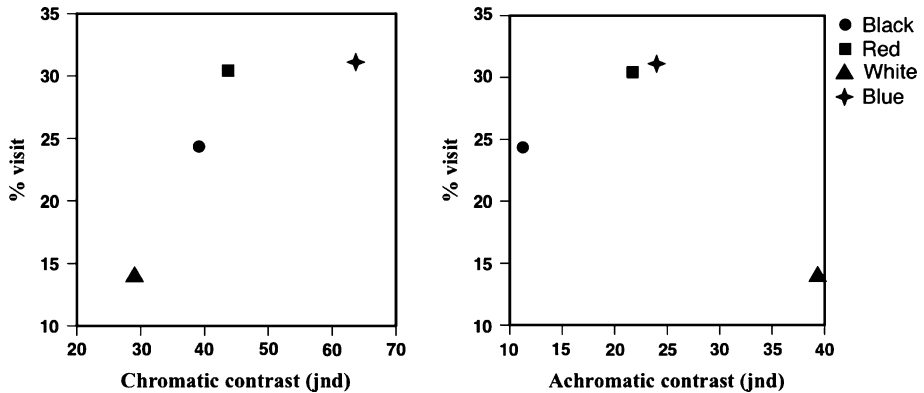


Fig. 3 Relationship between total percentage of detection and chromatic and achromatic contrasts of fruits against natural background (values of jnds)

forest ($34 \text{ jnds} \pm 2.4$ (mean \pm SE) ($t = 2.60$, $P = 0.01$) (Fig. 4). Achromatic contrasts of natural fruits did not differ between lowland species ($19 \text{ jnds} \pm 2.4$; mean \pm SE) and restinga species ($17 \text{ jnds} \pm 3.5$) ($t = 0.52$, $P = 0.60$) (Fig. 4).

Discussion

We found that patterns of fruit detection in the forest understory are mediated by chromatic contrasts. Achromatic contrasts do not explain fruit detection because higher achromatic contrasts did not result in higher probability of detection. Also, the inverse relationship between achromatic contrast and detection that the results of our experiment suggest is unlikely to explain general patterns of detection probabilities.

Our result that chromatic contrasts influence fruit detection by birds is based on the detection rates of only four different colors. Testing detection rate of a larger range of colors might yield different results. However, there are different lines of evidence for why we consider this possibility unlikely. First, in the lone experiment on this subject Schaefer et al. (2006) found that—similar to our results—crows prioritized chromatic over achromatic contrasts when searching for fruits among foliage. Second, our comparison between habitats, albeit restricted to two habitats, showed that fruits displayed in different illumination differed in their chromatic contrasts but not in their achromatic contrasts. Alternatively, fruit detection in our study might have been influenced by pre-existing color preferences rather than by fruit perception. However, studies that analyzed fruit consumption as a function of fruit colors and contrasts concluded that fruit removal is a function of contrasts and not of color per se (Schmidt et al. 2004; Schaefer et al. 2006). This conclusion is consistent with the generally inconsistent and transient color preferences of most frugivorous birds that are characterized by high inter- and intra-specific variability (Willson et al. 1990; Wilson and Comet 1993; Traveset and Wilson 1998; Schmidt et al. 2004). Finally, chromatic and achromatic contrasts of artificial fruits generally matched those of natural fruits at the study site, thus, we assume that chromatic contrasts rather than color preferences and pre-existing biases explain the patterns of fruit detection in our study.

We suggest that birds rely on chromatic contrast for fruit detection, probably because variation in chromatic composition of illumination is smaller than variation in achromatic

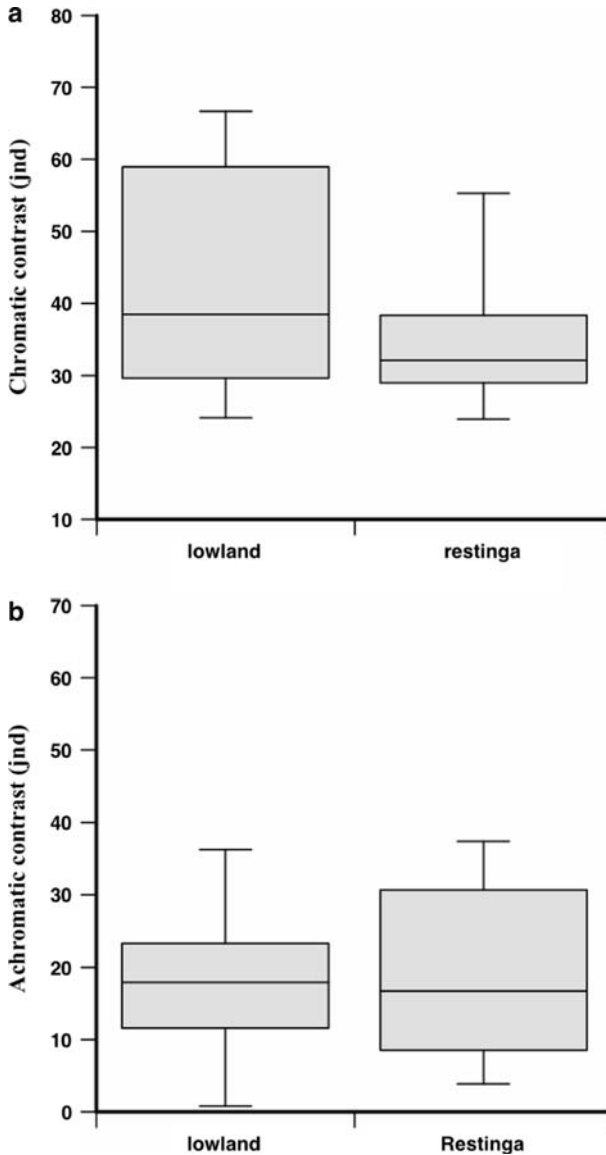


Fig. 4 Illustrated are the contrasts of natural fruits in the lowland forest ($N = 16$) and restinga forest ($N = 34$). **(a)** Chromatic contrasts (jnds) are higher in fruit species of the lowland forest than the restinga forest, **(b)** and achromatic contrasts (jnds) are similar between both forest types. Illustrated are medians, mid-quartiles, 90th and 10th percentiles

composition and consequently chromatic contrasts might be more reliable cues under changing light conditions (Troost 1998; Kelber 2005). This logic is especially applicable to the task of fruit detection against a background of foliage, because foliage consists of high achromatic variation owing to alternating patterns of sun spots and shadows. Analyzing color perception by frugivores primates, Summer and Mollon (2000) discussed the

importance of this effect for fruit detection. They concluded that achromatic fruit signals are difficult to detect for primates because of large achromatic variance in foliage.

In our experiment, fruit detection was not influenced by the presence of an artificial background. On the first glance this result is surprising because it is generally believed that the secondary structure associated with fruit display increases the consumption rates of frugivores birds (Morden-Moore and Willson 1982; Wheelwright and Janson 1985; Whelan and Wilson 1994). In our study the artificial background reduced the chromatic contrast between fruits and background to lower values compared to those against leaves but the background itself also contrasted with leaves. There are several possibilities to explain why the artificial background had no effect on detection. First, the reduction in chromatic contrasts was not strong enough to influence patterns of detection. In other words, contrasts between artificial fruits and artificial background were still high enough to warrant detection. Second, the artificial background we used was not big enough to affect the likelihood of detection. We consider this possibility unlikely given that our background was larger than the secondary structures that plants use to increase detection rates by birds (Burns and Dalen 2002). Lastly, the lack of influence of the artificial background might be explicable because its shape differed from that of plants' secondary structures and birds might not have associated this background with fruit rewards.

The model developed by Vorobyev and Osorio (1998) assumes that discrimination can be made quickly and under increasingly unfavorable conditions as values of "jnd" becomes higher than 1. The model is based on the receptor noise of the four cone types. It expects that all objects with values above 10 jnds are always detected because higher levels of noise are not physiologically plausible. The model fits with behavioral evidence in controlled settings in the laboratory (Maier 1992). We found that detection increased with contrasts (from white to black to red fruits) and that this relationship tends to become stable for values above 40 jnds (i.e., no increase in detection rates from red to UV-fruits). In visual searches the likelihood of detection will increase asymptotically until a target is so conspicuous that it will always be detected. The asymptotic curve resulting from our experiment (Fig. 1) might well describe detection thresholds for birds under variable light conditions, although we acknowledge that the conditions and the scope of our experiment are likely too limited to infer general patterns of fruit detection. Importantly, however, our results show that in natural conditions where light intensity and the distance between observer and prey vary, higher contrasts might increase the chances of detection. We emphasize that this applies particularly to the forest understory where rare but regular sun spots might be important distractors for visual searches.

Consistent with the importance of ambient light conditions on fruit detection by birds, we found that natural understory fruits of the lowland forest had higher chromatic contrasts but similar achromatic contrasts than fruit species growing in neighboring areas of restinga forest with bright illumination. To the best of our knowledge, this is the first broad comparative study showing that fruit colors differ between habitats and that this differentiation is likely linked to fruit detection rates by seed dispersers. Although this result is based on comparing two sites only, it fits the observation made by Summer and Mollon (2000) that understory fruits tend to have higher contrasts than fruits in the canopy. Based on our data we suggest that it is particularly important to maximize color chromatic contrasts for animal-dispersed species growing inside the forest under a relatively closed canopy with low light intensity.

In sum, this is the first work that evaluated the importance of chromatic and achromatic signals in fruit detection by birds in natural conditions. We concluded that birds attend primarily to chromatic contrasts probably because they are a more reliable signal under

changing light conditions. Thus, chromatic contrasts play an important role in fruit frugivore interaction by increasing the chances of fruit detection. Plants might therefore increase removal rates and, indirectly, their reproductive success by displaying fruit colors with strong chromatic contrasts against background.

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