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Fruit colour and edge effects poorly explains frugivorous bird-plant interactions in disturbed semideciduous forests

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ABSTRACT. Fruit colour is considered an important feature mediating interactions between plants and frugivorous birds. Despite that, colour mediated interactions are context-dependent, and habitat disturbances may affect how frugivorous birds perceive fruit colours. This study assessed the influence of fruit colour and edge effect on the consumption of artificial fruits by frugivorous birds in three disturbed semideciduous forests in southeastern Brazil. In each of those areas, we performed a field experiment in which we placed artificial fruits of three different colours on plants and recorded their consumption by birds. Red-coloured fruits were ingested more often than yellow, but neither of them was consumed differently from dark-blue. Edge effect only affected consumption of yellow fruits. Our data neither support the hypothesis of preferential consumption of the highest contrasting colours nor of increased fruit consumption in the forest interior. These findings indicate that colour and edge effects, as well as the interaction between them, may not be strong predictors of fruit choice by birds in disturbed environments, especially because generalist species, which are less sensitive to the physical alterations in forests, are favoured in these areas.

Keywords: frugivory; behaviour; plant signals; sensory ecology; plant-animal communication.

A cor dos frutos e o efeito de borda não explicam as interações entre aves frugívoras e plantas em fragmentos florestais semidecíduos alterados

RESUMO. A cor dos frutos é importante nas interações entre plantas e aves. Apesar disso, as interações mediadas por cores são contexto-dependentes e as alterações no habitat podem afetar a maneira como os frugívoros percebem a coloração dos frutos. Este estudo avaliou a influência da cor e do efeito de borda no consumo de frutos artificiais por aves em três florestas semidecíduas degradadas no sudeste brasileiro. Em cada uma dessas áreas, foi conduzido um experimento no qual foram colocados frutos artificiais de três cores diferentes nas plantas e foi registrado o seu consumo pelas aves. Os frutos vermelhos foram mais consumidos do que os amarelos, mas nenhum deles foi consumido mais frequentemente do que os azul-escuros. O efeito de borda afetou apenas o consumo de frutos amarelos. Nossos dados não suportam as hipóteses de consumo preferencial da coloração mais contrastante nem do aumento do consumo de frutos no interior dos fragmentos. Estes resultados indicam que a cor dos frutos, o efeito de borda e a interação entre estes dois fatores, não são fortes preditores da escolha do fruto por aves em ambientes degradados, principalmente pela ocorrência de espécies generalistas nestas áreas, que são menos sensíveis às alterações físicas nos fragmentos.

Palavras-chave: frugivoria; comportamento; sinais das plantas; ecologia sensorial; comunicação planta-animal.

Introduction

Fruit choice is a vital component of bird-plant interactions (Muñoz et al., 2016). It depends on the spatial context (Tiribelli, Amico, Sasal, & Morales, 2017), of frugivores' morphology and behaviour and also of plant traits such as phenology, crop size, fruit colour, accessibility, shape and size (Flörchinger, Braun, Böhning-Gaese, & Schaefer, 2010;

Sallabanks, 1993; Smith & McWilliams, 2014; Snow, 1971). For instance, fruits consumed by frugivorous birds are generally small, spherical, odourless and colourful (Galetti, Alves-costa, & Cazetta, 2003; Schmidt, Schaefer, & Winkler, 2004). Thus, understanding the underlying mechanisms of fruit consumption is of particular concern for evolutionary and conservation biology, since birds interact with many plant taxa and are the leading

seed dispersers in tropical ecosystems (Blendinger, Martín, Osinaga Acosta, Ruggera, & Araújo, 2016; Fleming & Kress, 2011; Kuhlmann & Ribeiro, 2016).

To be consumed, a fruit must first be detected. In the forest sub-canopy, where shading limits light availability (Endler, 1993; Wicklein, Christopher, Carter, & Smith, 2012), plants that compete for seed dispersers may increase signalling by producing contrasting fruit colours (Schaefer, Schaefer, & Vorobyev, 2007), which are hypothesised to have evolved in response to selection mediated by frugivores (Cazetta, Galetti, Rezende, & Schaefer, 2012). In fact, increased detectability may affect plant fitness through higher fruit consumption rates, enhanced seed dispersal, and plant recruitment (Cazetta et al., 2012; Lomáscolo & Schaefer 2010; but see Stournaras & Schaefer 2016).

Birds have a tetrachromatic vision and are well adapted for colour perception (Osorio & Vorobyev, 2008). Avian frugivores feed on fruits of a wide variety of colours (Fleming & Kress, 2011). Notwithstanding, colour hue alone may not explain patterns of bird-plant interactions because fruit detectability also depends on contrast against the background (i.e. conspicuousness) (Burns & Dalen, 2002; Cazetta et al., 2012; Duan, Goodale, & Quan, 2014; Schaefer, Levey, Schaefer, & Avery, 2006; Schaefer et al., 2007; Schmidt & Schaefer, 2004; Silva & Melo, 2011). For example, a particular colour may be conspicuous at close range but cryptic at long distances (Cazetta, Schaefer, & Galetti, 2009). Furthermore, conspicuousness may also vary seasonally, because background (specially foliage) and illumination may vary critically in time (Burns & Dalen, 2002; Camargo, Cazetta, Schaefer, & Morellato, 2013). Therefore, it is crucial to incorporate chromatic (wavelength related) and achromatic (intensity related) aspects of fruit colours for a broader and more elaborate understanding of frugivorous bird-plant mutualisms, since these contrasts take into account the differences in target size, distance from the signal receiver and illuminance intensity that may affect fruit detectability (Schaefer et al., 2006).

Habitat transformation due to anthropogenic disturbances may also affect bird-plant interactions (Donoso, García, Rodríguez-Pérez, & Martínez, 2016; Herrerías-Diego et al., 2008; Martínez & García, 2015; Menezes, Cazetta, Morante-Filho, & Faria, 2016). Such alterations change habitat structure, functioning, and quality, especially near the forest boundaries, where edge effects alter abiotic conditions and create a subset of

microhabitats (Aleixo & Vielliard, 1995). For example, Magrach, Santamaría, and Larrinaga (2013) demonstrated that fruit removal by birds increases with distance from forest edges, thus disrupting plant reproduction at forest boundaries (but see Bach & Kelly 2004; Galetti et al., 2003). Investigating how edge effects alter ecological interactions is imperative for habitat conservation, since disrupted interactions in forest edges may trigger negative cascading effects throughout the entire environment (Harper et al., 2005; Magrach et al., 2013).

One would expect that edges may alter biological interactions by changing colour perception in birds (Bach & Kelly, 2004; Cazetta et al., 2009; Galetti et al., 2003). Assuredly, habitat disturbances may change background heterogeneity, light incidence, and cause sight obstruction, influencing fruit visibility and conspicuousness (Camargo, Cazetta, Morellato, & Schaefer, 2014). Light intensity, for example, can vary drastically in forest environments and is usually higher at edges (Endler, 1993). In these environments, achromatic signals may be more important than chromatic ones for foraging birds (Cazetta et al., 2009; Schaefer et al., 2006). Despite that, so far there are no studies assessing the influence of edge effects on colour-mediated interactions between birds and plants.

In this study we aimed at investigating the influence of fruit colour and habitat disturbance on the consumption of artificial fruits by birds. We predicted that 1) highly contrasting colours would be preferred by birds over cryptic ones; 2) fruit consumption would decrease along the edge-interior gradient in forest fragments and 3) highly contrasting fruits would be more detected and consumed in the interior (shaded) than in the edge (brightened) of the forests.

Material and methods

Study areas

The study was conducted in October 2011 in three semideciduous forests in the Cerrado of Minas Gerais State: *Estação Ecológica do Panga* (Panga) (19°10'04" S and 48°23'41" W), *Fazenda Experimental do Glória* (Glória) (18°57'03" S and 48°12'22" W) and *Fazenda São José* (São José) (18°51'35" S and 48°13'53" W).

The Panga has 409 ha of area, and its vegetation is composed of a mosaic of different formations of the Cerrado, such as grasslands, cerrado *stricto sensu*, woodland, savanna, dry forests and riparian forests (De Faria Lopes & Schiavini, 2007). The Glória has ca. 30 ha of area and is mainly composed of woodland and riparian forest

surrounded by large agro-pastoral landscapes (Lopes et al., 2011). The São José is a woodland fragment of 20 ha surrounded by eucalyptus forest (Júnior et al., 2011).

Sampling design

We made 594 artificial spherical fruits (about 15 mm wide) using flour, water, vegetable oil, sugar and liquid paraffin (*sensu* Arruda, Rodrigues, & Izzo, 2008). We dyed artificial fruits into three colours: red, dark-blue and yellow. We chose these colours because they contrast distinctly with the background and occur naturally in many ripe fruits and arils that are consumed by frugivorous birds in the study areas and also in the Cerrado, such as those of *Birsonima* sp., *Miconia* sp., *Siparuna* sp., *Protium* sp. and *Calophyllum* sp. (pers. obs., Camargo et al., 2013). Moreover, these colours produce distinct chromatic and achromatic contrasts.

We attached the fruits to the plant branches by a thin brown polyester line (about 10 mm long). Then, we set all artificial fruits on non-fruiting and/or flowering understory plants with green leaves so that background and fruit presentation was standardised for all experimental colours and among the different areas (*i.e.* Camargo et al., 2014). We hung nine artificial fruits (three of each colour) on the plants. In each area, artificial fruits were set in 22 plants (10m away from one another) along two parallel transects (11 plants per transect), the first at forest edges and the last 100 m away from them (edge-interior gradient).

Fruits were left exposed for 72 hours. Only pecked artificial fruits were considered in the analyses, because either birds or other frugivores, such as monkeys or bats, could have consumed any missing fruits. At forest edges, plants were fully exposed to standard daylight, while from 10 meters onwards plants were under forest shade. We used the illuminance spectra provided by Pavo package (Maia, Eliason, Bitton, Doucet, & Shawkey, 2013), using arguments “forest shade” and “D65”. For all comparisons among fruit colours and the background, contrasts (chromatic and achromatic) did not differ between different illuminant conditions (Table 1), so we used the mean contrast between full sunlight and forest shade for each pair of colours in the analysis.

Fruit colour reflectance

In order to identify the physical properties of the colours studied, reflectance spectra of artificial fruit colours were measured with a

spectrophotometer (Jaz, Ocean Optics Inc., Dunedin, FL, U.S.A.) between 300–700 nm, which corresponds to the visible spectrum for birds (Hart, 2001). We measured the reflectance spectra of five fruits of each colour inside a black box, and calculated background reflectance as the mean reflectance of 30 leaves from common shrubs occurring in each area. We measured reflectance as the proportion of a standard white reference tile (WS-1-SS; Ocean Optics, Dunedin, FL, U.S.A.). The distance between the fruit and the optical sensor was held constant for all measurements and the angle of illumination and reflection was set at 45°. All reflectance measurements were processed with SpectraSuite® software.

We analyzed the chromatic and achromatic contrasts using Vorobyev and Osorio (1998) receptor noise-limited model to calculate colour distances. This model takes into account the receptor sensitivity of the four different cones (LWS, MWS, SWS, UVS) that make the visual system of most birds and quantify how each one is stimulated by a given color. Small to medium-sized Passeriformes are the main fruit consumers in the study areas and in the Cerrado, so we used the eye model based on the spectral sensitivities of the blue tit (*Cyanistes caeruleus*) (Cazetta et al., 2009).

In order to calculate single cone stimulation, we estimated quantum catch as:

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

where the subscript *i* denotes each single cone, $R_i(\lambda)$ the spectral sensitivity, $S(\lambda)$ the reflectance spectrum of the color and $I(\lambda)$ the illumination spectrum. We corrected for light adaptation and colour constancy by applying the Von Kries transformation (Vorobyev & Osorio, 1998).

To calculate color distances, we first needed to assign a noise value (ω) for each receptor class *i*, based on its Weber Fraction (v) and on the number of receptors of type *i* within it (n):

$$\omega_i = v_i/n_i \quad (2)$$

We used the noise values for the blue tit available in Hart, Partridge, Cuthill, and Bennett (2000).

Finally, colour distances can be calculated for tetrachromats by weighting the Euclidean distance of the photoreceptor quantum catches by the Weber fraction of the cones (ΔS).

Table 1. Mean \pm SD and p-values of T-tests results for comparisons of chromatic and achromatic contrasts of fruit colours and artificial background under different illuminant conditions (forest shade and standard daylight).

	Chromatic contrast			Achromatic contrast		
	Forest shade	Standard daylight	p	Forest shade	Standard daylight	p
Red	9.041 \pm 2.575	9.030 \pm 2.553	0.987	7.674 \pm 4.100	8.289 \pm 4.124	0.599
Yellow	7.910 \pm 3.763	8.322 \pm 4.041	0.710	14.310 \pm 3.428	14.340 \pm 3.445	0.969
Dark-blue	5.315 \pm 1.002	5.268 \pm 1.005	0.869	6.713 \pm 3.618	6.879 \pm 3.643	0.872

$$\Delta S = \sqrt{\frac{[(\omega_1\omega_2)^2(\Delta f_4 - \Delta f_3)^2 + (\omega_1\omega_3)^2(\Delta f_4 - \Delta f_2)^2 + (\omega_1\omega_4)^2(\Delta f_3 - \Delta f_2)^2 + (\omega_2\omega_3)^2(\Delta f_4 - \Delta f_1)^2 + (\omega_2\omega_4)^2(\Delta f_3 - \Delta f_1)^2 + (\omega_3\omega_4)^2(\Delta f_2 - \Delta f_1)^2]}{[(\omega_1\omega_2\omega_3)^2 + (\omega_1\omega_2\omega_4)^2 + (\omega_1\omega_3\omega_4)^2 + (\omega_2\omega_3\omega_4)^2]}} \quad (3)$$

Colour distances are measured in units of ‘just noticeable differences’ (*jnd*). According to Vorobyev and Osorio (1998), discrimination between objects increases as values of “*jnd*” become higher than one.

For achromatic contrasts (ΔL), discrimination among receptors is based solely on brightness differences (Δf_i):

$$\Delta L = \left| \frac{\Delta f_i}{\omega} \right| \quad (4)$$

Data analysis

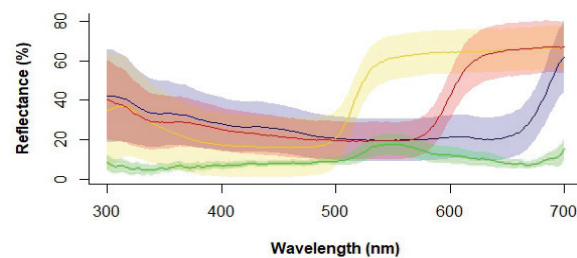
We performed an ANOVA to assess differences in contrasts among the different fruit colours and the background. We applied a two-way ANOVA on fruit consumption using colour and distance from the edge as factors. We applied a simple linear regression to test the relationship between fruit consumption and the edge-interior gradient. Spectral measurements were analysed on RStudio, using Pavo package (Maia et al., 2013). We used the non-parametric alternatives for the tests described above whenever data did not fit a normal distribution according to Shapiro-Wilk test (Zar, 2010).

Results and discussion

The reflectance spectrum of each colour of the artificial fruits is illustrated in Figure 1. All colours used in this study exhibited contrasts higher than one *jnd*. Red and yellow fruits had the highest chromatic contrasts ($H_{2,72} = 23.49$; $p < 0.001$), and yellow was the highest achromatic contrasting colour ($F_{2,72} = 29.39$; $p < 0.001$; Table 2).

Birds pecked 153 artificial fruits (Table 3). Fruit consumption varied amongst different colours ($F_{2,66} = 6.91$; $p = 0.001$). There was a difference between the consumption of red (2.03 ± 0.15) and yellow fruits (0.96 ± 0.19) ($p = 0.001$) per plant, but no difference between each of them and dark-blue fruits (1.51 ± 0.25) (Figure 2). There was no interaction between fruit colour and distance from the edge ($F_{20,66} = 0.922$; $p = 0.562$). Yellow was the only colour

whose consumption varied along the edge-interior gradient, decreasing with distance from the edge (Figure 3).

**Figure 1.** Mean reflectance spectra (lines) and standard deviations (shading) of the yellow, dark-blue and red fruit colours and the green background.**Table 2.** Multiple comparisons of mean (\pm SD) chromatic and achromatic contrasts (*jnds*) between artificial fruit colours and a standardized green background. Calculations were done using data from both illuminance conditions: full sunlight and shade conditions. Different letters in the same column represent statistical significance ($p < 0.05$).

Colours	Chromatic Contrast	Achromatic contrast
Red	9.035 \pm 2.564 ^A	7.981 \pm 4.108 ^b
Yellow	8.116 \pm 3.902 ^A	14.320 \pm 3.346 ^a
Dark-blue	5.291 \pm 0.201 ^B	6.796 \pm 3.624 ^b

Table 3. Number (and percentage) of artificial fruits of four different colours consumed in three semideciduous forests in southeastern Brazil.

Area	Fruit Colour			Total
	Red	Dark-blue	Yellow	
Panga	28 (41.79)	20 (29.85)	19 (28.36)	67
Glória	20 (43.48)	11 (23.91)	15 (32.61)	46
São José	19 (47.50)	19 (47.50)	2 (5.00)	40
Total	67 (43.79)	50 (32.68)	36 (23.53)	153

Our results show that each colour had distinct contrasts against the background, albeit colour preferences did not rely on conspicuousness. On the other hand, habitat structure (i.e. edge-interior gradient) influenced the role of chromatic and achromatic signals in fruit consumption, at least for yellow fruits.

We found that yellow had a high achromatic contrast against the leafy background and that it was the only colour for which consumption reduced along the edge-interior gradient.

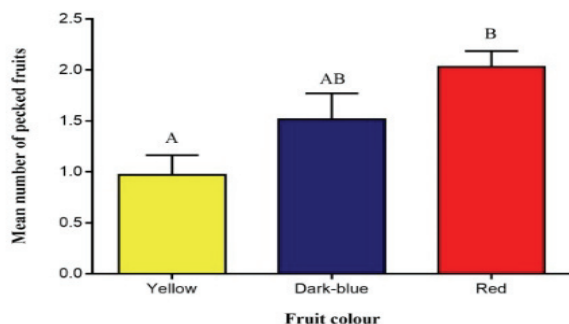


Figure 2. Mean number (\pm SE) of artificial fruit colours pecked per plant in three disturbed areas in the Cerrado. Different letters represent statistical significance ($p < 0.05$).

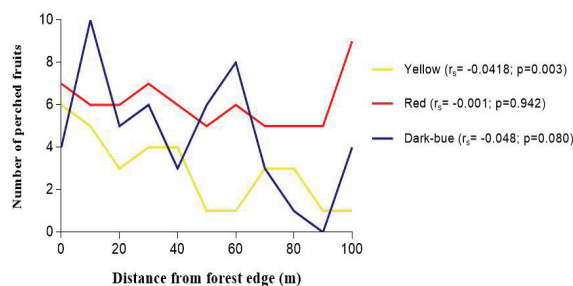


Figure 3. Consumption of three different artificial fruit colours along the edge-interior gradient.

Birds use achromatic signals when foraging at longer distances and constant light intensity, whereas chromatic signals become more reliable at shorter distances (Schaefer et al., 2006) and at low, inconsistent light intensity (Cazetta et al., 2009). At forest edges, birds have a broader visual field because there are often fewer structures (*e.g.* trees, leaves, branches, etc.) obstructing sight and light is not limited as in the forest interior. This scenario facilitates long distance foraging and the colours with high achromatic contrast, such as yellow, would attract frugivores from a distance. Towards the interior of the forest, foraging activities shift from long-distance to close quarters, owing particularly to limited, poor-quality light availability and denser vegetation in the understory. Therefore, we suggest that, for a single colour, the role of achromatic signals in frugivore attraction is more prominent in edge-like environments, which explains why yellow fruits were consumed less frequently in the forest interior, where high chromatic contrast would be more effective in attracting birds (Camargo et al., 2014; Flörchinger et al., 2010).

Despite its high achromatic contrast, yellow fruits were not consumed preferentially over red and/or dark-blue fruits at forest edges. Although conspicuousness increases the probability of

consumption because it allows for easier detection of fruits (Schmidt et al., 2004), colour preferences are much more complex because they also depend on innate and learned behaviours (Burns & Dalen, 2002; Camargo et al., 2015; Honkavaara, Siitari, & Viitala, 2004; Paluh, Kenison, & Saporito, 2015; Schaefer et al., 2007). For instance, some studies show that omnivorous birds have an unlearned preference for red or reddish fruits (Schmidt & Schaefer, 2004; Willson & Comet, 1993) and that fruit preferences match the frequency of natural colours in the community (Duan et al., 2014). Our findings are in accordance with these results, because red was the most consumed fruit colour, followed by dark-blue and yellow. Although yellow is a common fruit colour in the Cerrado (Camargo et al., 2013), red and dark fruits are overrepresented in the forests studied, especially for small, spherical fruits (unpubl. data), which suggests consumption based on learned preference by birds. Other underlying mechanisms for the colour preferences observed in this experiment and that require further investigation are the association of colour and nutritional rewards (Schaefer, McGraw, & Catoni, 2008) and exploitative competition with mammals for yellow fruits (Lomáscolo & Schaefer, 2010; Lomáscolo, Speranza, & Kimball, 2008).

The effects of habitat disturbance on plant-frugivore interactions may go beyond fruit detectability due to physical alterations of the habitat structure, affecting the whole community of foragers (Cordeiro & Howe, 2003; Moran, Catterall, & Kanowski, 2009). Kirika, Farwig, and Böhning-Gaese (2008) demonstrated that environmental disturbances significantly reduced frugivorous richness and functional variation, affecting mainly specialist birds. In disturbed habitats such as those in which this experiment was conducted, generalist, opportunistic, and edge-tolerant species are favoured and may be able to forage in forest edges, as well as in its interior (Cavarzere, Marcondes, Moraes, & Donatelli, 2012), compensating for the loss of disturbance-sensitive species (Menezes et al., 2016). Thus, generalist birds may still overexploit some fruits colours that are predominant in the community (*i.e.* red and dark-blue). Hence, a disruption of seed dispersal may occur since diversity of frugivores foraging in disturbed areas is reduced and dispersal effectiveness varies among different dispersers (Babweteera & Brown, 2009; Li, Li, An, & Lu, 2016).

Advances in the study of sensory ecology have broadened our understanding of how animals sense and interact with their environment (Renoult,

Kelber, & Schaefer, 2015). Nonetheless, our knowledge of animal senses and how they mediate plant-animal interactions is still very limited. Although fruit colour is an important feature mediating plant-frugivore interactions, our findings demonstrated that it is not a strong predictor of fruit choice by birds in disturbed areas. Those results demonstrate the need to gather evidence for alternative roles of fruit colour beyond plant-frugivore communication.

Conclusion

In this study, we found limited interaction between fruit colour and edge effect in determining frugivorous birds and plants interactions, since only yellow fruits were consumed more often on the edges than on the interior of the fragments. We suggest that the effects of habitat disturbance on the consumption of different fruit colours are mainly indirect, *i.e.* through the alteration of community composition, which would favour the prevalence of generalist species in disturbed environments. Further studies would benefit from the assessment of how edge effects alter habitat structure and whether and how these changes affect light conditions in forest fragments.

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