

Conspicuousness, not colour as foraging cue in plant–animal signalling

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The global prevalence of red and black fruits has still not been explained. Hypotheses based on innate consumer preferences have been tested and rejected. Though colour itself plays an important role in animal foraging, it is only one component of signals. Another major component are colour contrasts against background achieving the conspicuousness of signals. In order to evaluate which signal component determines consumers behaviour, we measured fruit colour and colour contrasts of 43 species against their natural background under ambient light conditions. Red and black fruits exhibit stronger contrasts and are therefore more conspicuous to consumers than fruits of other colours. Subsequently, trials were carried out to determine whether colour or conspicuousness influences avian food choice. Four bird species strongly preferred contrasting red–green or black–green over uni-coloured red, green, or black fruit displays, while no preference for particular hues was found. We therefore hypothesize that conspicuousness determines avian food selection and define the contrast hypothesis: Diurnal dispersers select fruit colours based on their conspicuousness and not their colour itself.

Because colour vision is an ancient trait, the entire heterogeneous group of frugivorous birds most likely perceives conspicuousness uniformly over evolutionary time spans. Conspicuousness has thus the potential to explain the global prevalence of red and black fruits.

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The significance of colour in ecological interactions and evolutionary processes is stunning. In visual communication, colour is widely used to transfer information, e.g. signalling mate quality during courtship, facilitating food recognition via search images, and avoiding predators through aposematism, mimicry, and mimesis. Many plants produce colourful fleshy fruits that are made to be eaten by animals often resulting in seed dispersal. However, the mechanisms of how fruit colours function as signals to foraging seed dispersers remain poorly known. Among the diversity of fruit colours, a

global prevalence of red and black hues has been noted totalling 50–70% of all ripe fruits in tropical and temperate areas (Wheelwright and Janson 1985, Willson and Whelan 1990). To explain this ubiquitous prevalence, several non-adaptive and adaptive hypotheses have been proposed (Willson and Whelan 1990), the latter focussed mainly on birds as selective agents due to their excellent colour vision (Goldsmith 1990, Hunt et al. 2001, but see Sumner and Mollon 2000). Numerous studies investigated avian selection for different hues, but found strong intra- and interspecific inconsistencies

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(Willson and Comet 1993, Traveset and Willson 1998). Hypotheses on directed selective pressures of birds on the evolution of global fruit colour patterns were therefore rejected (Willson et al. 1990). Considering that hue is only one component of colour signals, and that studies were conducted under differing light conditions, the contradicting results of birds colour preferences are not surprising. Few researchers have measured contrast patterns of fruit displays (Burns and Dalen 2002), which are an important component of colour signals as the strength of any signal lies in its distinction from background noise (Endler 1992, 1993, 2000). Alternatively to colour, fruits conspicuousness may thus influence consumers fruit selection.

Another limitation of studies on fruit colour conducted to date is the colour classification based mostly on human vision. This approach ignores the marked differences in visual systems among vertebrates potentially leading to erroneous conclusions (Bennett et al. 1994). Birds visible range extends into the UV, and they are equipped with a forth cone type and a system of oil droplets, which likely enables them to distinguish more hues than humans can perceive (Vorobyev et al. 1998). Currently, the most objective approach to colour assessment in ecological studies is the use of colour spectra obtained by spectrometric devices, as they are independent of specific colour space assumptions (Cuthill et al. 1999).

Thus, under these new premises, i.e. the employment of objective colour assessment and the measurements of contrast as an important aspect of fruit signals, the potential avian influence on the evolution of fruit colour patterns is again under scrutiny. We first hypothesize that not colour itself but conspicuousness is the key to attractive fruit displays. Therefore, we propose that the prevalence of red and black fruits is a result of their conspicuousness owing to strong colour contrasts against natural backgrounds. We tested this hypothesis by assessing the conspicuousness of 43 neo-tropical fruit species using colour spectra of both fruit and background under natural ambient light. Second, we propose that birds do not prefer red and black per se, but that contrasting displays enhance fruit consumption. Accordingly, we investigated, in choice experiments, whether colour or colour contrasts influence avian fruit selection both in natural and artificial red, black, and green fruits.

Methods

Spectral measurements and contrast calculation

Fieldwork was conducted from October to December 1998 and October 1999 to February 2000 at the Surumoni field station in a lowland rainforest in southern Venezuela (65°40'W, 3°10'N). We collected fruits in all forest strata, 33 fruit species inside the forest

and ten in a Llanos type savannah nearby. We measured the colour of 20 mature fruits and background structures of each plant species immediately after collection. For all measurements, a portable Ocean optics S2000 diode-array spectrometer and a Top Sensor System Deuterium-Halogen DH-2000 as a standardised light source were used. The combination yielded reliable readings between 350 and 900 nm. The sensor consisted of six 200 µm illuminating fibres, surrounding a seventh fibre, which transferred the reflected light into the spectrometer with an acceptance angle of 28°. We measured reflectance as the proportion of a standard white reference tile. Spectra were processed using SpectraWin 4.0 software and were calculated in 5 nm intervals between 350 and 700 nm using the software package ColorMaster (H. Winkler, unpubl.). To measure irradiance, we took ambient light spectra with a CC3 cosine-corrected irradiance sensor with a measuring surface of 6 mm in diameter, collecting incoming light over a solid angle of 180°. Depending on light intensity, the probe was connected with a 200 µm or a 50 µm optical fibre. The cosine correction adjusts for signal differences resulting from differing angles of the incoming light. Fruit spectra of each species were averaged. For background patterns, an average spectrum consisting of the estimated proportions contributed by each structure (leaves, bark etc.) was calculated. For each species, we photographed seven infructescences from 5 m distance and calculated the proportions of background structures to the nearest 10%. To obtain the colour spectra reaching the eye of a consumer, we multiplied averaged reflectance spectra of fruit and background with corresponding ambient light spectra (Endler 1990, 1993).

We used the Euclidean distance for the estimation of colour contrasts although its assumption of equal sensitivity might not apply to all wavelengths in birds. Due to the influence of ambient light intensity, spectra were normalised to the same brightness in order to only yield colour contrast (Endler 1990). The Euclidean distance D was then calculated as:

$$D = \sqrt{\sum [Q_f(\lambda) - Q_b(\lambda)]^2}$$

with Q being the colour light spectrum reaching the eye of the observer, Q_f and Q_b representing the products of fruit, respectively background reflectance spectra and ambient light spectrum; λ is the wavelength in nm, and the sum represents the entire spectrum of wavelength (350–700 nm). We conducted a Mann–Whitney test to compare colour contrasts of red and black fruits with those of other colours.

Study species

We tested the following thraupids: green honeycreeper (GH, *Chlorophanes spiza*), blue dacnis (BD, *Dacnis*

cayana), short-billed honeycreeper (SH, *Cyanerpes nitidus*), and purple honeycreeper (PH, *C. caeruleus*) in a cafeteria trial (GH n = 4, BD n = 5, SH n = 3), in a contrast trial with artificial fruit (GH n = 4, BD n = 5, SH n = 5), and natural fruits (BD n = 6; SH n = 5; PH n = 3; all wild caught). All birds were held individually in cages (62 × 40 × 39 cm) under constant conditions (LD 12:12; 25°C ± 1°C; app. 70% relative humidity). Birds were kept on a uni-coloured brown standardised food of dried insects, vegetable oil, protein, carbohydrates, cellulose, minerals, and vitamins. The maintenance food was supplied with artificial nectar (Nectar-Plus, Enderle Prod., Germany). Water was always provided ad libitum. Individuals were bought as captive bred in trade, most of them still in juvenile plumage, and held under license of the Weser-Ems District Government, Germany. During the experiments, birds maintained or increased their body mass. Birds caught at the field station were observed one month prior to capture and mist-netted after the breeding season. We fed birds a variety of natural fruits and a mixture of insects. Permits were given under No. 193 by the SADA-Amazonas Department, Pto. Ayacucho, Venezuela. Birds were acclimatized for two weeks before trials and released within four weeks after capture. The birds were colour-ringed and observed in their original mixed species flocks until the field season ended.

Preference of fruit colour

We investigated a general colour preference in a cafeteria design experiment. The species were simultaneously exposed to five artificial fruit cubes of different colours over two consecutive days. Cubes were gelatine-based with 2.5 g of indigestible cellulose to make fruits opaque (Schmidt 2002). We used "Crazy colours" by Brauns Heitmann GmbH, Germany, and titanium white as food dye. Colour shade was spectrometrically checked and fitted the range of natural fruit spectra of the same hue. The same colour shades were used for all trials. Birds were familiar with all artificial fruits before the trials and readily fed on them. We presented fruits in petri dishes with changing colour positions. After 45 min of exposure, we collected unconsumed fruits and food spills and determined the amounts eaten. To assess whether birds generally prefer a certain colour, we used a modified Hotelling's T^2 -test following Lockwood (1998). Amounts eaten of each fruit cube were calculated as proportions of individual total consumption. In a second step, a permutation test tested preferences for red fruits among the different species. Since the design was hierarchical (treatments, species, individuals) and repeated over individuals, permutations were carried out on values centred at zero within individuals (Mundry 1999). The results were statistically evaluated in 10 000

permutations to test for differences in the among-treatments variance versus the within-treatments variance. The permutation test was performed using unpublished software (H. Winkler, unpubl.).

Influence of contrasts

To test the influence of contrasts, we presented green artificial fruits simultaneously on a red and a green dish on three consecutive days. The same trial was repeated with red artificial fruits to avoid the potential influence of red in just one display. After 45 min, we collected food spills and uneaten food to determine the amount of fruit eaten from each display. For these trials, birds were held in indoor aviaries of 1.20 × 1.20 × 2.40 m. To test the effects of contrasts within a fruit display, we offered wild-caught birds in Venezuela two food cups with either 20 black, ripe fruits of *Goupia glabra*, or 13 black fruits with 7 green unripe *G. glabra* fruits. *G. glabra* has a multi-coloured ripening process with fruits of different ripening stages being simultaneously present. The aim of this trial was to test the effect of contrasts within a fruit display. We therefore presented fruits against a dark grey background. After 15 min, we counted black fruits left in both cups (birds did not eat green fruits). Trials were conducted on three consecutive days. For both experiments, we employed a χ -test to test whether birds preferred one type of display.

Results

Conspicuousness of fruit colours

Typical fruit and background reflectance spectra are shown in Fig. 1. The Euclidean distances of the brightness-normalised spectra of 43 fruit species showed clear differences between fruit colours. Red and black fruits contrasted more with their background than fruits of other colours (Mann-Whitney U-test; $U = 130.0$; $z = -2.435$; $n = 43$; $p = 0.015$; Fig. 2, Appendix 1). Colour contrasts did not differ between red and black fruits ($U = 52.0$; $z = -0.693$; $n = 25$; $p = 0.488$).

Experiments on fruit colour and conspicuousness

The bird species did not exhibit a preference for red fruits (permutation test: all species $p > 0.05$). Similarly, no overall preference for any fruit colour was found (Hotelling's $T^2 = 19.8942$, $df = [4, 8]$, $n = 9$; $p > 0.05$ /Fig. 3). When we presented green artificial fruits with a red or a green background, all species strongly preferred the contrasting food display on all days ($\chi^2 = 7.143$; $df = 1$; $n = 14$; $p = 0.008$ /Fig. 4A). A second trial with red fruits yielded a similar preference for a contrasting

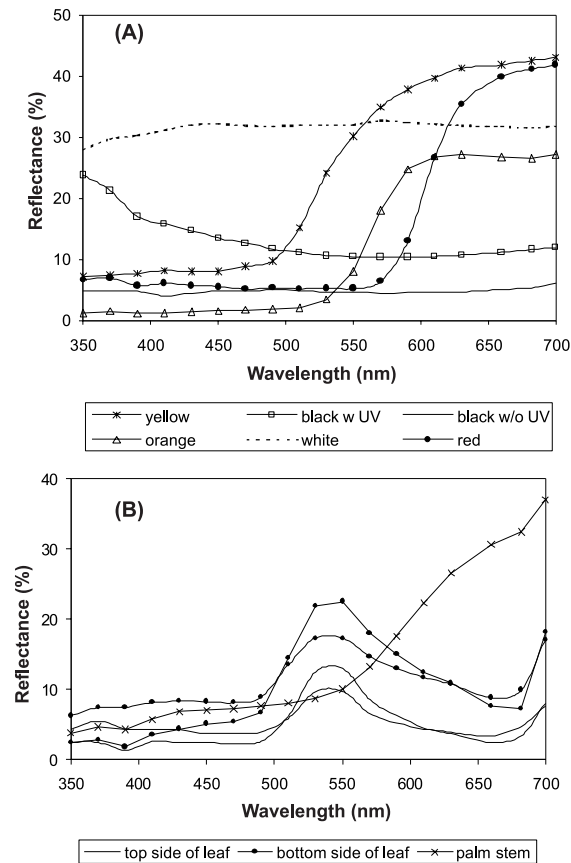


Fig. 1. (A) Typical fruit colour reflectance spectra. (B) Typical background colour spectra. Background structures were mainly green leaves or reddish brown stems.

display ($\chi^2 = 10.286$; $df = 1$; $p = 0.001$ /Fig. 4B). In experiments with the uni-coloured display of natural black ripe fruits and the bi-coloured display with

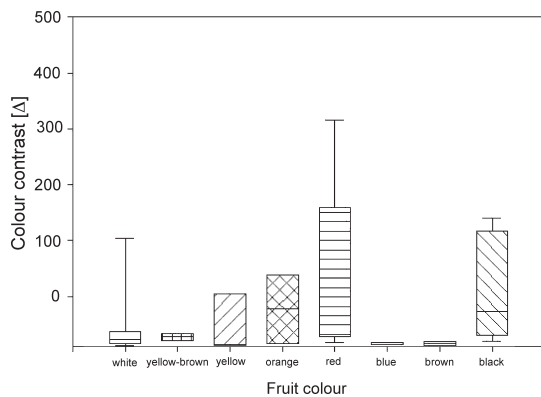


Fig. 2. Colour contrasts between brightness-normalised spectra of natural red and black fruits versus fruits of other colours. Contrasts are measured in Euclidean distance units. Fruit colours represented by only one fruit species are not included.

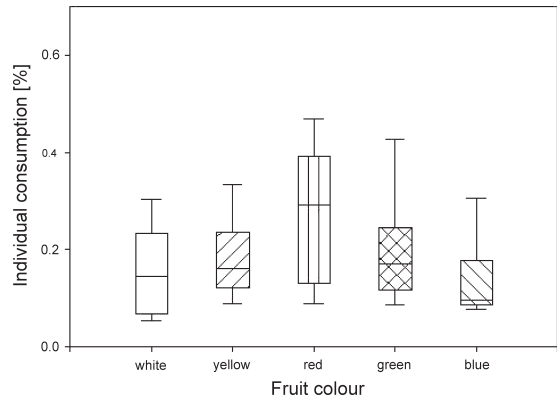


Fig. 3. Colour choice of three neo-tropical tanager species in cafeteria design experiments with five different fruit colours. Birds show no consistent colour preference.

additional green unripe fruits, birds of all species also favoured the contrasting display ($\chi^2 = 7.118$; $df = 1$; $n = 14$; $p = 0.008$ /Fig. 4C).

Discussion

This study presents the first objective assessment of fruit colour and conspicuousness of 43 fruit species of different families under natural illumination. In any light habitat (*sensu* Endler 1993), red and black fruits were the most conspicuous colours to background structures. Moreover, contrasts of these hues against background and not colour per se determined food choice in birds which preferred contrasting over uni-coloured displays. The global prevalence of red and black fruits appears thus to be explained by their greater conspicuousness against natural backgrounds compared to other fruit colours. The greater conspicuousness of these hues was also reported in *Coprosma* species using

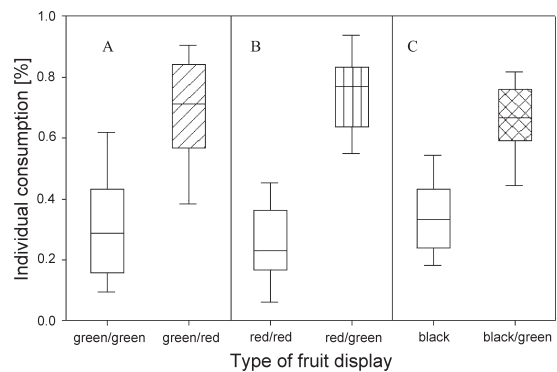


Fig. 4. Choice experiments with contrasting (barred) and uni-coloured (plain) food displays. Trials were conducted with artificial green (A) and red (B), and with natural ripe black and unripe green fruits (C).

standard illuminants and the CIE system developed for the human eye (Lee et al. 1994).

Considerations

Our experiments did not control for birds experience that may impact colour choices. However, birds of very different experience (wild caught vs captive bred and fed on an uncoloured diet more than six months prior to the trials) exhibited similar preferences for conspicuousness. Despite the short distance between food and consumers, conspicuousness determined fruit choice in four bird species regardless of fruits colour or context (artificial vs natural). We approached conspicuousness using only colour contrasts and not brightness patterns. Though contrasts increase numerically with brightness (Schmidt 2002), they are not necessarily perceived as greater in bright sunlight due to the Weber–Fechner law (Vorobyev et al. 1998) and the light-dark-adaptation mechanisms of the vertebrate eye. Hence, brightness-biased contrasts may not accurately reflect birds perception. Also, frugivorous silvereyes (*Zosterops lateralis*) used hue and not brightness as foraging cue (Puckey et al. 1996), and hue also defined signal content in mate choice in two bird species (Pearn et al. 2001, Heindl and Winkler 2003). Birds are sensitive to wavelengths from 320–700 nm (Honkavaara et al. 2002). Our contrast calculations extending from 350–700 nm do not measure contrasts in the extreme UV. However, our data cover the maximum UV wavelength absorbance in birds which is 360–370 nm or higher (Cuthill et al. 2000). Fruits with UV reflectance < 350 nm also reflect > 350 nm (Honkavaara et al. 2002) which we found in 2% of the fruits. Thus, we assume that our data provide a realistic approach to natural contrasts. Background structures such as leaves and bark do not reflect UV light (Endler 1993), which was also true for our sample.

The role of colour and conspicuousness

In our colour choice experiments, birds did not prefer any particular colour, but ate fruits randomly. Previous studies found mostly weak and transient avian colour preferences (Willson et al. 1990, Willson and Comet 1993). The only studies demonstrating consistent colour choices (red over orange, yellow, or white), recorded preferences for fruits presented against a green background of either cardboard or leaves (Puckey et al. 1996, Gervais et al. 1999). In this design, birds may have preferred red fruits because of their greater conspicuousness towards the green background, which has not been tested, instead of an innate preference for red.

The influence of conspicuousness on fruit selection rather than innate consumer preference has previously been proposed (Kerner 1895, Ridley 1930, Willson and

Hoppes 1989). Burns and Dalen (2002) demonstrated that red fruits displayed against a contrasting background had higher removal rates. However, the idea of the influence of conspicuousness has not yet been formally defined, and here we will term it the contrast hypothesis. The contrast hypothesis predicts that diurnal dispersers select fruit colours based on their conspicuousness and not their colour. We define conspicuousness at two spatial scales: (1) between the fruit display and its background and (2) within a fruit display i.e. between ripe fruits and coloured accessory structures (unripe fruits, stem, pedicles). The hypothesis assumes that greater contrasts of fruit displays increase the likelihood of dispersers fruit detection and subsequently consumption. If conspicuousness acts on dispersers decision in which plant to feed, it has impact on plant fitness and may lead to the evolution of conspicuous fruits.

Effects of disperser preferences

The fruit–frugivore system is characterized by complex interactions between a large heterogeneous group of plants and a very large heterogeneous group of consumers. Both groups differ considerably in generation length and the rate of evolutionary changes (Herrera 1985). Consequently, only traits ubiquitously present in consumers over evolutionary time have the potential to shape fruit traits. Colour vision is an ancient vertebrate trait presumably present in all contemporary diurnal avian frugivores and their ancestors (Neitz et al. 2001). Hence, selective pressures on conspicuousness persist even evolutionary changes in consumer assemblages because succeeding frugivorous bird species have similar colour perception. Acting prior to the various parameters that contribute to fruit selection (Schaefer et al. 2003), conspicuousness seems to be a fundamental key for plants to increase seed dispersal. Because colour vision is ubiquitously present in birds, conspicuousness has the potential to shape evolutionary processes in fruit species that are mainly consumed by diurnal dispersers. Conspicuousness will only translate into the evolution of fruit characters if opposing pressures of fruit pests do not eliminate the selective pressures of dispersers. Evidence on the function of fruit signals and on the visual perception of fruit pests is very limited. However, it is known that the visual perception of birds and insects differs strikingly in the lack of a long-wave receptor in many insect groups (Menzel and Backhaus 1990). Hence, colour contrasts of red fruits can act as a conspicuous long-distance signal on birds, while most insect fruit predators (wasps, beetles) will only perceive brightness contrasts. This difference in the visual perception of birds and insects may enable plants to use red fruit colour as a specific signal for dispersers only. This

does, however, not apply to black fruits. Birds and insects perceive black colour probably similarly because it is achromatic with an overall low reflectance. Differences in insect and bird perception of red but not black fruits lead to two assumptions: First, if red fruits are less conspicuous to frugivorous insects than black fruits, we predict that black fruits possess more effective defensive secondary compounds than red fruits to prevent insect damage. This conjecture expects, second, a higher frequency of invertebrate generalists feeding on red compared to black fruits. The prediction is yet to be tested by comparing secondary compounds or invertebrate feeding behaviour in red and black fruits.

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Appendix 1. Colour contrasts of brightness-normalised spectra between fruits and background with colours assigned to colour categories perceived by the human eye. Contrasts are measured in Euclidean distance units.

Species	Colour contrast [Δ]	Human colour categories
<i>Dacryodes microcarpa</i>	303.6	black
<i>Trattinickia bursereaefolia</i>	212.5	black
<i>Goupia glabra</i>	211.9	black
<i>Ouratea</i> sp. 2	199.0	black
<i>Ocotea</i> aff. <i>Amazonica</i>	190.9	black
<i>Miconia</i> sp. 1	141.3	black
<i>Oenocarpus bacaba</i>	56.7	black
<i>Euterpe precatoria</i>	53.4	black
<i>Cybianthus spicatus</i>	42.4	black
<i>Guatteria schomburgkiana</i>	26.0	black
<i>Dendrobanzia boliviana</i>	11.5	black
<i>Geonoma deversa</i>	1.6	black
<i>Ouratea</i> sp. 1	0.7	black
<i>Melastomataceae</i> Genus sp. 1	7.1	bluish black
<i>Melastomataceae</i> Genus sp. 2	0.8	bluish black
<i>Miconia</i> sp. 2	6.0	bluish black
<i>Clusia columnaris</i>	437.4	red
<i>Heisteria scandens</i>	354.0	red
<i>Pseudolmedia laevigata</i>	213.3	red
<i>Xylopia venezuelana</i>	188.0	red
<i>Iryanthea elliptica</i>	55.2	Light red
<i>Retiniphyllum schomburgkii</i>	43.8	red
<i>Iryanthea jurensis</i>	19.2	Light red
<i>Trichilia</i> sp.	12.6	red
<i>Fabaceae</i> sp.	2.0	red
<i>Paullinia capriollata</i>	211.8	white
<i>Phoradendron pellucidulum</i>	26.6	white
<i>Protium</i> sp.	14.5	white
<i>Dacryodes</i> c.f. <i>glabra</i>	9.8	white
<i>Diclinanona calycina</i>	5.1	white
<i>Psychotria</i> sp.	0.6	white
<i>Orthomene schomburgkii</i>	182.7	yellow
<i>Melastomataceae</i> Genus sp. 3	2.9	yellow
<i>Pouteria</i> sp. 1	1.9	yellow
<i>Picramnia</i> sp.	1.4	yellow
<i>Kutchubaea</i> sp.	7.7	brown
<i>Iriantella setigera</i>	1.4	brown
<i>Caryocar glabrum</i>	22.4	brownish-yellow
<i>Pouteria</i> sp. 2	10.6	brownish-yellow
<i>Emmotum acuminatum</i>	137.5	orange
<i>Tovomita</i> c.f. <i>umbellata</i>	5.3	orange
<i>Noranthea</i> sp.	125.9	pink
<i>Couma utilis</i>	68.2	green