Detectability and content as opposing signal characteristics in fruits

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Although often associated with consumers, fruit colours have rarely been assessed as signals. Here, we investigate the signal principles of 'detectability' and 'content' in bird-dispersed fruits. We determined detectability as the contrast between fruit and background and signal 'content' by correlating fruit colours and compounds. Red and black, the most common fruit colours globally, contrast more against background than other colours but do not indicate compounds. In other colours, 60% of the variation in long- to shortwave light correlated with protein, tannin and carbohydrate content. Because macronutrients stimulated fruit removal, while phenols, but not tannins, deterred it, signalling these macronutrients probably increases seed dispersal. Phenolic content was not signalled because it would reduce plants' fitness. Signalling tannins might be directed towards fruit pests rather than dispersers. In conclusion, plants may employ differential signalling strategies matching conspicuous signals in red and black fruits while other colours signal fruit quality. The latter implies that nutrient quality and fruit defence are communicated visually.

1. INTRODUCTION

Although fruit colours have interested ecologists and evolutionists for more than 100 years (Kerner 1895; Willson & Whelan 1990), a recent article states that 'the ecological and evolutionary processes responsible for fruit colour diversity are not well understood' (Burns & Dalen 2002). This might be owing to the paucity of adequate colour measurements and quantitative assessments of signalling functions in fruits. However, applying the extensive knowledge on signals in animal communication (Espmark *et al.* 2000) to fruit colours may yield new insights.

As a rule, senders and receivers use signals to increase their fitness. Accordingly, plants use fruit colours to trigger seed dispersal, while dispersers increase their fitness through nutrient intake. To track signal evolution, it has been useful to distinguish between the content and detectability of a signal (Schluter & Price 1993). Andersson (2000) demonstrated that these two aspects of signals

might sometimes be in conflict. He suggested that signals with an emphasis on detectability should be conspicuous and cheap, while content-related signals should correlate with the quality of the sender, be costly to produce, but not necessarily conspicuous. Assuming such a dichotomy from the perspective of the receivers, the colour of a fruit can either emphasize its detectability or indicate the reward that the disperser gains in nutrients. Fruit colours that were classified according to the human eye did not correlate with fruit contents (Wheelwright & Janson 1985). However, neither the variation in colour nor its relationship to allelochemicals was previously quantified. The detectability of a signal depends on the signal-to-noise ratio of object and background and can be measured as the contrasts between fruit and background. The most prevalent fruit colours globally, red and black (Wheelwright & Janson 1985), were more conspicuous against backgrounds in *Coprosma* species (Lee *et al.* 1994) and in a tropical plant community (Schmidt *et al.* 2004). In the latter sample, the fruit removal of all dispersers was stimulated by macronutrients and deterred by phenols whereas condensed tannins had no effect (Schaefer *et al.* 2003*a*). As fruits are generally characterized by high interspecific variation in contents (Herrera 1987), the low potential for interspecific variation within a colour, especially in black, may restrict the possibility for content indicating signals in red and black fruits. For simplicity, we thus hypothesize that red and black fruits have more relative emphasis on detectability, whereas other colours are better described as content signals indicating the nutrient quality of the fruit.

Knowing consumer preferences in the tropical plant community, we assumed effective content signals to be related to macronutrients but not to phenols. Therefore, we explicitly tested the predictions that red and black fruits are (i) less correlated with fruit compounds than are other fruit colours and (ii) cheaper in macronutrients. We (iii) explore the relationship between colour and deterrent (phenols) and non-deterrent (condensed tannins) allelochemicals.

2. MATERIAL AND METHODS

Fieldwork was conducted from October to December 1998 and October 1999 to February 2000 in a lowland rainforest in Venezuela (65°40′ W, 3°10′ N). We measured the reflectance spectra of 45 fruit species belonging to 25 families with a portable spectrometer (see Appendix A). For chemical analyses of energy, lipid, protein, carbohydrate, condensed tannin, total phenols (as per cent dry weight) and water contents and a list of the fruit species see Schaefer *et al.* (2003*a*).

According to the reflectance spectra, we categorized fruits into two groups: black/red versus other colours. We applied principal-component analyses (PCA) separately to the reflectance spectra of both groups to identify trends in colour variation. A PCA is advantageous because it is independent of assumptions on colour vision and thus applies to all consumers. The PCA transforms the many correlated variables of reflectance into a few orthogonal variables that are a weighted linear sum of the original data. The principal component coefficients of each species are the weights and they reflect which variation each principal component captures (figure 1). In fruits, we analysed energy, water and lipid, protein, carbohydrate, total phenol and tannin content. Only energy and water correlated with other variables and were dropped for subsequent multiple regressions (table 1). We employed stepwise multiple regressions on the log-transformed fruit compounds with the PCA reflectance scores as the dependent variable. Here, each principal component of each of the two colour groups was tested separately because they are by definition independent. A phylogenetic correction was not included in our regressions because previous analyses of fruit removal yielded no phylogenetic effects in this sample (Schaefer *et al.* 2003*a*). The costs of pigmentation in wild fruits remain unexplored. To assess costs,

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Table 1. Correlation matrix for fruit compounds in neither red nor black fruits.

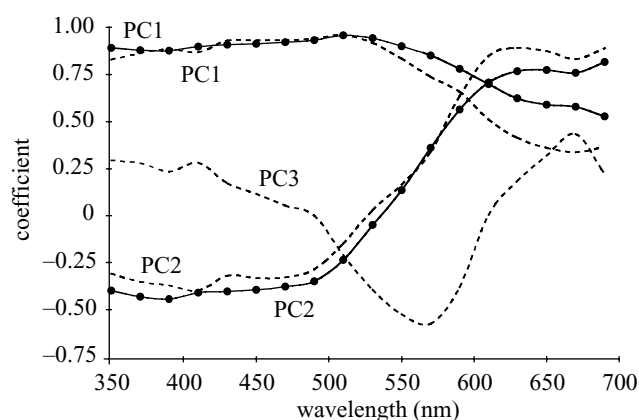|	carbohydrates	protein	lipid	phenol	tannin	water
energy	0.17	0.4*	0.94***	−0.17	−0.32	−0.32
carbohydrates		−0.22	−0.14	−0.05	−0.15	0.46**
protein			0.34	0.19	−0.06	−0.22
lipid				−0.19	−0.28	−0.47**
phenol					0.08	0.06
tannin						−0.17

$*p < 0.05$; $**p < 0.01$; $***p < 0.001$.

Figure 1. Principal component coefficients relating principal components to reflectance spectra. The dashed lines represent the three principal components of red and black fruits and solid lines with black circles represent the two principal components of other colours.

we measured the nutritional content because it directly represents the reward that the receiver is interested in. We had no *a priori* assumption regarding which component involves the costs necessary for content signals, so we tested for differences in all macronutrients between red and black fruits and those of other colours.

3. RESULTS

PCAs of reflectance spectra yielded three components in red and black fruits explaining 98% of variance while two components accounted for 95% of variance in other fruit colours. In both groups, variation in reflectance was similar with nearly identical principal component coefficients. PC1 represented variation in mean reflectance (brightness) characterized by positive coefficients of similar magnitude up to 550 nm and decreasing coefficients towards 700 nm. PC2 captured subsequent variation between the relative amount of long- to short-wavelength light with negative values at shorter wavelengths and positive values at long wavelengths (figure 1). In red and black fruits, concentrations of none of the fruit compounds correlated with any of the three PCs in multiple regressions. In other fruit colours, the first PC (brightness) was not linked to fruit contents ($r^2 = 0.125$, d.f. = 3, $F = 0.57$, $p > 0.05$). The second PC, however, explaining 27% of total variance in reflectance correlated positively with proteins and negatively with tannins and carbohydrates. A total of 60% of this variation in long- to shortwave light was explained by these three variables ($r^2 = 0.597$, d.f. = 3,

Table 2. Result of multiple regression on the correlation between fruit compounds and colour variation (PC2) in neither red nor black fruits.

variables	β	t	p-value
tannin	−0.534	−3.853	< 0.001
protein	0.521	3.707	< 0.001
carbohydrates	−0.336	−2.394	< 0.05
lipid	−0.165	−0.902	n.s.
phenol	−0.042	−0.206	n.s.

$F = 10.877$, $p < 0.0001$; table 2). Fruits with high PC2 scores were high in proteins but low in carbohydrates and tannins and vice versa in fruits with low PC2 scores. Red and black fruits did not differ from those of other colours in lipid, protein or carbohydrate contents (Mann–Whitney test: $n_1 = 20$, $n_2 = 25$, $z = −0.344$; all $p > 0.53$).

4. DISCUSSION

Black and red fruits are more conspicuous (Schmidt *et al.* 2004), but do not indicate fruit compounds. Conversely, 60% of the variation of long- to shortwave light in other colours correlated with the content of tannins, proteins and carbohydrates. Red and black colours thus have different signal functions than other fruit colours. The greater contrasts of red and black fruits match with signals emphasizing detectability, while other colours signal the quality of a fruit. This distinction is based on the relative emphasis of the signal and is not absolute; some yellow fruits exhibited more contrasts than some black or red fruits (Schmidt *et al.* 2004). Our results on the signal functions of fruit colours contrasts with work finding no association between fruit colour and compounds (Wheelwright & Janson 1985; Traveset & Willson 1998). The variation in colour was, however, not previously quantified with a PCA. This method captures the overall variation in reflectance. Most variation (typically greater than 90%; Cuthill *et al.* 1999) correlates invariably with brightness (PC1) which rarely carries signal information (Endler 2000). The correlation between PC2 and fruit compounds was not complete. The remaining variation might be explained by other compounds, but owing to the opposing β-values of nutrients (table 2), not by the caloric content of fruits.

Birds prefer conspicuous over low contrasting fruit displays even in short-distance experiments (Schmidt *et al.* 2004). Consequently, we reason that emphasizing

detectability by contrasting red and black colours increases the likelihood of rapid detection and fruit removal. We did not support the prediction that red and black fruits are less costly in nutrients, probably because it was too simplistic. If fruits of a certain colour had lower nutritional gains, consumers will quickly learn to avoid non-rewarding fruits because they make an association between the context and nutritional gain of foods (Hurly & Healy 1996). Whether the costs required for maintaining honest signals originate in the costs of pigmentation itself needs to be investigated. The correlation between colour (PC2) and fruit compounds in neither red nor black fruits illustrates that fruits of a saturated orange or yellow hue signal high protein, saturated blue fruits signal high carbohydrate and low tannin content, and white fruits (no variation in long- to shortwave light) are intermediate. Despite a similar reward in macronutrients, dispersers may still preferentially feed on fruits that indicate fruit quality because they can specifically complement their diets (Whelan *et al.* 1998; Witmer 2001), thereby avoiding the costs related to nutrient deficiency or excess. Such content signals are most effective if fruits are abundant and consumers can afford to be choosy. We thus predict a higher proportion of content signalling during the main fruiting seasons. Content-indicating signals will be especially effective in stimulating fruit removal if they signal rare fruit compounds. Because protein is generally limited in fruits (Herrera 1987), indicating high protein contents seems advantageous to plants. Fruits low in protein had high carbohydrate contents. Signalling the latter, these fruits will still be attractive to consumers because they preferentially consume high-sugar diets (Schaefer *et al.* 2003*b*).

The degree of indicating allelochemicals through content signals depended on their effect on dispersers. Plants did not signal phenols because, given that dispersers avoid phenols in fruits (Schaefer *et al.* 2003*a*), phenol-related signals would not increase plants' fitness. Conversely, condensed tannins, having no impact on the fruit removal of dispersers (Schaefer *et al.* 2003*a*), are signalled in low-protein fruits. If foods had a low protein-to-carbohydrate ratio, tannins inhibited the food intake of insects (Simpson & Raubenheimer 2001). Owing to the low protein-to-carbohydrate ratio in blue fruits (table 2), signalling tannin content might reduce insects' fruit attack. Red has been suggested to decrease insect predation through increased crypsis because some insect groups have low sensitivities to red light (Willson & Whelan 1990), but in non-red fruits signalling deterrence may be an efficient alternative strategy. In conclusion, our results demonstrate that fruit colours possess different, even opposing, signal properties that address multiple receivers (pests, dispersers) and may translate into differential signalling strategies of plants. A corollary is that the conventional approach of univariate fruit colour assessments is inappropriate to portrait plants' signals and to understand the ecological and evolutionary processes leading to fruit colour diversity.

APPENDIX A: SPECTROMETRIC MEASUREMENTS

We measured the colour of 20 mature fruits and 20 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 standardized light source were used. We measured reflectance as the proportion of a standard white reference tile (Top Sensor System WS-2). Spectra were processed with SPECTRAWIN v. 4.0 software and calculated in 5 nm intervals between 350 and 700 nm using the software package COLOURMASTER (H. Winkler, unpublished data). Our reflectance data from 350 to 700 nm were limited by spectrometer scope and do not measure contrasts in extreme ultraviolet (UV) light. However, our data cover the maximum UV wavelength absorbance in birds which is 360–370 nm or higher (Cuthill *et al.* 2000). Ambient light spectra were taken with a CC3 cosine-corrected irradiance sensor with a measuring surface of 6 mm in diameter, measuring incoming light over a solid angle of 180°. For irradiance measurements, we calibrated the spectrometer with a calibration lamp (Ocean Optics LS-1-Cal) of known spectral energy distribution. The probe was connected with a 200 or a 50 μm optical fibre, depending on light intensity. The cosine correction adjusts for signal differences resulting from differing angles of the incoming light. Reflectance and irradiance data were transformed into units of photon flux according to the methods described in Endler (1990). To obtain the colour spectra reaching the eye of a consumer, we multiplied the averaged reflectance spectra of each fruit species with corresponding ambient light spectra (Endler 1990, 1993). For each species, we photographed seven infructescences from 5 m distance and calculated the proportions of background structures (leaves, bark, pedicles, exocarp) within 1 m^2 to the nearest 10%. We used the average proportion of each background structure and calculated the Euclidean distance for the estimation of colour contrasts between the overall background and fruits. The Euclidean distance D was calculated as

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

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 spectrum of wavelength (350–700 nm). Owing to the influence of ambient light intensity, spectra were normalized to the same brightness (Endler 1990).

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