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Are Fruit Colors Adapted to Consumer Vision and Birds Equally Efficient in Detecting Colorful Signals?

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Online enhancement: table.

ABSTRACT: Reproduction in plants often requires animal vectors. Fruit and flower colors are traditionally viewed as an adaptation to facilitate detection for pollinators and seed dispersers. This long-standing hypothesis predicts that fruits are easier to detect against their own leaves compared with those of different species. We tested this hypothesis by analyzing the chromatic contrasts between 130 bird-dispersed fruits and their respective backgrounds according to avian vision. From a bird's view, fruits are not more contrasting to their own background than to those of other plant species. Fruit colors are therefore not adapted toward maximized conspicuousness for avian seed dispersers. However, secondary structures associated with fruit displays increase their contrasts. We used fruit colors to assess whether the ultraviolet and violet types of avian visual systems are equally efficient in detecting color signals. In bright light, the chromatic contrasts between fruit and background are stronger for ultraviolet vision. This advantage is due to the lesser overlap in spectral sensitivities of the blue and ultraviolet cones, which disappears in dim light conditions. We suggest that passerines with ultraviolet cones might primarily use epigamic signals that are less conspicuous to their avian predators (presumably with violet vision). Possible examples for such signals are carotenoid-based signals.

Keywords: avian color vision, frugivory, plant animal interactions, visual discrimination, sexual selection, coevolution.

Studies modeling the evolution of signals identified the detectability of a signal as one of the major components

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driving signal evolution (Schluter and Price 1993). Numerous studies supported this model documenting that animals seek out favorable environmental conditions to increase the detectability of their signals (e.g., Endler and Théry 1996). By contrast, plants are unable to move to favorable signaling sites, and whether or not plant signals evolved to maximize detectability is a contentious issue (Schaefer et al. 2004). Plant signals can be relatively simple, as fruits dispersed by diurnal consumers are mainly advertised by a single sensory channel: color (Korine et al. 2000; Schaefer et al. 2004). The detectability of fruit colors can be determined by measuring the contrasts between fruit and background color as seen by a fruit consumer.

Traditionally, the colors of fruits and the secondary structures associated with fruit displays (e.g., nongreen colored bracts and stems) are viewed as an adaptation to increase their detectability for seed dispersers (Kerner 1895; Willson and Whelan 1990; Schmidt et al. 2004). This assumption seems intuitively plausible given that most fruits change color during ripening and become more conspicuous when ripe, at least to the human eye. In an adaptive scenario where plants coevolve with seed dispersers, it is expected that fruit colors contrast strongly with background foliage (Burns and Dalen 2002). Because phylogenetic constraints on fruit colors are relatively weak (Voigt et al. 2004), certain colors are thought to have evolved in response to specific consumer guilds, for example, red and black fruits are associated with seed dispersal by birds (Wheelwright and Janson 1985; Willson and Whelan 1990). Innate preferences of some bird species for red fruits (Schmidt and Schaefer 2004) and for highly contrasting red and black fruit displays (Schmidt et al. 2004) might explain how such patterns have evolved.

A limitation to these studies, however, is that fruit signals were either classified by human observers or measured as the Euclidean distance between fruits and backgrounds and not according to the specific properties of the avian color vision system (i.e., the spectral sensitivities; Burkhardt 1982; Bennett et al. 1994). Thus, it remains unclear whether signal evolution in bird-dispersed fruits has indeed been driven to maximize the detectability for birds.

Adaptations of plant signals to their animal vectors might be difficult to prove (Vorobyev and Menzel 1999), but they undoubtedly occur, for example, in flowers that change color after pollination, thereby increasing the foraging efficiencies of their pollinators (Weiss 1991). Because plants show generally strong interspecific variation in leaf color (Lev-Yadun et al. 2004), the predominant background of fruit displays, under the premise that plant signals are adapted to consumer vision, we expect that fruit signals show maximized contrasts toward their own leaves.

The question whether such an adaptation in plant signals exists becomes more intriguing in light of recent studies demonstrating variation in the visual system of birds, one of the main seed-disperser groups. Depending on the position and spectral absorbance of the four cone types used for color discrimination, birds can be categorized into two groups. Parrots and most passerines possess an ultraviolet visual spectrum (UVS) system, with peak absorbance of the shortwave receptor around 360 to 375 nm. By contrast, most nonpasserines so far known and crows and tyrants possess a visual system that is shifted toward the violet part of the spectrum (VS), with peak absorbance at 405 to 425 nm (Bowmaker et al. 1997; Hart 2001; Ödeen and Hastad 2003). Both groups contain fruit-eating birds, such as parrots (UVS), manakins, and trogons (both VS). It remains as yet uncertain whether the differences in the visual systems translate into a differential ability to detect fruits or visual signals in general. If so, fruit signals might not only target specific disperser species while being less conspicuous to other birds, but the signals used by birds in other contexts, such as mate choice, might also differ between both groups.

To test whether fruit colors are adapted to consumer vision, we modeled how fruit signals are perceived by birds of both visual systems, assuming that discrimination is limited by receptor noise (Vorobyev and Osorio 1998). This model describes behavioral data on spectral sensitivity in a variety of animals, including humans, dichromatic mammals, bees, and birds (Goldsmith and Butler 2003). First, we tested whether 130 bird-dispersed fruit species exhibit contrasts to their own background structures different than to the mean of all 129 foreign backgrounds according to the spectral sensitivities of the avian UVS and VS systems. Second, we assessed whether secondary structures increase the contrasts of fruit displays relative to the contrasts between fruits and background. Because it has been suggested that mimicry occurs in sympatric fruit species (Burns 2005), we also assessed birds' abilities to discriminate different fruit species under different light conditions. Finally, we used the chromatic contrasts between fruits and backgrounds and asked whether UVS and VS vision are equally efficient to detect and discriminate visual stimuli.

Methods

Color Measurements

We measured the reflectance spectra of ripe fruits from 130 bird-dispersed temperate to subtropical plant species (see table A1 in the online edition of the *American Naturalist*) and their respective backgrounds with an Ocean Optics USB2000 spectrometer and a Top Sensor Systems deuterium-halogen DH-2000 as a standardized light source. Reflectance was measured as the proportion of a standard white reference tile (Top Sensor Systems WS-2). For the color measurements, we used a coaxial fiber cable (QR400-7, Ocean Optics) that was mounted inside a matte black plastic tube to exclude biases by ambient light. The angle of illumination and reflection was fixed at 45° to minimize the objects' glare. Spectra were processed with SpectraWin 4.0 software and calculated in 5-nm intervals from 300 to 730 nm.

Fruit Sample

Nearly half of the fruit species (43%) were collected from August 2003 to July 2004 in forests and open habitats consisting of woodlands and hedges in the vicinity of Freiburg, Germany. This sample comprises more than 80% of fruits present in that area. To test whether contrasts in a subtropical flora differ from those of the temperate flora in central Europe, we included fruits (20% of the sample) collected from February to April 2004 in the hardwood hammocks of northern Florida (United States) in the vicinity of Gainesville. The final 37% of species represent all species that ripened in the botanical gardens at Freiburg from October 2003 to July 2004. We included these species to be able to derive general conclusions about the contrasts of fruit signals that hold for a larger diversity of fruit colors (including pink, blue, brown, and orange) than found in the two floras. We classified the plant species belonging to 36 families as bird-dispersed according to published information, to direct observations of fruit removal, or to the assumption that fruits were bird-dispersed if they matched congeneric bird-dispersed fruits (according to published information) in size and fruit morphology. We consider all nongreen structures associated with the fruit display—such as bracts, stems, and unripe fruits—in sequentially ripening species as secondary structures. Fruit color is generally among the last traits that change during ripening (Regan et al. 2001), and we categorized a fruit as ripe if it was easy to detach from the plant, if it was relatively soft, and if it did not further change color. We used the average spectra of 20 ripe fruits and of 10 background spectra for each species and analyzed the chromatic contrasts as perceived by the avian eye.

Avian Eye Model

The cone spectral sensitivities of a bird having a UVS cone—the starling *Sturnus vulgaris*—and of a bird having a VS cone—the peacock *Pavo cristatus* (fig. 1)—were modeled using analytical approximation of cone visual pigment and oil droplet spectra (Govardosvskii et al. 2000; Hart and Vorobyev 2005) and microspectrophotometric data of pigment's peak positions, transmittance of oil droplets, and ocular media (Hart et al. 1998; Hart 2002). The model of detection thresholds (Vorobyev and Osorio 1998; Vorobyev et al. 2001) is based on the assumption that detection is mediated by chromatic (color opponent) mechanisms and that thresholds are set by noise originating in cones. Comparisons of behavioral thresholds with the predictions of the model indicate that these assumptions are valid (Maier and Bowmaker 1993; Vorobyev and Osorio 1998; Goldsmith and Butler 2003). The noise-to-signal ratio of a receptor mechanism is described by a Weber fraction (Vorobyev et al. 1998; Vorobyev et al. 2001). The relative values of Weber fractions of cone mechanisms were estimated from the ratio of cone numbers (Vorobyev and Osorio 1998; Vorobyev et al. 1998), and the absolute value of the Weber fraction was calculated from behavioral thresholds measured in Pekin robins *Leiothrix lutea* (Maier and Bowmaker 1993; Vorobyev et al. 2001).

First, we calculated the quantum catch of each class of single cones (long-wavelength sensitive [LWS], medium-wavelength sensitive [MWS], short-wavelength sensitive [SWS], ultraviolet sensitive [UVS]), denoted by the subscript i , as the integrated product over the wavelength λ of the receptor sensitivity spectrum $R_i(\lambda)$, reflectance spectrum $S(\lambda)$, and illumination spectrum $I(\lambda)$:

$$Q_i = \int_{\lambda} R_i(\lambda) S(\lambda) I(\lambda) d\lambda. \quad (1)$$

The quantum catches are used to find relative contrasts between fruits and leaves as the log of the quotient of quantum catches from both spectra (the use of logarithms is appropriate for photoreceptor intensity coding). The result of this calculation is the contrast Δf for each receptor type i :

$$\begin{aligned} \Delta f_i &= \ln(Q_i \text{ fruit}) - \ln(Q_i \text{ background}) \\ &= \ln(Q_i \text{ fruit}/Q_i \text{ background}). \end{aligned} \quad (2)$$

The contrast, so defined, does not depend on how the receptor spectral sensitivities are scaled, and hence, the model does not require assumptions about the adaptation of receptors. Note that where $(Q_i \text{ fruit})$ is similar to $(Q_i$

background), $\Delta f_i = \Delta Q_i / (Q_i \text{ background})$, where $\Delta Q_i = (Q_i \text{ fruit}) - (Q_i \text{ background})$.

To quantify discrimination using signals of four types of single cones, each receptor class is first assigned a limiting Weber fraction, ω_i , based on the noise-to-signal ratio of an individual cone, v_i , and the number of cones per receptive field, η_i (Vorobyev et al. 2001):

$$\omega = \frac{v_i}{\sqrt{\eta_i}}. \quad (3)$$

The ratios of avian cone numbers is LWS 4 : MWS 2 : SWS 2 : UVS 1 (Vorobyev and Osorio 1998). Equation (3) explicitly assumes that the relative noise in cone channels does not depend on the signal, that is, that the Weber law holds. This law is valid in conditions of bright illumination. In conditions of dim light, the Weber law is no longer valid, and both the internal noise in the photoreceptors and the fluctuations of the number of absorbed photons set the threshold. In this case,

$$\omega = \sqrt{\frac{v_i^2}{\eta_i} + \frac{1}{Q_i}}, \quad (4)$$

where Q_i is the quantum catch per receptive field and integration time. Obviously, thresholds calculated using equation (4) depend on the illumination level. Here, we present the calculations assuming that the quantum catch for the long-wavelength-sensitive double cone viewing a 100% reflecting white surface cones is equal to 1,000 photons per integration time.

Then, we calculate discrimination values for the tetrachromatic visual systems:

$$\begin{aligned} (\Delta S)^2 &= (\omega_1 \omega_2)^2 (\Delta f_4 - \Delta f_3)^2 + (\omega_1 \omega_3)^2 (\Delta f_4 \Delta f_2)^2 \\ &+ (\omega_1 \omega_4)^2 (\Delta f_3 - \Delta f_2)^2 + (\omega_2 \omega_3)^2 (\Delta f_4 \Delta f_1)^2 \\ &+ (\omega_2 \omega_4)^2 (\Delta f_3 - \Delta f_1)^2 \\ &+ \frac{(\omega_3 \omega_4)^2 (\Delta f_2 - \Delta f_1)^2}{(\omega_1 \omega_2 \omega_3)^2 (\omega_1 \omega_2 \omega_4)^2 + (\omega_1 \omega_3 \omega_4)^2 + (\omega_2 \omega_3 \omega_4)^2}. \end{aligned} \quad (5)$$

Results of calculations using equation (5) provide the chromatic distance (ΔS) separating the perceptual values of two spectra in receptor space. The units for ΔS are JNDs (just noticeable differences): 1 JND is at the threshold of discrimination, values <1 JND indicate that two colors are indistinguishable, and values >1 JND indicate that spectra can be discriminated (Osorio and Vorobyev 1996). However, the absolute value of noise may vary because the

viewing conditions affect the degree of spatial and temporal summation. To account for such variations, we performed calculations assuming several values of noise. Increase of the noise level results in the corresponding increase of the threshold distance. We first assume that the limiting Weber fraction of the LWS cone mechanism is 0.05 and refer to the corresponding threshold as 1 unit distance. Note that the limiting Weber fraction of LWS cones estimated from the behavioral data of Maier and Bowmaker (1993) is 0.1. We consider the possibility that the noise is increased up to 0.5; such value corresponds to 10 units distance. Because noise above 0.5 is physiologically implausible, we assume that all fruits whose distance to background exceeds 10 units can always be detected.

Because visual signals depend on the ambient light conditions, we assessed the color contrasts of fruits in two different light environments. We chose the two most distinct ones: green light as in the forest understory and white daylight (D65) as present in open gaps (Vorobyev et al. 1998). For both light environments, we calculated chromatic distances of fruits in bright and dim light conditions. The model has obvious limitations: it cannot be used for very dark (black) spectra because the contrast to 0 is not defined. We assumed that fruits are black for birds if the quantum catch of all cones did not exceed 2% of the quantum catch corresponding to a 100% reflecting white surface (Regan et al. 2001). We only used fruits that produced higher quantum catches.

Statistical Analysis

Color contrast values for a given pair of species are likely to depend on their phylogenetic proximity or taxonomic distance. To explore how contrast patterns are related to taxonomic affinity, we analyzed the autocorrelograms of fruit-background contrast values on taxonomic distance. A taxonomic distance matrix (Gittleman and Kot 1990) was obtained for the studied species. We used “library ape” in the R package (R Development Core Team 2003) to estimate the autocorrelogram describing variation in taxonomic autocorrelation (Moran’s I) of contrast values for successively distant taxonomic categories (genera, family, order, subclass and class). A significant autocorrelogram for a given taxonomic level would indicate a “phylogenetic signal” at that level for the contrast values.

Results

Fruit Signals

For avian UVS vision, fruits did not contrast differently against their own background compared to the median

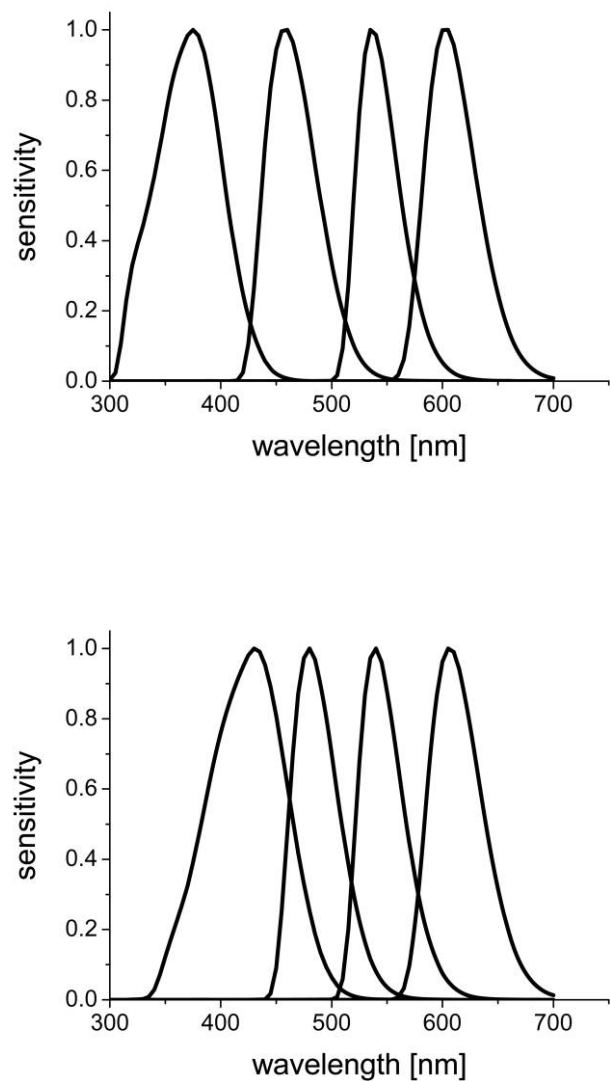


Figure 1: Spectral sensitivities of the four avian cone types. Characteristic for the UVS system is the starling (*top*) and for the VS system is the peacock (*bottom*). Note the lesser overlap between shortwave cones in the starling.

contrast of the 129 pairings to nonspecies-specific backgrounds (sign test, $P > .05$) in standard daylight (D65) and in green light. For the avian VS visual system, fruits contrasted less to their own background than to nonspecies-specific backgrounds (sign test, $P < .05$). We found a marginally significant autocorrelation value for fruit contrasts only at the genus level (Moran’s I = 0.14080, $P = .084$, $N = 130$), with higher taxonomic levels showing nonsignificant values and decreasing autocorrelation with increasing taxonomic distance. This suggests a trend for congeners to show similar fruit-foliage contrast patterns, although high within-genus variation exists.

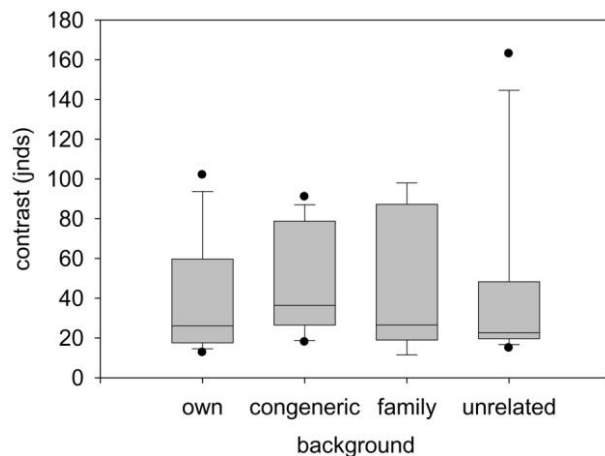


Figure 2: Contrasts between fruits and their own background, the background of congeneric species, of species from different genera within the same family, and of unrelated species. Indicated are median, midquartiles, ninetieth and tenth percentiles, and fifth and ninety-fifth percentiles as outliers.

To assess the effects of congeneric species within our fruit sample, we repeated the analyses of fruit contrasts twice, first using only one randomly chosen species from each genus and then using only a single randomly chosen species from each family. With one species per genus, the results were the same: for the UVS vision, fruits did not contrast differently against their own background compared to foreign backgrounds (sign test, $P > .05$), and fruits contrasted less to their own background for the VS vision (sign test, $P < .05$). With only one species per family, fruits had in both types of avian vision similar contrasts against their own background and against the backgrounds of other species (both sign tests, $P > .05$). Similarly, repeating the analysis using only genera that were represented by at least two species yielded similar results: the contrasts between fruits ($n = 90$) and their species-specific background do not differ from the contrasts of these fruits to the background of congeneric species, the background of species from different genera of the same family or from different families (ANOVA, $F = 0.09$, $P > .05$; fig. 2). We therefore conclude that plants do not optimize the chromatic contrasts of fruit colors toward the background.

Colored secondary structures, however, show larger chromatic distances to the background than the corresponding fruits. They therefore increase the contrasts of the entire fruit display for both visual systems (Wilcoxon test, $n = 22$, UVS: $z = -1.96$, $P < .05$, VS: $z = -2.81$, $P < .01$, fig. 3). Secondary structures also had larger chromatic contrasts to background than fruits when we used only one species per genus (Wilcoxon test, $n = 12$, UVS:

$z = -2.11$, VS: $z = -2.51$, both $P < .01$). Repeating this analysis with only one species per family yielded no differences between the contrasts of secondary structures and fruits to background (Wilcoxon test, $n = 8$, UVS: $z = -1.12$, VS: $z = -1.68$, both $P > .05$).

Fruits originating from Germany, Florida, and the botanical garden did not differ in their contrasts to background (mean \pm SE, UVS: Germany: 25.6 ± 3.0 , Florida: 25.7 ± 3.7 , botanical garden: 23.6 ± 2.3 , VS: 20.1 ± 1.7 , 17.5 ± 1.2 , 18.2 ± 1.2 , respectively) in both visual systems (ANOVA, UVS: $F = 0.17$, VS: $F = 0.75$, both $P > .05$). This result persisted when we used only a single species per genus or per family for each group (ANOVA, UVS: $F < 0.21$, VS: $F < 0.53$, both $P > .05$). To analyze group-specific differences in the contrasts created by secondary structures, we had to unite the three species from Florida with the six species from the botanical garden into one group. There was no difference in the contrasts between fruits from that group and fruits from Germany (t -test, $t = 0.95$, $P > .05$).

Comparison of Avian Visual Systems

The majority of fruits (UVS: 97%, VS: 96%) showed chromatic contrasts above five units toward their background (median UVS 19.2, range 1.9–108.2; median VS 17.3, range 1.0–50.2 units). Under bright light conditions, fruits had stronger chromatic contrasts toward the background in the UVS compared with the VS visual system in both green and white light (Wilcoxon test, $n = 130$, white light:

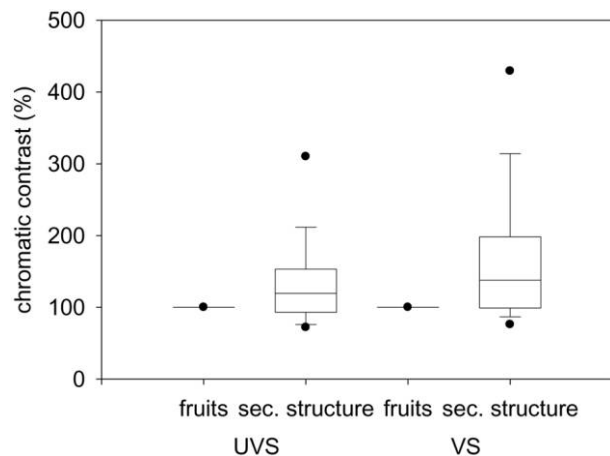


Figure 3: Secondary structures, that is, nongreen bracts or unripe fruits, increase the contrasts between ripe fruits and leaves for birds with ultraviolet and violet vision. The contrasts of secondary structures are given relative to those of ripe fruits that are illustrated as 100%. Indicated are median, midquartiles, ninetieth and tenth percentiles, and fifth and ninety-fifth percentiles as outliers.

Table 1: Chromatic contrasts of fruit as seen by birds of the UVS and VS systems (see fig. 4)

Spectra in figure 4	Species	Hue	Contrast	
			UVS	VS
a	<i>Cotoneaster divaricata</i>	Red	38.3	26.5
b	<i>Crataegus crusgalli</i>	Red	13.2	13.4
c	<i>Symphoricarpos albus</i>	White	25.3	12.6
d	<i>Phoradendron serotina</i>	White	13.8	13.7
e	<i>Cotoneaster nigra</i>	Black	14.8	4.8
f	<i>Phellodendron amurense</i>	Black	6.9	6.3

$z = -5.67$, green light: $z = -6.02$, both $P < .001$). We repeated this comparison excluding all fruits with chromatic distances above 10 units in order to avoid the result being biased by large differences in stronger contrasting fruits. Such differences might not be relevant if fruits above a certain threshold are detected with 100% probability regardless of the magnitude of contrasts. Again, these low-contrasting fruits had stronger chromatic contrasts for the UVS than for VS vision (Wilcoxon test, <10 units, $n = 22$, $z = -2.93$, $P < .01$). Fruits differ in their detectability for UVS and VS vision (table 1) if their reflectance changes in a relatively narrow spectral area (e.g., 410–425 nm or 470–490 nm; fig. 4) where both systems differ in their spectral sensitivity. In dim light conditions, however, birds of both visual systems perceive the chromatic contrasts of fruits similarly (Wilcoxon test, $n = 130$, D65: $z = -0.16$, green: $z = -0.32$, both $P > .05$). All fruits had much lower chromatic contrasts in dim light compared with bright light (fig. 5).

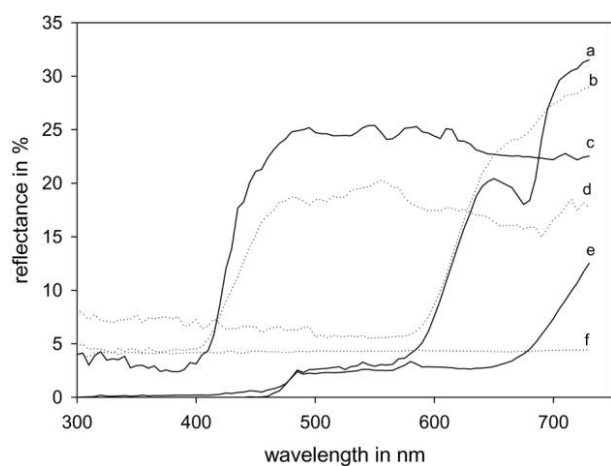


Figure 4: Solid lines denote the reflectance spectra of white, red, and black fruits (as perceived by humans) with stronger contrasts for birds with ultraviolet cones, whereas white, red, and black fruits contrasting similarly for both types of avian vision are indicated by dotted lines. Contrasts and names of these fruits are given in table 1.

Discrimination of Fruits

To estimate the potential of birds with UVS and VS visual systems to discriminate fruits from each other, we calculated the chromatic distance between all fruits. We limited our analysis to those pairs of fruits whose distance did not exceed 10 units, assuming all other fruits can be reliably discriminated. Under bright light conditions, birds with UVS systems discriminated fruits better than birds with VS systems (Wilcoxon test, D65: $n = 61$, $z = -4.23$, $P < .0001$; green: $n = 72$, $z = -4.01$, $P < .0001$; fig. 6). In dim white light, chromatic distances were similar for birds with UVS and VS systems (Wilcoxon test, D65: $n = 298$, $z = -0.84$, $P = .4$). In dim green light, however, birds with a UVS system were better in discriminating colored stimuli ($n = 298$, $z = -2.22$, $P < .05$).

Discussion

Considerations

Because we used a conservative method including different cues that are not based on color to assess the ripeness of fruits, we consider it unlikely that our classification of ripeness biased the results reached in this study. Furthermore, from the plants' perspective, a fruit is ripe when the seeds are viable, which is often the case in green fruits and usually happens before the changes in fruit traits that we used (Foster 1977). A distinctive feature of our analysis of colors is that we used a model based on the avian eye design and behavioral studies of color thresholds (Maier and Bowmaker 1993; Goldsmith and Butler 2003; Hart and Vorobyev 2005). The model is based on the assumption that detection is mediated by chromatic mechanisms alone. It describes color thresholds in birds when tested with relatively large stimuli (Maier and Bowmaker 1993; Goldsmith and Butler 2003), that is, in conditions that favor detection by chromatic mechanisms (Giurfa and Vorobyev 1998; Vorobyev and Osorio 1998). However, it remains uninvestigated how birds detect colored stimuli in more natural conditions, for example, fruits that vary in size and distance to them. It is also important to note that the model does not predict to which fruits birds attend first; it only predicts whether a fruit is detected or not, once a bird is looking at it.

Fruit Signals

The plants of our sample did not optimize the chromatic contrasts between fruits and foliage according to the visual perception of birds. Although we found the tendency that congeneric species show similar fruit-foliage contrasts, this result seemed robust against phylogenetic biases because it remained unaltered when we limited the analyses to a single species per genus or family. Because we did not find

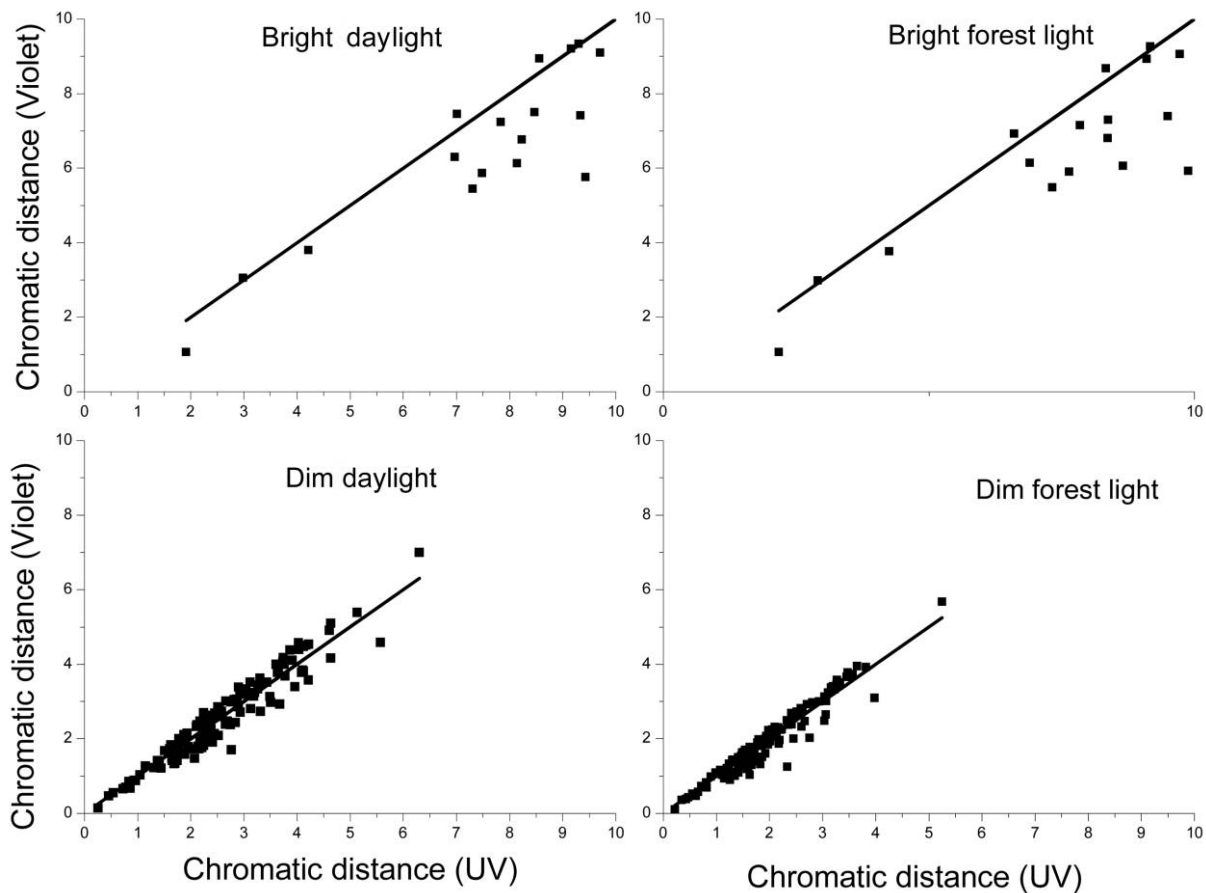


Figure 5: Efficiency in fruit detection against the background of leaves of avian ultraviolet (UV) and violet vision differs depending on light intensity. Each fruit with chromatic contrasts below 10 units is indicated by a point, and the solid line denotes equal detectability for both visual systems. In bright light, the UV vision perceives contrasts of fruit signals as greater; that is, points deviate to the right of the solid line, whereas there is no difference in dim light.

any difference between fruits from the three groups that we sampled, this result applies to the temperate flora of central Europe and to the subtropical flora of Florida. We therefore reject our coevolutionary hypothesis (termed “foliage-color contrast hypothesis”; Burns and Dalen 2002); that is, fruit colors evolved specifically to increase detectability to avian frugivores. Secondary structures, however, increase the conspicuousness of fruit displays but are uncommon (22 out of 146 species), as in a previous study (Herrera 1987). Again, this result persisted when we considered only a single species per genus. Restricting the analysis to a single species per family did not result in increased contrasts of secondary structures, most probably due to the small sample size ($n = 8$).

Our study is the first to investigate the perception of fruits according to avian vision. The possible coevolution between fruit colors and consumer vision has, however, been inten-

sively studied in primates. Eye models on primate color vision predict that trichromacy is advantageous—compared to dichromacy—for finding fruits against foliage (Osorio and Vorobyev 1996). In trichromatic primates, photopigments are optimized for finding fruits and other colored targets, for example, young reddish leaves against a background of mature leaves (Sumner and Mollon 2000a; Regan et al. 2001). However, fruit color is not as important as background heterogeneity, that is, variance in the chromaticities of leaves in determining the optimal set of photopigments in primates (Sumner and Mollon 2000a). This conclusion might explain the current controversy over the relative advantage of trichromacy in experimental studies (Dominy et al. 2003; Smith et al. 2003). Similar to our study, Sumner and Mollon (2000a) rejected the coevolutionary hypothesis that fruit colors evolved in response to the visual perception of primates because primates are adapted to de-

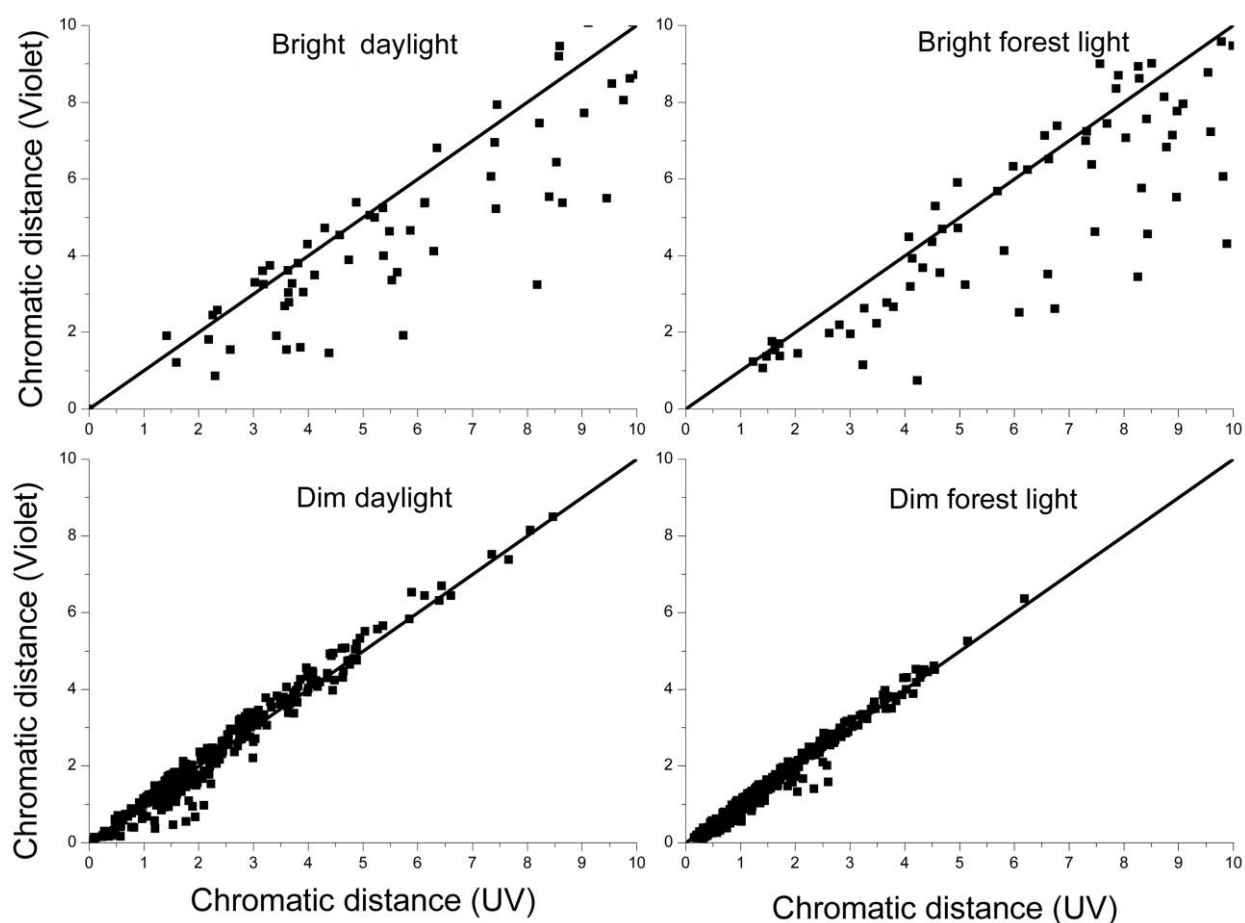


Figure 6: Efficiency in discriminating fruits from each other of avian ultraviolet and violet vision differs depending on light intensity. See legend to figure 5.

tect anything that is not a mature leaf and because only a portion of the fruits consumed by them matched the primate dispersal syndrome.

How can the lack of signal optimization toward consumer vision in our fruit sample be explained if birds prefer contrasting fruit displays (Schmidt et al. 2004)? For birds, the majority of fruits (87% for the UVS type and 84% for VS type) exhibit considerable contrasts above 10 units toward their background. If contrasts of more than 10 units lie above the threshold critical for detection, the majority of fruits are sufficiently easy to detect, and the evolution of fruit signals is unlikely to be driven toward further contrast maximization. This conclusion is consistent with the low frequency of secondary structures that enhance the contrasts between fruits and backgrounds. We emphasize, however, that the detection threshold depends on the size of the target and the distance between fruit and observer. For example, in primate-dispersed fruits,

chromatic contrasts are inversely related to fruit size (Sumner and Mollon 2000b). This is consistent with an adaptive view on fruit signaling because smaller fruits of the same contrast are more difficult to detect than larger fruits.

Other possible explanations for the lack of signal optimization are that less contrasting fruit colors may indicate specific fruit compounds and thus represent a different signaling strategy (Schaefer and Schmidt 2004). Alternatively, pleiotropic effects of correlated selection acting on fruit color alleles, such as defense against pathogens or predators (Whitney and Stanton 2004), may prevent plant signals from adapting to consumer vision. In this scenario, signal evolution in plants represents a trade-off between the defensive functions and the attraction of animal vectors through visual signals. The combined selective pressures of fruit pests and seed dispersers might then select for those pigments that simultaneously serve both functions. Our result that plants have not maximized the

conspicuousness of fruit signals strongly suggests that the traditional paradigm of analyzing fruit signals solely in respect to consumer vision is outdated.

Comparison of Avian Visual Systems

In bright light, the chromatic contrasts of fruit signals relative to their background and to other fruits are stronger for the avian UVS compared to the VS system. However, this difference in the efficiency of both visual systems disappears under dim light conditions, except for the fruit-fruit comparison in green light. If, as in bright light, UV and violet-sensitive cones have the same level of noise, UV vision is beneficial for discriminating color signals, corroborating previous results on bird plumage (Vorobyev et al. 1998). The relative advantage of UV vision is caused by the lesser extent of overlap between the violet and blue-sensitive cone types (fig. 1). Reduction of cone overlap generally leads to an increase in the number of discriminable colors (Govardosvskii 1983; Vorobyev 2003). This advantage disappears in dim light because the noise of UV cones increases to higher levels than in violet cones owing to the lower quantum flux in the UV part of the spectrum.

The two types of avian vision differ strikingly in their ability to discriminate color. White (for humans) fruits steeply increasing in reflectance at 410 to 425 nm are more contrasting to the UVS than to the VS system, as are black and red fruits with a modest increase in reflectance at 470 to 485 nm (table 1). At 410 to 425 nm, the UVS system possibly outperforms the VS system because its blue-sensitive cone catches more light quanta in this range. At 470 to 485 nm, the lesser overlap of blue and violet cones produces a more distinct output in the UVS system, probably allowing for better wavelength discrimination. By contrast, birds from both types of visual systems perceive chromatic signals similarly if they change reflectance above 550 nm (yellow red) or in the blue part of the spectrum at 440 to 460 nm (fig. 4, line *b*), areas where both systems are equally sensitive.

We conclude that the position of maximal wavelength change in a signal—that is, hue—does not reliably predict its detectability, neither for conspecifics nor for predators. Instead, we show that the detectability of a signal might be determined by minor changes in reflectance if they occur in an area of relatively high spectral sensitivity of the avian eye. This result has important implications for the study of animal signals. Since signal design is a trade-off between efficient signaling to intended (mate) and inefficient signaling to unintended (predator) receivers (Endler 2000), the sender of a signal will benefit if it has higher detectability for conspecifics than for predators. We predict that plumage signals that increase contrasts to background in the wavelength range between 410 to 425

and 470 to 485 nm will be common in passerine birds with UVS vision because they are less conspicuous to hawks with VS vision (Ödeen and Hastad 2003; Håstad et al. 2005). It has to be cautioned, however, that the classification of hawks as possessing VS vision is based on the molecular data of very few species and that no physiological data are currently available. Possible examples for signals with such characteristics are carotenoid-based colors, which change reflectance in the area of high spectral sensitivity of the passerine eye (Hunt et al. 2003; MacDougall and Montgomerie 2003). At present, the relative contribution of reflectance between 400 to 500 nm to the detectability of carotenoid-based signals remains unexplored, mainly because most research focused on variation in the yellow and red part of the spectrum. We emphasize the need to study epigamic color signals in those parts of the visible spectrum in which mates and predators might differ in their ability to discriminate visual signals.

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