The role of chromatic and achromatic signals for fruit detection by birds

H. Martin Schaefer,[a] Douglas J. Levey,[b] Veronika Schaefer,[a] and Michael L. Avery[c]
[a]Albert Ludwigs-Universität Freiburg, Institute of Biology 1, Hauptstrasse 1, 79104 Freiburg, Germany,
[b]Department of Zoology, University of Florida, PO 118525, Gainesville, FL 32611-8525, USA, and
[c]United States Department of Agriculture, Animal and Plant Health Inspection Service, Florida Field
Station, 2820 E. University Avenue, Gainesville, FL 32641, USA

Fruit color changes during ripening are typically viewed as an adaptation to increase signal efficacy to seed dispersers. Plants can increase signal efficacy by enhancing chromatic (wavelength related) and/or achromatic (intensity related) contrasts between fruit and background. To assess how these contrasts determine the detectability of fruit signals, we conducted 2 experiments with free-flying crows (*Corvus ossifragus*) under seminatural conditions in a 2025 m^2 aviary. Crows searched first for artificial red and black fruits and detected red fruits from a larger distance. Because artificial red fruits had higher chromatic and lower achromatic contrasts against foliage than artificial black fruits, crows apparently prioritized chromatic contrasts. Thus, the common change in fruit color from red to black during ripening does not increase signal efficacy to crows. In a second trial, crows searched for UV-reflecting and black blueberries (*Vaccinum myrtillus*) against backgrounds of foliage and sand. Against foliage, UV-reflecting berries had higher chromatic and achromatic contrasts than black berries, and crows detected them from a larger distance. Against sand, UV-reflecting berries had low achromatic contrasts and black berries low chromatic contrasts. Crows detected both fruit types equally, suggesting that they used chromatic contrasts to detect UV-reflecting berries and achromatic contrasts to detect black berries. Birds prioritized chromatic contrasts when searching for artificial red fruits in foliage but not when searching for blueberries on sand. We suggest that the relative importance of chromatic and achromatic contrasts is contingent on the chromatic and achromatic variance of the background. Models of signal perception can be improved by incorporating background-specific effects. *Key words:* eye model, frugivory, fruit color, perception, seed dispersal, vision. *[Behav Ecol 17:784–789 (2006)]*

Organisms use signals to communicate information about their phenotypic or genotypic quality. Simulation models predict that receivers select for easily detectable and honest signals (Schluter and Price 1993). Thus, hypotheses on signal evolution focus on efficacy (detectability) of signals and on reliability of the information transferred by signals (Guilford and Dawkins 1991; Endler 2000). Although it is usually assumed that plants use conspicuous colors to attract animal vectors to fruits and flowers (Borges et al. 2003; Schaefer and Schmidt 2004), it remains unclear how most animals perceive those signals (Endler 1993). This is important because differences in perception by different animal taxa may underlie widespread patterns in fruit and flower color (Schaefer et al. 2004).

Two recent studies concluded that birds, the largest taxon of seed dispersers, prefer high-contrast over low-contrast fruit signals (Burns and Dalen 2002; Schmidt et al. 2004). A limitation of these studies is that contrasts were not quantified according to avian visual perception. Physiological models of eye function (Vorobyev and Osorio 1998; Hart 2001; Vorobyev et al. 2001) increasingly allow such quantification (Heiling et al. 2003; e.g., Thery and Casas 2002).

Although models of avian vision are widely used to explain color patterns in prey (Siddiqi et al. 2004; Bruce et al. 2005; Thery et al. 2005), their ability to predict birds' detection of colored stimuli under natural conditions is untested. Such a test is important because eye models make no predictions on signal detectability if the intensity of illuminating light

varies (Vorobyev and Osorio 1998) or if targets differ in size and distance to the signal receiver. Of particular relevance, color signals may be conspicuous at close range and cryptic when viewed from a distance (Endler and Thery 1996; Marshall 2000; Heindl and Winkler 2003). Moreover, even in constant conditions, both birds and insects apparently use different signal parameters depending on the size of the target. Chromatic (wavelength related) aspects of color are important for the detection of large objects, whereas achromatic (intensity related) aspects are important for the detection of small objects (Osorio et al. 1999; Spaethe et al. 2001). The relative importance of chromatic and achromatic contrasts is not incorporated into eye models for assessing signal efficacy. There is, however, indirect evidence that birds primarily attend to chromatic contrasts because avian predators select for reduced chromatic but not achromatic contrasts in prey (Stuart-Fox et al. 2004; Håstad et al. 2005).

We conducted 2 experiments on avian fruit detection in a large (2025 m^2) seminatural aviary. Our goals were 1) to test predictions of physiological eye models under field conditions and 2) to test the relative importance of chromatic and achromatic contrasts in signal detection. Specifically, we observed the distance at which crows (*Corvus ossifragus*) detected red versus black fruits and UV-reflecting versus black (non–UV reflecting) fruits. We tested detection of red and black fruits because these colors are the most common colors of bird-dispersed fruits and because many fruits change from red to black during ripening (Wheelwright and Janson 1985; Willson and Whelan 1990). Assuming that fruit color changes during ripening are adaptive in the context of signal theory (i.e., if color changes increase detectability), we predict that black fruits will be detected from a larger distance than red fruits.

We tested for detection of UV reflection because many bird-dispersed fruits have a UV "bloom" that is assumed to target

avian seed dispersers, which can perceive UV (Burkhardt 1982; Altshuler 2001). Comparing fruit detection of UV-reflecting and black fruits against foliage also allowed us to test the core prediction of an avian eye model (Vorobyev et al. 2001) that targets (fruits) with higher chromatic and achromatic contrasts will be detected at a larger distance than targets with lower contrasts. We also used a second type of background, sand, because UV-reflecting fruits were only distinguishable from sand by chromatic contrasts and black fruits only by achromatic contrasts. This design allowed us to test the relative importance of these contrasts for fruit detection. If birds prioritize one type of contrast over the other, we predicted differences in the distance from which UV-reflecting and black fruits would be detected against sand.

METHODS

Species selection

We chose crows as a study species because they commonly consume fruits and adapt well to the large aviary we used. Furthermore, their relatively large size made it possible for us to keep them in sight and to closely observe their foraging behavior.

Diurnal birds use 4 retinal cone types for color vision and are classified into 2 distinct groups by the peak sensitivity of the short-wave cone (Ödeen and Hastad 2003; Endler and Mielke 2005). In the U-system group, peak sensitivity is shifted to the UV part of the spectrum, and in the V-system, it is shifted to the violet part of the spectrum (Ödeen and Hastad 2003). Each group contains frugivorous birds. Crows have been assigned to the V-system group, based on molecular data (Ödeen and Hastad 2003). Knowledge of cone sensitivities in different bird species is limited (Hart 2001), but interspecific variability in each group is considered relatively small (Håstad et al. 2005). Therefore, our results are likely to apply to other frugivorous species with the V-system. We caution against applying them to species with the U-system.

Experimental design

From December 2003 to February 2004, we captured 23 crows in Alachua County, Florida (United States), using a modified Australian crow trap (Gadd 1996). We maintained crows in groups of 2–4 in cages (1.2 × 1.2 × 1.8 m) at the National Wildlife Research Field Station in Gainesville, Florida. Birds were caught no more than 6 weeks prior to trials and were released immediately afterward. Nine days prior to a given crow's trial, the bird was placed alone in a cage and provided with 2 black and 2 red beads (artificial fruits; see below) that were wired together and attached to a food cup, allowing the crow to associate the color signal with a food reward without developing a color preference. Food cups were hung in front of palm leaves. After 7 days of habituation, crows were released singly into a large seminatural aviary (45 × 45 × 5 m), which contained various nonfruiting bushes and trees, including 22 lady palms (*Rhaphis* spp; height 2–2.5 m) that were regularly spaced on a large patch (30 × 30 m) of bare sand.

We conducted 2 experiments on fruit detection. In both trials, we defined detection distance as the distance between a fruit display and where a crow started to fly or walk directly toward that display. If, however, the crow did not consume the nutritional reward associated with the display within 1 min (usually much less) after moving toward it, we assumed the display had not been detected. This happened only 5 times. In most cases, abrupt head movements and an instant alteration of flight or gait reliably indicated when and where detection occurred. All cases in which the point of detection was un-

certain were omitted from analyses. Both experiments ended when the crow had discovered half of the displays or after 90 min.

In the first experiment, we compared detection of red and black fruits. Anthocyanins are the pigments that impart red color at low concentrations and dark purple to black color at high concentrations (Lancaster et al. 1997). Because anthocyanins possess high antioxidant capacity, they might be selected by crows as nutritional rewards (Cipollini 2000; Schaefer et al. 2004). Thus, to isolate color cues from nutritional cues, we used artificial fruit displays, which consisted of four 1.2-cm (diameter) wood beads painted either red or black. For a nutritional reward, we attached one piece of dog food (ca. 5 mm) to the end of a thin (<1 mm) green metal wire projecting from the bottom of each artificial infructescence. The dog food was placed inconspicuously beneath the infructescence to reduce the possibility that crows might use the reward to detect displays rather than vice versa. The night before a trial, we placed 8 infructescences (4 black and 4 red) into 8 randomly chosen palms. Thus, all infructescences were displayed against a standardized and natural background in an otherwise unpredictable manner. We used palms as a background because many species of palm, including several species native to Florida, produce red or black fruits that attract avian frugivores. At dawn, as soon as the crow started to forage, we watched from a blind outside the aviary as it searched for fruits, recording detection distances and the color of detected fruits. Birds readily detected the displays and consumed the dog food.

At the end of the first experiment, 2 observers entered the aviary. Within 5 min, one person placed one blueberry (*Vaccinium myrtillus*; 1-cm diameter) in each of the 8 randomly chosen palms at the end of a wire protruding approximately 3 cm from the leaves and 8 blueberries in random locations on the sand. At the same time, the other person distracted the crow to prevent it from observing where the fruits were placed. The UV-reflecting waxy bloom of 4 blueberries in each set of 8 was rubbed off so that half of the berries had their peak reflectance in the UV (UV+) and the other half did not (black).

We used sand as second type of standardized background because blueberries exhibit strikingly different chromatic and achromatic contrasts against foliage and sand. Importantly, sand is a natural background for native blueberry species that grow in the dry and sandy pine flatwoods of northern Florida. It is not uncommon for blueberries of these species to fall to the ground and be consumed. Regardless of how frequently this occurs, however, the intent of this experiment was to present blueberries against 2 types of backgrounds with substantially different contrasts, not to perfectly mimic the species-specific backgrounds. To keep fruit traits constant, we only used blueberries that were of similar shape, size, and ripeness. Crows in north central Florida regularly encounter and consume blueberries; in fact, they are considered a major pest by blueberry farmers (Avery et al. 1992).

Fruit color measurements

We measured the color of 20 blueberries, 10 artificial red and 10 black fruits, and 20 background structures (10 palm leaves and 10 patches of sand) with an Ocean Optics USB2000 diode-array spectrometer. We used a Top Sensor System Deuterium-Halogen DH-2000 lamp as a standardized light source and a coaxial fiber cable (QR400-7, Ocean Optics) that was mounted inside a matt black plastic tube to exclude ambient light. Reflectance was measured as the proportion of a standard white reference tile (Top Sensor Systems WS-2). The angle of illumination and reflection was fixed at 45° to minimize glare. Spectra were processed with SpectraWin 4.0

software and calculated in 5-nm intervals from 300 to 730 nm. The reflectance spectra of the artificial fruits matched those of natural temperate fruits, including those that occur in Florida (100 species in total; HM Schaefer, unpublished data; Figure 1). In blueberries, the removal of the bloom led to a significant reduction in UV and overall reflectance (Figure 2). Chromatic contrasts of the mean reflectance of fruits and the different background measurements were calculated by Misha Vorobyev (University of Brisbane) following the calculations detailed in Siddiqi et al. (2004). For this analysis, we used an eye model of the peacock (*Pavo cristatus*) (Hart 2002) because it most likely estimates the vision of crows (Ödeen and Hastad 2003). Contrasts were characterized in units of "just noticeable differences" (jnds), following Vorobyev's models (for details, see Vorobyev et al. 1998, 2001). One jnd is at the threshold of discrimination for birds, values <1 jnd indicate that 2 colors are indistinguishable, and values >1 jnd indicate how much above this threshold a pair of spectra is discriminated (Osorio and Vorobyev 1996). Similar to the chromatic contrasts, we calculated achromatic contrasts for the double cone of birds, assuming a Weber fraction of 0.05 (for details, see Siddiqi et al. 2004).

Depending on the outcome of the trials, we had 1–4 measurements of detection distances for the different fruit types on each background for each individual crow. For statistical analyses, we used the mean detection distance of individual crows for each fruit type and background. We analyzed the 2 × 2 factorial design of the blueberry trial with a 3-way analysis of variance (ANOVA). The dependent variable was mean detection distance, whereas fruit color (UV+, black) and background (palm, sand) were entered as fixed factors and individual crows as random factors. When necessary, we transformed variables to meet the assumption of homoscedascity.

RESULTS

Nineteen of 23 crows found the artificial red and black fruit displays rapidly (mean trial length = 18 ± 2 min); the remaining 4 crows found only 2 or 3 displays before they stopped foraging. All birds consumed the dog food immediately after initially approaching a fruit display, indicating that they associated the artificial infructescence with a food reward. The distance from which the fruit signals were detected differed. Crows detected artificial red fruits from a larger median distance (6.0 m) than artificial black fruits (3.7 m; *t*-test: $n = 23$, $t = -2.353$, $P < 0.05$; Figure 3) corresponding to a 60% increase in detection distance. The difference in detection distance is explainable because artificial red and black fruits differed in their achromatic and chromatic contrasts against leaves (*t*-test: $t = 193.41$ and $t = 128.56$, respectively; both $P < 0.001$). Achromatic contrasts of red fruits were below the threshold of discrimination (0.8 ± 0.1 jnds; mean ± SE), whereas achromatic contrasts of black fruits were well above the threshold (11.0 ± 0.1 jnds). Conversely, red fruits had higher chromatic contrasts (22.3 ± 0.2 jnds) than black fruits (16.0 ± 0.1 jnds). The larger detection distance of artificial red fruits suggests that crows attended primarily to chromatic cues.

When blueberries were presented against foliage, most crows (17 out of 23) found 8 fruits within 41 min (±7min); the remaining birds found only 4–6 fruits before they stopped foraging. Crows' detection of blueberries depended on fruit colors, the type of background, and the interaction between both factors, but not on crow identity (3-way ANOVA, $F = 7.59$, $P < 0.001$). Overall, blueberries were detected from a larger distance against palms compared with sand ($F = 12.53$, $P < 0.001$) and UV-reflecting fruits from a larger distance than black fruits ($F = 5.66$, $P < 0.05$). The interaction between color and background ($F = 5.11$, $P < 0.05$) indicates
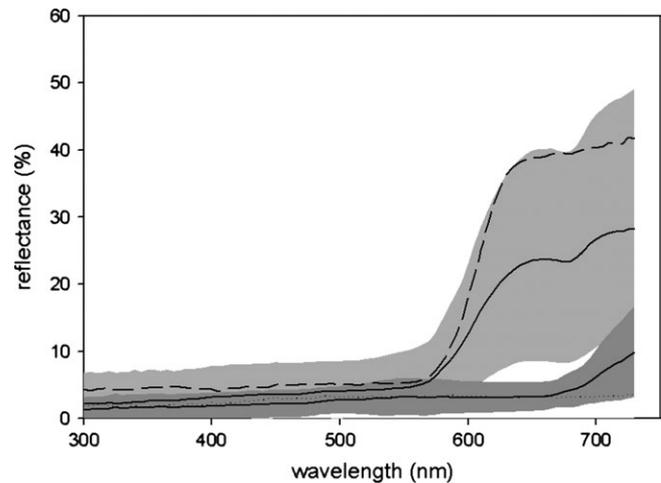

Figure 1
Reflectance spectra of artificial and natural red ($n = 62$) and black ($n = 38$) fruits. Solid lines denote the mean reflectance of natural red and black fruits, the long-dashed line denotes artificial red fruits, and the dotted line denotes artificial black fruits. The light gray area shows the standard deviation of natural red fruits and the dark gray area shows the standard deviation of natural black fruits. Note that the reflectance spectra of artificial fruits matched those of natural fruits—i.e., they lie within the standard deviation.

that fruit contrasts are important in explaining fruit detection. Against foliage, crows detected UV+ fruits from a greater distance than black fruits. The difference in detection distance was large—UV+ fruits were detected from 60% farther than black fruits (median UV+: 5.7 m, black: 3.1 m; Figure 4). The difference in detection distance resulted in a higher consumption of UV-reflecting blueberries (*t*-test, $t = 3.37$, $P < 0.01$). That crows found UV-reflecting blueberries from farther away is consistent with the core prediction of the eye model because UV+ blueberries had stronger chromatic (19.7 ± 0.1 jnds) and achromatic (10.8 ± 0.1 jnds) contrasts against foliage than black blueberries (16.7 ± 0.1 and 9.1 ± 0.1 jnds, respectively; *t*-test, $t = 123.72$ and $t = 108.65$, both $P < 0.001$).

On sand, the distance from which crows detected both fruit types did not differ (Figure 4), and crows consumed equal numbers of UV-reflecting and black blueberries (*t*-test,
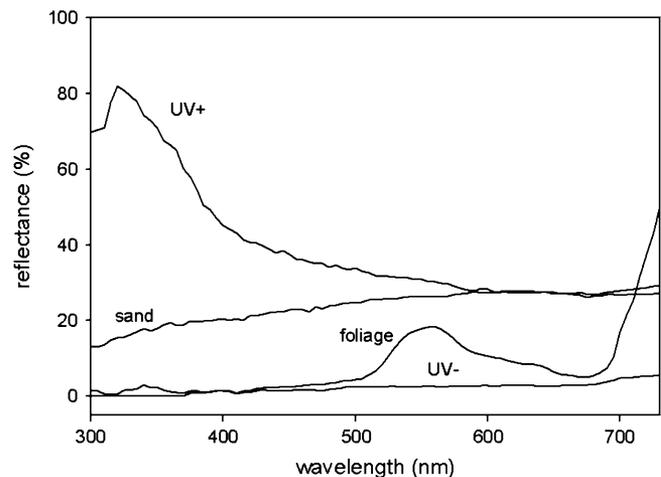

Figure 2
Reflectance spectra of UV-reflecting (UV+) and black (UV−) blueberries and background structures over the range of wavelengths visible to birds.
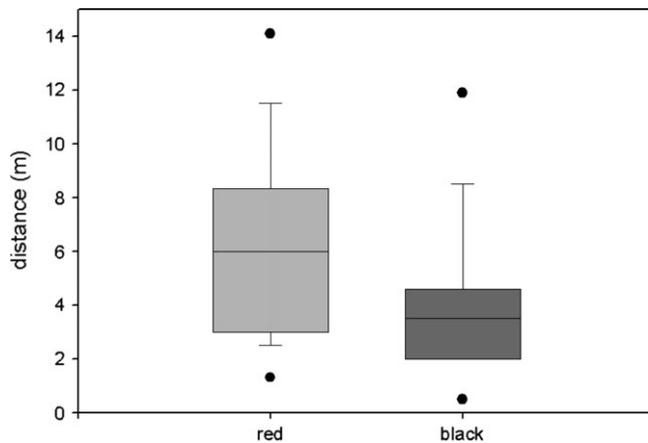
Figure 3
Artificial red fruits were detected from a larger distance than artificial black fruits. Illustrated are medians, mid-quartiles, 90th and 10th percentiles, and 95th and 5th percentiles as outliers.

$t = -0.14$, $P > 0.05$). UV+ fruits were indistinguishable from the background by achromatic contrasts (0.8 ± 0.1 jnds), and black fruits were difficult to detect by chromatic contrasts (1.0 ± 0.1 jnds). UV+ fruits had higher chromatic contrasts than black fruits (5.6 ± 0.6 jnds vs. 1.0 ± 0.1 jnds, respectively; t-test, $t = 84.53$, $P < 0.001$), and black fruits had higher achromatic contrasts than UV+ fruits (17.0 ± 0.2 jnds vs. 0.8 ± 0.1 jnds, respectively; t-test, $t = 110.43$, $P < 0.001$). These results suggest that both chromatic and achromatic cues were important for detecting fruits against sand.

DISCUSSION

Results from the experiment with artificial red and black fruits do not agree with the prediction that black fruits have higher detectability than red fruits. In fact, we found the opposite result: artificial red fruits were detected from a greater distance than artificial black fruits. Thus, the color shift from red to black during fruit ripening cannot be attributed to increased detectability.
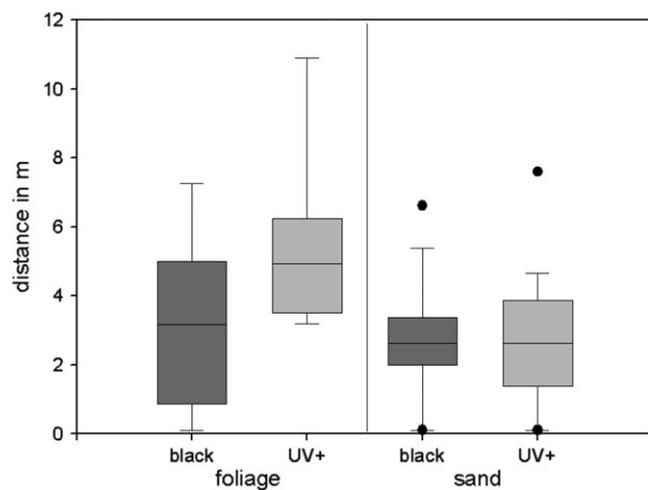

Figure 4
Crows detected UV-reflecting (UV+) fruits from a larger distance than black fruits against a background of foliage but not against that of sand. Illustrated are medians, mid-quartiles, 90th and 10th percentiles, and 95th and 5th percentiles as outliers.

Importance of chromatic and achromatic contrasts for signal detection

Results from the second trial generally validate the avian eye model (Vorobyev and Osorio 1998; Vorobyev et al. 2001). In an environment with natural lighting, blueberries with higher chromatic and achromatic contrasts (UV+ against foliage) were detected at much greater distances than blueberries with lower chromatic and achromatic contrasts (black against foliage). When one fruit was only detectable by chromatic contrast (UV+ against sand) and the other fruit only by achromatic contrast (black against sand), birds detected both fruit types equally. This result does not match that from the first trial, in which artificial red fruits were detected at much larger distances than artificial black fruits, despite the higher achromatic contrasts of black fruits. Because achromatic contrasts are thought to be more important than chromatic contrasts for the detection of small objects (Osorio et al. 1999), this inconsistency between trials might be explainable by differences in fruit presentation. In trial 1, instead of presenting a single fruit (as in trial 2), we used 4 beads that exceeded blueberries in size. The large size of the beads may have caused crows to attend primarily to chromatic cues when searching for artificial infructescences.

Results of the 3-way ANOVA illustrate a significant effect of background on fruit detection: blueberries were detected from larger distances when displayed against palm leaves than against sand. The difference might be explainable by the stronger contrasts of blueberries against palm leaves. Crows detected the single spherical berry of our presentation from various angles (in flight, from perches, and from the ground) on both backgrounds. We consider it therefore unlikely that the orientation of that berry (vertical in palms and horizontal on sand) influenced fruit detection. For example, a vertically displayed fruit in palms becomes a horizontal display (as on sand) if detected in flight. Likewise, it is unlikely that the background-specific effect on fruit detection is explicable by an association of food rewards with palms from trial 1 because crows did not find blueberries faster on palms compared with on sand (data not shown).

We suggest that the relative importance of chromatic and achromatic contrasts is contingent on the background, a conjecture that has not been incorporated into current models of visual detection and signal theory. It is generally believed that achromatic contrasts are important for edge or pattern discrimination and more frequently used for long-distance detection (Osorio et al. 1999). However, because illumination (i.e., light intensity) can vary drastically, intensity-related achromatic contrasts are considered to be less reliable for object identification (Kelber et al. 2003). This logic is especially applicable to foliage because the patterns of sun flecks and shadows that characterize a background of foliage produce high variation in illumination.

Sumner and Mollon (2000) discussed the importance of this effect for the detectability of fruits. Analyzing fruit perception in frugivorous primates, they concluded that achromatic fruit signals are difficult to detect for primates because of large achromatic variance in foliage. Variation in the chromatic composition of illumination is comparatively small, and the chromatic aspect of a signal might therefore be a more reliable cue under variable light conditions (Troost 1998). This might explain why crows detected artificial red fruits from a larger distance (our study) or why hawk moths appear to base foraging decisions on chromatic, not achromatic, contrasts (Kelber 2005).

Our results suggest, however, that crows do not generally prioritize chromatic over achromatic contrasts. Crows probably attended to both types of contrasts when detecting

UV-reflecting and black blueberries on sand. On sand, UV+ fruits were indistinguishable by achromatic contrasts and had low chromatic contrasts—conditions that might have favored the use of achromatic contrasts to detect the alternative black blueberries. Also, sand has lower variance in brightness than foliage, which might result in a higher detectability of the achromatic fruit signal and thus explain the seemingly contradictory results between trials 1 and 2. However, to pinpoint the effect of background heterogeneity on signal detection in birds, a study including a larger number of bird species, colored targets, and backgrounds is needed.

Fruit signals

Both a previous study on primates (Sumner and Mollon 2000) and our study conclude that color changes from red to black during fruit ripening are apparently not an adaptation to increase fruits' conspicuousness to seed dispersers because of the high importance of chromatic red signals. If fruit detection by crows is representative of that of other seed dispersers, the color shift during ripening is not explicable by signal theory. The high frequency of black fruits (up to 40%) in bird-dispersed plants (Wheelwright and Janson 1985) might rather be explained by physiological processes within the plant (see Schaefer and Wilkinson 2004; Schaefer and Rolshausen 2006) or by pleiotropy (Whitney and Stanton 2004). Because black fruits are more common than red fruits in the flora of Florida (Long 1971), we consider it unlikely that crows detected red fruits from a larger distance because they had previously developed a search image for red fruits.

To the best of our knowledge, our experiments are the first behavioral validation of the applicability of an avian eye model under conditions that mimic what birds encounter in the wild. Eye models are based on the molecular data of retina composition (Hart 2001) as well as on the behavioral data of a sophisticated laboratory experiment (Maier 1992). Our results show that predictions based on these models, which are widely used to explain the proximate selective pressures in signal evolution, probably also apply to more natural conditions. Thus, using such models provides a powerful tool for assessing the evolutionary ecology of signals.

Signal perception in crows, for example, might provide a functional explanation for the occurrence of accessory signals such as preripe red fruits or red bracts in fruit displays (Stiles 1982; Wheelwright and Janson 1985; Burns and Dalen 2002). Such accessory signals increase the conspicuousness of fruit displays (Schaefer et al., Forthcoming). Adding preripe red fruits to fruit displays increased birds' removal rates of ripe black fruits in solitary infructescences but not in clumped infructescences (Morden-Moore and Willson 1982; Willson and Melampy 1983). Red fruits presumably enhance fruit conspicuousness in both presentations, but the effect of enhanced detectability is not apparent if black fruits are presented at sufficiently short distances in clumped distributions, which enable birds to easily perceive the achromatic signal. We caution, however, that our results pertain to the specific conditions of our study. It is currently unknown whether the search behavior of crows in the simplified habitat of a large aviary more generally reflects the detection of colored targets in birds.

Like other studies (Siddiqi et al. 2004; Thery et al. 2005), we based our analysis on signal detectability entirely on the cone sensitivities of the avian retina, assuming that the double cone functions to detect achromatic signals. It is still unknown how birds process chromatic and achromatic signals and how neuronal processing affects signal detectability. Although future studies might shed light on this question, an emerging lesson of our study is that visual signals are more complex than commonly assumed and that the relative importance of chromatic and achromatic contrasts is contingent on the background.

SUPPLEMENTARY MATERIAL

The Figures 1, 3, and 4 are provided in color in the Supplementary Material which can be found at http://www.beheco.oxfordjournals.org/.

REFERENCES

Altshuler D. 2001. Ultraviolet reflectance in fruits, ambient light composition and fruit removal in a tropical forest. Evol Ecol Res 3:767–78.

Avery ML, Nelson JW, Cone MA. 1992. Survey of bird damage to blueberries in North America. Proceedings of the Eastern Wildlife Damage Control Conference. Volume 5. Raleigh, NC: North Carolina Cooperative Extension Service. p 105–10.

Borges RM, Gowda V, Zacharias M. 2003. Butterfly pollination and high-contrast visual signals in a low-density distylous plant. Oecologia 136:571–3.

Bruce MJ, Heiling AM, Herberstein ME. 2005. Spider signals: are web decorations visible to birds and bees? Biol Lett 1:299–302.

Burkhardt D. 1982. Birds, berries and UV. Naturwissenschaften 69:153–7.

Burns KC, Dalen JL. 2002. Foliage color contrasts and adaptive fruit color variation in a bird-dispersed plant community. Oikos 96:463–9.

Cipollini ML. 2000. Secondary metabolites of vertebrate-dispersed fruits: evidence for adaptive functions. Rev Chil Hist Nat 73:421–40.

Endler JA. 1993. Some general comments on the evolution and design of animal communication systems. Philos Trans R Soc Lond B Biol Sci 340:215–25.

Endler JA. 2000. Evolutionary implications of the interaction between animal signals and the environment. In: Espmark Y, Amundsen T, Rosenqvist G, editors. Animal signals. Trondheim: Tapir Academic Press. p 11–46.

Endler JA, Mielke PW. 2005. Comparing entire colour patterns as birds see them. Biol J Linn Soc 86:405–31.

Endler JA, Thery M. 1996. Interacting effects of lek placement, display behavior, ambient light and color patterns in three neotropical forest-dwelling birds. Am Nat 148:421–52.

Gadd P. 1996. Use of the modified Australian crow trap for the control of depredating birds in Sonoma County. Proc Vertebr Pest Conf 17:103–7.

Guilford T, Dawkins MS. 1991. Receiver psychology and the evolution of animal signals. Anim Behav 42:1–14.

Hart NS. 2001. The visual ecology of avian photoreceptors. Prog Retin Eye Res 20:675–703.

Hart NS. 2002. Vision in the peafowl (Aves: *Pavo cristatus*). J Exp Biol 205:3925–35.

Håstad O, Victorsson J, Ödeen A. 2005. Differences in color vision make passerines less conspicuous in the eyes of their predators. Proc Natl Acad Sci USA 102:6391–4.

Heiling AM, Herberstein ME, Chittka L. 2003. Crab-spiders manipulate flower signals. Nature 421:334.

Heindl M, Winkler H. 2003. Interacting effects of ambient light and plumage color patterns in displaying Wire-tailed Manakins (Aves, Pipridae). Behav Ecol Sociobiol 53:153–62.

Kelber A. 2005. Alternative use of chromatic and achromatic cues in a hawkmoth. Proc R Soc Lond B Biol Sci 272:2143–7.

Kelber A, Vorobyev M, Osorio D. 2003. Animal colour vision—behavioural tests and physiological concepts. Biol Rev Camb Philos Soc 78:81–118.

Lancaster JE, Lister CE, Reay PF, Triggs CM. 1997. Influence of pigment composition on skin color in a wide range of fruit and vegetables. J Am Soc Hortic Sci 122:594–8.

Long RW. 1971. A flora of tropical Florida. Coral Gables, FL: University of Miami Press.

Maier EJ. 1992. Spectral sensitivities including the ultraviolet of the passeriform bird *Leiothrix lutea*. J Comp Physiol A 170:709–14.

Marshall NJ. 2000. Communication and camouflage with the same "bright" colours in reef fishes. Philos Trans R Soc Lond B Biol Sci 355:1243–8.

Morden-Moore AL, Willson MF. 1982. On the ecological significance of fruit color in *Prunus serotina* and *Rubus occidentalis*: field experiments. Can J Bot 60:1554–60.

Ödeen A, Hastad O. 2003. Complex distribution of avian color vision systems revealed by sequencing the SWS1 opsin from total DNA. Mol Biol Evol 20:855–61.

Osorio D, Miklósi A, Gonda Z. 1999. Visual ecology and perception of coloration patterns by domestic chicks. Evol Ecol 13:673–89.

Osorio D, Vorobyev M. 1996. Colour vision as an adaptation to frugivory in primates. Proc R Soc Lond B Biol Sci 263:593–9.

Schaefer HM, Rolshausen G. 2006. Plants on red alert—do insects pay attention? Bioessays 28:65–71.

Schaefer HM, Schaefer V, Levey DJ. 2004. How plant-animal interactions signal new insights in communication. Trends Ecol Evol 19:577–84.

Schaefer HM, Schaefer V, Vorobyev M. 2006. Are fruit colors adapted to consumer vision and birds equally efficient in detecting colorful signals? Am Nat. Forthcoming.

Schaefer HM, Schmidt V. 2004. Detectability and content as opposing signal characteristics in fruits. Proc R Soc Lond B Biol Sci 271:S370–3.

Schaefer HM, Wilkinson DM. 2004. Red leaves, insects and coevolution: a red herring? Trends Ecol Evol 19:616–8.

Schluter D, Price T. 1993. Honesty, perception and population divergence in sexually selected traits. Proc R Soc Lond B Biol Sci 253:117–22.

Schmidt V, Schaefer HM, Winkler H. 2004. Conspicuousness, not colour as foraging cue in plant-animal interactions. Oikos 106:551–7.

Siddiqi A, Cronin TW, Loew ER, Vorobyev M, Summers K. 2004. Interspecific and intraspecific views of color signals in the strawberry poison frog *Dendrobates pumilio*. J Exp Biol 207:2471–85.

Spaethe J, Tautz J, Chittka L. 2001. Visual constraints in foraging bumblebees: flower size and color affect search time and flight behavior. Proc Natl Acad Sci USA 98:3898–903.

Stiles EW. 1982. Fruit flags: two hypotheses. Am Nat 120:500–9.

Stuart-Fox D, Moussalli A, Johnston GR, Owens IPF. 2004. Evolution of color variation in dragon lizards: quantitative tests of the role of crypsis and local adaptation. Evolution 58:1549–59.

Sumner P, Mollon JD. 2000. Chromaticity as a signal of ripeness in fruits taken by primates. J Exp Biol 203:1987–2000.

Thery M, Casas J. 2002. Predator and prey views of spider camouflage. Nature 415:133.

Thery M, Debut M, Gomez D, Casas J. 2005. Specific color sensitivities of prey and predator explain camouflage in different visual systems. Behav Ecol 16:25–9.

Troost JM. 1998. Empirical studies of color constancy. In: Walsh V, Kulikowski J, editors. Perceptual constancy. Cambridge, UK: Cambridge University Press. p 262–82.

Vorobyev M, Brandt R, Peitsch D, Laughlin SB, Menzel R. 2001. Colour thresholds and receptor noise: behaviour and physiology compared. Vision Res 41:639–53.

Vorobyev M, Osorio D. 1998. Receptor noise as a determinant of colour thresholds. Proc R Soc Lond B Biol Sci 265:351–8.

Vorobyev M, Osorio D, Bennett ATD, Marshall NJ, Cuthill IC. 1998. Tetrachromacy, oil droplets and bird plumage colours. J Comp Physiol A 183:621–33.

Wheelwright NT, Janson CH. 1985. Colors of fruit displays of bird dispersed plants in two tropical forests. Am Nat 126:777–99.

Whitney KD, Stanton ML. 2004. Insect seed predators as novel agents of selection on fruit color. Ecology 85:2153–60.

Willson MF, Melampy MN. 1983. The effect of bicolored fruit displays on fruit removal by avian frugivores. Oikos 41:27–31.

Willson MF, Whelan CJ. 1990. The evolution of fruit color in fleshy-fruited plants. Am Nat 136:790–809.