Ultraviolet vision aids the detection of nutrient-dense non-signaling plant foods

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ABSTRACT

To expand our understanding of what tasks are particularly helped by UV vision and may justify the costs of focusing high-energy light onto the retina, we used an avian-vision multispectral camera to image diverse vegetated habitats in search of UV contrasts that differ markedly from visible-light contrasts. One UV contrast that stood out as very different from visible-light contrasts was that of nutrient-dense non-signaling plant foods (such as young leaves and immature fruits) against their natural backgrounds. From our images, we calculated color contrasts between 62+ species of such foods and mature foliage for the two predominant color vision systems of birds, UVS and VS. We also computationally generated images of what a generalized tetrachromat, unfiltered by oil droplets, would see, by developing a new methodology that uses constrained linear least squares to solve for optimal weighted combinations of avian camera filters to mimic new spectral sensitivities. In all visual systems, we found that nutrient-dense non-signaling plant foods presented a lower, often negative figure-ground contrast in the UV channels, and a higher, often positive figure-ground contrast in the visible channels. Although a zero contrast may sound unhelpful, it can actually enhance color contrast when compared in a color opponent system to other channels with nonzero contrasts. Here, low or negative UV contrasts markedly enhanced color contrasts. We propose that plants may struggle to evolve better UV crypsis since UV reflectance from vegetation is largely specular and thus highly dependent on object orientation, shape, and texture.

1. Introduction

Ultraviolet (UV) vision is common amongst animals with color vision (Bowmaker, 2008; Briscoe & Chittka, 2001; Douglas & Jeffery, 2014; Emerling, Huynh, Nguyen, Meredith, & Springer, 2015), and researchers have made great strides over the past decades in determining what it is good for, especially in insects. Many insects use specialized UV receptors in the dorsal rim area of the eye to visualize the pattern of polarization in the sky. Although a clear sky is more polarized and brighter in the blue part of the spectrum, skylight polarization patterns are more consistently discernible under different weather and habitat conditions in a UV than blue channel (Barta & Horváth, 2004; Wang, Gao, & Fan, 2014). Some insects also use UV receptors to localize open areas, i.e. the so-called open space reaction (Scherer & Kolb, 1987), because of the high UV contrast between the sky and ground. UV components of flower, fruit, and animal signals also attract a lot of research attention (Altshuler, 2001; Bennett & Cuthill, 1994; Chittka, Shimda, Troje, & Menzel, 1994), but we currently have no well-supported theory as to why UV signals should generally be more selected for than visible-light signals (Cronin & Bok, 2016).

The prevalence of UV vision remains a bit of an enigma since UV vision must come with costs in terms of an elevated demand for DNA repair machinery in the retina (Pattison & Davies, 2006), especially for long-lived animals in which UV-induced mutations and other types of molecular damage can be expected to accumulate over time. In spite of this, UV receptors peaking below 380 nm are widespread even in the longest-lived birds, the Psittaciformes (parrots and cockatoos) (Carvalho, Knott, Berg, Bennett, & Hunt, 2011), many of which live 50+ years (Brouwer, Jones, King, & Schiffter, 2000). The utility of UV vision in everyday visual tasks is still not fully understood because we ourselves cannot easily visualize how UV light behaves in natural environments. In recent years, we have been taking a new approach to exploring what UV vision is good for by using a multispectral camera to visualize habitats such that lighting geometry and object position are undisturbed and completely natural. This method allows us to quickly spot areas of contrast in the UV that differ dramatically from contrasts in

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the visible channels. The method has the additional advantage of decreasing the number of assumptions commonly employed in visual modeling, in which all objects are treated as perfect diffuse reflectors and the color of light incident on objects is assumed to be the same from all directions (Endler & Mielke, 1991; Vorobyev & Osorio, 1998). Using the camera, we recently showed that because most light comes from above, and because leaves transmit little UV light, there are striking UV contrasts between upper and lower leaf surfaces in natural habitats. We proposed that such contrasts could improve animals’ perception of the geometry of leafy environments. To better understand our results, we developed an optical model to describe them, which revealed that mirror-like specular reflections of the sky and surrounding vegetation vastly increase leaf reflectance, and also vary in color depending on the color of light incident at the appropriate angle to be specularly reflected toward the observer (Tedore & Nilsson, 2019). Here we highlight another type of discrimination task in natural environments that our multispectral camera has shown to be especially helped by UV vision—detection of nutrient-dense non-signaling plant foods, such as young, expanding plant leaves and immature fruits. As we will propose in the Discussion, the utility of a UV receptor for this task likely derives, at least in part, from the geometry of lighting and specular reflections in natural habitats; however, rigorous tests of this hypothesis remain to be done.

Nutrient-dense non-signaling plant parts are an important source of food for many animals. Growing leaf buds and young leaves tend to be chemically and structurally less defended than mature leaves, are more nutritious and easier to digest (Kursar & Coley, 1991; Mattson, 1980; White, 2011, 2012), and as a consequence, allow animals to grow faster (Ayers & MacLean, 1987; Damman, 1987; Kelber, 1999; Mutze, 2007). Growing leaf buds and young leaves are commonly targeted by birds, mammals, insects, and reptiles (White, 2012). Seeds are high in protein, even when immature, and many animals consume and digest immature seeds from both non-fleshy and fleshy fruits, rendering them unable to germinate (Cramp, 1994; Marchant et al., 1990-2006; Mattson, 1980; Sebastián-Gonzalez et al., 2019; White, 2011, 2012). Indeed, many animals preferentially feed on seeds from immature fleshy and non-fleshy fruits, even when mature fruits are available, apparently because they are better able to digest the seeds before they dry and harden (Hamilton & Galdikas, 1994; Matsuda, Tuuga, & Higashi, 2009; Mutze, 2007; Nagy & Shemanski, 2009). Many bird species time their reproduction such that the peak of nesting feeding coincides with the flush of immature seeds, and preferentially feed nestlings immature seeds (Allen & Humé, 1997; Renton, 2001; Wilson, Karl, Toft, Beggs, & Taylor, 1998). Indeed, the adult zebra finch Taeniopygia guttata is able to maintain its body condition on mature grass seeds alone, but is unable to breed without immature grass seeds (Allen & Humé, 1997). Insect damage of unripe fleshy fruit disrupts fruit development and introduces bacteria, fungi, and fecal pellets into the fruit. This can cause the fruit to become distasteful and avoided by frugivores when it ripens. Many plants abort developing fruits that have been damaged by insects, apparently to avoid investing further resources in a fruit that is unlikely to produce offspring (Sallabanks & Courtney, 1992). Plants would therefore seem to face a rather large cost when immature leaves and fruits are eaten. However, plants may occasionally benefit if immature fruits are dropped or cached and forgotten, provided the fruit is capable of maturing when prematurely detached from its parental tree (Sebastián-González et al., 2019).

To quantify the utility of a UV receptor for detecting nutrient-dense non-signaling plant foods against their natural backgrounds, we analyze all multispectral images we have taken that include immature leaves or fruits. This comprises 84 scenes with at least 62 different food species. The multispectral camera has been previously described in Tedore and Nilsson (2019), but briefly, has spectral filters custom-made to mimic the two predominant tetrachromatic color vision systems of birds (UVS and VS, or U and V for brevity). UVS birds have UV and blue cones that peak at shorter wavelengths than those of VS birds (Fig. 1A). The UVS visual system appears to be the ancestral condition of birds (Aidala et al., 2012; Hart, Mountford, Davies, Collin, & Hunt, 2016), although birds have flipped between visual systems multiple times over their evolutionary history (Odeen, Håstad, & Alstrom, 2011; Odeen & Håstad, 2013). We therefore focus on testing the effects of shifting UV receptors to longer wavelengths, i.e. from U to V, as well as a complete loss of a UV receptor, on color contrasts between nutrient-dense non-signaling plant foods and their visual backgrounds.

Thus far, the functional significance of transitions between U and V remains unclear, although we recently found the V-cone to be advantageous for resolving leaf contrast in closed habitats due to relatively longer-wavelength specular reflections from leaves in such habitats (Tedore & Nilsson, 2019). Birds living in light-limited habitats can also be expected to collect larger absolute numbers of photons with a V-cone than a U-cone since there is more downwelling light available in the sensitivity range of the V-cone (Endler, 1993; Johnsen et al., 2006). Unfortunately, even on a clear day, our camera’s maximum exposure time was too short to take photos after the sun had dropped about half a degree below the horizon. Thus, all photos were taken under what were likely photopic conditions (Olsson, Lind, & Kelber, 2015), and the effect of light limitation on the relative benefit of U- versus V-cones could not be examined.

Avian S-, M-, and L-cones have pigmented oil droplet filters which sit distal to their photoreceptive segments and absorb the UV light that would otherwise be absorbed by the opsin β-band, i.e. the secondary
peak of an opsin sensitivity curve. Pigmented oil droplets and other types of spectral filters are common in birds, reptiles, and butterflies, but are rare in other taxonomic groups, such as amphibians, mammals, and many insects (Stavenga, 2006; Toomey & Corbo, 2017). To test whether our object contrast results in birds might generalize to animals lacking oil droplets or other spectral filters, we develop and describe a new method which uses the above-described avian filters to computationally generate filters mimicking new spectral sensitivities. The method uses constrained linear least squares to solve for optimal weighted additive combinations of photos taken through different filters to achieve new spectral sensitivities. In this way, we generate images that approximate how a generalized tetrachromat without oil droplet filters would see these plant foods. In addition, we generate images approximating avian double cone vision, an achromatic channel not involved in color vision (Jones & Osorio, 2004; v. Campenhausen & Kirschfeld, 1998), in order to gain some insight into the relative importance of color and achromatic vision in detecting nutrient-dense non-signaling plant foods. This method of developing computational filters was not able to produce as close of fits to the desired spectral sensitivity curves as the originally fabricated bird filters did (Fig. 1). However, the fits were close enough to allow us to test whether our results in oil droplet-filtered birds can be expected to generalize to other taxa without spectral filters. Future work will demonstrate that using eight filters, rather than six, produces much closer fits to a wide range of spectral sensitivity curves, offering researchers the flexibility to model a broad range of visual systems with only eight filters.

2. Methods

2.1. Multispectral imaging & computational filters

The camera and filters used were previously described in (Tedore & Nilsson, 2019). To computationally generate new spectral sensitivities from the existing filters, we used the MATLAB (version 2018b) ‘lsqmin’ function, which solves constrained linear least squares problems. We tasked the function with finding a set of six coefficients (a, b, c, d, e, and f) to multiply by the effective spectral sensitivities of the six camera channels such that the spectral shape of the sum of the six channels, each weighted by a different coefficient, would match a specified spectral sensitivity curve. We constrained the solution such that no coefficient would be allowed to drop below zero; this constraint is critical for preventing erroneous results. The effective spectral sensitivity of each camera channel i was calculated as:

\[ F_i(\lambda) = S_{sensor}(\lambda)T_{ lens}(\lambda)T_{IRblock}(\lambda)T_{filter}(\lambda) \]

where \( S_{sensor}(\lambda) \) is the spectral sensitivity of the camera sensor, \( T_{ lens}(\lambda) \) is the transmittance spectrum of the camera lens, \( T_{IRblock}(\lambda) \) is the transmittance spectrum of an infrared blocking filter mounted on the front of the lens, and \( T_{filter}(\lambda) \) is the transmittance spectrum of camera filter i. Then, we tasked the ‘lsqmin’ function with finding the best-fitting set of non-negative coefficients a, b, c, d, e, and f that would satisfy the equation:

\[ R_j(\lambda)T_{ obj}(\lambda)T_{ lens}(\lambda) = aF_1(\lambda) + bF_2(\lambda) + cF_3(\lambda) + dF_4(\lambda) + eF_5(\lambda) + fF_6(\lambda) \]

where \( R_j(\lambda) \) is the spectral sensitivity of photoreceptor \( j \) (generated by the template of Govardovskii, Fyhruquist, Reuter, Kuzmin, and Donner (2000)), \( T_{ obj}(\lambda) \) is the transmittance spectrum of the oil droplet associated with photoreceptor \( j \) (generated by the template of Hart and Vorobyev (2005)), and \( T_{ lens}(\lambda) \) is the transmittance spectrum of the optical media associated with UVS birds (Lind, Mitkus, Olsson, & Kelber, 2014). The effective spectral sensitivities of the real and computational filters are shown in Fig. 1.

Of 308 photographed scenes from diverse terrestrial habitats in Skåne, Sweden and Queensland, Australia, we found 84 that contained nutrient-dense non-signaling plant foods. Some foods had been photographed specifically because we or a local naturalist had observed birds feeding on them. The majority were identified to species level with the help of field guides and local botanists (Cooper & Cooper, 2004; Mossberg & Stenberg, 2006) (Graham Bell, Honor C. Prentice, Christina Suttner, and Torbjörn Tyler, personal communication) (Table A.1). A total of 62 distinct species were identified. Taxonomic levels of plant food categories known to be eaten by birds are marked with asterisks in Table A.1 (Boyés & Perrin, 2009; Carleton & Smith, 2016; Cramp, 1994.; Forshaw & Cooper, 1989; Grajal, Strahl, Parra, Gloria Dominguez, & Neher, 1989; Mountfort, 1957; Newton, 1964, 1967; Peponen, 1974; Renton, 2001; Reynolds, 2003; Schaefer & Schmidt, 2002; Sebastián-González et al., 2019; Selman, Perrin, Hunter, & Dean, 2002; Snow & Snow, 1988; Symes & Perrin, 2003).

Fruit is the botanically correct term for any seed-bearing structure in flowering plants, and can be further subdivided into fleshy and non-fleshy types of fruits. Non-fleshy fruits often consist of a pod-like structure that contains one or more seeds, but no fleshy material; well-known examples include grass seed spikelets and acorns. Fleshy fruits, by contrast, consist of a fleshy outer casing enclosing one or more seeds; when ripe, this flesh often serves to attract seed-dispersing frugivores. When we refer to immature fruits, we refer to both fleshy and non-fleshy types of fruits. Both types were photographed as we found them on the plant without manipulation of any kind.

Photographs were taken on calm days or portions of the day to minimize noise due to wind-induced motion of branches and leaves. When possible, we photographed objects at different heights in the canopy, assisted by canopy towers, walks, bridges, etc. Field excursions were planned to maximize the range of lighting conditions sampled, from overcast to clear skies, and from sunrise to sunset. Sun elevation was determined by entering the location, date, and time each photo was taken into sunCalc.org. Cloud cover was estimated by eye and recorded on a scale from 1 to 5 (1 = 0% cloud cover; 2 = 25% cloud cover, 3 = 50% cloud cover, 4 = 75% cloud cover, 5 = 100% cloud cover). Occlusion of the sun by clouds or the horizon was also estimated by eye on a scale from 1 to 5 (1 = no occlusion; 5 = full occlusion). The sun was considered to be fully occluded by clouds when the layer of clouds obscuring it was thick enough to hide its position in the sky. Occlusion levels 2–4 corresponded to thin layers of clouds that reduced the intensity of the sun but did not obscure its position in the sky. Due to the subjective nature of estimating the thickness of clouds obscuring the sun, as well as the danger of looking directly at the sun, estimates from 2 to 4 should be treated as only rough approximations. Taking multispectral photos with a partially occluded sun is difficult due to the fact that the clouds obscuring the sun must be stationary in order for the lighting not to change drastically between photos taken through successive camera channels. Our sampling was therefore unavoidably biased towards conditions with either a completely unoccluded or completely occluded sun. When the dynamic range of the camera was insufficient to capture much of the dynamic range of the scene, multiple sets of photographs were taken at different exposures and combined later, in MATLAB, to create high dynamic range (HDR) images.

2.2. Quantifying contrasts from photographs

The output of the camera sensor scaled linearly with light intensity, so no non-linearity corrections were required. Dark noise was constant across exposures and was subtracted from all pixel values. Each pixel value of real and computational filter images represented the quantum catch (in arbitrary but quantal units) by the simulated photoreceptor class at a single point in space. To adapt quantum catches to the intensity of the background (i.e. convert to relative quantum catches) (Vorobyev, Osorio, Bennett, Marshall, & Cuthill, 1998), each pixel value was normalized by the mean of all pixel values in the image.

Using the pixel selection feature of the software Evince (Prediktera, Umeå, Sweden), we hand-selected pixels corresponding to different
object categories, selecting the same pixels across all six photographs. Although grass leaves often do not have morphologically distinct upper and lower surfaces, we classified grass leaf surfaces that were more upward-oriented as upper leaf surfaces, and surfaces that were more downward-oriented as lower leaf surfaces. Certain object categories were highly variable in appearance, such as different branches of the same tree. Some of the plant foods we were targeting also had distinct color patches. These were all treated as separate selections. If some objects in an image were illuminated by direct sunlight, they were selected separately. Contrasts were only calculated between objects that were under similar illumination (i.e. both in direct sunlight or both in the shade). Other object categories were more uniform within an individual plant, such as upper leaf surfaces and lower leaf surfaces and many of the plant foods. In such cases, all objects of a given category were grouped together in a single selection. We avoided selecting senescent leaves and regions of branches that were covered by moss or lichen. We also avoided regions very close to object or color patch edges.

We exported the indices of the selected pixels from Evince and then imported them into MATLAB 2018b, which we used to calculate the median of the exposed pixels in any channel, these pixels were excluded from all calculations across all channels.

We chose this non-linear transformation rather than log transformation because log transformation can produce spurious results in calculations across all channels. We avoided selecting senescent leaves and regions of branches that were covered by moss or lichen. We also avoided regions very close to object or color patch edges in order to mitigate artifacts due to chromatic aberration and slight wind-induced motion between images. If there were any over- or under-exposed pixels in any channel, these pixels were excluded from all calculations across all channels.

We calculated the median relative quantum catch \( P \) of each object category across each photograph. These medians were then converted to non-linear receptor excitation values following (Naka & Rushton, 1966),

\[
E = \frac{P}{P + 1} \tag{3}
\]

We chose this non-linear transformation rather than log transformation because log transformation can produce spurious results in subsequent calculations of receptor noise-limited (RNL) contrast when relative quantum catch is less than one (Gawryszewski, 2018). Within-channel differences in receptor excitation \( E \) between foods and visual background objects were then calculated for all six channels \( i \),

\[
\Delta E_i = E_{\text{food}} - E_{\text{background}} \tag{4}
\]

Finally, RNL color contrast \( \Delta S \) was calculated by plugging the various \( \Delta E_i \) values into the RNL color contrast equation (Vorobyev et al., 1998; Vorobyev & Osorio, 1998). The \( \Delta S \) metric was originally formulated as a means to calculate whether a target is discriminable from its background, with a \( \Delta S \) equal to one corresponding to the target being just over the discrimination threshold. However, the transformation in Eq. (3) cannot be assumed to yield just-noticeable differences equal to one; behavioral tests are still needed to determine what unit of RNL contrast would correspond to a just-noticeable difference when this alternative nonlinear transformation is used. Since its introduction, the \( \Delta S \) metric has been widely adopted as a measure of color contrast (Santiago et al., 2020). For tetrachromats, \( \Delta S \) was calculated as

\[
\Delta S = \sqrt{\frac{(\omega_1 \omega_2)^2 (\Delta E_1 - \Delta E_3)^2 + (\omega_1 \omega_3)^2 (\Delta E_1 - \Delta E_4)^2 + (\omega_1 \omega_4)^2 (\Delta E_1 - \Delta E_5)^2 + (\omega_2 \omega_3)^2 (\Delta E_2 - \Delta E_4)^2 + (\omega_2 \omega_4)^2 (\Delta E_2 - \Delta E_5)^2 + (\omega_3 \omega_4)^2 (\Delta E_3 - \Delta E_5)^2}{(\omega_1 \omega_2 \omega_3)^2 + (\omega_1 \omega_2 \omega_4)^2 + (\omega_1 \omega_3 \omega_4)^2}} \tag{5}
\]

and for trichromats, as

\[
\Delta S = \sqrt{\omega_1^2 (\Delta E_1 - \Delta E_3)^2 + \omega_2^2 (\Delta E_2 - \Delta E_3)^2 + \omega_3^2 (\Delta E_3 - \Delta E_4)^2}{(\omega_1 \omega_2)^2 + (\omega_1 \omega_3)^2 + (\omega_2 \omega_3)^2}} \tag{6}
\]

where \( \omega_i \) is the standard deviation of the noise in cone channel \( i \), and is calculated as

\[
\omega_i = \frac{\nu}{\sqrt{\eta_i}} \tag{7}
\]

where \( \nu \) is the noise in a single photoreceptor and \( \eta_i \) is the relative number of cones in cone class \( i \). The noise in a single photoreceptor and relative numbers of cone classes were computed as Order-level means of all published estimates of terrestrial-foraging birds. The mean noise in a single photoreceptor was 0.12 (Lind, Mitkus, et al., 2014; Olsson et al., 2015) and mean relative cone numbers were 1:1:7:2:5:3 for U/V:S:M:L (Baumhardt, Moore, Doppler, & Fernández-Juricic, 2014; Ensminger & Fernández-Juricic, 2014; Hart, 2001; Kram, Mantey, & Corbo, 2010; Rahman, Yoshida, Maeda, Tanaka, & Sugita, 2010). The associated \( \omega_{UV} \), \( \omega_S \), \( \omega_M \), and \( \omega_L \) were calculated to be 0.12, 0.092, 0.075, and 0.069, respectively, and were used in our tetrachromatic color contrast calculations.

There is a trade-off between the number of cone classes an animal has and the signal to noise ratio in each channel. We model this trade-off in our trichromatic calculations by allocating the single U/V cone of the tetrachromat to the visible cones such that the total cone number, as well as the S:M:L cone ratios, remain the same as in the tetrachromat. This reduces the noise in each channel of the trichromat such that \( \omega_S \), \( \omega_M \), and \( \omega_L \) become 0.086, 0.071, and 0.065, respectively.

In addition to color contrast, we also calculated an RNL achromatic contrast (Olsson, Lind, & Kelber, 2018):

\[
\Delta S = \frac{\Delta E_\text{a}}{\omega_\text{a}} \tag{8}
\]

where \( \Delta E_\text{a} \) is the difference in the excitation of the double cones between foods and visual background objects, and \( \omega_\text{a} \) is the standard deviation of the noise of the double cone channel. We calculated an Order-level average \( \omega_\text{a} \) of 0.24 from previous behavioral and electrophysiological studies (Ghim & Hodos, 2006; Hodos, Ghim, Potocki, Fields, & Storm, 2002; Jarvis, Abeyesinghe, McMahon, & Wathes, 2009; Lind, Chavez, & Kelber, 2014; Lind, Sunesson, Mitkus, & Kelber, 2012; Lind, Karlsson, & Kelber, 2013).

### 2.3. Object contrast statistics

All statistics were run using MATLAB 2018b. Significant effects were tested with linear mixed effects models (‘lme4’). Separate models were run for each category of object comparison. To compare within-channel differences in the UV channel to those in each of the other color channels, we ran a separate model for each channel comparison, with the alternate color channel as the fixed effect.

To test the effect of different compositions of cone classes on RNL color contrast in birds (with oil droplets), we calculated color contrasts for birds with the following cone compositions: US\(_{1/2}\)ML, VS\(_{1/2}\)ML, VS\(_{3/4}\)ML, and S\(_{1/2}\)ML. We then ran a model with three fixed effects: 1) V-cone presence, 2) S\(_{1/2}\)-cone presence, and 3) U/V-cone absence. To test whether avian double-cone achromatic contrasts were consistently lower than even the worst-performing oil droplet-filtered tetrachromatic avian color vision model (VS\(_{1/2}\)ML), we ran a model with one fixed effect: type of contrast (achromatic or chromatic).

Finally, to test the effect of a loss of the UV photoreceptor in a generalized tetrachromat (without oil droplets), we calculated color
interaction between object unique IDs. Although some receptor excitations and RNL contrasts were not perfectly normally distributed, residual plots indicated that linear models were nevertheless a good fit to the data.

2.4. Visualizing relative cone excitation values across entire images

To visualize the relative excitation of each cone class on a pixel-by-pixel basis, we normalized receptor excitations \( E_i \) by the maximum receptor excitation value across all six color channels photographed. We then adjusted the resulting values to undo the sRGB gamma scaling of most digital display devices in order to make excitation values scale linearly with pixel brightness. The same values were plugged into each of the R-, G-, and B-channels of the computer display in order to obtain a grayscale image. This gives receptor excitation images in which bright pixels correspond to high excitation and dark pixels to low excitation.

Next, we generated false-color images to help see what additional information is added by a UV channel that is not already present in the visible-light channels. Contrasts in the UV most resemble those in the blue, so we alternately plugged the S- and U-cone excitation images into the R-channel, the M- and L-cone excitation images plugged into the G-channel, and the L- and M-cone excitation images plugged into the B-channel of the computer display, respectively.

2.5. Visualizing the uniqueness of plant food colors across entire images

Next, we wanted to demonstrate and visualize how a UV channel contributes to the uniqueness of the color of nutrient-dense non-signaling plant foods, helping them to pop out from a cluttered visual background. To do this, we calculated the difference in receptor excitation values between all possible dichromatic comparisons for each pixel of each image:

\[
\Delta E_{ij} = E_i - E_j. 
\]

For each comparison of channels \( i \) and \( j \), we used a histogram to display the \( \Delta E_{ij} \) values of all pixels across all images of a given plant food category, with the position of the median \( \Delta E_{ij} \) value of each plant food category food plotted for comparison. The closer the plant food to the tail of the distribution, the more unique its color. For ease of comparison, we also displayed the percentage of all image pixels with values below this median value. We also generated \( \Delta E_{ij} \) images in which the receptor excitation images described above (before the correction for gamma scaling) were subtracted from each other. To make full use of the computer display’s dynamic range, while keeping \( \Delta E_{ij} = 0 \) at half the maximum pixel intensity, we found the absolute value of the most extreme positive or negative \( \Delta E_{ij} \) value across all six dichromatic comparisons, and then stretched and shifted \( \Delta E_{ij} \) thusly:

\[
\Delta E_{ij} = \Delta E_{ij} \max \left\{ \Delta E_{ij} : i = 1, \ldots, 6, j = 1, \ldots, 6 \right\} \times 0.5 + 0.5 \tag{10}
\]

Finally, we adjusted the resulting values to undo sRGB gamma scaling in order to make \( \Delta E_{ij} \) values scale linearly with pixel brightness.

2.6. Visualizing tetrachromatic vision with only three channels

To include information from all four cone channels in a single color image, we plugged select \( \Delta E_{ij} \) images into each of the three channels of an RGB image. We chose the three dichromatic comparisons that Osorio, Vorobyev, and Jones (1999) found behavioral support for in chickens, plugging the S-U comparison into the R-channel, the M-L comparison into the G-channel, and the U-M comparison into the B-channel. To make full use of the computer display’s dynamic range, we shifted the \( \Delta E_{ij} \) values by the same amount in all three channels such that the minimum \( \Delta E_{ij} \) value was zero. We then normalized by the maximum \( \Delta E_{ij} \) value across all three channels and adjusted the resulting values to undo sRGB gamma scaling.

3. Results

Photographs were taken across a broad range of lighting conditions. The distributions of different weather conditions photographed are plotted per image (Fig. 2A–C) and per object comparison (Fig. 2D–F). For a complete breakdown of weather conditions per category of object comparison, see Supplementary Fig. 1.

Nutrient-dense non-signaling plant foods (delineated in Table A.1) presented significantly lower (and often negative) contrast in the U channel than in the longer-wavelength channels when viewed against upper leaf surfaces and branches (Fig. 3A,C, Tables A.2–3). The same was not always true when lower leaf surfaces were the background object, owing to the fact that leaves transmit almost no UV light, and
Fig. 3. Low or negative figure-ground contrast in the UV channel between nutrient-dense non-signaling plant foods and background objects enhanced overall color contrast for birds (with oil droplets) and a generalized tetrachromat (with peak sensitivities approximating those of UVS birds but unfiltered by oil droplets). Within-channel contrasts (A,C) and RNL color contrasts (B,D) in birds (A,B) and a generalized tetrachromat (C,D). Within-channel contrasts are the inputs to the RNL model, and the distances between such contrasts help one to understand how within-channel UV contrasts enhance color contrasts. “Upper” refers to upper leaf surfaces and “lower” refers to lower leaf surfaces. (A,C) Stars indicate channels in which the within-channel contrast is significantly different from the within-channel contrast in the U-channel. (B) Within each object comparison, a gray star indicates that double-cone RNL achromatic contrast was significantly lower than VS\textsubscript{ML} RNL color contrast. A purple star indicates a significant effect of the V-cone, a blue star indicates a significant effect of the S\textsubscript{V}-cone, and (B,D) a black star indicates a significant effect of a complete loss of the U/V receptor on RNL color contrast. Note that all effects in B and D were negative. Boxplots show the median, interquartile range (IQR), and lowest and highest data. See Tables A.2-6 for details of statistical tests. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
most of the incident light in natural habitats comes from above (Tedore & Nilsson, 2019).

The avian achromatic channel, the double cones, saw much lower contrast than the modeled avian tetrachromatic visual systems (Fig. 3B, Table A.4). When compared in an opponent color vision system, a shift from U to V, as well as a complete loss of the U/V receptor, nearly always significantly lowered color contrast (Fig. 3B,D, Tables A.5–6). By inspecting Fig. 3, it can be seen that the larger the gap between the within-channel contrasts in the UV and visible channels (Fig. 3A,C), the greater the decrease in color contrast with the loss of a UV photoreceptor.

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**Fig. 4.** A study in the color of leaf buds. Receptor excitation images of Betula leaf buds as viewed by (A) the avian U, V, S_U, S_V, M, L, and double cone channels and (B) the generalized tetrachromat’s U, S, M, and L channels. Dark pixels correspond to low receptor excitation and light pixels to high receptor excitation. (C) Histograms show the distribution of differences in receptor excitation across all pixels of all images of leaf buds. The median difference in receptor excitation for leaf buds themselves is indicated by a vertical yellow line (with the value printed on top) within each distribution. The closer this median value is to the tail of the distribution, the more unique the color. Also displayed is the percentage of all image pixels falling below this median value. (D) Exemplar images showing the difference between zoomed-out versions of the receptor excitation images in (A). (E) False-color images of the scene in (D) with differences in receptor excitation values (left) and receptor excitation values (center and right) of the indicated avian channels plugged into each of the RGB channels of the computer screen. For details of image processing, see Methods. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)
class (Fig. 3B,D). On the other hand, a shift of the avian $S_u$-cone to the
$S_v$-cone only twice had a significant effect on color contrast (Fig. 3B
(blue boxplots), Table A.5), and the effects were small and negative.

In the distributions of receptor excitation differences across all pixels
of all images, nutrient-dense non-signaling plant foods plotted at or near
the tail of the distributions involving a UV receptor, i.e. U-S, U-M, and U-
L. Plant foods’ S-M and S-L differences were similar to their U-M and U-L
differences, respectively, but less extreme and less unique. Conversely,
in distributions of M–L differences, plant foods tended to plot near the
distribution center (Figs. 4–7).

4. Discussion

Nutrient-dense non-signaling plant foods generally radiated little UV
light. Sometimes this resulted in near-zero contrast with the background in a UV channel, whereas in other cases, the contrast was obviously negative, generating strong negative target-ground contrast. Low or negative contrast in the UV channel, when compared in a color opponent system to the higher or more positive contrast in the visible channels, markedly enhanced color contrast, even when accounting for the greater receptor noise experienced by a tetrachromat than a trichromat. The same was true regardless of whether vision was modeled with or without oil droplets. Importantly, the foods photographed presented much smaller double cone (achromatic) contrasts than color contrasts. This demonstrates the importance of color vision for the detection of nutrient-dense non-signaling plant foods.

It is obvious that negative contrast, in which an object reflects less light than its background, will enhance color contrast, but it is less obvious how a UV contrast close to zero could enhance color contrast. However, if one examines how color contrasts are computed in the receptor-noise-limited model developed by Vorobyev et al. (1998) and Vorobyev and Osorio (1998) (Eqs. (4)–(6) in the Methods section), one can see that it is the difference in contrasts seen by different receptors, i.e. the difference of differences, that affects color contrast. To consider a simple example, imagine a UV-blue-green trichromat that sees a contrast of 1 in the green channel, a contrast of 1 in the blue channel, and a

Fig. 6. A study in the color of unripe non-fleshy fruits. Legend otherwise as in Fig. 4. Exemplar images feature immature non-fleshy fruits of *Melicope rubra*. 
contrast of 0 in the UV channel. If we strip Eq. (6) of its noise terms for simplicity, one can see that color contrast in such an animal would be computed by taking $\sqrt{(1 - 1)^2 + (1 - 0)^2 + (0 - 1)^2} = 1.4$. If, on the other hand, the contrast in the UV channel were 1, then color contrast would be $\sqrt{(1 - 1)^2 + (1 - 1)^2 + (1 - 1)^2} = 0$. Thus, a UV contrast of zero can significantly enhance color contrast if contrasts in the other channels differ from zero.

Earlier work hinted at the importance of UV cues for animals foraging for nutrient-dense non-signaling plant foods. Kelber (1999) investigated how the swallowtail butterfly *Papilio aegeus* might use color information to identify the young leaves of its host plant, since she found that caterpillars hatching from eggs on young leaves grow faster than those that hatch on mature leaves. She used behavioral assays and visual and statistical modeling to determine which receptors were most likely mediating the butterfly’s choice of artificial leaves on which to oviposit. The best-fitting model indicated that the UV receptor had the strongest influence, such that artificial leaves low in UV reflectance were favored by the butterflies. However, this model was discarded because it was difficult to interpret due to the arena light source radiating little UV light and the experimental stimuli all reflecting similarly low amounts of UV light. However, our results suggest that this finding was real and not an artifact of limitations in the experimental design.
One might question why nutrient-dense non-signaling plant foods do not develop better UV crypsis so as to better avoid detection by herbivores. We would hypothesize that UV crypsis is difficult to achieve in vegetated habitats. Much of the UV light emitted by leafy backgrounds comes from mirror-like specular reflections of the surrounding habitat from waxy plant cuticles (Brakke, 1994; Tedore & Nilsson, 2019; Vandelblilt & Grant, 1985), and the magnitude of specular reflections depends on object orientation. Because mature leaves are generally oriented with their flat surfaces oriented toward the sky, and because specular reflections increase with increasing angle of incidence, specular reflections of UV light from skyward-oriented upper leaf surfaces are high when viewed by an observer looking horizontally. Nutrient-dense non-signaling plant foods often have shapes and orientations that make it impossible for them to match the specular reflections of the mature leaves surrounding them when viewed from this horizontal viewpoint, even if they have a well-developed waxy cuticle. In the UV image of Citrus in Fig. 7, for example, one can see intense specular reflections from the skyward-oriented waxy surface of the fruit, but as this presents a relatively small surface area, most of the fruit appears dark. Similarly, young leaves are often oriented with their flat surfaces perpendicular to the sky (e.g. Atractocarpus benthamianus and Acradenia euodiformis in Fig. 5). This prevents the strong specular reflections seen from more horizontally-oriented mature leaf surfaces. If, however, an observer were flying above the vegetation, taking down, or obliquely down, such that their gaze was perpendicular to mature leaf surfaces, specular reflections would be reduced due to the lower angle of incidence of specular reflections of the sky reaching the observer. Nutrient-dense non-signaling plant foods may therefore appear more cryptic from this downward-looking viewpoint. That said, when an animal searches from a horizontal viewpoint, there are more lower leaf surfaces visible than when it searches from a downward-looking viewpoint. Like nutrient-dense non-signaling plant foods, lower leaf surfaces radiate little UV but much green light, and may act as visual clutter or distractors during a horizontally-directed visual search. It would be interesting to test whether animals favor a particular viewing angle when searching for such foods.

Even if a nutrient-dense non-signaling plant food had the orientation required to specularly reflect a lot of sunlight, there are other reasons why it may not specularly reflect as much UV light as a mature leaf. Emerging leaves often have a crinkly surface and an underdeveloped waxy cuticle (Jeffree, 2006), both of which will reduce the intensity of specular reflections. And the surfaces of non-fleshy fruits are often not smooth enough to specularly reflect much light (e.g. Melicope rubra in Fig. 6).

It is also possible that immature and/or rapidly-growing plant tissues upregulate expression of sunscreen pigments. Sunscreen pigments absorb UV, making the plant tissue appear dark in a UV channel. It is known that leaves exposed to high levels of UV light upregulate their production of UV sunscreen pigments such as phenolic compounds, flavonoids, and hydroxyccinnamate esters (Behn, Schurr, Ulbrich, & Noga, 2011; Bieza & Lois, 2001; Hahlbrock & Scheel, 1989). It could be that immature leaves, without the benefit of a fully developed waxy cuticle to reflect and absorb UV light (Day, Martin, & Vogelmann, 1993; Solovchenko & Merzlyak, 2003), upregulate production of sunscreen pigments compared to mature leaves. This seems unlikely, however, since studies of rye and pecan leaves have found UV sunscreen pigment concentration to increase over development (Burchard, Bilger, & Weisenbock, 2000; Qi, Bai, & Heitz, 2003).

Earlier studies of other types of non-signaling, apparently cryptic foods have not yielded such a consistent relationship between food target UV reflectance and background UV reflectance. Cryptic caterpillars, for example, have been found to diffuse reflect low but varying amounts of UV light relative to the leaves and twigs they stand on, which also diffusely reflect little UV light - i.e. sometimes more and sometimes less (Church, Bennett, Cuthill, Hunt, et al., 1998; Church, Bennett, Cuthill, & Partridge, 1998). It would be useful to visualize such caterpillars against leaves and twigs using multispectral imaging to determine how cryptic they are when mirror-like specular reflections are taken into account. It seems likely that the round shape of the caterpillar body and the wrinkled texture of the caterpillar cuticle would prevent strong specular reflections and, in a UV channel, cause them to stand out as dark targets against the strong specular reflections of mature leaves and smooth twigs.

Distributions of differences in receptor excitation values across entire images, as well as the associated difference images, made it clear that all potential dichromatic UV channel comparisons markedly enhance the uniqueness of nutrient-dense non-signaling plant food colors, helping them to pop out against a cluttered background (Figs. 4–7). This was especially true of leaf buds, immature lower leaf surfaces, and immature non-fleshy fruits. For immature non-fleshy fruits, although U-S differences were the smallest of the UV channel comparisons, they were the most unique (Fig. 5). Thus, animals relying on immature non-fleshy fruits would especially benefit from retinal circuitry supporting a U-S comparison. Although the opponent comparisons made by animals are, in general, poorly known, and are not fully characterized in birds (Baden & Osorio, 2019; van der Kooi, Stavenga, Arikawa, Belusie, & Kelber, 2020), it is interesting to note that Osorio et al. (1999) provided behavioral evidence that chickens do indeed compare U- and S-cone outputs. Conversely, M–L differences in all classes of nutrient-dense non-signaling plant foods were slight and plotted near the center of the distributions of M–L differences across entire images. This indicates that, at least under photopic conditions, a UV receptor should be more useful than a red receptor for picking out nutrient-dense non-signaling plant foods against a cluttered visual background.

Another of our key findings was that the avian U-cone usually saw lower, or more negative, within-channel contrast than the avian V-cone. This translated into higher color contrast for birds with U-cones. The U-cone should therefore be favored in birds specializing on nutrient-dense non-signaling plant foods. And, more generally, animals specializing on such plant foods should have UV photoreceptors peaking at shorter wavelengths. Interestingly, parrots and cockatoos possess a U-cone (Odeen & Hästad, 2013) and are particularly notorious for predating on the seeds of unripe fruits (Toft & Wright, 2015; White, 2011). Sulfur-crested cockatoos, for example, are known to dig into the unripe fruits of Melicope and Citrus shown in Figs. 6 and 7 to eat the seeds within (Christina Suttner, personal communication). Most passerine seed-eating specialists, including finches, tits, chickadees, waxbills, buntings, and sparrows also possess the UVS cone variant, as do many passerines that feed on seeds and young leaves during only certain times of year (del Hoyo et al., n.d.; Odeen et al., 2011). That being said, passerine seed-eating specialists are closely related to one another, making it difficult to disentangle the effects of selection and common ancestry. Evolutionary transitions between UVS and VS visual systems in the avian phylogeny are uncommon enough (Odeen et al., 2011; Odeen & Hästad, 2013) to make it difficult to rigorously test for significant correlations between visual system and diet, especially since diet records are often not as specific as needed in the taxa surrounding evolutionary transitions. Frequently, birds are recorded as feeding on buds or fruits without any specification as to whether they eat leaf, flower, or branch buds, or unripe, ripened, or fully ripe fruit.

Most insects have photoreceptors peaking at or below the wavelength of peak sensitivity of the avian U-cone. Thus, most insect visual systems are well-tuned to detect nutrient-dense non-signaling plant foods, and indeed, many insects do specialize on such foods (White, 2011, 2012). However, many insects do not specialize on such foods, so there are likely other important factors driving or constraining UV-photoreceptor spectral tuning among insects, and among birds as well. The polarization pattern of the sky must be of particular importance to insects, since so many possess a specialized dorsal rim area sensitive to polarized UV light, and for this, UV photoreceptors peaking at shorter wavelengths will perform better under challenging viewing conditions, such as under cloudy skies or a forest canopy (Barta & Horváth, 2004;
Wang et al. (2014). It is unclear whether birds see polarized light (Muheim, 2011); however, there are other selective forces that can be expected to influence the spectral tuning of their UV cone. The avian V-cone should be favored in light-limited habitats since there are more photons available in its range of sensitivity than in the sensitivity range of the U-cone. The V-cone should also be favored in closed habitats due to the higher leaf contrast seen by the V-cone in such habitats (Tedore & Nilsson, 2019). Many birds are active at dawn and dusk, and for them, the V-cone’s ability to catch more photons may be of critical importance, outweighing any benefits of the U-cone. Moving forward, as we develop a more complete picture of the UV world and the information it contains, and as animal diet, habitat, and circadian activity records become more complete and specific, it will become more feasible to test for evolutionary losses, gains, and shifts in UV sensitivity in response to different selective factors to try to discern their relative importance for the evolution of UV photoreceptors.

5. Data statement

All data and code used in the manuscript can be found at figshare.com under the DOI https://doi.org/10.6084/m9.figshare.11473293.

CRediT authorship contribution statement

Cynthia Tedore: Conceptualization, Data curation, Formal analysis, Investigation, Methodology, Project administration, Software, Validation, Visualization, Supervision, Project administration, Writing - original draft. Dan-Eric Nilsson: Conceptualization, Funding acquisition, Supervision, Project administration, Resources, Writing - review & editing.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.vires.2021.01.009.

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