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Ultraviolet reflectance in fruits, ambient light composition and fruit removal in a tropical forest

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ABSTRACT

Ultraviolet (UV) reflectance patterns in fruits and UV perception ability in frugivores were linked through a fruit survey and with a field experiment that examined fruit removal under varying light conditions. The reflectance spectra were measured for fruits from 57 tropical plant species on Barro Colorado Island, Panama. Relationships among UV reflectance in fruits, colour vision of the dispersal agents, light regime and fruit ripening were examined using both non-phylogenetic tests and the concentrated changes test to analyse the phylogenetic distributions of these traits. Ultraviolet-reflecting fruits occurred in both open and closed light habitats and were strongly associated with dispersal by birds and rodents, both of which perceive UV radiation. In addition, only mature fruits reflected UV. Natural rates of fruit removal were studied experimentally over 3 months in the understorey shrub *Psychotria emetica* (Rubiaceae). Ambient light was manipulated by placing a UV-absorbing filter over fruiting plants, with control treatments of plants under clear filters (UV-transmitting) and plants without filters. Fewer fruits were removed when ambient UV was filtered out, establishing that ultraviolet reflectance can be an important attractant for some fruit dispersers. The results indicate a prominent role for UV reflectance in plant–frugivore relations and demonstrate a link between the perceptual abilities of animals and the colour of the fruits they consume.

Keywords: dispersal agent, fruit phenology, fruit removal, light habitat, *Psychotria emetica*, ultraviolet-reflecting fruits.

INTRODUCTION

Vertebrate ultraviolet-A (UV) perception (i.e. sensitivity to wavelengths 320–400 nm) was first documented 30 years ago in birds (Huth and Burkhardt, 1972; Wright, 1972). It is now assumed that all diurnal birds, like most insects, can perceive UV (Bennett and Cuthill, 1994). Some mammals, most notably rodents, have very refined UV vision; others, including ungulates, carnivores and primates, probably lack UV vision (Jacobs, 1993, 1996; Jacobs *et al.*, 1991, 1998). The functional roles for UV perception in vertebrates have been the subject of recent experiments on avian mate choice and foraging decisions. In the former, it has been documented that many male birds reflect UV and are preferred over non-reflecting

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birds by females (Bennett *et al.*, 1996; Andersson *et al.*, 1998; Hunt *et al.*, 1998; Sheldon *et al.*, 1999). The role of UV reflectance as a foraging cue has also been investigated in the laboratory, with the intriguing results that birds prefer both insects and fruits that reflect UV over non-reflecting ones (Church *et al.*, 1999; Siitari *et al.*, 1999). Thus, UV is common in objects of interest to birds with UV sensitivity and affects choice of both mates and food items. The aims of the present study were to assess the evolutionary conditions influencing UV reflectance in fruits (using the comparative method) and to determine experimentally if UV reflectance affects fruit removal rates in the field.

Many bird-dispersed fruits reflect UV when ripe. A study of fruit reflectance spectra for plants in Germany found that 14 of 24 species (58%) had fruits that reflect UV (Burkhardt, 1982). A similar study in Illinois found that 21 of 53 plants (40%) had UV-reflecting fruits (Willson and Whelan, 1989). All of the fruits surveyed from temperate-zone plants were fleshy drupes and almost all the fruits reflecting UV were covered by a protective, waxy cuticle referred to as a ‘bloom’. This bloom appears whitish to humans and reflects light structurally across all wavelengths, including UV. Removal of the bloom eliminated UV reflectance and generally made the fruits appear somewhat duller. Thus, most of the temperate fleshy fruits reflect UV from the waxy bloom instead of from pigments.

Perception of fruit colour is influenced by a suite of characters, including the perceptual abilities of the perceiver, the reflectance properties of the fruit, the visual background and the spectral composition of ambient light (Endler, 1990). The forest mosaic of trees, large gaps, riparian areas and clearings leads to various habitats that differ in ambient light composition (Endler, 1993). Briefly, open clearings and large gaps have the highest total light intensity, followed by small gaps, woodland shade and then forest shade. The relative UV irradiance (proportional to the human visual spectrum) is similar among the habitats with one exception: woodland shade has proportionally more UV irradiance than forest shade (Endler, 1993).

Discrimination of fruits against leaves is aided by cone pigments with sensitivity peaks at the wavelengths of the background reflectance and the object of interest, and the extent of colour contrast between the fruits and the leaves (Regan *et al.*, 1998). Because leaves containing chlorophyll strongly reflect green light and strongly absorb UV irradiance, UV-reflecting fruits will be very conspicuous against green leaf backgrounds. Birds and rodents have cone pigments with peak sensitivities in the UV (350–370 nm) and green (520–530 nm) wavelengths (Jacobs *et al.*, 1991; Hart *et al.*, 1998). Thus, UV fruit reflectance should be a particularly good signal against green leaves for birds and rodents in any habitat.

Fruit colour is presumed to function primarily to attract seed dispersers, but the ecological and evolutionary correlates of fruit colour, particularly UV reflectance, are unclear (Wheelwright and Janson, 1985; Willson and Whelan, 1990). Based upon the aforementioned studies of animal behaviour and visual abilities, and the light properties of habitats, I made four predictions concerning the function of UV reflection in fruits:

1. Ultraviolet fruit reflectance is present in fruits dispersed by birds and rodents but not in fruits dispersed by monkeys and bats.
2. Fruits with UV-reflecting components will occur in both open and closed light habitats.
3. Ultraviolet reflectance is an advertisement of fruit ripeness.
4. Fruits reflecting UV are dispersed at higher frequencies than non-reflecting fruits.

The first three predictions were addressed by a field survey that measured colour properties for fruits on Barro Colorado Island in Panama. The fourth prediction was tested using a field experiment designed to detect differences in removal rate with different UV reflectance of fruits.

METHODS

Field collections and experiments were performed between 1 June 1996 and 4 February 1997 on Barro Colorado Island, Panama, a 1560 hectare reserve administered by the Smithsonian Tropical Research Institute. Barro Colorado Island is a seasonal moist forest that receives 2600 mm of rain a year during a light rainy season from May to August, a heavy rainy season from September to December and a dry season from January to April. The island contains over 1300 species of vascular plants, of which 1263 (≈97%) are angiosperms (Croat, 1978).

The fruit survey consisted of collecting fresh fleshy fruits along every trail on the island and then bringing these back to the lab clearing to measure reflectance spectra. Collections were made two to three times per week during 2–6 h walks. Trails were chosen haphazardly and routes closest to the lab clearing were surveyed more frequently.

Measurements of fruit radiance were made with a portable spectroradiometer (LI-COR, LI-1800) and telescope receptor (LI-COR, 1800-06). Scans were made outside in a large clearing when the sky was either completely clear or uniformly cloudy, using the sun as a natural light source. The fruits were placed 0.2 m in front of the telescope receptor and all scans were made at an angle of 90° relative to the fruit surface. Radiance was measured at 2 nm intervals across wavelengths from 350 to 700 nm. A scan was first made of the fruit's surface, which was immediately followed by a scan of a white standard (pressed barium sulphate). Percent reflectance was calculated by dividing the fruit radiance scan by the white radiance scan. One radiance scan was made for each fruit and 1–4 fruits were scanned per plant species. When possible, scans were made of developing as well as ripe fruits. I classified species as UV-reflecting if the fruit reflectance between 350 and 400 nm was ≥20% or if it was <20% but with a peak in the colour curve below 400 nm.

Data on dispersal agent, light habitat and fruit encapsulation for all surveyed plants were compiled from a plant guide for Barro Colorado Island (Croat, 1978), primary articles (Foster, 1982; Glanz *et al.*, 1982; Howe, 1982; Oppenheimer, 1982; Smythe *et al.*, 1982; Worthington, 1982) and correspondence (S.J. Wright, personal communication). All survey data were converted to the following discrete, binary variables:

- *dispersal agent*: UV-blind (monkeys and bats) or UV-perceiving (rodents and birds); and
- *light habitat*: closed (fruits from the understorey) or open (fruits from the canopy, lakeshore, gaps or clearings).

Phylogenetic relationships among families were assigned using a three-gene angiosperm phylogeny (Soltis *et al.*, 1999). Relationships among genera were assigned using other studies that considered lower-order relationships (Hufford, 1992; Herre *et al.*, 1996; Nepokroeff *et al.*, 1999). Relationships between UV reflectance and the three discrete variables were tested with and without phylogenetic consideration. The phylogeny was used in conjunction with the concentrated changes test, which tests for non-random association of a dependent character state (in this case, UV reflectance) within clades of the tree that possess an independent character of interest (Maddison, 1990). Because of the size of the angiosperm tree, the concentrated changes test was performed through 10^6 simulations in the program MacClade version 3.03 (Maddison and Maddison, 1992). Non-phylogenetic associations were tested using χ^2 tests of contingency.

The fruit removal experiment was designed to test if removal rates are lower for plants that have ambient UV light removed from the fruit display. The null hypothesis was that fruit removal is unaffected by manipulations of UV reflectance. *Psychotria emetica* (Rubiaceae) was chosen as the focal plant species for the experiment for the following reasons:

1. *P. emetica* has strong reflectance in UV wavelengths.
2. Unpublished avian emetic data from a study by Poulin and Lefebvre (1996) indicated that these fruits are dispersed by a resident ground-foraging dove, *Leptotila cassinii*, and by the migratory thrushes *Catharus minimus* and *C. ustulatus* (B. Poulin, personal communication).
3. Adult plants are short (13–40 cm high) and narrow (diameter ≈ 30 cm), so that manipulations of ambient light above the plants were technically feasible.

Ripe fruits of *P. emetica* appear violet blue to humans, whereas unripe fruits are green and mature over several weeks. Fruiting plants contain 4–16 ripe fruits. Twenty-five plants were included in the experiment and were randomly assigned to one of three treatments:

1. In the 'UV filter' treatment ($n = 10$), the ambient ultraviolet light was filtered out by placing a 1 m^2 piece of UV-absorbing plexiglas (Fig. 1b) 50–100 cm above and directly over the plant. Although the 1 m^2 filters removed ambient light from above but not the sides, most of the UV irradiance was removed under the UV plexiglas filters (Fig. 1d). One of the plants from the 'UV filter' treatment was subsequently damaged by a branch fall and was excluded from the analyses.
2. Fruits in the 'clear filter' treatment ($n = 10$) were covered by a 1 m^2 UV-transmitting (Fig. 1a) piece of plexiglas placed in the same configuration.
3. The 'no filter' treatment ($n = 5$) contained plants that were monitored without any plexiglas filter.

Data on the number of fruits of each colour class (corresponding to unripe and ripe fruits) were collected once every 7 days between 7 August 1996 and 4 February 1997. The filters were also cleaned on these days and the ground examined for evidence of fallen fruit. The percentages of fruit removed were compared among the three treatments using a one-way analysis of variance and a Tukey *post-hoc* test, with filter treatment as the independent variable and the proportion of fruit removed as the response variable. To meet the assumptions for a parametric test, the proportions of fruit removed were square-root transformed.

RESULTS

Spectral radiance was measured for the fruits of 57 plant species on Barro Colorado Island. Scans of completely ripe fruits were available for 39 species, of which 24 (61.5%)

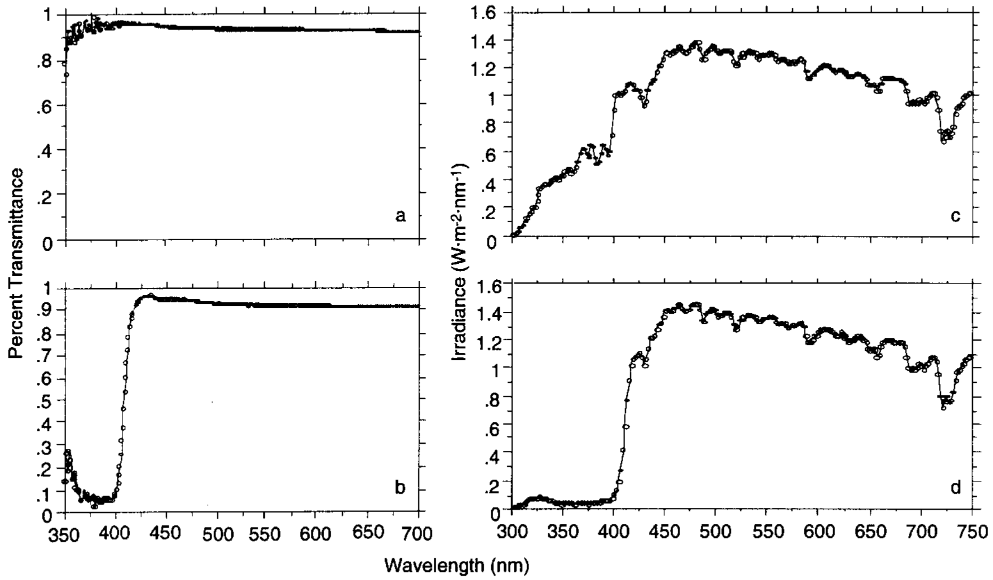

Fig. 1. Percent transmission through (a) the clear (UV-transmitting) and (b) the ultraviolet (UV-absorbing) plexiglas filters measured with a UV-visible spectrophotometer (Varian, Cary 100). The ambient light spectra were measured under clear (c) and UV plexiglas filters (d) using the portable spectroradiometer (LI-COR, LI-1800) and its remote cosine receptor (LI-COR 1800-11). The spectroradiometer was calibrated before and after each set of irradiance scans using an optical radiation calibrator (LI-COR, LI-1800-02).

reflected UV (Table 1). No fruits were covered by a bloom and rubbing did not affect reflectance spectra.

In addition to frugivory by birds, monkeys and bats, fruits from plants were also consumed, hoarded and dispersed by several rodents, including agoutis (*Dasyprocta punctata*), pacas (*Agouti paca*) and red-tailed squirrels (*Sciurus granatensis*). Dispersal by birds and rodents was positively correlated with UV reflectance in fruits. The non-phylogenetic analysis revealed a strong association between UV-reflecting fruits and dispersal by birds and rodents with UV sensitivity (χ^2 = 5.652, P = 0.017). The concentrated changes test also revealed an unusually high concentration of UV reflectance evolving within clades of avian- and rodent-dispersed fruits ($P = 0.005$).

Ultraviolet-reflecting fruits did not differ in their distribution between open and closed habitats ($\chi^2 = 0.652$, $P = 0.420$). Furthermore, UV components to fruit displays were equally likely to evolve in plants occurring in either open or closed habitats according to the concentrated changes test (P = 0.13). Scans of developing fruits were available for 28 of the 57 plants species but no fruits reflected UV.

Fruits of *Psychotria emetica* were slightly less bright under the clear filters at all wavelengths, and were completely dull in UV wavelengths when placed under the UV-absorbing filter (Fig. 2). Most fruits were removed within 10 weeks of ripening. Other fruits disappeared from plants in later months during the peak rainy season, but many of these fruits

Table 1. The plant species surveyed in Panama

Species	UV reflectance	Dispersal agent	Light regime	Capsule
Annona hayesii	Strong	Rodents (monkeys)	Closed	No
Anthurium friedrichstelii	Strong	?	Closed (open)	No
Calophyllum longifolium	No UV	Monkeys	Closed (open)	No
Cestrum magalophylum	Slight	?	Closed	No
Chamaedorea tepejilote	No UV	?	Both	No
Coccoloba acuminata	No UV	Birds	Open	No
Connarus turczaninowii	Strong	Birds, rodents	Open (closed)	Yes
Cupania rufescens	Strong	Birds (monkeys)	Closed	Yes
Doliocarpus major	Strong	Birds, rodents, monkeys	Open (closed)	Yes
Faramea occidentalis	No UV	Birds (rodents, monkeys)	Closed	No
Ficus colubrinae	No UV	Birds, rodents, monkeys	Closed (both)	No
Ficus insipida	Slight	Rodents, monkeys	Open	No
Ficus obtusifolia	No UV	Bats	Open	No
Ficus yopenensis	No UV	Bats	Open	No
Gustavia superba	No UV	Rodents, monkeys	Open	Yes
Heisteria longipes	No UV	Birds, rodents, monkeys	Closed	No
Heliconia catheta	Slight	Birds (rodents)	Open	No
Herrania purpurea	Strong	Birds, rodents	Closed	Yes
Lacistema aggregatum	Slight	Birds	Closed	Yes
Lacmellea panamensis	Strong	Rodents	Closed	No
Maripa panamensis	Slight	Rodents	Open (closed)	Yes
Miconia nervosa	Slight	Birds	Closed	No
Oenocarpus panamanus	Slight	Rodents, monkeys	Closed	Yes
Ormosia amazonica	Slight	?	Open	No
Paullinia pterocarpa	Slight	Birds, rodents, monkeys	Closed	Yes
Piper cordulatum	No UV	Bats (monkeys)	Closed	No
Pourouma guinensis	Slight	Monkeys, rodents	Open	No
Psychotria acuminata	Slight	Birds	Closed	No
Psychotria chagrensis	No UV	Birds	Closed	No
Psychotria emetica	Slight	Birds	Closed	No
Psychotria hoffmannseggiana	No UV	Birds	Closed	No
Psychotria limonensis	Slight	Birds	Closed	No
Psychotria marginata	No UV	Birds	Closed	No
Socratea exorisza	No UV	Monkeys (rodents)	Closed	No
Tabernaemontana arborea	No UV	Monkeys	Closed	Yes
Tetrathylacium johansenii	Strong	Rodents, monkeys	Closed	No
Trema micrantha	Slight	Birds	Open	No
Virola surinamensis	Slight	Birds, monkeys, rodents	Open	Yes
Vitis tiniifolia	Slight	Birds (rodents)	Open	No

Note: Agents and habitats in parentheses are less frequent. The mean number of fruits scanned per species was 2.67.

were rotten or desiccated by that time. Accordingly, I only analysed removal data for the first 10 weeks after ripening.

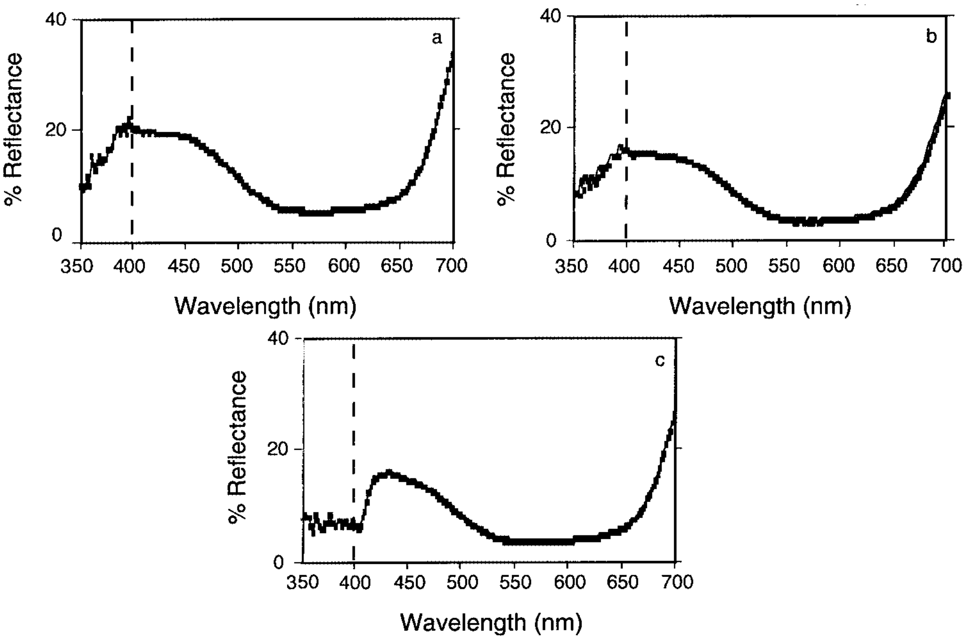

Fig. 2. Percent reflectance in *Psychotria emetica* (Rubiaceae) under no filter, a clear filter and a UV-absorbing filter. The reflectance scan of fruits under no filter (a) is a scan of unmanipulated fruits. The scan of the fruits under the clear filter (b) shows the same shape as the no filter scan but with slightly less overall reflectance. The scan of the fruits placed under the UV-absorbing filter (c) has the same reflectance curve as underneath the clear filter with the exception that these fruits are totally dull in UV wavelengths. The radiance measures in (b) and (c) were performed by dividing the fruit scan under the filter by a white standard scanned without a filter.

Plants from the three treatments did not differ in the total number of fruits per plant ($F_{2,21} = 1.100$, $P = 0.351$). Almost 100% of the fruits were removed from the 'no filter' treatments, a high proportion were removed from the 'clear filter' treatment and a very small proportion were removed from the 'UV filter' treatment (see Fig. 3; $F_{2,21} = 6.561$, $P < 0.01$). *Post-hoc* analysis revealed that the proportion of fruit removed did not differ between the 'clear filter' treatment and the 'no filter' treatment ($P = 0.483$), although 'UV filter' treatments had a lower percent fruit removal than both the 'no filter' treatment ($P = 0.008$) and the clear filter treatment ($P = 0.036$).

DISCUSSION

Fruit colour is assumed to function primarily in attracting seed dispersers to ripe fruits. Linking the colour components of fruits to the perceptual abilities of the dispersers lends strong support to this hypothesis. Janson (1983) proposed that tropical birds and mammals feed upon fruits that fall into two colour syndromes: mammalian-dispersed fruits appear orange, yellow, brown or green to humans, whereas avian-dispersed fruits typically appear red, black, white, blue, purple or multicoloured to humans. However, avian-dispersed fruits

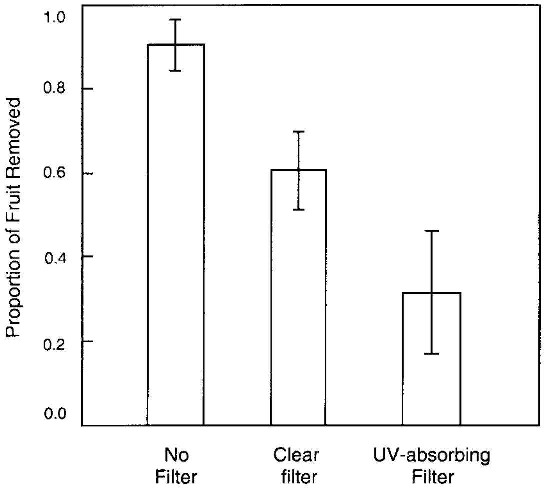

Fig. 3. Fruit removal in *Psychotria emetica* (Rubiaceae) under no filters, clear filters and UV-absorbing filters. Bars represent means and error bars are standard errors.

from both temperate and tropical sites can be black, red, white, orange, brown, blue, yellow or green when ripe (Wheelwright and Janson, 1985) and many bird-dispersed fruits in Australia fit better in Janson's (1983) mammal colour syndrome (Willson and Irvine, 1989).

Many fruits are presented in bi-coloured displays (Wheelwright and Janson, 1985) and birds preferentially consume fruits from bi-coloured displays than uni-colour displays (Willson and Melampy, 1983; Whelan and Willson, 1994). However, birds do not exhibit strong preference among colours presented in uni-coloured displays (Willson *et al.*, 1990). A suite of evolutionary hypotheses has been proposed for the selective value of particular fruit colours but none has received strong support (Willson and Whelan, 1990). Because most animal colour vision is different from our own, much of the confusion concerning fruit colour and disperser behaviour has probably resulted from using human colour vision for colour quantification (Bennett *et al.*, 1994).

Tropical fruits in this study reflected UV through a different mechanism than temperate fruits from other studies. The tropical fruits were not covered by bloom and probably reflect UV through pigments. In contrast, most of the temperate fruits were covered by a waxy bloom and reflected UV through Tyndall scattering (Burkhardt, 1982; Willson and Whelan, 1989). Wax cuticles on fruits also provide protection against fungal pathogens and desiccation and are involved in gas exchange (Rosenquist and Morrison, 1989). If modified waxy blooms have evolved on temperate fruits to increase UV reflection, these structural changes would probably affect other features of fruit physiology. A larger survey from multiple latitudes would be necessary to determine if the mechanisms of UV reflectance truly differ among biomes. Irrespective of the mechanistic differences, the proportion of fruits reflecting UV in the tropical survey (61.5%) was similar to that in the two aforementioned surveys of temperate fruits (58% and 40%). Thus, the evolutionary forces promoting UV colour reflectance may be operating at a similar magnitude and direction at tropical and temperate latitudes.

Ultraviolet reflectance in fruits was predicted to be a signal for attracting vertebrate dispersers possessing UV-sensitive cone pigments. This prediction was tested by comparing the associations between UV reflectance in fruits and UV perception abilities of dispersers. The tests of association between UV reflectance in fruits and UV perception received strong support from both non-phylogenetic and phylogenetic methods.

Ultraviolet reflectance in fruits was not associated with habitat light characteristics. Because the discrimination of fruits against green leaf backgrounds is greatest with cone sensitivities matching that of fruits and leaves (Regan *et al.*, 1998), it would appear that birds and rodents can discriminate UV-reflecting fruits against green leaf backgrounds despite lower short-wave irradiance in the forest understorey (Endler, 1993).

The third prediction tested was that fruits reflect UV only when ripe. This hypothesis received strong support because no immature fruits reflected UV. This pattern could result from a convergence on UV reflectance as a ripeness signal to the majority of seed-dispersing species. In addition, it is beneficial for fruits to appear dull during development to decrease conspicuousness to herbivores. Taking the results of the comparative study of fruit colour and ecological characteristics together, it would appear that UV reflectance in fruits serves to advertise ripeness to UV-perceiving birds and rodents. It is also possible that UV displays function as a bi-coloured advertisement (associated with chlorophyll-containing leaves) in both open and closed habitats.

These hypotheses were explicitly tested in the fruit removal experiment. Two previous studies examined avian removal of UV-reflecting fruits. Each of these experiments tested for discrimination between conspecific fleshy fruits with or without a waxy bloom responsible for the UV colour component. Willson and Whelan (1989) conducted both aviary and field experiments with artificially placed fruits. In neither case did birds discriminate between fruits with or without the bloom. In contrast, Siitari *et al.* (1999) found that birds in the laboratory preferred fruits with bloom if the fruits were illuminated with UV ambient light. Fruits with blooms that were not illuminated with ambient UV were not preferred over fruits without bloom. In addition to using artificial UV illumination, Siitari *et al.* (1999) used green backgrounds, whereas Willson and Whelan's (1989) artificial placements may have led to unnatural background colour and more difficulty in discriminating colour. The effect of background colour on avian foraging behaviour has been studied for blue tits (*Parus caeruleus*) foraging on UV-reflecting caterpillars against black and cabbage-coloured backgrounds (Church *et al.*, 1999). This experiment also found discrimination between UV-reflecting and non-reflecting caterpillars but the birds did not discriminate based on the two background colours. However, black and cabbage-coloured backgrounds may be close to natural background colours of dirt and the foraging substrate respectively. Taken together, it would appear likely that UV reflectance in fruits is a distinguishable cue only in the relevant context of both ambient light and contrast with background colour.

The current study removed UV from the ambient light reaching the plant, but also by leaving plants in their natural background. Because of the height of the plants and the ground foraging behaviour of *Leptotila cassinii*, the overhead placement of filters is unlikely to have interfered physically with fruit removal. The significant decrease in fruit removal for plants under UV-absorbing filters is a strong indication that fruits with UV reflectance are preferentially removed relative to UV-dull fruits in closed habitats.

Roles for UV vision are known for mate choice and foraging. Evidence is presented here for evolutionary forces promoting UV reflectance in fruits. This study lays the groundwork for understanding plant–animal interactions in the context of the animal visual system.

A combination of comparative analyses and concomitant experiments may help to shed light on the sensory modalities of animals and their ecological correlates.

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