

VISUAL FRUIT PREFERENCES OF VISAYAN TARICTIC HORNIBILLS, *Penelopides panini panini* (BUCEROTIFORMES: BUCEROTIDAE), AND MUSKY FRUIT BATS, *Ptenochirus jagori* (MEGACHIROPTERA: PTEROPODIDAE), IN CAFETERIA EXPERIMENTS

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ABSTRACT

Cafeteria-choice experiments revealed preferences of Visayan Tarictic Hornbills (Penelopides panini panini) and Musky Fruit Bats (Ptenochirus jagori) for test fruits with different wavelength reflection characteristics. Preferences for certain colors were assessed by offering artificially colored fresh fruit cubes of banana pulp ('test fruits'). Findings indicate that while hornbills preferred red and blue test fruits, fruit bats showed a preference for yellow and red test fruits. Although fruit bats are color blind, reflection properties of fruits might support visual guidance for foraging bats under dim light conditions. Samples of reflectance measurements of 'typical' bat and bird fruits in the wild are given.

Introduction

Hornbills and fruit bats are known to be important seed dispersal agents and therefore essential for the maintenance of tropical rainforests (e.g. Marshall 1985, Kemp 1995, Corlett 1998, Whitney & Smith 1998, Hamann & Curio 1999). Many studies have reported distinct fruit preferences by frugivores that may effect seed dispersal. Plant characteristics, such as fruit color, fruit, and seed size, as well as plant life forms are often assumed to be adapted for certain seed dispersal agents (e.g. Marshall 1983, Howe & Westley 1986, Fleming & Estrada 1993): factors such as fruit display, crop size, and the spatial distribution of food plants influence food choice of bats and birds (e.g. Moermond & Denslow 1983, Heithaus et al. 1975, Uzzurum 1995).

Following the early concepts of fruit syndromes (Ridley 1930, van der Pijl 1969), it is possible to define fruit characteristics in relation to the main dispersers of certain plant species (Howe & Westley 1986). Bat-dispersed fruits are often described as having dull green colors (Kalko et al. 1996, Korine et al. 1998), emit musky, strong odors (van der Pijl 1969, Howe & Westley 1986, Luft 2002), and contain a high proportion of carbohydrates, while being poor in lipids and proteins (Korine et al. 1998, Ruby et al. 2000, Wendeln et al. 2000). By contrast, typical bird fruits are thought to be black, violet, red, or blue (Knight & Siegfried 1983, Howe & Westley 1986), nearly odorless, and offer a pulp rich in sugars and, occasionally, lipids (Howe & Westley 1986, Corlett 1998, Schabacker & Curio 2000). Furthermore, ultra-violet reflection of certain fruits seems to be strongly associated with dispersal by birds and rodents both of which could perceive UV radiation (Altschuler 2001).

In cafeteria-choice experiments, we tested one hornbill and one fruit bat for fruit color preferences. Fruit bats are thought to possess no color vision (Suthers 1970, Neuweiler 1993, Nowack 1999). In spite of this, we included a fruit bat in the cafeteria experiment since fruit bats are likely to perceive colors as various shades of grey. Kalko et al. (1996) hypothesized that ripening fruits of red, orange, or yellow coloration should be attractive to pteropodids as they stand out against the surrounding vegetation and are presumably easier to detect visually in dim light than cryptic greenish fruits (see Burns and Dalen 2002). Unlike fruit bats, most birds have a highly developed color vision (e.g. Martin & Lett 1985, Kreithen & Eisner 1978, Jane & Bowmaker 1988) including UV-vision in several species (e.g. Goldsmith 1980, Emmerton & Delius 1980, Burkhardt 1983). For example, at least one species (*Buceros bicornis*) displays a sexual dimorphism in the UV reflection of certain head structures (Burkhardt 1989). Unfortunately, the color vision of hornbills has not been studied in detail. Nevertheless, there are several ecological and

behavioral observations demonstrating the importance of fruit colors for foraging hornbills (e.g. Whitney & Smith 1998, Poulsen et al. 2002).

Although much is already known about the importance of frugivore-plant relationships in the tropics, aspects of fruit characteristics and how they relate to physiology, sensory capabilities, morphology, and behavior of the animals eating the fruits and dispersing the seeds are still generally understudied. This paper addresses the fruit color preferences of two Philippine fruit-eaters, the Visayan Tarictic Hornbill (*Penelopides panini panini*) and the Musky Fruit Bat (*Ptenochirus jagori*), in an experimental setup and discusses the ecological backgrounds of the findings.

Materials and Methods

The study was conducted in and around the research station of the Philippine Endemic Species Conservation Project (PESCP) in the NW Panay peninsula, Philippines (11°49,2' N, 121°58,1' E). The station lies at 450 m a.s.l. and is surrounded by a mosaic of primary and secondary forest. Three adult Tarictic Hornbills, *Penelopides panini panini*, and ten adult Musky Fruit Bats, *Ptenochirus jagori*, with both species coming from NW Panay, were kept in the PESCP-Rehabilitation-Center.¹ While bats were kept isolated from each other in cages (1.2 x 1.0 x 1.5 m), hornbills were housed as a pair and a single male in large aviaries (5.0 x 2.5 x 3.0 m).

The purpose of the cafeteria experiments was to reveal the animals' potential color preferences while feeding on fruits. In order to standardize fruits, we used cubes of ripe banana pulp (2 cm³), which were treated with food colors (National Foods Inc., Manila) in red, green, blue, and yellow in watery solution. Uncolored banana cubes of the same size, which were dipped in water prior to each trial, served as controls. Fruits were offered simultaneously in white (birds, bats) or green dishes (bats) (flat plastic plates of 20 cm diameter) in equal numbers (bats: 4 fruit cubes of

each color; birds: 10 fruit cubes of each color). The colors were mixed randomly in the dish. The feeding bowls for *P. jagori* were suspended under the roof at one narrow end of the cage while those for the *P. p. panini* were placed on a feeding stand 1.6 m from the ground. This setup ensured equal access to both bats and birds. After placing the dishes in the cages, we noted the number of fruit pieces removed and eaten every 15 min (0-75 min) for bats and every minute (0-10 min) for birds. This difference in timing was necessary because of the varying feeding modes of birds (swallowing whole fruits in a short time) as compared to fruit bats (processing each fruit over minutes). Each bat was tested on three evenings ($n_{\text{trials}} = 30$) and hornbills on four days ($n_{\text{trials}} = 12$). These data were analyzed following Rodger's (1984) suggestion of an appropriate measure of preference by calculating the area under each cumulative consumption curve standardized to a maximum of 1.0. The areas under curves were estimated using the following formula (Sachs 1999):

$$\text{Area} = \frac{1}{2} \sum_{i=0}^{n-1} (t_{i+1} - t_i)(y_i + y_{i+1})$$

where $n + 1$ are numbers of observations y_i at times t_i with $i = 0, 1, \dots, n$ (birds) or $i = 0, 15, 30, \dots, n$ (bats). These preference scores were then standardized to the range 0-1.0 by the formula (Krebs 1989):

$$R_i = \frac{A_i}{\max(A_i)}$$

where Rodgers' index of preference for species i (R_i) is calculated by dividing the area representing the cumulative proportion eaten by this species (A_i) by the largest value of the A_i ($\max(A_i)$) of hornbills or fruit bats, respectively.

The results of R_i of fruit bats for each color were tested with the Friedman test and pairwise comparisons were made using Wilcoxon-Wilcox tests (Sachs 1999) because values of R_i are not independent. Prior to the analysis, R_i values were transformed ($\arcsin \sqrt{R_i}$).

¹ As per MOA with the DENR

To quantify the color data of the tested banana cubes and some wild fruits eaten by fruit bats, we used a miniature fiber optic spectrometer (Ocean Optics, Inc., model S2000) attached to a Tungsten Halogen Lightsource (HL2000) with a wavelength range of 360-1100 nm. As fiber optic probes, R200 Reflection probes which consist of 7 optical fibers (6 illuminating fibers, 1 read fiber; each 200 μm diameter) in combination with a Reflection Probe Holder with 45° aperture were used. Spectrawin 4.0-Software was used to analyze the reflection data of fruits.

Results

The cafeteria experiments revealed that hornbills preferred red, blue, and uncolored banana cubes more than yellow and green cubes (Fig. 1). The differences in preference indices of the three favorites are small ($R_i = 0.82-1.0$), but there is a clear difference between green and yellow fruits ($R_i = 0.07-0.15$). This is also obvious when the proportion of eaten fruits over time is considered (Fig. 2), although the magnitude of variation among trials is high (e.g. first time interval (1 min): red 28.3 \pm 23.7%, yellow 0%, control 14.2 \pm 21.1%, blue 18.3 \pm 25.2%, green 0%; all mean \pm SD, n = 12 trials).

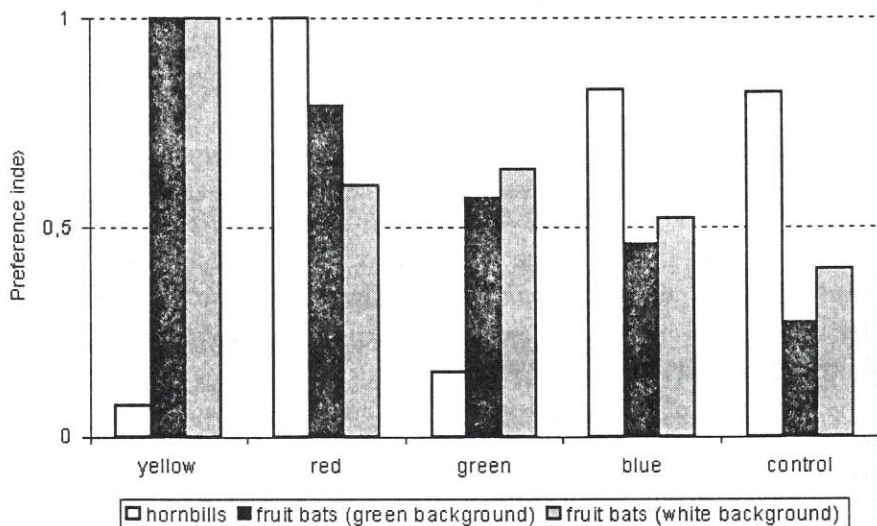


Fig. 1: Preference indices for fruit-bats (*P. jagori*) and hornbills (*P. p. penelopides*) of color choice in cafeteria experiments.

When presented with the colored fruit cubes set against a green background, fruit bats exhibited the strongest preference for yellow fruits ($R_i = 1$), followed by red ($R_i = 0.79$), and green ($R_i = 0.57$) cubes. Blue ($R_i = 0.46$) and uncolored ($R_i = 0.27$) banana cubes were least attractive choice to bats (Fig. 1). Similar to the results of hornbills, the proportion of eaten fruits over time (see Fig. 3) varies much among trials (e.g. first time interval (15 min): red 16.7 ± 12.9 %, yellow 20.8 ± 24.5 %, control 0 %, blue 12.5 ± 20.9 %, green 4.1 ± 10.2 ; all mean \pm SD, $n = 30$ trials).

A Friedman test revealed a significant difference in visual preferences ($\chi^2 = 15.83$, d.f. = 4, $p = 0.00325$). Pairwise comparisons showed that fruit bats preferred yellow test fruits over blue and uncolored fruits (Wilcoxon-Wilcox test, $D_{\text{yellow vs blue}} = 20.0$, $p < 0.05$; $D_{\text{yellow vs control}} = 23.0$, $p < 0.01$). All other pairwise comparisons did not reveal any significant results. When colored test fruits were set against a white background, yellow fruit cubes were preferred by fruit bats over other colored cubes. However, differences between red, green, and blue fruits almost vanished ($R_i = 0.52$ - 0.64) and uncolored banana cubes still yielded the lowest R_i (0.40) of all (Fig. 1).

Fig. 4 demonstrates the reflectance measurement from one typical bat-dispersed fruit (*Ficus variegata*, Moraceae) and one typical bird dispersed fruit (*Pygeum vulgare*, Rosaceae). While ripe *F. variegata* var. *elangooides* figs appear greenish-yellow (high percentage of reflectance between 540 and 600 nm), *P. vulgare* fruits are purplish-black (reflectance mainly > 750 nm wavelength). Table 1 shows the results of reflectance measurements of seven *Ficus* species and three fruits of other genera regularly eaten by bats. Most fruits eaten by bats seem to have yellowish green colors, but red and purple colors likewise occur. The latter fruit species are preferentially taken by birds (pers. obs.).

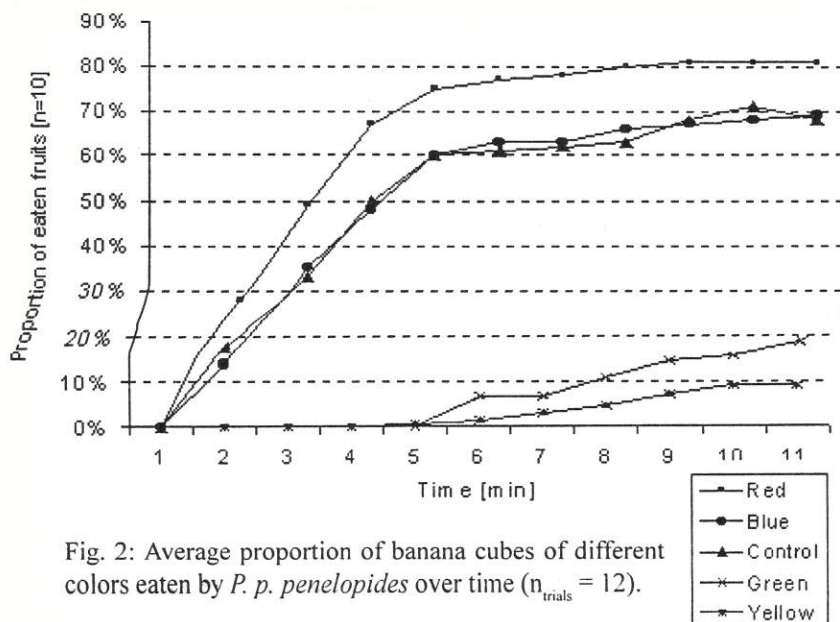


Fig. 2: Average proportion of banana cubes of different colors eaten by *P. p. penelopides* over time ($n_{\text{trials}} = 12$).

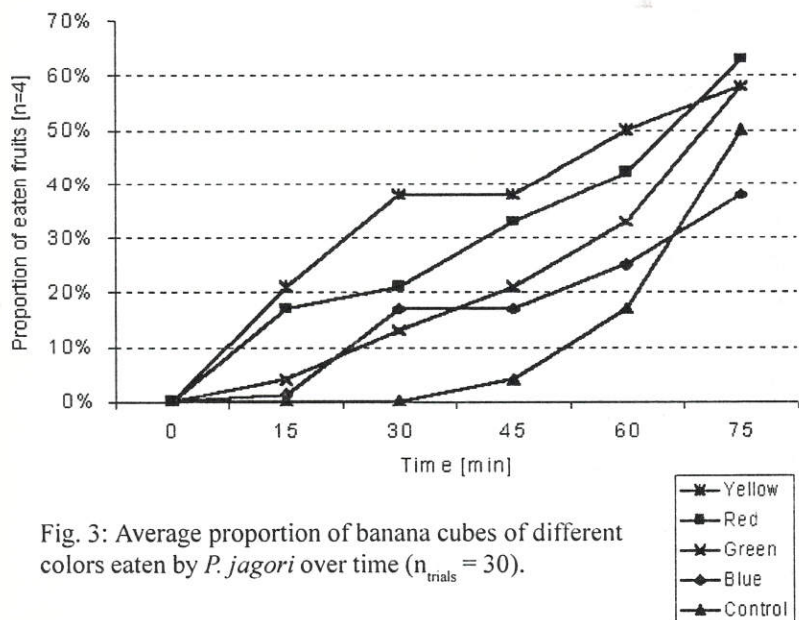


Fig. 3: Average proportion of banana cubes of different colors eaten by *P. jagori* over time ($n_{\text{trials}} = 30$).

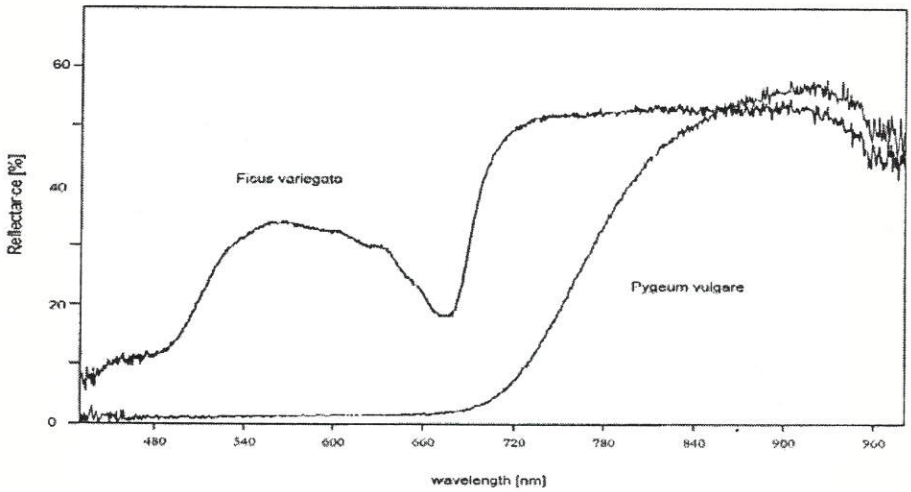


Fig. 4: Reflectance measurements of *Ficus variegata* (bat fruit) and *Pygeum vulgare* (bird fruit).

Table 1: Color impressions and reflectance maxima of ten fruit species eaten by bats in the study area. Only ripe fruits were considered.

<i>Fig species</i>	<i>Reflectance maxima</i>	<i>Color impression</i>
<i>Ficus congesta</i>	540-640 nm	yellowish green
<i>F. septica</i>	510-630 nm	yellowish green
<i>F. sp., P351</i>	570-630 nm	orange yellow
<i>F. variegata var. elangoides</i>	540-640 nm	yellowish green
<i>F. variegata var. variegata</i>	590-630 nm	red with a tinge of green
<i>F. pseudopalma</i>	630-650 nm	dark red to purple
<i>F. sp., P350</i>	540-650 nm	yellowish green
<i>Columella corniculata</i>	690-900 nm	purplish red
<i>Gnetum indicum</i>	660-900 nm	red
<i>Saurauia latibractea</i>	550-660 nm	green with red parts

Discussion

The results obtained for Visayan Tarictic Hornbills confirm the seemingly universal preference of birds for red and/or purple-black fruits. A recent study in Africa supporting the separation of

primate and hornbill diets reveal that fruits eaten by hornbills differ in color from those eaten by primates. Primates prefer green and brownish fruits whereas the majority of hornbill fruits are red and purple (Poulsen et al. 2002). Other birds similarly prefer diets of red, purple, and black fruits (e.g. Gautier-Hion et al. 1985, Wheelwright & Janson 1985). Knight & Siegfried (1983) found that birds favor black, orange, and red whereas mammals favor species with yellow, orange, and green fruits. In this study the relatively high preference index among hornbills for uncolored banana might be a consequence of their diet of bananas in the rehabilitation facility. Bats were also fed bananas but they were only kept for a few days before being released.

While the color vision of frugivorous birds is generally well developed, fruit bats are expected to be color blind (Suthers 1970, Neuweiler 1993, Nowack 1999). Nevertheless, the sensory systems for vision and olfaction of frugivorous bats are well developed (Schneider 1957, Kolb 1971, Bhatnagar & Kallen 1975, Baron et al. 1996), and represent an adaptation to their feeding habits (Phillips 2000). Based on this premise, one would expect that plants relying on pteropodids for their dispersal should have relatively exposed fruits to facilitate visually guided access. Kalko et al. (1996) hypothesized that fruits turning red, orange, or yellow when ripening should be attractive to Megachiroptera as they stand out from the mostly greenish background even under dim light conditions. On the other hand, grey shades of different colors can be confusingly similar to a colorblind animal, such that it will not be able to find a colored object that has been mixed with identical objects of several shades of grey (Von Frisch 1988). Fruit bats exhibited a higher preference index for yellow fruits presented against a green background over all other colors tested. This result is not surprising because many figs, a main component of the natural diet of *P. jagori*, turn from green to yellow, or yellowish green when ripening. Similarly, red fruits are represented by some species in the diet of the Musky Fruit Bat (e.g. *Veitchia merrillii*), while blue fruits are very rare. Green banana cubes

might resemble unripe fruits and thus are less attractive to bats. Although Utzurrum (1995) found that smaller bats like *P. jagori* select fruits based on color while larger bats choose their food based on crop size, her work does not explain how fruit color might effect the food choice of colorblind (!) pteropodids.

How can fruit color influence the choice of colorblind fruit bats? In general, each surface has a characteristic reflection function which describes the proportion of incident light that is reflected by the surface at each wavelength (Stroppe 1990). Brightness or lightness of a color is an attribute of a visual sensation according to which an area appears to exhibit more or less light (Purves et al. 2002). It follows that colors differing substantially in their reflection show a high brightness contrast (e.g. black with c. 3 % reflection of light and white with c. 97 % reflection of light show the greatest brightness contrast). Furthermore, the lightness of the background influences the way in which colors or shades of grey are perceived (Burns & Dalen 2002). This effect is called simultaneous brightness contrast (Purves et al. 2000). Megachiropterans are able to detect brightness differences accurately even under dim light conditions (Suthers 1970, Neuweiler 1993). Thus fruit reflection properties and brightness contrasts between fruits and background vegetation are likely to influence the visual detection of fruits.

In addition to visual cues, flying foxes use their well-developed sense of smell to find and assess the quality of fruit resources (e.g. Acharya & Krishna 1998, Luft 2000, 2002). Moreover, many plant species used by Megachiroptera offer their fruits openly, probably to allow better visual detection. For example, *Alpinia haenkii* (Zingiberaceae) produces fruits at the outer tips of branches away from leaves. In many cases, figs (Moraceae), as well as genera like *Saurauia* sp. (Altinidiaceae) or *Syzygium* sp. (Myrtaceae) show cauliflory, and fruits often grow in clusters. At least one fig species in the study area (*Ficus* sp., P351) loses its leaves when fruits are ripe, which is likely to be adapted to fruit

bats as the main seed dispersers of this species. The results of the choice experiments suggest that certain colors like yellow and red may facilitate visual detection of fruits by bats. How visual fruit properties may affect the detection by fruit bats is still largely unstudied. Experiments with free ranging fruit bats might provide further insights to this aspect of fruit bat ecology. It might be promising to study fruits in the natural environment of megachiropterans, for instance, by manipulating their color and/or odor. This is likely to yield useful information about the relationship between fruit characteristics and the choice behavior of foraging pteropodids under natural conditions.

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APPENDIX A**Definitions:**

Reflectance: The ratio of reflected power to incident power generally expressed in dB or percent.

Reflection: The abrupt change in direction of a wave front at an interface between two dissimilar media so that the wave front returns into the medium from which it originated. *Note 1:* Reflection may be specular (*i.e.*, mirror-like) or diffuse (*i.e.*, not retaining the image only the energy) according to the nature of the interface. *Note 2:* Depending on the nature of the interface *i.e.*, dielectric-conductor or dielectric-dielectric the phase of the reflected wave may or may not be inverted.

Brightness is a subjective attribute of light to which humans assign a label between very dim and very bright (brilliant). Brightness is perceived not measured. Brightness is what is perceived when lumens fall on the rods and cones of the eye's retina. The response is non-linear and complex. The sensitivity of the eye decreases as the magnitude of the light increases and the rods and cones are sensitive to the luminous energy per unit of time (power) impinging on them.

Simultaneous brightness contrast is defined as the same surface looking differently bright in different surrounds. Here the same gray target—the circular patch—looks brighter in a darker surround than in a lighter one (*left*).

Luminance is the luminous intensity per unit area projected in a given direction.

Light is radiant energy that is capable of exciting the retina and producing a visual sensation. This definition is the one most meaningful for display professionals although it differs from the definition frequently used by physicists. Our definition excludes ultraviolet (UV) and infrared (IR) wavelengths. UV is shorter in wavelength than light as we have defined it and IR is longer. The visible wavelengths of the electromagnetic spectrum extend from about 380 to 770 nm. The unit of light energy is the lumen second.

Luminous intensity is the luminous flux per solid angle emitted or reflected from a point. The unit of measure is the lumen per steradian or candela (cd). (The steradian is the unit of measurement of a solid angle.) The Intensity control on an oscilloscope adjusts the magnitude of the luminous intensity and consequently the luminance and the brightness of the light output. Luminance and brightness are defined below.

Luminance is the luminous intensity per unit area projected in a given direction. The SI unit is the candela per square meter which is still sometimes called a nit. The footlambert (fL) is also in common use ($1 \text{ fL} = 3.426 \text{ cd/m}^2$). The concept of luminance is challenging and deserves detailed discussion. First let us look at what is meant by "projected area." Think of a slide projector containing a slide that is opaque except for a small clear spot at the center. When d_1 and d_2 are correctly related to the focal length of the lens light passing from the lamp through the clear spot in the slide is focused by the lens onto the receiving surface. This in-focus image of the spot is the projected area. The size of the projected area can be adjusted by changing the focal length of the lens d_1 and d_2 and/or the size of the spot - the aperture - on the slide. Replacing the projection lamp with a photodetector and the projected area with a source of light - either self-luminous or reflected provides the basic elements of a luminance photometer. Most luminance photometers' have special optics that allow the user to view the source and bring the projected area into focus. Any luminous flux that leaves the source - as defined by the projected area - and passes through the lens will also pass through the Aperture. That luminous flux will enter the photodetector and permit a luminance measurement. What is being measured is power - the rate at which energy is being transferred from source to detector - but there can be no power without energy.

To see how luminous intensity contributes to luminance review the definition of luminous intensity. Each of the points - such as P1 and P2 - on the projected area emits luminous flux over a solid angle of 2 PI steradians. However only that portion of the flux that falls within the cone defined by the effective area of the lens and the distance d from the lens to the point on the source succeeds in arriving at the detector.

There is a little cone for every point on the projected area. Two cones of angles 1 and 2 are shown. For each point on the projected area there will be a corresponding solid angle. The greater the projected area the greater will be the luminous flux collected by the lens. The larger the lens diameter the greater will be the luminous flux from each point collected by the lens and directed through the Aperture to the photodetector. P1 and P2 are two of the many points on the object source plane. The optics form the images P1' and P2' of these points at the aperture plane. A point on the source is focused by the lens onto the aperture plane. There is no need to focus on the photodetector because all of the light that passes through the aperture must fall on the photodetector. If the projected area were to be reduced to one-half the number of little cones would be reduced to one-half and the luminous flux collected by the lens and arriving at the photodetector would

be reduced by one-half. This assumes that the projected area is uniformly luminous. If the projected area is not uniformly luminous the photodetector will average the luminous flux over the projected area.

The luminous flux collected by the photometer lens (and directed to the photodetector) is proportional to the projected area. This is important in for example measuring the luminance of a display. The placement of the projected area on the luminous source of a display - such as a symbol stroke - is important when making a luminance measurement.

Luminance is the measurable quantity which most closely corresponds to brightness. The luminance photometer and the human eye both have a lens and both receive light from specific directions. The photometer has a single photodetector - maybe three for color - while the eye has a very large number of sensors (rods and cones). One may think (loosely) of each cone in the fovea - the area near the center of the retina - as being part of a human light meter using a common lens.

Illuminance is the luminous flux incident on a surface e per unit area. The SI unit is the lux or lumen per square meter. The foot-candle (fc) or lumen per square foot. is also used ($1 \text{ fc} = 10.764 \text{ lux}$). An illuminance photometer measures the luminous flux per unit area at the surface being illuminated without regard to the direction from which the light approaches the sensor. Using cosine correction to correct for changes in the illuminated area of a surface as a function of angle of incidence guarantees that the measured value of illuminance is independent of the direction from which the light approaches the sensor.

Let us try to say that again in a more intuitive way. If a flashlight is aimed perpendicular to a nearby surface it produces a circle of light on the surface. Tilt the flashlight and the illuminated spot increases in area and becomes elliptical in shape. The same luminous flux is now spread over a larger area as the angle between the axis of the flashlight and the normal to the surface increases. For a given luminous flux the illuminance decreases as the illuminated area increases.

If you have an illuminance photometer handy make an illuminance measurement with the light directly over the sensor. Now make a measurement with the light off axis by a given number of degrees from the normal. The off-axis reading should be equal to the on-axis reading times the cosine of the angle. If it is the meter is cosine corrected. This experiment requires the meter sensor to be smaller than the projected area.

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