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Light levels used during feeding by primate species with different color vision phenotypes

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Abstract The intensity of available light is important in determining how well a diurnal animal can distinguish color. Primates with different types of color vision may exhibit behaviors that maximize visual contrast during critical activities such as feeding. We hypothesized that (1) trichromatic taxa will feed in a wide range of light conditions because color constancy permits stabilized color appearance across changes in illumination, and (2) that taxa with a high proportion of dichromatic individuals will tend to feed at higher light levels to increase color contrast. We recorded light levels during feeding bouts of seven primate taxa with varying degrees of color vision: the dichromatic *Lemur catta*, two polymorphic species, *Propithecus v. verreauxi* and *Ateles geoffroyi*, and the routine trichromats, *Alouatta palliata*, *Colobus guereza*, *Ptilocolobus badius*,

and *Cercopithecus ascanius*. Results were equivocal for our hypotheses. While routinely trichromatic taxa used varying light levels, the pattern of results did not differ from the dichromatic *Lemur catta*. However, polymorphic taxa not only sought the highest light, but females, which are the only individuals in polymorphic taxa that can be trichromatic, fed in higher light levels than males when eating non-green foods. This result is consistent with selection operating to maintain a balanced polymorphism in these taxa, though the connection between light levels and color vision type for the females is unclear. Our results further suggest that trichromatic vision may afford a selective advantage because it permits foraging under a greater range of light levels.

Keywords Color vision · Diurnality · Light levels · Primate foraging

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Introduction

Relationships between light environments and color variation have been thought to affect a wide array of behaviors, including crypsis and sexual selection in guppies (Endler 1991) and birds (Endler and Thery 1996; Gomez and Thery 2004), signal detection and species recognition in lizards (Leal and Fleishman 2004), and predation in orb-spinning spiders (Craig et al. 1996). In primates, changes in light levels have been linked to activity cycles over both daily (e.g., onset and cessation of activity; Pariente 1974; Kavanau and Peters 1976; Overdorff 1988; Richard and Dewar 1991; Curtis et al. 1999; Suchi and Rothe 1999; Wright 1999; Erkert and Kappeler 2004) and seasonal (e.g., estrus and concomitant reproductive cycles; Pereira et al. 1999; Wright 1999) periods. However, although the role of light on the daily behavior of some nocturnal and cathemeral primates has been studied fairly extensively (Pariente 1974; Kavanau and Peters 1976; Overdorff 1988; Erkert 1989; Curtis et al. 1999; Donati et al. 2001; Fernandez-Duque 2003; Kappeler and Erkert 2003), few studies have

examined light and its effects on the activities of strictly diurnal primates for which color perception is potentially critical for foraging activity.

Four kinds of light spectra, termed ambient, reflectance, radiance, and absorbance, affect the colors perceived by diurnal primates (Endler 1990, 1993, 1997). An ambient spectrum characterizes the light striking an object, while a reflectance spectrum is the fraction of ambient light reflected from it. The radiance is the product of the ambient and reflectance spectra and has a critical effect on the ability of the photoreceptors in the cone cells of the primate retina to capture light at each wavelength of the radiance spectrum. The overall pattern of photon capture by the eye is called the absorbance spectrum and depends not only on the radiance, but also on the characteristics of the cone photopigments of the primate involved. Research over the last decade has shown that these photopigments vary greatly within the order Primates. The Catarrhini as a clade have routinely trichromatic color vision, enabled by three cone photopigments responding to short, medium, or long wavelengths of light (Jacobs 1993; Jacobs 1995; Arrese et al. 2002; Surridge et al. 2003). Trichromacy depends genetically on an autosomal short-wavelength-sensitive (S) opsin gene and middle (M) and long-wavelength-sensitive (L) genes on the X-chromosome. The howler monkey genus (*Alouatta* spp.) is the only one in the New World with routine trichromatic color vision (Jacobs et al. 1996). In contrast, nearly all other species of New World monkey are polymorphic, possessing one autosomal cone pigment and some combination of three different M/L alleles at a single locus on the X-chromosome (Shyue et al. 1995). This results in only heterozygous females (approximately 2/3 of all females) being trichromatic. All other females, and all males, are dichromatic. Until recently, all prosimians had been considered dichromatic, but recent studies have shown that some are polymorphic in a manner similar to many New World monkeys (NWM; Tan and Li 1999; Jacobs et al. 2002). For example, *Propithecus* appear to be polymorphic, whereas *Lemur* have only two photopigments and are dichromatic (Tan and Li 1999; Jacobs et al. 2002; Jacobs and Deegan 2003). However, unlike NWM, which have three M/L alleles, *Propithecus* have only two alleles, enabling up to half of all females to be heterozygous and thus trichromatic (Jacobs et al. 2002).

Recent findings on the evolution of color vision photopigments suggest that the selective pressure driving routine trichromacy may have been the need to feed on young leaves (Dominy and Lucas 2001). In the tropics, leaves very often flush red against a mature leaf background of dark green leaves. Any folivore, such as *Alouatta*, which could perceive this color contrast, would have an advantage, especially if there is a shortage of other resources (i.e., fruits). Here, we concentrate on another aspect of the absorbance spectrum—the ambient light available in different forest environments. Available light is important for interpreting behaviors for which color plays a prominent role and in which a complex mosaic of light environments differing in both brightness and color can occur. Brightness (or value) is the average height of a curve plotting inten-

sity on the y-axis against wavelength on the x-axis. More correctly though, it is the area under such a curve over a defined interval of wavelengths (Endler 1997). Color has two components: hue and chroma. Hue is the vernacular sense of blue, green, red, etc., and is proportional to wavelength. Chroma (or saturation) is a measure of color strength. Endler (1993) describes five kinds of daylight: forest shade, woodland shade, small gaps, large gaps, and early/late. These can all be found in a variety of different kinds of forest, both temperate and tropical. Effects of different light environments on color perception can be profound. For example, if an orange-red food item (reflecting > 600 nm) is illuminated by forest shade, it will not appear bright because the ambient spectrum is deficient in long wavelengths. On the other hand, if the same food target is illuminated by sunlight passing through gaps in the canopy or early/late light, it will be much brighter (Endler 1997). In contrast, a yellowish-green food object (reflecting middle wavelengths ca. 520–620 nm) will be brightest under forest shade and least bright in early/late light conditions. The ambient light spectrum thus affects both the color of a food item as well as its contrast with the visual background (e.g., mature leaves).

Given the importance of the light environment to discerning the color and brightness of objects, such as food targets, it stands to reason that primates may forage under light conditions that optimize their ability to discriminate color and contrast. In this regard, the use of light among primate taxa will likely differ according to their perceptual abilities.

In the present study, we examine light levels (illumination) during feeding throughout the day in seven species of primates that span the range of color vision capabilities within the order. We compare three groups of sympatric species: the dichromatic *Lemur catta* (ringtailed lemur) and the polymorphic trichromat *Propithecus v. verreauxi* (sifaka) in Madagascar; the routine trichromat *Alouatta palliata* (mantled howler monkey) and the polymorphic trichromat *Ateles geoffroyi* (black-handed spider monkey) in Costa Rica; and three routinely trichromatic Old World monkeys (OWM), *Colobus guereza* (black-and-white colobus), *Ptilocolobus badius* (red colobus), and *Cercopithecus ascanius* (red-tailed guenon), in Uganda.

The purpose of the paper was to assess whether species with different color vision use ambient light levels in a predictable manner when feeding. In doing so, we assumed that foods that can be distinguished from a mature leaf background are attractive to primate herbivores and that the ability to discriminate them was a key factor in the evolution of color vision (Lucas et al. 1998; Regan et al. 1998; Sumner and Mollon 2000; Dominy and Lucas 2001; Lucas et al. 2003; Riba-Hernández et al. 2004). We hypothesized that (1) trichromatic taxa will feed in a wide range of light conditions because color constancy permits stabilized color appearance across changes in illumination, and (2) that taxa with a high proportion of dichromatic individuals will tend to feed at higher light levels to increase color contrast. We started by simply comparing light levels used by dichromatic,

polymorphic, and routinely trichromatic species, then tested predictions based on general light levels used, associated food hues, and time spent feeding on foods of different hues. Specifically, we predicted that the dichromatic *Lemur* would use higher light levels more consistently than the polymorphic (*Ateles/Propithecus*) and routinely trichromatic (*Colobus/Piliocolobus/Cercocebus/Alouatta*) taxa when feeding.

In addition, anticipating differences in light levels used when feeding on foods of different colors, we hypothesized that the dichromatic species would forage on non-green foods at higher light levels than on green foods as compared to the polymorphic and routinely trichromatic species. We examined patterns of feeding at dusk, when ambient light levels are at their lowest, to test this supposition. We concentrated on the two polymorphic species in our sample because we expected to find that females within these populations would be more variable in their behavior when feeding on non-green foods as a result of their mixed visual capabilities. Since we had no information on the genetic makeup of individual females, we conducted the analysis simply at a male vs female level since the former are always dichromatic. Finally, we expected that animals with better color discrimination would spend more feeding time on non-green foods simply as a result of their enhanced color discrimination.

Materials and methods

Study sites and species

Two diurnal lemur species (*Lemur* and *Propithecus*) were studied in the deciduous tropical dry forest of Beza Mahafaly special reserve (25°30' S, 44°40' E) in southwestern Madagascar. This region is characterized by distinct wet and dry seasons. During the course of this study, the wet season, from November to March, had 772 mm rainfall with average daily temperature maxima and minima of 38°C and 21°C. In contrast the dry season had 94 mm rainfall and average temperatures of 34°C and 12°C. *Lemur* are characterized as generalist herbivores (Sauther et al. 1999). *Propithecus* are morphological folivores; that is, they have specializations of the gastrointestinal tract that are specifically related to processing a fibrous diet (Campbell et al. 2000). *Propithecus* spp., which have been studied in both dry forests and rainforests, include a high percentage of leaf material in their diets in addition to combinations of seeds and fruits (Yamashita 1996; Hemingway 1998).

Two diurnal New World monkeys (*Alouatta* and *Ateles*) were studied in northeastern Costa Rica in the Guanacaste Conservation Area in the Murciélago zone (10°55' N 85°43' E). This area has been classified as tropical dry forest and receives approximately 1.5 m rain per year with an average annual temperature of 23°C (Holdridge 1967; Hartshorn 1983). The forest is largely deciduous and is characterized by a dry season from December to April. *Alouatta* are large (5–10 kg) arboreal monkeys that principally for-

age on young leaves, however, fruit also comprises a substantial part of their diet in some habitats during part of the year (Glander 1975; Milton 1980; Estrada 1984; Stoner 1996). *Ateles* are one of the largest arboreal New World monkeys (5–9 kg) and they forage principally on ripe fruit, which comprises 56–77% of their diet (Cant 1977; Chapman 1987; Riba-Hernández 2004).

Cercopithecus, *Colobus*, and *Piliocolobus* were studied in Kibale National Park (0°13' N to 0°41' N and 30°19' E to 30°32' E) in Uganda, where rainfall is bimodal in distribution, occurring in two distinct rainy seasons: March–May and August–November. Mean annual rainfall is 1,750 mm (1990–2001; Chapman et al. 2003). The forest varies from moist evergreen (closely related to moist montane forest because the elevation is between 1,100–1,590 m) to lowland tropical rainforest (with affinities to both montane rainforest and mixed tropical deciduous forest; Struhsaker 1997). *Piliocolobus* and *Colobus* fed primarily on young leaves, while *Cercopithecus* spent roughly equal amounts of time on fruits, leaves, and other objects (Dominy and Lucas 2004).

Foraging data collection

Foraging data on lemurs (*Lemur* and *Propithecus*) were collected 5 days a week from February 1999 to February 2000, alternating study species daily. Observations were facilitated by identifying collars and pendants on all *Propithecus* individuals in six groups and on at least one group member, usually a female, in the six to seven *Lemur* study groups. Foraging data were collected using 10-min focal animal observations (Altmann 1974). Focal animals were randomly changed after each 10-min observation. Data collection began slightly after sunrise at 0700 hours and continued until dusk at approximately 1800 hours. Data collection was usually suspended from 1200–1400 hours while the lemurs were inactive. Total hours of observation were 247 for *Lemur* and 242 for *Propithecus*.

Foraging data were collected from a single troop of *Alouatta* with 33 individuals and one troop of *Ateles* with 30 individuals from March 1999 to March 2000, alternating study species daily. Fifteen of the *Alouatta* could be distinguished by individual marks (National Resource Council 1981) and the rest were identified to sex and age-class. All *Ateles* could be distinguished using identifying marks. Foraging data were collected using 2-min focal animal observations (Altmann 1974), and focal animals were randomly changed after each 2-min observation for a total of 503 h of observation for *Ateles* and 595 for *Alouatta*. Data collection began slightly after sunrise at 0600 hours and continued until dusk at 1730 hours.

Between one to three habituated groups of each monkey species were observed at Kibale from January to November 1999, with a different species followed each day in rotational order. Total hours of observation were 330 for *Cercopithecus*, 378 for *Colobus*, and 412 for *Piliocolobus*. Focal animals were observed as at Beza. Feeding data included here refer to adults of specified sex.

At all sites, data were collected on all aspects of feeding, including plant species, food type (e.g., leaves, fruits, flowers, seeds), developmental stage, food color, and time spent feeding on each food item. The authors were distributed at the sites as follows: N.Y. at Beza Mahafaly, K.E.S. and P.R.-H. at Murciélago, and N.J.D. and P.W.L. at Kibale.

Measurement of light levels

Light levels were recorded during all feeding bouts. A handheld Sekonic photographic exposure meter (Flashmate L-308BII) was used to register light levels at different times of the day. The light meter can be set to take readings of either illuminance or reflected light. This latter setting was used to measure light reflecting off animals at Beza where focal animals were at variable distances from the observer, from 1–5 m away. In most cases the reading from the reflected light setting was similar to the illuminance setting. As a check, light levels were compared via both reflected and illuminance measurements when the animals were on the ground. Discrepancies were resolved by accepting the modal reading. In cases where the animals were some distance away, illuminance readings were taken by positioning the light meter in similar light to that used by the focal animal. For example, if the focal was in full sun, then the reading was taken in full sun at ground level. Ambient conditions were measured as illuminance at the level of the observer with the light meter oriented to the horizontal in at least three different directions. Only light levels during activities were recorded. If the animals were resting at their sleepsite, the light level was not included.

Illuminance measurements were taken at Murciélago and Kibale. Focal animals were typically 5–15 m above the observer and illuminance readings were taken by positioning the light meter in similar light to that used by the focal animal. Illuminance and reflectance readings were later compared to check for possible discrepancies. The correlation between the two sets of readings was strongly linear (least squares regression, $R^2 = 0.869$, $P < 0.001$).

Analyses and statistics

We compared light levels used while the seven species of primates foraged to determine if species with particular color vision capacities used different light levels. Light level readings were recorded once per feeding bout. Individuals within species were sampled approximately equally in those species with identifiable individuals. Readings were initially pooled for each species, and then they were subdivided by sex and food color. Food colors were divided into green and non-green for comparisons. Non-green foods were red, orange, yellow, brown, and purple. White, black, and blue foods were excluded since the spectral range of these colors lie toward the shorter wavelengths of the spectrum. The next analysis compared light levels used while foraging by males and females for the two polymorphic species. We then compared time spent feeding on green

and non-green foods. A final analysis compared light levels during the last recorded activity of the day for each species. At Beza light levels during feeding were compared with those during non-feeding activities or with measurements taken on the ground (ambient).

Exposure value (EV) readings were converted to standard lux units (lx). Since there was considerable variation in this parameter between sites as a result of differences in canopy cover, data were further standardized with Z-scores within each site to enable comparisons of relative light levels between sites. All data were analyzed with non-parametric Mann-Whitney U , Kruskal-Wallis, or χ^2 goodness-of-fit tests. Because of disparities between sites in light levels, we used non-parametric statistical tests as a conservative method for comparing datasets.

Results

Light levels used when feeding

We predicted that the dichromatic species (*Lemur*) would use the highest light levels (LL), followed by the polymorphic species (*Ateles* and *Propithecus*) and lastly the trichromatic taxa (*Alouatta*, *Colobus*, *Ptilocolobus*, and *Cercopithecus*).

The seven species differed significantly from one another (Kruskal-Wallis $\chi^2 = 162.90$, $df = 6$, $P < 0.001$) in LLs used. The two polymorphic species, *Propithecus* and *Ateles*, used higher light levels than the other species at their respective

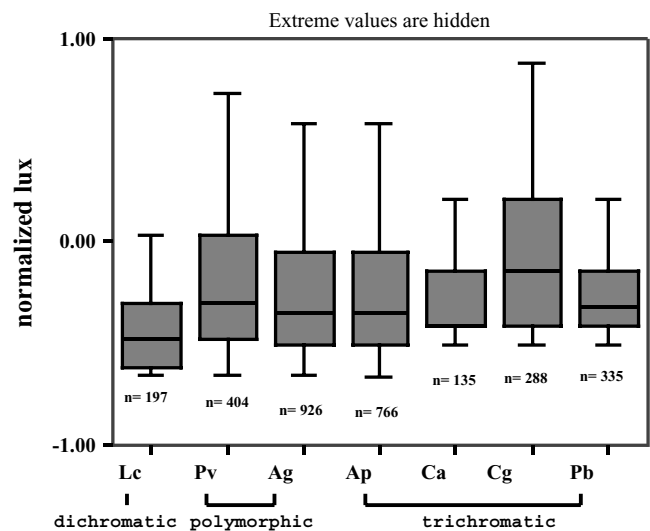
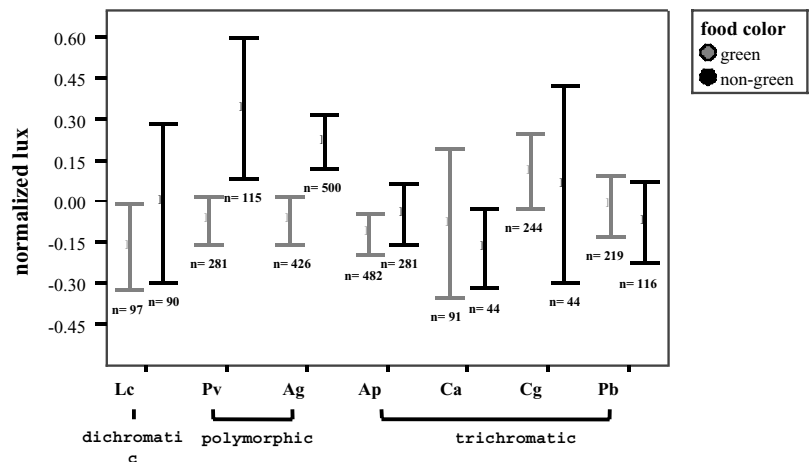


Fig. 1 Light levels used by primates while feeding. Centers represent mean values and whiskers are 95% confidence intervals of the mean (*Lc**Lemur catta*, *Pv**Propithecus verreauxi*, *Ag**Ateles geoffroyi*, *Ap**Alouatta palliata*, *Ca**Cercopithecus ascanius*, *Cg**Colobus guereza*, *Pb**Ptilocolobus badius*). Normalized lux values represent Z-scores standardized across sites.

Table 1 Interspecific comparisons of light levels used while feeding^a (*LcLemur catta*, *PvPropithecus v. verreauxi*, *ApAlouatta palliata*, *AgAteles geoffroyi*, *CgColobus guereza*, *CaCercopithecus ascanius*)

	Dichromatic	Polymorphic		Trichromat		
	<i>Lc</i>	<i>Pv</i>	<i>Ag</i>	<i>Ap</i>	<i>Ca</i>	<i>Cg</i>
<i>Propithecus</i>	-5.76 (0.001)					
<i>Ateles</i>	-3.40 (0.001)	-4.36 (0.001)				
<i>Alouatta</i>	-1.79 (0.073)	-7.24 (0.001)	-2.83 (0.005)			
<i>Cercopithecus</i>	-4.86 (0.001)	-1.32 (0.188)	-1.64 (0.001)	-3.74 (0.001)		
<i>Colobus</i>	-8.28 (0.001)	-2.83 (0.005)	-6.13 (0.001)	-9.46 (0.001)	-4.91 (0.001)	
<i>Piliocolobus</i>	-7.75 (0.001)	-1.34 (0.180)	-5.11 (0.001)	-8.62 (0.001)	-3.70 (0.001)	-1.97 (0.049)

^a Mann-Whitney *U* Z scores (*P*-values). Bonferroni method used to calculate α levels, which yielded significance at <0.002 (0.05/21). Normalized lux values used in analysis

Fig. 2 Light levels used by species when feeding on foods of different colors. Centers represent mean values and whiskers are 95% confidence intervals of the mean. See Fig. 1 caption for explanation of abbreviations.

sites, and at all sites with the exception of *Colobus* in Kibale (Fig. 1, Table 1). Contrary to expectations, *Lemur* did not use higher light levels than the polymorphic species.

Relationship of food color and light levels

We compared light levels (LL) used with respect to the color of the food eaten. When all species were pooled, LLs for feeding on green vs non-green foods (red, orange, yellow, brown, purple foods) were not significantly different from one another ($Z = -1.42$, $P = 0.156$). However, when the data were examined by species (Fig. 2), significant among-species variation was observed in LLs used when eating green and non-green foods (green: Kruskal-Wallis $X^2 = 144.91$, $df = 13$, $P < 0.001$; non-green: $X^2 = 77.33$, $df = 13$, $P < 0.001$). Within-species comparisons between LLs used when eating green and non-green foods were significantly different for *Propithecus* ($Z = -2.85$, $P = 0.004$) and *Ateles* ($Z = -5.17$, $P < 0.001$). Results run counter to predictions for the dichromatic *Lemur*, which did not use higher LLs when eating non-green foods. The routinely trichromatic *Alouatta* and the OWM also showed no differences in LLs when eating green as opposed to non-green foods.

Comparison of polymorphic species

Light intensities used by males and females of the two polymorphic species, *Propithecus* and *Ateles*, indicate that

sexes do not differ in light levels used within species (Fig. 3; *Propithecus*: $Z = -1.02$, $P = 0.310$; *Ateles*: $Z = -1.31$, $P = 0.190$). All the males of these species are dichromatic, while the females are a mix of dichromats and trichromats. Color vision capabilities of specific individuals were unavailable for our sample, so we were unable to segregate the trichromatic females from the rest.

When light levels used when eating green vs non-green foods were separated, there were significant differences between sexes within these species (Fig. 4, Table 2). Among the polymorphs, *Propithecus* females used significantly higher light levels when eating non-green foods (Table 2), and there was significant separation in both *Ateles* sexes. *Lemur* and *Piliocolobus* females and *Alouatta* males also used higher LLs (Table 2).

Time spent feeding on green vs non-green foods

We expected that species with better color vision would spend more feeding time on non-green foods exclusive of the light levels used. The overwhelming majority of foods eaten by the species were green, and these foods were eaten throughout the day (X^2 goodness-of-fit = 437.67, $df = 6$, $P < 0.001$ for comparison of green vs all non-green foods; Fig. 5). Comparing time spent on non-green foods only, the trichromats as a group uniformly spent more time on red foods than other food colors ($X^2 = 52.60$, $df = 1$,

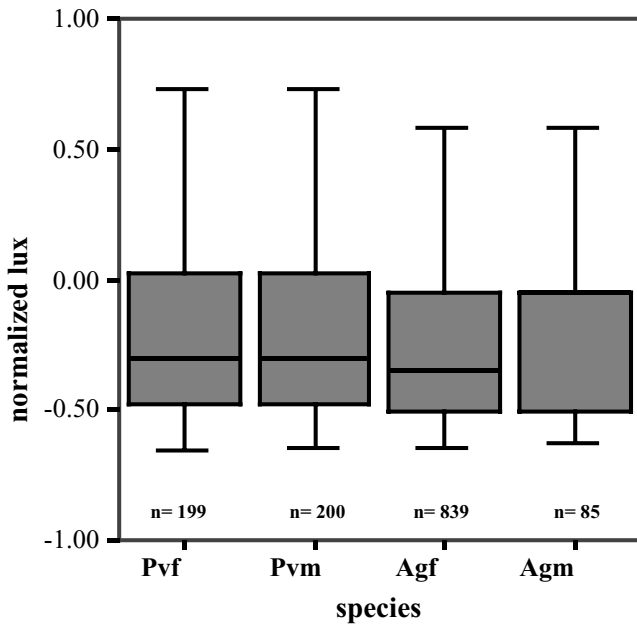


Fig. 3 Light levels used by females and males of species polymorphic for trichromatic color vision. *Boxes* represent central half of data divided by median line, *whiskers* depict data range excluding outliers.

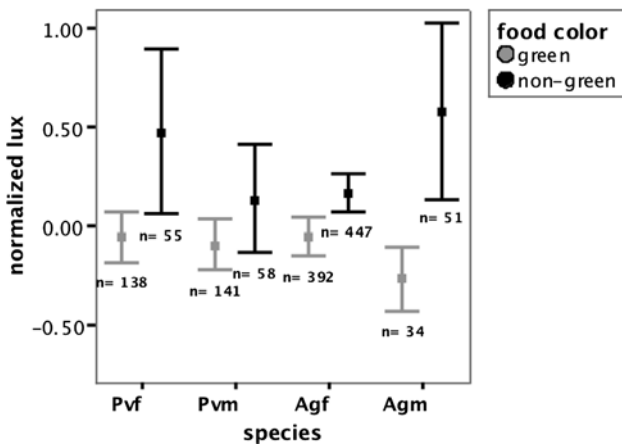


Fig. 4 Light levels used by polymorphic species when eating green vs non-green foods. *Centers* represent mean values and *whiskers* are 95% confidence intervals of the mean.

Fig. 5 Percent time spent feeding by food color. Time spent feeding in minutes divided by total feeding time. Data are pooled observations for each species. *Gray bars* Green foods, *black bars* red foods, *white bars* brown, yellow, orange, and purple foods. See Fig. 1 caption for explanation of abbreviations.

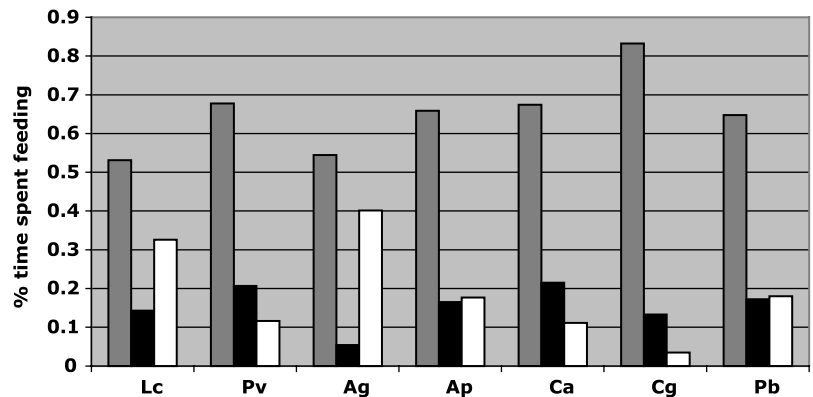


Table 2 Light levels used when eating green vs non-green foods separated by sexes^a

Species	Female	Male
<i>Lemur catta</i>	-2.01 (0.044)	-0.39 (0.696)
<i>Propithecus verreauxi</i>	-2.59 (0.010)	-1.46 (0.145)
<i>Ateles geoffroyi</i>	-4.63 (0.001)	-2.45 (0.014)
<i>Alouatta palliata</i>	-1.33 (0.185)	-2.52 (0.012)
<i>Cercopithecus ascanius</i>	-0.42 (0.675)	-0.95 (0.342)
<i>Colobus guereza</i>	-1.32 (0.187)	-1.24 (0.215)
<i>Ptilocolobus badius</i>	-2.09 (0.041)	-0.02 (0.988)

^a Mann-Whitney *U* Z scores (*P*-values). Normalized lux values used in comparisons

P < 0.001), whereas the polymorphs ($X^2 = 7.90, df = 1, P = 0.005$) and the dichromat ($X^2 = 35.52, P < 0.001$) spent more time on non-red foods. Within species, only *Alouatta* ($X^2 = 0.003, df = 1, P = 0.958$) and *Ptilocolobus* ($X^2 = 2.17, df = 1, P = 0.141$) spent equal time on red and non-red foods, and *Lemur* ($X^2 = 35.52, df = 1, P < 0.001$) and *Ateles* ($X^2 = 156.75, df = 1, P < 0.001$) spent more time on non-red than red foods. Pairwise comparisons of the species yielded only two non-significant comparisons, between *Propithecus* and *Cercopithecus* ($X^2 = 0.41, df = 1, P = 0.524$) and *Alouatta* and *Ptilocolobus* ($X^2 = 0.18, df = 1, P = 0.675$) in red vs non-red. In terms of other food colors, *Lemur* devoted feeding time to brown foods; *Propithecus* to brown and yellow; *Ateles* to yellow and orange foods; *Alouatta* to yellow and brown; the Kibale monkeys to yellow with the addition of brown to the diet of *Ptilocolobus*.

Comparisons at dusk

Comparisons in the late afternoon can provide the clearest discrimination of differences between light levels and feeding preferences (food color, feeding time) since the animals react in several predictable ways to falling light intensities: they can continue feeding at the lower light level, they can move to higher light to eat, or they can stop feeding. Their choices with regard to food color and light level may be indicative of their abilities to distinguish color.

The Beza and Murciélago species were not significantly different from one another in LLs taken during their

last recorded feeding bouts (Beza: Mann-Whitney U , $Z = -0.75$, $P = 0.454$; Murciélago: $Z = -0.04$, $P = 0.967$). The Kibale monkeys, however, used different LLs from one another at dusk (K-W $X^2 = 8.90$, $df = 2$, $P = 0.012$). At Beza, light levels used when feeding were significantly higher than ambient light for both *Lemur* ($Z = -2.35$, $P = 0.019$) and *Propithecus* ($Z = -2.72$, $P = 0.007$). Ambient light levels did not differ between species ($Z = -1.01$, $P = 0.311$).

When light levels were lowest in the late afternoon, *Alouatta* spent more feeding time on non-green (mostly yellow) foods (Fig. 6). Light levels remained constant

between color categories but feeding U time increased for non-green foods. *Propithecus* light levels were higher in the afternoon when eating non-green foods compared to green foods; time spent feeding on non-green foods also rose. The *Ateles* pattern followed that of *Lemur* rather than that of *Propithecus* with both species showing little difference in either light levels or changes in feeding time when eating green vs non-green foods at the end of the day. The OWM all decreased feeding time on non-green foods at dusk compared to green foods with the exception of *Cercopithecus*, which slightly increased feeding time on

Fig. 6 Time spent feeding throughout the day plotted with light levels. Green foods are in the left column, non-green foods on the right. Time spent feeding in minutes divided by numbers of observations in AM and PM separately to offset unequal observations in mornings and afternoons. Time of day on the x -axis standardized among sites (species at different sites had different start and end times). Time spent feeding on the lefthand y -axis, log lux on the right.

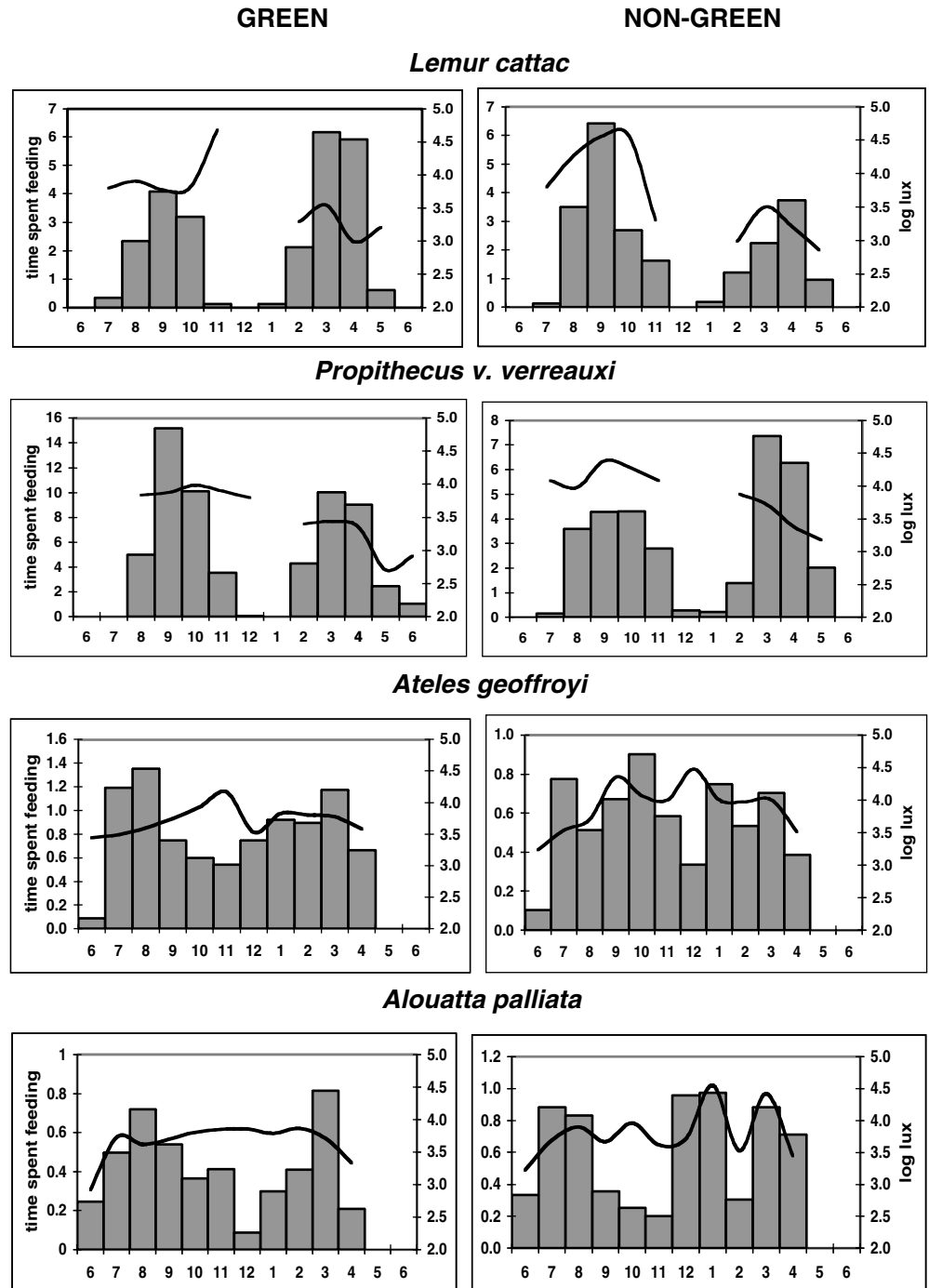
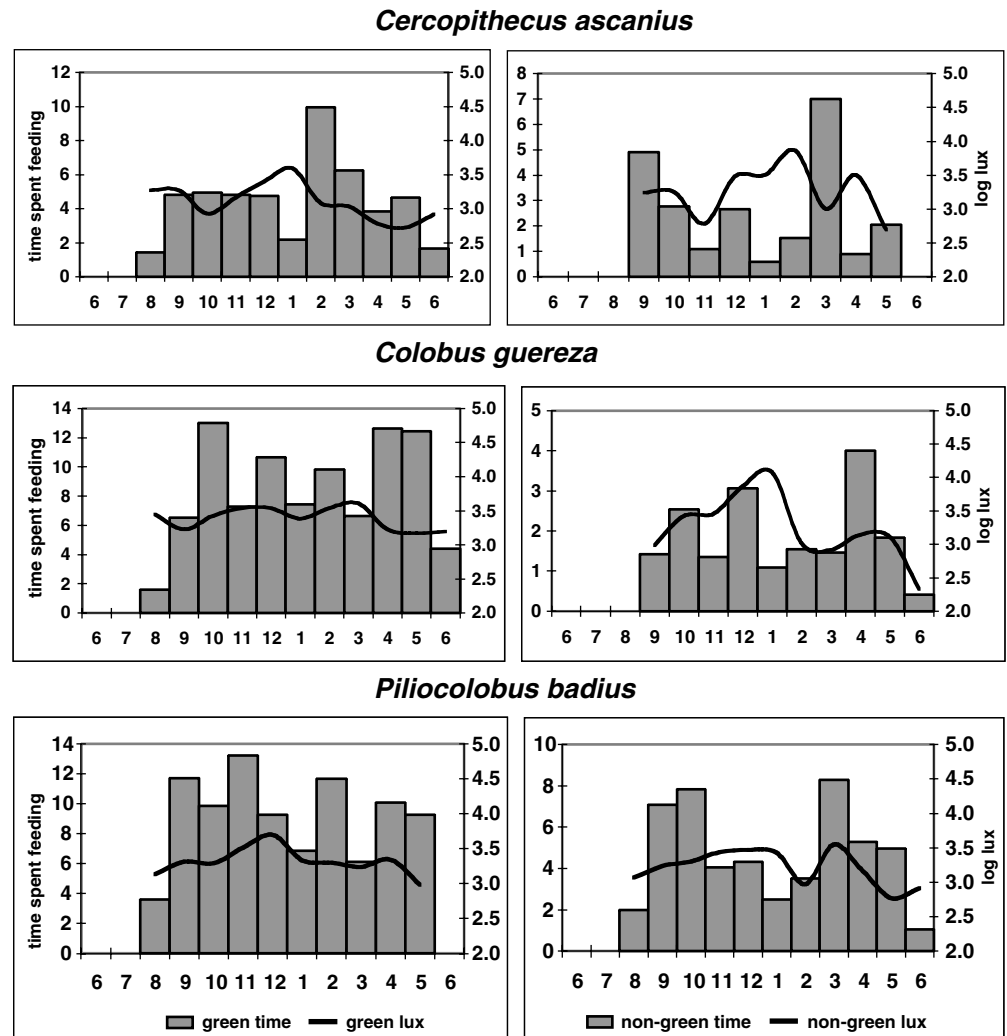


Fig. 6 Continued



non-green foods. *Piliocolobus* maintained light levels used between food color categories, while the two other species decreased LLs when eating non-green foods at dusk.

Discussion

The initial purpose of this study was to assess how species with different types of color vision used light when feeding. We expected that animals would use light to maximize their color vision capabilities, such that the poorer the color discrimination, the higher the light level used. The dichromats did not conform to this pattern and used lower LLs than expected. Generally, it appears that the dichromatic animals do not make a distinction in light level when eating green and non-green foods, and using higher light intensities does not help them make the contrast. However, we found two major results in our study of the relationship between light levels and food. First, the routine trichromats used a wide range of LLs when feeding, as predicted, and, interestingly, the polymorphic species not only used the highest LLs when feeding but both sexes consistently used higher LLs when feeding on non-green foods.

Polymorphic species

We predicted that animals with better color discrimination would use more variable light levels overall when feeding on non-green foods against a background of mature leaves. The species polymorphic for color vision should more commonly use higher LLs than the routine trichromats because of their more variable composition in terms of color vision capability. This proved correct up to a point. With respect to food color, only the polymorphic species consistently made discriminations in light levels when eating green vs non-green foods (Fig. 2). Within these species, females generally used higher light than the males. [*Ateles* males, however, also showed significant differences in LLs while eating green and non-green foods. This observation is congruent with the recent findings reported by Riba-Hernández et al. (2004), which showed that in *Ateles* dichromatic males could detect 95% of the fruit species consumed by this species. This would account for male *Ateles* using higher LLs than expected when feeding on non-green foods.] Given our prediction that individuals with greater color discrimination should use lower light, this result is surprising. However, the separation by sex within the

polymorphic species is exactly the pattern one would expect to find if selection were acting to maintain a balanced polymorphism within these species. A balanced polymorphism indicates that the trait under selection is advantageous in the heterozygous state. Because the M/L alleles for color vision are carried on a sex chromosome, only heterozygous females will directly benefit in a polymorphic species. The gene duplication of the alleles on the X-chromosome that led to routine trichromacy for all individuals is most parsimoniously interpreted as having occurred twice in primates (SurrIDGE et al. 2003), implying that it is a rare event. Once routine trichromacy was achieved, selection no longer had to act on the heterozygous females to maintain the trait, and indeed, we find no general distinction in light levels used by either sex in the fully trichromatic species.

As for being advantageous, trichromacy is thought to have evolved for rapid identification of non-green fruits and leaves against a background of mature leaves (Regan et al. 1998; Dominy and Lucas 2001; Riba-Hernández et al. 2004). A captive study supports the theory of trichromatic advantage for food detection tasks. Smith et al. (2003b) demonstrated that trichromatic saddleback (*Saguinus fuscicollis*) and red-bellied (*Saguinus labiatus*) tamarins more quickly selected ripe fruits against a leaf background than dichromatic individuals. However, other tamarin studies have found equivocal results when investigating the potential advantages to females in these polymorphic species. In a study of saddleback and mustached (*Saguinus mystax*) tamarins, Smith et al. (2003a) did not find that trichromatism was a necessary condition for troop leadership since some troops did not contain trichromatic females and those that did were not uniformly led by them to food trees. Likewise, Dominy et al. (2003a) did not find that trichromatic female saddleback and emperor (*Saguinus imperator*) tamarins had an advantage in locating yellow foods at feeding stations. Finally, a recent study on a wild population of *Ateles* modeled fruit detection by various color vision phenotypes in this species and found that all trichromat phenotypes had an advantage over dichromats, even though 95% of the fruit species could be detected by dichromats (Riba-Hernández et al. 2004). While the evolution of trichromacy for detecting leaves and fruits remains the most likely hypothesis, these conflicting results underscore the need for continued study of wild populations.

Using a strict interpretation of the capabilities of the polymorphic animals, the dichromatic males in our study should have difficulties discriminating green from non-green foods. Apparently, their association with trichromatic females enables them to 'act like trichromats' when feeding, at least for food crops where individual discriminatory abilities are not paramount once the food crop is located (e.g., all fruits in a patch are ripe). The same should be true for dichromatic females, but in this particular study the color vision of the females was unknown. In the absence of this information, we expected that the female range would encompass that of the male since the female sample was composed of both dichromats and trichromats (Fig. 3). However, the two were similar.

The dichromatic males used lower light than the females when eating non-green foods, which is consistent with the dichromatic *Lemur* also using lower light than expected. However, these males are still feeding in higher light than any other group except for females of the same taxa. Why the females are feeding in high light is unclear and runs counter to the expectation that trichromats can feed at all light levels. The link between light levels and feeding on non-green foods appears to operate differently in polymorphic taxa.

Females may be feeding in brighter light for other reasons. They may feed higher in the canopy, where the LLs are also higher, to obtain better quality foods. Fruits at the top of the canopy tend to be of higher quality than fruits lower down (Houle and Chapman, unpublished data), and they may be more abundant, though, in this last case, fruits in the lowest layer and mid-canopy had higher caloric content (Schaefer et al. 2002). Canopy leaves also have higher levels of protein but are tougher than those in the understory (Dominy et al. 2003b). While there is some evidence to suggest that foods in the canopy are of better quality, there is no consistent pattern of our study animals feeding on these foods that would explain the observed differences in LLs used by the polymorphic species.

Light and feeding at dusk

The fully trichromatic *Alouatta* maintained similar light levels throughout the day when eating both green and non-green foods, but increased feeding time on non-green foods at the end of the day when light levels began to fall (Fig. 6). The polymorphic *Propithecus*, in contrast, followed the light of the setting sun up tree crowns (higher light level relative to *Lemur* as seen in Fig. 6) when feeding at dusk on non-green foods. It appears that the trichromatic *Alouatta* could discriminate red foods from a dark green background at dusk, whereas *Propithecus* requires brighter light to make the same discrimination. The other polymorph, *Ateles*, made no discrimination in light levels and spent more time on green foods at the end of the day. *Lemur* also spent similar amounts of feeding time on green and non-green foods, and it slightly increased light levels on green foods (Fig. 6). The OWMs in Kibale varied in time spent feeding on non-green foods. However, they used much dimmer light throughout the day compared to the species at the other sites when the data were not normalized. They are under a year-round rainforest canopy, in contrast to the deciduous dry forests of the other sites, which explains the lower light levels found. Their LLs used at dusk were either lower when eating non-green foods or were the same.

According to Endler (1997), different light environments can affect color perception. For example, early/late light occurs at sun angles less than 10° from the horizon early and late in the day and is rich in purplish or reddish-purple light. Because forest shade light is dominated by shorter wavelengths, orange-red foods (reflecting > 600 nm) are not strongly illuminated. They are much brighter under

early/late light. Consistent with this pattern, *Propithecus* appears to take advantage of the reddish light at dusk to illuminate non-green foods by ascending to the top of the canopy to feed.

The pattern of light usage by the routinely trichromatic species (Figs. 2, 6) suggests that they may be able to discriminate colors at lower light levels than polymorphic or dichromatic animals. Our results indicate that the trichromatic species generally used lower light than the species polymorphic for color vision. Fully trichromatic animals may not require higher light to distinguish color. There is some data suggesting that vertebrates resort to achromatic signals in dim light (Vorobyev and Osorio 1998; Kelber et al. 2003). Color vision deteriorates with decreasing light (Schneider and von Campenhausen 1998). In high light conditions (photopic), only cones are active and rods are saturated, and the opposite is the case in low light (scotopic). However, in the mesopic conditions of dusk both rods and cones are active (Brill 1990). Trichromatic animals may be able to use their more acute color perception advantageously even in the dim light of twilight.

Conclusions

The dichromatic taxon, *Lemur*, did not use the highest light levels when feeding, presumably because higher light intensities did not help it in contrasting non-green foods from a mature leaf background. The polymorphic species (*Propithecus*, *Ateles*) used the highest light levels when feeding and were the only species that consistently used higher light levels when eating non-green foods. Both sexes in the polymorphic species made a distinction in light levels used when eating green vs non-green foods, and females in these taxa were significantly different. Although the polymorphs as a group used higher LLs than the other taxa studied, the males used lower light than the females when eating non-green foods, which is a similar pattern to that found for the dichromatic *Lemur*. That the females used higher light confounds expectations for trichromats. Males and dichromatic females are presumably taking advantage of the discriminatory abilities of trichromatic females. The separation between males and females in LLs when eating non-green foods suggests that selection is acting on trichromatic females within the polymorphic species to maintain a balanced polymorphism, though the relationship between LLs and color vision for these taxa is as yet unclear.

The routine trichromat *Alouatta* did not make discriminations in light levels used when feeding on foods of different colors and did not feed at higher light levels than the sympatric, polymorphic *Ateles*. The trichromatic Kibale monkeys also used lower light when feeding, especially when eating non-green foods. A possible explanation for this may be that fully trichromatic animals do not enjoy a net benefit from increasing light levels to see color. By virtue of their 'better' color vision, trichromats may be more flexible in seeing color at all light levels.

This study demonstrates that the interplay of the light environment and underlying visual capacities of primate

species influences food color perception and subsequent food choice. The extent to which color and ambient light affects food choice during foraging could be further explored in other species that are at least partially diurnal.

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