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

Received: 11 June 2004 / Revised: 11 February 2005 / Accepted: 14 February 2005 / Published online: 1 June 2005
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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

Communicated by P. Kappeler

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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

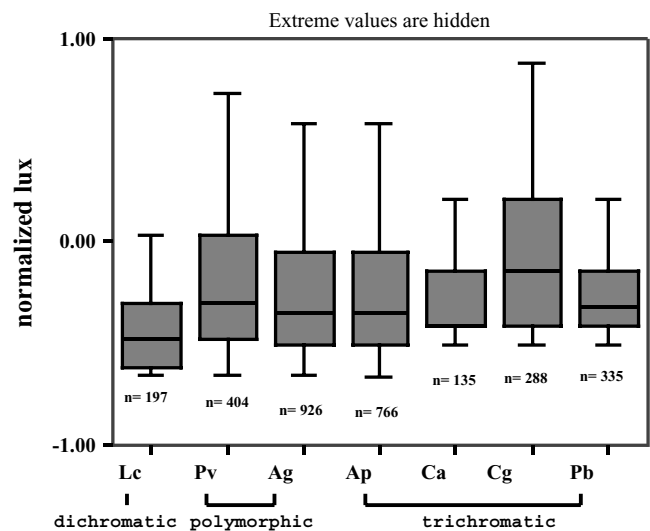
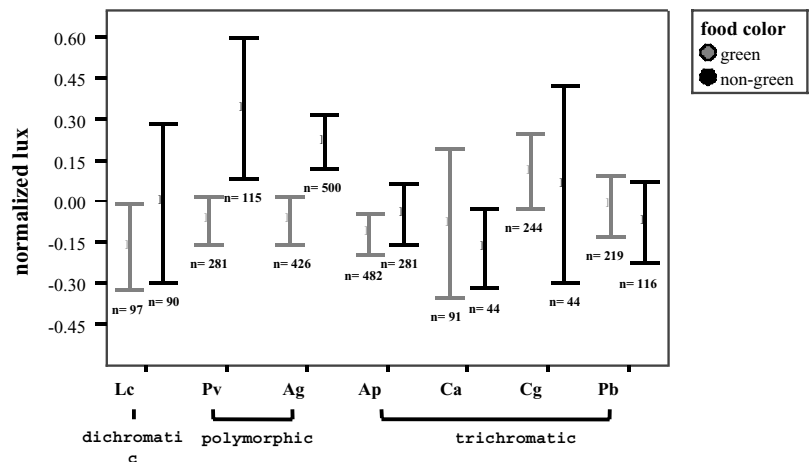


Fig. 1 Light levels used by primates while feeding. Centers represent mean values and whiskers are 95% confidence intervals of the mean (*Lc**Lemur catta*, *Pv**Propithecus verreauxi*, *Ag**Ateles geoffroyi*, *Ap**Alouatta palliata*, *Ca**Cercopithecus ascanius*, *Cg**Colobus guereza*, *Pb**Ptilocolobus 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 ($X^2 = 52.60$, $df = 1$,

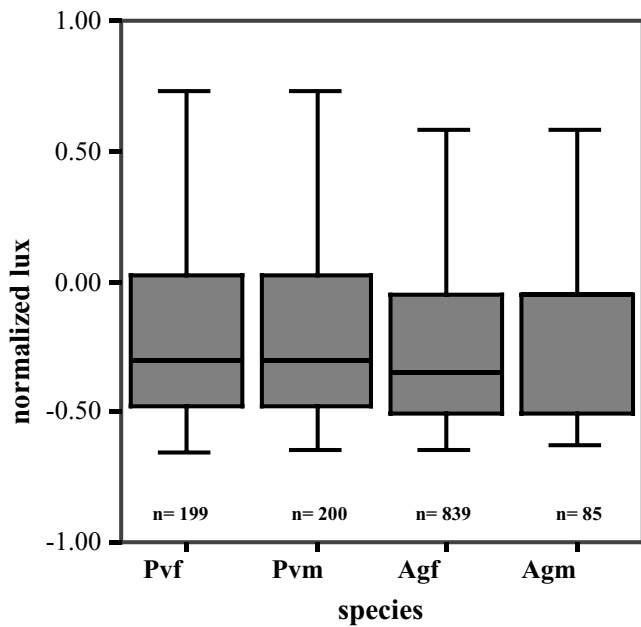


Fig. 3 Light levels used by females and males of species polymorphic for trichromatic color vision. *Boxes* represent central half of data divided by median line, *whiskers* depict data range excluding outliers.

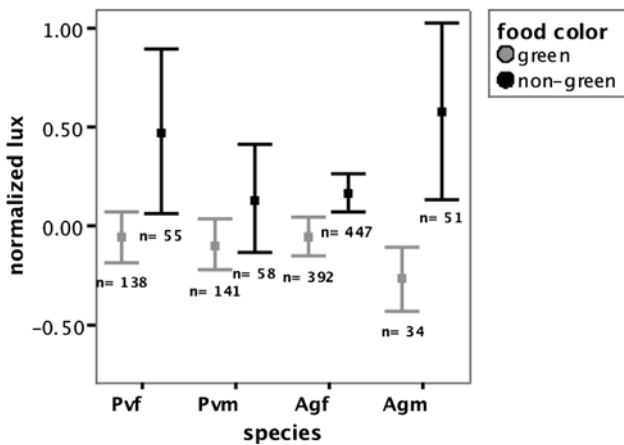


Fig. 4 Light levels used by polymorphic species when eating green vs non-green foods. *Centers* represent mean values and *whiskers* are 95% confidence intervals of the mean.

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.

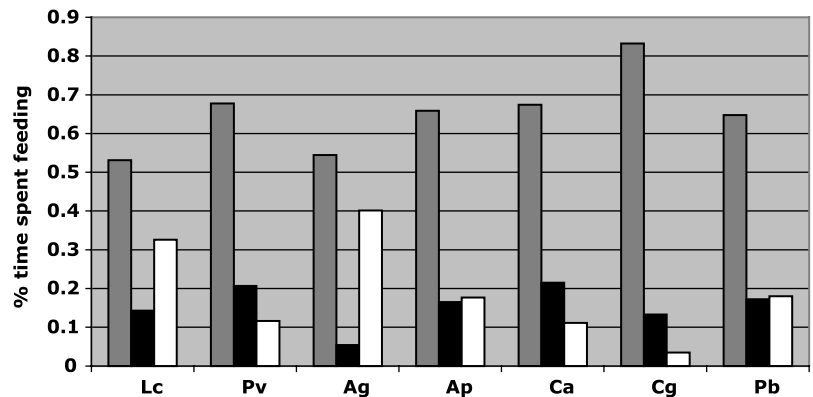


Table 2 Light levels used when eating green vs non-green foods separated by sexes^a

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

