

COMMENTARY

Why Aye-Ayes See Blue

AMANDA D. MELIN^{1*}, GILLIAN L. MORITZ², ROBERT A. E. FOSBURY³, SHOJI KAWAMURA⁴, AND NATHANIEL J. DOMINY^{1,2}¹Department of Anthropology, Dartmouth College, Hanover, New Hampshire²Department of Biological Sciences, Dartmouth College, Hanover, New Hampshire³European Southern Observatory, Garching bei München, Germany⁴Department of Integrated Bioscience, University of Tokyo, Kashiwa, Chiba Japan

The capacity for cone-mediated color vision varies among nocturnal primates. Some species are colorblind, having lost the functionality of their short-wavelength-sensitive-1 (SWS1) opsin pigment gene. In other species, such as the aye-aye (*Daubentonia madagascariensis*), the SWS1 gene remains intact. Recent studies focused on aye-ayes indicate that this gene has been maintained by natural selection and that the pigment has a peak sensitivity (λ_{\max}) of 406 nm, which is ~20 nm closer to the ultraviolet region of the spectrum than in most primates. The functional significance behind the retention and unusual λ_{\max} of this opsin pigment is unknown, and it is perplexing given that all mammals are presumed to be colorblind in the dark. Here we comment on this puzzle and discuss recent findings on the color vision intensity thresholds of terrestrial vertebrates with comparable optics to aye-ayes. We draw attention to the twilight activities of aye-ayes and report that twilight is enriched in short-wavelength (bluish) light. We also show that the intensity of twilight and full moonlight is probably sufficient to support cone-mediated color vision. We speculate that the intact SWS1 opsin pigment gene of aye-ayes is a crepuscular adaptation and we report on the blueness of potential visual targets, such as scent marks and the brilliant blue arils of *Ravenala madagascariensis*. *Am. J. Primatol.* 74:185–192, 2012. © 2012 Wiley Periodicals, Inc.

Key words: *Daubentonia*; color vision; opsin; nocturnal behavior; *Ravenala*; scent marking

INTRODUCTION

Mammals possess a duplex retina with two classes of photoreceptors—rods and cones—that enable vision at different light intensities. Although cone activation is approximately inversely proportional to background illumination (Weber's law) [Fain et al., 2001], basic categories of light intensity follow simple benchmarks of photoreceptor activity. Scotopic (dark), mesopic (dim), and photopic (bright) light intensities are based on the overlapping transition from rod- to cone-mediated vision (Fig. 1) [Stockman & Sharpe, 2006]. Such terms are anthropocentric, but useful heuristic tools for discussing nonhuman visual systems. Accordingly, mammals are assumed to require mesopic or photopic light levels for cone-mediated color vision [Manning & Brainard, 2009]. They must also possess two or more cone classes with different spectral sensitivities. Intriguingly, the peak sensitivities (λ_{\max}) of cone photoreceptors can vary widely among mammals. Depending on species, the short-wavelength-sensitive (S-) cones can range from ultraviolet (UV) to blue regions of the spectrum (360–450 nm), whereas the λ_{\max} of the middle-to-

long-wavelength-sensitive (M/L-) cones can range from green to yellow regions of the spectrum (500–560 nm).

In recent years, a growing number of studies have described the variable presence and λ_{\max} of S-cones in lineages of mammals with profoundly scotopic visual ecologies [Peichl, 2005]. For example, some bats have maintained functional UV-sensitive S-cones for millions of years, whereas others have accumulated deleterious mutations to their short-wavelength-sensitive-1 (SWS1) opsin pigment gene, effectively dispensing with color vision [Müller

Contract grant sponsor: David and Lucile Packard Foundation; contract grant sponsor: 2007-31754.

The authors declare no conflict of interest.

*Correspondence to: Amanda D. Melin, Department of Anthropology, Dartmouth College, Hanover, NH 03755. E-mail: amanda.d.melin@dartmouth.edu

Received 27 August 2011; revised 7 November 2011; revision accepted 19 November 2011

DOI 10.1002/ajp.21996

Published online in Wiley Online Library (wileyonlinelibrary.com).

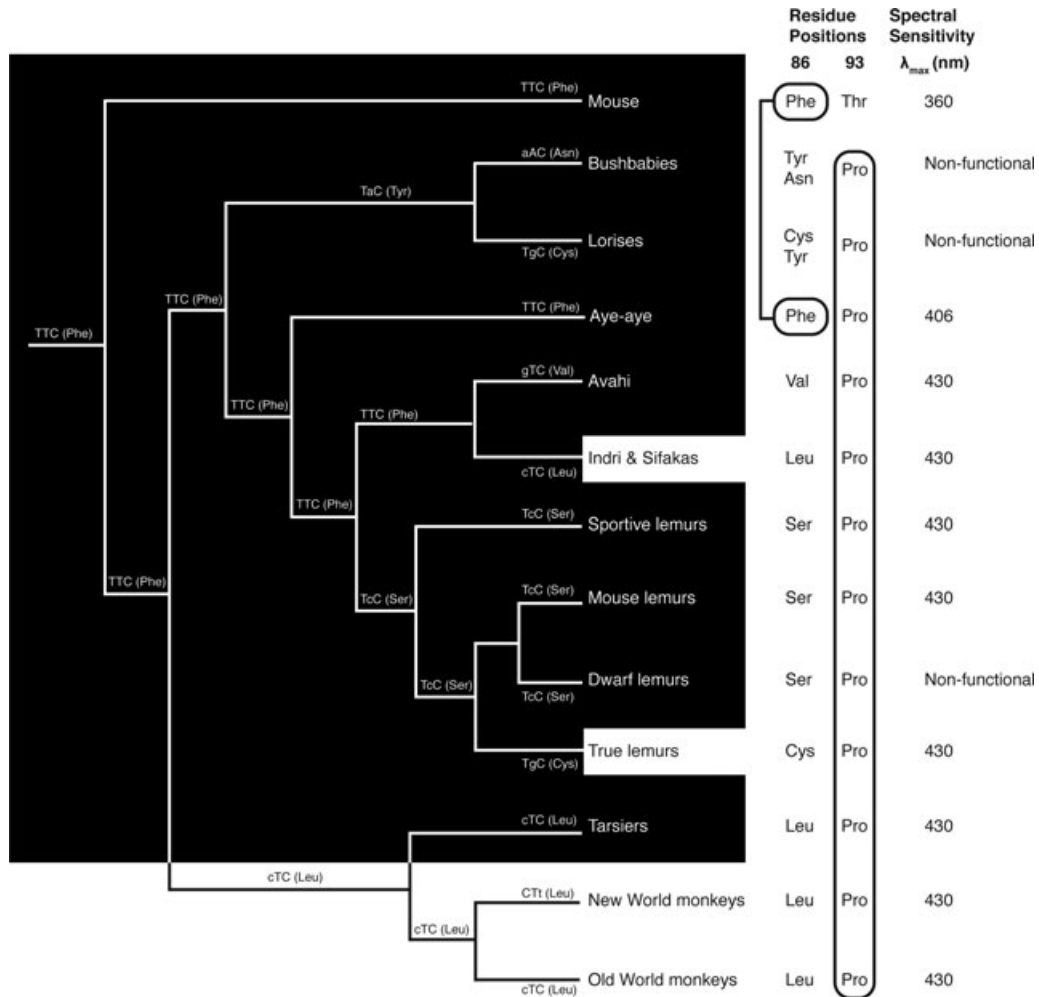


Fig. 1. Phyletic position of the aye-aye and its functional SWS1 (short-wavelength-sensitive-1) opsin pigment gene. The distinction between nocturnal (black zone) and diurnal (white zone) activity patterns is depicted along with different residues found at site 86 of the SWS1 gene, together with the corresponding codon sequences. Lower case letters are used to indicate substitutions in codon 86. Branch lengths do not reflect evolutionary distances. For aye-ayes, the retention of Phe at site 86 (Phe86) has raised the possibility of UV sensitivity, as in other mammals (see text). However, a change from Thr to Pro at site 93 exists in all primates and it appears to preclude UV sensitivity. Thus the tandem effects of Phe86 and Pro93 give the aye-aye a uniquely intermediate λ_{max} of 406 nm [Carvalho et al., 2012], which is plausibly the ancestral character state of euprimates.

et al., 2009; Zhao et al., 2009a,b). The functional significance of this variation is uncertain, and it is paralleled to an extent among nocturnal primates.

Nocturnal Primates and Color Vision

Nocturnal primates vary in their retention of functional opsin genes (Fig. 1). The SWS1 opsin pigment gene of some primates—the dwarf lemurs, lorises, and night monkeys—has acquired deleterious mutations [Jacobs et al., 1996; Kawamura & Kubotera, 2003, 2004; Tan et al., 2005]. As a result, these species cannot see color. In other lineages—the mouse lemurs, *Avahi*, *Lepilemur*, aye-ayes, and tarsiers—the SWS1 opsin pigment gene is intact and thus the presence of dichromatic color vision is inferred [Tan et al., 2005]. This finding was inter-

preted initially as an anachronism, a functionless vestige retained from a diurnal ancestor [Tan et al., 2005]. However, a signature of purifying selection at the SWS1 opsin gene locus of Bornean tarsiers [Kawamura & Kubotera, 2004] and aye-ayes [Perry et al., 2007] favors an adaptive interpretation, and indicates that these species benefit from having functional S-opsin pigments. Yet many of our colleagues have voiced private skepticism with this view, and suggest that it might be overly Panglossian.

Debate on the function of color vision among nocturnal primates must now account for a new and surprising finding. In a recent study, Carvalho et al. [2012] focused on the amino acid residues present at site 86 of the SWS1 gene. Among vertebrates, variation at this site affects the λ_{max} of the S-opsin

pigment, which can range from UV (360–400 nm) to blue (400–450 nm) regions of the spectrum. Aye-ayes are the only primates known to possess phenylalanine at site 86 (Phe86), a residue that, in other mammals, is associated with a UV-sensitive S-opsin pigment with a λ_{\max} \sim 360 nm [e.g., mouse, Fig. 1; Yokoyama et al., 1998; Hunt et al., 2004, 2007, 2009; Carvalho et al., 2006]. To explore the effects of Phe86 on the spectral tuning of the S-opsin pigment of aye-ayes, Carvalho et al. [2012] reconstituted, expressed, and measured the absorbance of the pigment in vitro. With a λ_{\max} of 406 nm, the S-opsin pigment was sensitive to violet rather than UV wavelengths. The absence of UV sensitivity was attributed to an amino acid change from Thr to Pro at site 93. This change (denoted Thr93Pro) exists in all primates and appears to preclude UV sensitivity (Fig. 1). Thus, the tandem effects of Phe86 and Pro93 appear to result in a λ_{\max} that is \sim 20 nm closer to the UV region of the spectrum than in most primates (Fig. 1).

Can Aye-Ayes See Blue?

The deductive intuition on whether or not aye-ayes benefit from color vision can be summarized as follows: if aye-ayes are nocturnal and therefore active under scotopic light levels, then their cone cells cannot function; thus there can be no selective advantage to maintaining a functional SWS1 opsin pigment gene for color vision. Perry et al. [2007] anticipated this reasoning when they suggested that aye-ayes might discriminate color only under the brightest moonlit conditions. Full moonlight is classified as dim mesopic light (Fig. 2A); however, the extent to which it can support primate color vision is yet unknown.

Light environments can vary by many orders of magnitude. A moonless night is \sim 100 million times darker than bright sunshine; and, in a tropical rainforest, light in the understory is \sim 100 times dimmer than incident light in the canopy overstory [Chazdon & Fetcher, 1984a,b]. A few animals can discriminate color under scotopic conditions, including at least one vertebrate, the helmet gecko *Tarentola chazaliae* [Roth & Kelber, 2004; Kelber & Roth, 2006]; however, these species have specialized optical adaptations [Roth et al., 2009; Kelber & Lind, 2010]. Among vertebrates with comparable optics to aye-ayes, estimates of color vision intensity thresholds are few and limited to humans, domestic horses, and two species of Australian parrot [Roth et al., 2008; Lind & Kelber, 2009]. The similar intensity thresholds (\sim 0.02 cd m⁻²) of two mammals with different color vision phenotypes—dichromatic horses and trichromatic humans—provides a compelling line of evidence that primates with di- or trichromatic vision have the potential for cone-mediated color vision under equally dim light, including twilight and bright moonlight

(Fig. 2A). Such findings motivate the question: Are aye-ayes active under twilight? The preservation and unusual λ_{\max} of the S-opsin pigment of aye-ayes is plausibly a crepuscular adaptation.

Activity in the Twilight Zone

To explore whether aye-ayes initiate activity at twilight, we reviewed the published literature and used the US Naval Observatory data service [<http://aa.usno.navy.mil/>] to classify light conditions at the time and location of observational field studies. We found that aye-ayes routinely initiated activity under twilight conditions, typically 17:30–18:45 hr [Ancrenaz et al., 1994; Andriamasimanana, 1994]. One study [Iwano, 1991] reported feeding behaviors at times that corresponded with the transition from civil twilight (when the solar elevation angle, θ_s , is between 0° and -6°) to nautical twilight (when θ_s is between -6° and -12°).

Yet twilight is a challenging visual environment. The rate of solar and lunar elevation change near the horizon is ca. 1° every 4–6 min [Johnsen et al., 2006], and a wide range of changes in the intensity and color of light can occur over a span of 2–4 hr [e.g., Tkačik et al., 2011]. For example, the spectral composition of twilight differs from day and night, being enriched in short wavelengths and distinctly purplish in Madagascar [Pariante, 1980] and at northern latitudes [Endler, 1993; Lee & Hernández-Andrés, 2003; Johnsen et al., 2006]. Such color results from the oblique angle of sunlight and the attenuation of middle wavelengths in the Chappuis band of atmospheric ozone [Fosbury et al., 2011]. However, these earlier measures of spectral irradiance were taken under unobstructed skies—a forest canopy not only dims downwelling light by orders of magnitude, it can also affect its spectral composition [Endler, 1993]. Thus, at twilight, aye-ayes are expected to encounter a wide range of mesopic light intensities and varying levels of purplishness as they travel and forage in both the forest overstory and dim understory [Sterling, 1993; Ancrenaz et al., 1994].

To explore the properties of this distinctive visual environment, we measured the intensity and spectral irradiance of twilight in the understory of a tropical rainforest. We used a multichannel spectrometer with a highly sensitive photomultiplier detector and an integrating sphere to ensure a cosine angular response (OL-770VIS, Gooch & Housego, Orlando, FL). Spectra were taken at 1-nm intervals from 380 to 700 nm on 12 July 2011 in Sabah, Malaysia (4°50'N–5°00'N and 117°35'E–117°45'E). At the end of civil twilight (18:50 hr), when θ_s was -6°, and in the presence of moonlight (38.9° elevation, 91% full), we recorded an understory irradiance spectrum with a broad peak around 450 nm (Fig. 2B). Such a spectrum agrees well with twilight irradiance

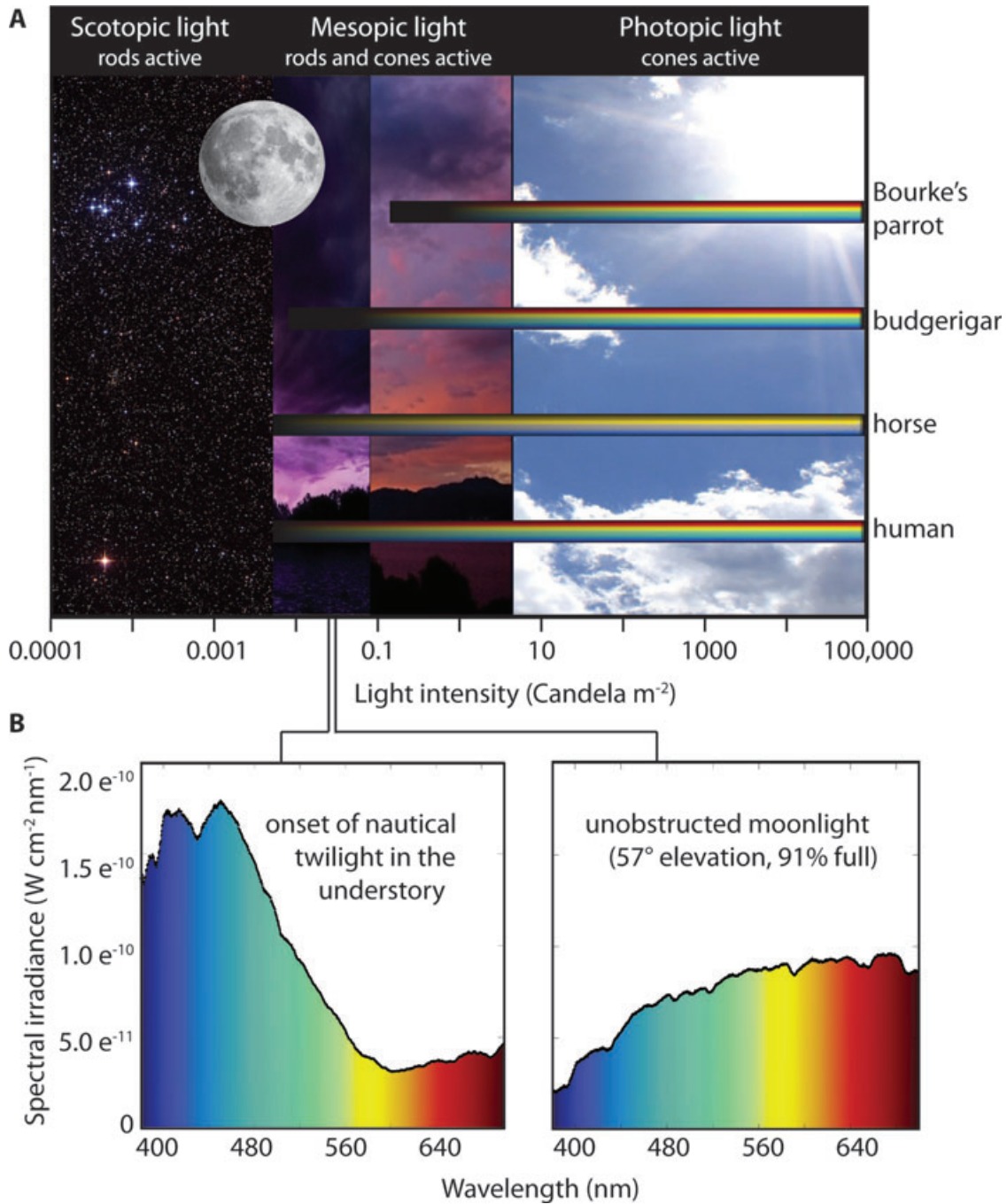


Fig. 2. Range and classification of light intensities experienced by vertebrates with visual optics comparable to those of aye-ayes. (A) Intensity thresholds of color vision in two species of Australian parrot [Lind & Kelber, 2009] and horses and humans [Roth et al., 2008]. The parrots and humans are represented with a trichromatic visible light spectrum, whereas the horse is represented with a dichromatic (protanope) light spectrum [simulated with VischeckJ v. 1.1 plug-in for ImageJ v. 1.44]. Figure concept modified from Kelber & Lind [2010]. (B) Irradiance spectra and intensities of two kinds of mesopic light with relevance to nocturnal primates: downwelling nautical twilight in the forest understory and unobstructed moonlight.

spectra from other latitudes [Endler, 1993; Johnsen et al., 2006] and indicates that a similar pattern can be expected in Madagascar [cf. Pariente, 1980]. Importantly, the intensity of this dim blue light, 0.046 cd m⁻², was above the color vision intensity threshold of horses and humans (Fig. 2A). We also

recorded the irradiance spectrum of unobstructed moonlight at 20:40 hrs (57° elevation, 91% full). This spectrum was shifted to longer wavelengths and nearly indistinguishable from a typical daylight spectrum, though at a much lower intensity (0.062 cd m⁻²; Fig. 2B).

Why Aye-Ayes See Blue

The preservation and unusual λ_{\max} of the S-opsin pigment of aye-ayes excites our curiosity, and it motivates us to speculate on why aye-ayes see blue. The aim of the present commentary is to describe current debate and to fuel interest in the visual ecology of nocturnal primates, a topic with the potential to inform hypotheses on the adaptive origins of primates [Tan et al., 2005]. In this vein, our analysis of the literature indicates that aye-ayes often initiate activity at twilight; and we show that the intensity of subcanopy twilight and bright moonlight is adequate to support cone-mediated color vision in mammals such as horses and humans, and presumably also aye-ayes. We also show that the spectral composition of understory twilight is enriched in blue wavelengths, which is expected to augment the brightness of blue stimuli due to their similar spectral shapes [hereafter termed "Endler's Rule"; cf. Rule 1, Endler, 1993]. Endler's Rule raises the possibility that the S-opsin pigment of aye-ayes contributes to the detection of blue targets under twilight conditions. To explore this hypothesis, we draw attention to stimuli with the potential to reflect short wavelengths.

Aye-ayes are nectar consumers and pollinators of the traveler's tree (*Ravenala madagascariensis*; Strelitziaceae), a plant widely cultivated for ornamental purposes (Fig. 3A). The fruit of *R. madagascariensis* has a brilliant blue aril that aye-ayes appear to use as a cue to detect aril- and seed-eating insects (Fig. 3B, C) [Sterling & McCreless, 2006]. The potential for coevolution between aye-ayes and the traveler's tree has long been recognized [Kress et al., 1994], yet the role of blue as a facultative color stimulus during lemur-plant interactions has received little attention [Sussman & Raven, 1978; Birkinshaw & Colquhoun, 1998].

The traveler's tree is also one of few plants to produce the animal protein bilirubin [Pirone et al., 2010], which might enhance the yellowness and overall visibility of lemur urine. In contrast to the glandular scent markings of most lemurs, the scent marks of aye-ayes are urine-based (Fig. 3E) [Sterling & Richard, 1995; Delbarco-Trillo et al., 2011]. Such marks are normally conceived as olfactory signals, but the possibility that S-opsin pigments can facilitate the visual detection of urine is an active area of research [Chávez et al., 2003; Kellie et al., 2004; Peichl et al., 2005].

To measure the reflectance spectra of these stimuli, we used a spectrometer (USB2000, range 200–850 nm; Ocean Optics, Dunedin, FL) and a deuterium tungsten halogen light source (DT-1000, range 200–1100 nm; Analytical Instrument Systems, Flemington, NJ) calibrated against a diffuse reflectance standard (WS1; Ocean Optics). All measurements were taken at a 45° angle. We found that the arils of *R. madagascariensis* (Fig. 3B, C) have

reflectance peaks in the violet and blue regions of the spectrum (Fig. 3F). We also examined the anther sheath of a more derived species in the family Strelitziaceae, *Strelitzia reginae* (Fig. 2D) [Kress et al., 1994]. Although *S. reginae* is endemic to South Africa, the spectral reflectance of the anther sheath (Fig. 3E) is a close match to the λ_{\max} of the S-opsin pigment of aye-ayes. This finding is relevant to aye-ayes insofar as it highlights how an S-opsin pigment might contribute to efficient foraging on the nectar-rich flowers of relict plant families. In Madagascar, similar floral structures might have played an important role in the evolution of lemur visual systems.

To examine the urine-based signals of aye-ayes, we measured the reflectance spectra of dried scent marks from captive animals. These marks were visible to us only when viewed under a UV flashlight, which caused the emission of yellow-green fluorescence (Fig. 3E). We measured this spectrum, but note that the excitation of the urine with our DT-1000 light source obscured the difference between reflectance and fluorescence, both of which were recorded as high levels of reflectance by the spectrometer. The urine spectra had marginal blue components (Fig. 3F), but there was a low level of short-wavelength chromatic contrast between them and the underlying tree bark, a typical substrate that is absorbent in this range. This result suggests that aye-ayes are unable to see conspecific scent marks; however, dried urine can lose its short-wavelength attributes [Chávez et al., 2003] and compounds from a natural diet could induce large spectral changes [Huitu et al., 2008].

DISCUSSION

Taken together, the studies of Perry et al. [2007] and Carvalho et al. [2012] indicate that the unusual color vision of aye-ayes has been maintained by natural selection. However, the extent to which aye-ayes actually discriminate color is unknown. We infer that the S-opsin pigment is in fact expressed in cone photoreceptors and that the transmission properties of the ocular media facilitate the absorbance of shorter wavelengths. Given these assumptions, and in the spirit of fostering and guiding future fieldwork, we have reported on the intensity and spectral composition of mesopic light in a tropical rain forest. We found that unobstructed, nearly full moonlight (measured here at 0.062 cd m⁻²) appears to be adequate for cone-mediated color vision in mammals, as Perry et al. [2007] hypothesized.

In addition, we have shown that dim subcanopy twilight is enriched in blue wavelengths and sufficient for color vision. Endler's Rule maintains that such light will enhance the brightness of blue targets, and we demonstrate that at least one relevant stimulus—the aril of *R. madagascariensis*—is blue.

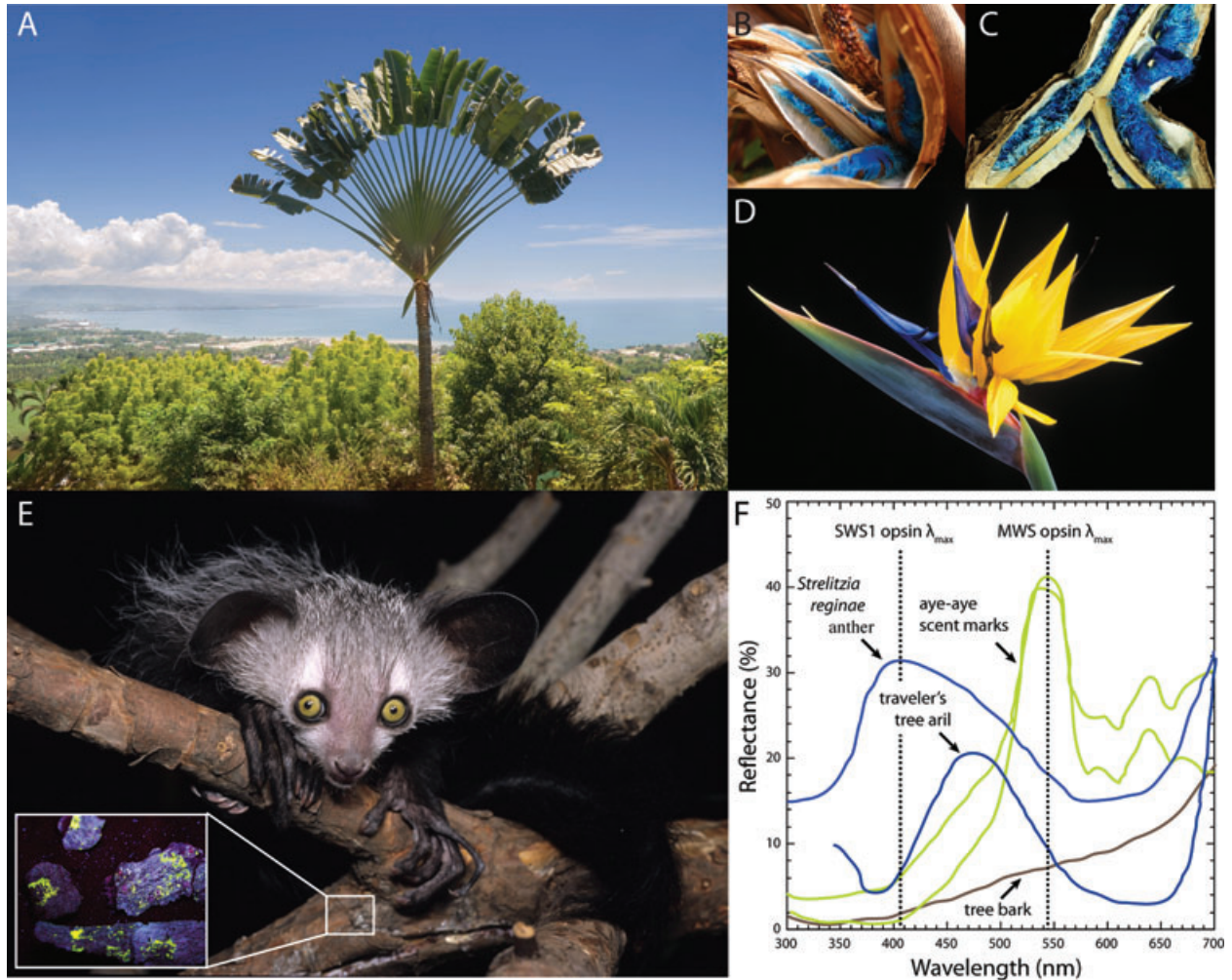


Fig. 3. Potential or analogous visual targets of aye-eyes. (A) The traveler's tree (*Ravenala madagascariensis*). (B, C) Fruit, seeds, and arils of *R. madagascariensis* (photograph 2B by C. Brattain, used with permission). (D) Flower of *Strelitzia reginae* with distinctive violet anther sheath. (E) The aye-aye (*Daubentonia madagascariensis*) (photograph by D. Haring, used with permission) and its fluorescent urine marks. (F) λ_{\max} values of the aye-aye's short-wavelength-sensitive-1 and middle-wavelength-sensitive (MWS) opsin pigments [Tan et al., 2005; Carvalho et al., 2012] and the reflectance spectra of each potential or analogous stimulus.

We hypothesize that aye-eyes see blue because it is advantageous for crepuscular foraging behaviors. However, it is plausible that the color vision of aye-eyes is unrelated to specific visual targets, but rather a general means of enhancing contrast under twilight conditions [Peichl et al., 2000; Vorobyev, 2004]. For example, the maintenance of intact SWS1 opsin pigment genes among tree-roosting bats (and conversely in few cave-roosting bats) might be related to the early onset of flight under twilight conditions—a period that is light enough to use visual cues for efficient travel to feeding sites, but dark enough to minimize the risk of predation from canopy raptors (Müller et al., 2007, 2009; Zhao et al., 2009a).

To test any of these hypotheses, it will be important to collect detailed behavioral observations in association with data on the spectral characteristics of light and visual targets. If possible, it is also important to determine the density and distribution

of cone types across the retina and the transmission properties of ocular media such as the cornea and lens [e.g., Müller et al., 2009; Hogg et al., 2011]. We conclude by suggesting that aye-eyes represent a promising avenue of future research for understanding the evolution and ecology of color vision among mammals.

ACKNOWLEDGMENTS

We are grateful to three anonymous reviewers for comments on prior versions of this commentary. Many thanks are extended to S. Zehr for permitting access to scent marks and to H. Bernard, K. Wells, and F. Tuh for logistical assistance in Malaysia. We also acknowledge C. Brattain and D. Haring for permission to reproduce their photographs. This research adhered to the American Society of Primatologists principles for the ethical treatment of primates.

REFERENCES

- Ancrenaz M, Lackman-Ancrenaz I, Mundy N. 1994. Field observations of aye-ayes (*Daubentonia madagascariensis*) in Madagascar. *Folia Primatol* 62:22–36.
- Andriamasimanana M. 1994. Ecoethological study of free-ranging aye-ayes (*Daubentonia madagascariensis*) in Madagascar. *Folia Primatol* 62:37–45.
- Birkinshaw CR, Colquhoun IC. 1998. Pollination of *Ravenala madagascariensis* and *Parkia madagascariensis* by *Eulemur macaco* in Madagascar. *Folia Primatol* 69:252–259.
- Carvalho LS, Cowing JA, Wilkie SE, Bowmaker JK, Hunt DM. 2006. Shortwave visual sensitivity in tree and flying squirrels reflects changes in lifestyle. *Curr Biol* 16:R81–R83.
- Carvalho LS, Davies WL, Robinson PR, Hunt DM. 2012. Spectral tuning and evolution of primate short-wavelength-sensitive visual pigments. *Proc R Soc B*. 279:387–393
- Chazdon R, Fetcher N. 1984a. Light environments of tropical forests. *J Ecol* 72:553–564. In: Medina E, Mooney H, Vazquez-Yanes C, editors. *Physiological ecology of plants of the wet tropics*. Boston: Dr W Junk Publishers. pp 27–36.
- Chazdon R, Fetcher N. 1984b. Photosynthetic light environments in a lowland tropical rain forest in Costa Rica. *J Ecol* 72:553–564.
- Chávez AE, Bozinovic F, Peichl L, Palacios AG. 2003. Retinal spectral sensitivity, fur coloration, and urine reflectance in the genus *Octodon* (Rodentia): implications for visual ecology. *Invest Ophthalmol Vis Sci* 44:2290–2296.
- Delbarco-Trillo J, Burkert BA, Goodwin TE, Drea CM. 2011. Night and day: the comparative study of strepsirrhine primates reveals socioecological and phylogenetic patterns in olfactory signals. *J Evol Biol* 24:82–98.
- Endler JA. 1993. The color of light in forests and its implications. *Ecol Monogr* 63:1–27.
- Fain G, Matthews H, Cornwall MC, Koutalos Y. 2001. Adaptation in vertebrate photoreceptors. *Physiol Rev* 81:117–151.
- Fosbury R, Koch G, Koch J. 2011. Ozone: twilight skies, and (exo-)planet transits. *ESO Messenger* 143:27–31.
- Hogg C, Neveu M, Stokkan K-A, Folkow L, Cottrill P, Douglas R, Hunt DM, Jeffery G. 2011. Arctic reindeer extend their visual range into the ultraviolet. *J Exp Biol* 214:2014–2019.
- Huitu O, Helander M, Lehtonen P, Saikkonen K. 2008. Consumption of grass endophytes alters the ultraviolet spectrum of vole urine. *Oecologia* 156:333–340.
- Hunt DM, Carvalho LS, Cowing JA, Davies WL. 2009. Evolution and spectral tuning of visual pigments in birds and mammals. *Philos Trans R Soc Lond B Biol Sci* 364:2941–2955.
- Hunt DM, Carvalho LS, Cowing JA, Parry JW, Wilkie SE, Davies WL, Bowmaker JK. 2007. Spectral tuning of shortwave-sensitive visual pigments in vertebrates. *Photochem Photobiol* 83:303–310.
- Hunt DM, Cowing JA, Wilkie SE, Parry JW, Poopalasundaram S, Bowmaker JK. 2004. Divergent mechanisms for the tuning of shortwave sensitive visual pigments in vertebrates. *Photochem Photobiol Sci* 3:713–720.
- Iwano T. 1991. An ecological and behavioral study of the aye-aye (*Daubentonia madagascariensis*). *Afr Study Monogr* 12:19–42.
- Jacobs GH, Neitz M, Neitz J. 1996. Mutations in S-cone pigment genes and the absence of colour vision in two species of nocturnal primate. *Proc R Soc Lond B* 263:705–710.
- Johnsen S, Kelber A, Warrant E, Sweeney AM, Widder EA, Lee RL, Hernández-Andrés J. 2006. Crepuscular and nocturnal illumination and its effects on color perception by the nocturnal hawkmoth *Deilephila elpenor*. *J Exp Biol* 209:789–800.
- Kawamura S, Kubotera N. 2003. Absorption spectra of reconstituted visual pigments of a nocturnal prosimian, *Otolemur crassicaudatus*. *Gene* 321:131–135.
- Kawamura S, Kubotera N. 2004. Ancestral loss of short wave-sensitive cone visual pigment in loriform prosimians, contrasting with its strict conservation in other prosimians. *J Mol Evol* 58:314–321.
- Kelber A, Lind O. 2010. Limits of colour vision in dim light. *Ophthalmic Physiol Opt* 30:454–459.
- Kelber A, Roth LSV. 2006. Nocturnal colour vision—not as rare as we might think. *J Exp Biol* 209:781–788.
- Kellie A, Dain SJ, Banks PB. 2004. Ultraviolet properties of Australian mammal urine. *J Comp Physiol A* 190:429–435.
- Kress WJ, Schatz GE, Andrianifahanana M, Morland HS. 1994. Pollination of *Ravenala madagascariensis* (Strelitziaceae) by lemurs in Madagascar: evidence for an archaic coevolutionary system? *Am J Bot* 81:542–551.
- Lee RL, Hernández-Andrés J. 2003. Measuring and modeling twilight's purple light. *Appl Optics* 42:445–457.
- Lind O, Kelber A. 2009. The intensity threshold of colour vision in two species of parrot. *J Exp Biol* 212:3693–3699.
- Manning J, Brainard, D. 2009. Optimal design of photoreceptor mosaics: why we do not see color at night. *Visual Neurosci* 26:5–19.
- Müller B, Glösmann M, Peichl L, Knop GC, Hagemann C, Ammermüller J. 2009. Bat eyes have ultraviolet-sensitive cone photoreceptors. *PLoS ONE* 4:e6390.
- Müller B, Goodman S, Peichl L. 2007. Cone photoreceptor diversity in the retinas of fruit bats (Megachiroptera). *Brain Behav Evol* 70:90–104.
- Pariente GF. 1980. Quantitative and qualitative study of the light available in the natural biotope of Malagasy prosimians. In: Charles-Dominique P, Cooper HM, Hladik A, Hladik CM, Pages E, Pariente GF, Petter-Rousseaux A, Petter JJ, Schilling A, editors. *Nocturnal Malagasy primates: ecology, physiology and behaviour*. New York: Academic Press. p 117–134.
- Peichl L. 2005. Diversity of mammalian photoreceptor properties: adaptations to habitat and lifestyle? *Anat Rec A* 287:1001–1012.
- Peichl L, Künzle H, Vogel P. 2000. Photoreceptor types and distributions in the retinae of insectivores. *Visual Neurosci* 17:937–948.
- Peichl L, Chavez AE, Ocampo A, Mena W, Bozinovic F, Palacios AG. 2005. Eye and vision in the subterranean rodent cururo (*Spalacopus cyanus*, Octodontidae). *J Comp Neurol* 486:197–208.
- Perry GH, Martin RD, Verrelli BC. 2007. Signatures of functional constraint at aye-aye opsin genes: the potential of adaptive color vision in a nocturnal primate. *Mol Biol Evol* 24:1963–1970.
- Pirone C, Johnson J, Quirke J, Priestap H, Lee D. 2010. Bilirubin present in diverse angiosperms. *AoB Plants* plq020.
- Roth LSV, Balkenius A, Kelber A. 2008. The absolute threshold of colour vision in the horse. *PLoS ONE* 3:e3711.
- Roth LSV, Kelber A. 2004. Nocturnal colour vision in geckos. *Proc R Soc Lond B* 271(Suppl 6):S485–S487.
- Roth LSV, Lundström L, Kelber A, Kröger RHH, Unsbo P. 2009. The pupils and optical systems of gecko eyes. *J Vision* 9:1–11.
- Sterling EJ. 1993. Behavioral ecology of the aye-aye (*Daubentonia madagascariensis*) on Nosy Mangabe, Madagascar [PhD Dissertation]. New Haven, CT: Yale University.
- Sterling EJ, McClellan EE. 2006. Adaptations in the aye-aye: a review. In: Gould L, Sauther ML, editors. *Lemurs: ecology and adaptation*. New York: Springer. p 159–184.
- Sterling EJ, Richard AF. 1995. Social organization in the aye-aye (*Daubentonia madagascariensis*) and the perceived distinctiveness of nocturnal primates. In: Alterman L, Doyle GA, Izard MK, editors. *Creatures of the dark: the nocturnal prosimians*. New York: Plenum Press. p 439–451.
- Stockman A, Sharpe LT. 2006. Into the twilight zone: the

- complexities of mesopic vision and luminous efficiency. *Ophthalm Physl Opt* 26:225–239.
- Sussman RW, Raven PH. 1978. Pollination by lemurs and marsupials: an archaic coevolutionary system. *Science* 200:731–736.
- Tan Y, Yoder AD, Yamashita N, Li W-H. 2005. Evidence from opsin genes rejects nocturnality in ancestral primates. *Proc Natl Acad Sci USA* 102:14712–14716.
- Tkačik G, Garrigan P, Ratliff C, Milčinski G, Klein JM, Seyfarth LH, Sterling P, Brainard DH, Balasubramanian V. 2011. Natural images from the birthplace of the human eye. *PLoS ONE* 6:e20409.
- Vorobyev M. 2004. Ecology and evolution of primate colour vision. *Clin Exp Optom* 87:230–238.
- Yokoyama S, Radlwimmer FB, Kawamura S. 1998. Regeneration of ultraviolet pigments of vertebrates. *FEBS Lett* 423:155–158.
- Zhao H, Rossiter SJ, Teeling EC, Li C, Cotton JA, Zhang S. 2009a. The evolution of color vision in nocturnal mammals. *Proc Natl Acad Sci USA* 106:8980–8985.
- Zhao H, Xu D, Zhou Y, Flanders J, Zhang S. 2009b. Evolution of opsin genes reveals a functional role of vision in the echolocating little brown bat (*Myotis lucifugus*). *Biochem Syst Ecol* 37:154–161.