

RESEARCH ARTICLE

Mutational Changes in S-Cone Opsin Genes Common to Both Nocturnal and Cathemeral *Aotus* Monkeys

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Aotus is a platyrrhine primate that has been classically considered to be nocturnal. Earlier research revealed that this animal lacks a color vision capacity because, unlike all other platyrrhine monkeys, *Aotus* has a defect in the opsin gene that is required to produce short-wavelength sensitive (S) cone photopigment. Consequently, *Aotus* retains only a single type of cone photopigment. Other mammals have since been found to show similar losses and it has often been speculated that such change is in some fashion tied to nocturnality. Although most species of *Aotus* are indeed nocturnal, recent observations show that *Aotus azarai*, an owl monkey species native to portions of Argentina and Paraguay, displays a cathemeral activity pattern being active during daylight hours as frequently as during nighttime hours. We have sequenced portions of the S-cone opsin gene in *A. azarai* and *Aotus nancymae*, the latter a typically nocturnal species. The S-cone opsin genes in both species contain the same fatal defects earlier detected for *Aotus trivirgatus*. On the basis of the phylogenetic relationships of these three species these results imply that *Aotus* must have lost a capacity for color vision early in its history and they also suggest that the absence of color vision is not compulsively linked to a nocturnal lifestyle. *Am. J. Primatol.* 69:1–9, 2007. © 2007 Wiley-Liss, Inc.

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INTRODUCTION

Owl monkeys (*Aotus* spp.) are the only nocturnal anthropoids and, partially because of that distinction, their behavior and ecology have been subject to considerable study [for reviews, see Erkert, 1999; Fernandez-Duque, 2007; Kinzey, 1997; Muller & Thalmann, 2000; Wright, 1994]. Robert W. Martin popularized the view that the nocturnality of *Aotus* was acquired secondarily following a diurnal past [Martin, 1990]. This conclusion is supported by the fact that, although *Aotus* displays features characteristically found in nocturnal mammals, such as a small body, large eyes, and lowered basal metabolic rate, a number of structural aspects of the eye itself imply diurnal ancestry [Wright, 1989]. The latter include the absence of a reflective tapetum as well as the sporadic presence of a fovea in some individuals [Martin & Ross, 2005]. The fossil record has been interpreted to suggest that the nocturnality of *Aotus* is of long standing, probably having emerged at least 12–15 mya [Setoguchi & Rosenberger, 1987].

The retina of *Aotus* contains a spatially heterogeneous mixture of rod and cone photoreceptors [Ogden 1975]. In mammals cone photoreceptors subserve a range of daylight visual capacities and typically contain two classes of photopigment, one type absorbs maximally in the short wavelengths (S-cones) while the other one has maximal absorption in the middle to long wavelengths (M/L cones) [Jacobs, 1993]. Although both classes of cone photoreceptors can be reliably identified with immunocytochemical labeling techniques in a wide range of mammalian retinas [Szel et al., 2000], an examination of the *Aotus* retina revealed a robust population of M/L cones (ranging in density from 2,000 to 7,000/mm²), but failed to detect the presence of any S-cones [Wikler & Rakic, 1990]. A joint behavioral and electrophysiological study verified this conclusion, finding clear evidence for a single class of M/L cones, but no evidence of S-cones [Jacobs et al., 1993].

The proximate explanation for the absence of S-cones was revealed by a sequence analysis of the cone opsin genes in *Aotus*. Although owl monkeys have an S-cone opsin gene that is highly homologous to the human S-cone opsin gene, the gene in *Aotus* harbors deleterious mutational changes that obviate the expression of viable S-cone photopigment [Jacobs et al., 1996]. Two implications were drawn from this discovery: (a) an ancestor of modern *Aotus* had a functional S-cone opsin gene and, by extension, a population of S-cones and the visual capacities normally supported by the presence of such cones, and (b) the loss of a functional S-cone gene might be linked to the evolution of nocturnality in *Aotus*, since the principal role of mammalian S-cones is to support a color vision capacity that might be expected to be of little adaptive value in a nocturnal species. The second argument gained support from the fact that a stringently nocturnal strepsirrhine, the bush baby (*Otolemur crassicaudatus*), also has an S-cone opsin pseudogene [Jacobs et al., 1996]. Subsequent research has revealed that the retinas of numerous terrestrial and marine mammal species lack functional S-cones [reviewed by Peichl, 2005]. Although it is true that many of those species are nocturnal, some are not. Accordingly, a general explanation for the loss of mammalian S-cones remains elusive.

Owl monkeys provide an interesting opportunity to examine the possible relationship between the loss of S-cones and patterns of activity in mammals, since closely related owl monkey species differ in their activity patterns [Fernandez-Duque, 2007; Wright, 1989]. Although the systematics of *Aotus* continues to be refined, the traditional position of all owl monkeys being

identified as *Aotus trivirgatus* is no longer accepted. Depending on the criteria employed, between five and 13 species are now recognized [Defler, 2004; Fernandez-Duque, 2007; Ford, 1994; Groves, 2001; Hershkovitz, 1983; Rylands et al., 2000]. Although most of the species are considered strictly nocturnal the Azara's owl monkeys (*Aotus azarai*) of the Argentinian and Paraguayan Chaco are active during daylight hours as well as during the night, and the pattern persists across the seasons [Fernandez-Duque, 2003; Fernandez-Duque & Erkert, 2006; Wright, 1994]. An activity profile like this one has also been described for a number of Malagasy strepsirrhines and for a variety of other mammals [Curtis & Rasmussen, 2006], and is now conventionally referred to as "catheMERal" [Tattersal, 1987]. *Aotus* thus provides a unique case where closely related animals differ dramatically in their photic activity cycles. To ask whether this variation in photic lifestyle might be paralleled by variation in the presence of functional S-cone photopigments and the visual capacities they support we have compared portions of the S-cone opsin gene structure in the catheMERal *A. azarai* with those in the nocturnal *Aotus nancymaeae*.

METHODS

Standard molecular genetic techniques were used to evaluate a portion of the S-cone opsin genes derived from five *A. azarai* and six *A. nancymaeae* individuals. The techniques used previously by Jacobs et al. [1996] on *A. trivirgatus* were essentially replicated for this investigation. DNA samples were obtained from the collection maintained at the Center for Reproduction of Endangered Species (CRES) of the Zoological Society of San Diego. *A. azarai* samples were obtained from monkeys in the catheMERal population under study in the Argentinean Chaco; *A. nancymaeae* samples came from the Dumond Conservancy for Primates and Tropical Forests, Miami, Florida. Homologous DNA sequences for humans (AH003620; [Nathans et al., 1986]) and *A. trivirgatus* [S82618; Jacobs et al., 1996] were obtained from Genbank.

Nucleotide sequence data were obtained using polymerase chain reaction (PCR) and dideoxy-chain-terminator cycle sequencing [Sanger et al., 1977]. For PCR, 1.0 μ l of nuclear DNA (~50 ng/ μ l) was amplified in a 50 μ l mixture containing 37.75 μ l of water, 5.0 μ l of $\times 10$ PCR buffer (500 mM KCl, 100 mM Tris-HCl, pH 8.3, and 20 mM MgCl₂), 3.0 μ l of mixed dNTP's (10 mM), 1.5 μ l of sense and anti-sense oligonucleotide primer (10 μ M), and 0.25 μ l of *Taq* DNA polymerase (5 units/ μ l). Amplification was achieved by placing the reaction through 35 cycles of denaturing at 90°C for 45 s, annealing at 55°C for 60 s, and extension at 72°C for 90 s, as well as a final extension period of 5 min at 72°C. Oligonucleotide primers "5" and "6" from Jacobs et al. [1996] were employed in a PCR to amplify a ~600 base pair fragment of the S-cone opsin gene. The amplified fragment included a small portion of the 5' pre-coding region, as well ~300 bases of the first exon of the S-cone opsin gene. PCR products were analyzed by size with ethidium-bromide-stained agarose-gel electrophoresis. The desired PCR products were purified and concentrated using Qiagen (Valencia, California) Qiaquick™ PCR purification columns and then sequenced directly using Applied Biosystem's (ABI; Foster City, California) Big Dye™ chemistry on an ABI 377 auto-sequencer. Both sense and anti-sense primer products were sequenced. Once obtained, the sequences were aligned for comparison using ClustalW [Thompson et al., 1994] and these alignments were confirmed by eye.

RESULTS AND DISCUSSION

S-Cone Opsin Pseudogenes in *A. azarai* and *A. nancymae*

A partial alignment of the obtained S-cone opsin sequences showing the first 114–118 bases of the first exon of S-cone opsin gene is presented in Figure 1 (because of gaps in the sequence the actual numbers differed slightly for the four species, as follows: *A. trivirgatus*, 114; human, 117; *A. azarai*, and *A. nancymae*, 118). S-cone opsin sequences obtained from humans [Nathans et al., 1986] and *A. trivirgatus* [Jacobs et al., 1996] are shown for comparison. No intra-species variations were detected in the sequences obtained for any of the individuals of either *A. azarai* or *A. nancymae*; consequently, only a single sequence is shown for each species. Both species show the same mis-sense mutation, earlier detected in *A. trivirgatus* [Jacobs et al., 1996]. This substitution of guanine with an adenine residue at nucleotide 66 (from the numbering of the alignment in Fig. 1) creates a translational alteration in the S-cone opsin gene, resulting in the premature introduction of a stop codon that is positioned just 21 residues into the ~330 residue protein. A second mis-sense mutation, a frame-shifting two-nucleotide deletion at nucleotide 92, also occurs in both *A. azarai* and *A. nancymae*. These changes indicate that the S-cone opsin genes of *A. azarai* and *A. nancymae* are pseudogenes, and thus cannot code for fully functional S-cone opsin proteins.

Given the presence of mis-sense mutations in the S-cone opsin genes similar to those found in *A. trivirgatus*, one would predict that the retinas of *A. azarai* and *A. nancymae* do not contain viable S-cone photopigments. Consequently, visually guided behavior in both cathemeral and nocturnal owl monkeys must be derived from signals generated by only a single type of photopigment, even under illumination conditions that would favor cone operation (i.e., daylight). This finding may contribute to our knowledge on the history of loss of S-cone function in *Aotus*, as well as to our understanding of the possible linkages between activity patterns and cone photopigment complement.

History of the Loss of S-Cones in *Aotus*

It seems reasonable to suppose that the loss of S-cone photopigment has occurred uniquely during the evolution of *Aotus* since all other contemporary platyrrhine lineages maintain a functional population of S cones (reviewed in Jacobs, 1998; 2007). Comparative analyses of four different DNA datasets and

	10	20	30	40	50	60
Human S cone	atgagaaaaa	tgctcggagga	agag~t	tatctgttca	aaaatatctc	ttcagtgagg
<i>A. trivirgatus</i>	atgagcaaga	tgctcagagga	agaggagttt	tatctgttca	a~catctc	ctcggtgagg
<i>A. nancymae</i>	atgagcaaga	tgctcagagga	agaggagttt	tatctgttca	agaacatctc	ctcggtgagg
<i>A. azarai</i>	atgagcaaga	tgctcagagga	agaggagttt	tatctgttca	agaacatctc	ctcggtgagg
	70	80	90	100	110	120
Human S cone	ccgtgggatg	ggcctcagta	ccacattgcc	cctgtctggg	ccttctacct	ccaggcagct
<i>A. trivirgatus</i>	ccgtgagatg	ggcctcagta	c~attgcc	cctgtctggg	ccttctacct	ccaggcagct
<i>A. nancymae</i>	ccatgagatg	ggcctcagta	ccacattgcc	c~gtctggg	ccttctacct	ccaggcagct
<i>A. azarai</i>	ccgtgagatg	ggcctcagta	ccacattgcc	c~gtctggg	ccttctacct	ccaggcagct

Fig. 1. Partial nucleotide alignment of the obtained S-cone opsin sequences of *Aotus azarai* (Genbank accession number DQ518239) and *Aotus nancymae* (DQ518238) shown in comparison to corresponding sequences derived for *Aotus trivirgatus* (S82618) and human (AH003620). The sequences have been shortened to show only the region corresponding to part of the first exon of the S-cone opsin gene. Dashes (~) denote internal gaps.

calibration of the molecular clock to the Oligocene–Miocene boundary have led to the suggestion that the family Cebidae split into constituent subfamilies, Cebinae and Aotinae, at about 22–23 mya [Schneider et al., 2001]. Hershkovitz [1983] first divided the genus *Aotus* into two groups—the so-called “gray-necked” and “red-necked”—that had characteristic chromosome differences and were largely geographically segregated north and south of the Amazon river, respectively. The gray-necked group has been regarded as being ancestral with subsequent diversification of the genus accompanying migration both northward and southward [Ford, 1994]. A cladistic interpretation of *Aotus* on the basis of a multidimensional analysis of craniodental morphometric data and pelage-coded data suggests *A. trivirgatus* is significantly divergent from both *A. nancymae* and *A. azarai* with *A. trivirgatus* closely linked to the original northern group, whereas *A. nancymae* is most closely linked to the original southern populations of *Aotus* [Ford, 1994].

The mis-sense mutation of the S-cone opsin gene found earlier in *A. trivirgatus* is also present in the two other species of owl monkeys analyzed here. The fact that all three species share the same mutational change suggests that the loss of a functional S-cone pigment probably occurred early in the history of *Aotus*, presumably before the divergence of the lineages leading to the modern-day northern and southern species. By implication, one might expect that all *Aotus* will be found to have the same gene defect.

The data obtained from *A. azarai* and *A. nancymae* reveal the presence of a second mis-sense mutation in their S-cone opsin genes, a two-nucleotide deletion at position 93. This defect, which would also render this gene nonfunctional, is not seen in the sequence derived for *A. trivirgatus* [Jacobs et al., 1996]. Consequently, that change probably occurred after the divergence of northern and southern groups of *Aotus*.

Photopigments, Vision, and Cathemeral Activity in *Aotus*

There are well-documented polymorphic variations in the M/L cone photopigments of most platyrrhine primates, of a few strepsirrhine genera, and among human populations [Jacobs, 1996]. Beyond those cases, however, most other mammalian genera appear to have no significant intra-species photopigment variations. *Aotus* seems to fall in this latter category. The observations reported here indicating a genus-wide absence of a functional S-cone confirms earlier experimental observations leading to the conclusion that, unlike all other platyrrhines, the photopigment complement of *Aotus* appears to consist of only two types of photopigment: a rod pigment having peak absorption at about 500 nm, and a single type of M/L cone containing a pigment with a sensitivity peak falling in the range of 539–543 nm [Hiramatsu et al., 2004; Jacobs et al., 1993].

In mammals, a principal role of S-cones is to provide signals that can be used in conjunction with those derived from M/L cones to jointly support a dimension of color vision [Calkins, 2001]. The existence of cathemeral owl monkeys raised the possibility that perhaps they had retained two functional classes of cone that would provide them color vision when it is most useful, during daylight. For example, various pieces of evidence indicate that the retinas of *Eulemur*, which are exclusively cathemeral [Kirk, 2006], contain functional populations of both S and M/L cones and, by inference, this allows for dichromatic color vision under conditions of photopic illumination [Jacobs & Deegan, 1993; Kawamura & Kubotera, 2004; Tan & Li, 1999]. In contrast, our results showing the lack of

functional S-cones in cathemeral owl monkeys indicate that cathemerality in primates is not necessarily linked to the presence of color vision.

Our results suggest that cathemeral owl monkeys are functionally monochromatic. The impressively large size of the owl monkey dilated pupil, combined with a large population of rods that reaches its maximum density ($\sim 450,000/\text{mm}^2$; Ogden [1975]) in the central part of the retina, provide this taxon with the visual tools for success under dim illumination conditions. As illumination is increased, the sensitivity of mammalian cones begins to exceed that of the rods. For *Aotus*, this point is reached in laboratory tests when the luminance of an adapting source viewed through the natural pupil exceeds $0.3\text{--}1\text{ cd/m}^2$ [Jacobs, 1977a]. In animals with duplex retinas the rods and cones share a range of luminance, where both are operational. For example, in humans, rods and cones are jointly active over a span covering approximately $4\log_{10}$ units of light intensity before rod signals saturate at the upper end of this range, a point reached at luminances of $1.94\text{--}3.3\log\text{ cd/m}^2$ [Buck, 2004; Makous, 2004]. Although analogous data are not available for *Aotus*, it seems undeniable that the daytime light levels at which *A. azarai* is behaviorally active [Fernandez-Duque, 2003; Fernandez-Duque & Erkert, 2006; Fernandez-Duque, 2007] are well within photopic range for this monkey. Consequently, although it is theoretically possible to derive some color discrimination under conditions where rods and cones are jointly active [Buck, 2004], for a significant fraction of its activity cycle *A. azarai* must be functionally monochromatic.

In recent years much attention has been focused on the functional utility of primate color vision. Both computational and observational studies indicate that color vision in platyrrhine monkeys can provide crucial information for successful foraging of fruits and foliage [Osorio et al., 2004; Regan et al., 2001]. Given that *Aotus* is a monochromat, incapable of exploiting any potential chromatic cues, it would be of interest to examine what sensory capacities are utilized in their detection and evaluation of foraging targets. The daytime diet of the cathemeral *A. azarai* includes both fruits and tree flowers [Arditi, 1992; Giménez & Fernandez-Duque, 2003; Wright, 1981, 1989, 1994, 1996]. In other platyrrhines these choices might be interpreted as involving the use of color cues. What alternative sources of information might cathemeral owl monkeys employ during foraging? There is evidence that *Aotus* may employ olfactory cues in foraging to a greater extent than do diurnal platyrrhines [Bolen & Green, 1997]; other possibilities include a greater reliance on the use of more proximate sensory capacities such as taste and texture in the mouth [Dominy et al., 2001].

Despite the absence of color vision, *Aotus* has significant daylight visual capabilities to support object discrimination. Earlier measurements of both temporal and spatial contrast sensitivity provided evidence that *A. trivirgatus* enjoys reasonable acuity in both of these key dimensions. For example, the limit of visual acuity in *Aotus* was estimated to be approximately 10 c/deg (\sim equivalent to a Snellen acuity of 20/80), a value distinctly lower than for the diurnal platyrrhines, but still nearly twice that of the domestic cat [Jacobs et al., 1979]. Similarly, *A. trivirgatus* individuals proved capable of successfully discriminating flickering lights at frequencies up to about 42 Hz, a value not much lower than that for equivalently tested humans [Jacobs, 1977b].

A number of hypotheses have been proposed to explain the evolution of cathemerality, including predation pressure, minimizing resource competition, and reducing exposure to unfavorable lighting or temperature conditions [Curtis & Rasmussen, 2006]. An adjustment of activity patterns in response to changes in ambient temperature seems to be at least a partial explanation for the occurrence of cathemerality in owl monkeys of the Argentinean Chaco [Fernandez-Duque,

2003, 2007; Fernandez-Duque & Erkert, 2006]. Finally, it has recently been argued that animals in the cathemeral genus *Eulemur* display variations in eye morphology that are intermediate to those of close nocturnal and diurnal relatives; specifically, in the relative sizes of their corneas [Kirk, 2006]. Although there are no comparable measurements that can be used to contrast *A. azarai* with the more typically nocturnal species of *Aotus*, we know of no evidence to suggest that there are any significant differences in gross morphology of the eye across the genus. And perhaps none would be expected in an animal whose eye, as noted above, already retains a number of features reflective of a diurnal past.

Mutational Loss of S-cones

The mutational loss of S-cone opsins was first described in *Aotus* monkeys. Since then, a number of species drawn from three families of terrestrial mammals and two families of marine mammals have been similarly found to have lost functional S-cones through opsin gene mutation [Peichl, 2005]. Although surveys for the loss of S-cones are still somewhat limited, two distributional patterns can be discerned. In some, the loss across the family is sporadic implying that it has occurred only in the distal branches of the family lineages. For example, some species in the family Procyonidae have lost S-cone function, while others have not [Jacobs & Deegan, 1992]. In other groups, for example among Cetaceans, Pinnipeds, and Lorisiform primates, the loss of S-cone function appears to be universal implying that the loss occurred early in the evolution of these groups [Kawamura & Kubotera, 2004; Levenson & Dizon, 2003; Levenson et al., 2006]. Whereas documenting the loss of S-cone function has become relatively straightforward, understanding the reasons behind these losses remains a challenge. As noted above, it has been suggested that the loss may be linked to nocturnality since S-cone signals are likely of less importance under low-light conditions. But there are difficulties in accepting the hypothesis of a unidirectional linkage between nocturnality and the loss of S-cone function. For instance, some of the taxa that have lost S-cone function may still be active under photopic illumination conditions and, on the other hand, many nocturnal mammals have retained S-cone function. It is similarly unclear at this stage whether the loss of S-cone function reflects an adaptive change, as might be inferred from the homogeneity of loss across all individuals, or whether it is a neutral event. Finally, although there is no documentation for the claim as yet, it has been suggested that the loss of S-cone opsin may in fact predate the radiation of *Aotus*, thus obviating its linkage to nocturnality [Tan et al., 2005]. However, these issues are eventually resolved, our data on *A. azarai* show clearly that the loss of S-cone function and a complete absence of color vision are not insurmountable barriers to visual success under daylight conditions.

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