

Comparative Morphology of the Eye in Primates

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ABSTRACT

Comparative studies of mammalian eye morphology have shown that relative cornea size is an important correlate of visual ecology. Nocturnal species tend to have large corneas relative to eye size as an adaptation for increasing visual sensitivity. By contrast, diurnal species tend to have smaller corneas relative to eye size because their eye morphology maximizes visual acuity. Although qualitative analyses suggest that activity pattern may have a similar influence on eye morphology in primates, various current hypotheses have proposed that either diurnal anthropoids or diurnal lemurs have visual systems that diverge from those of other diurnal mammals. The goal of this analysis is to quantify the relationship between eye morphology and activity pattern in primates and to determine whether primates exhibit variation in eye morphology comparable to that of other mammals. Data on eye size and cornea size were collected for 147 specimens of 55 primate species. These data reveal that, within primate suborders, diurnal species have significantly smaller relative cornea sizes than nocturnal or cathemeral species. Both haplorhines and strepsirrhines thus exhibit variation in eye morphology that is consistent with functional expectations. However, comparisons between the two primate suborders demonstrate that haplorhines and strepsirrhines differ significantly in eye morphology. Whereas strepsirrhines have relative cornea sizes that are similar to nonprimate mammals of comparable activity pattern, diurnal anthropoids have smaller relative cornea sizes than most nonprimate mammals. This derived eye morphology in anthropoids probably evolved in the anthropoid stem lineage as a result of selection for highly acute diurnal vision. © 2004 Wiley-Liss, Inc.

Key words: eye; cornea; activity pattern; anthropoid; lemuriform; cathemeral; disequilibrium

The time of day that a mammalian species is awake and active can usually be classified as falling at some point along a continuum. At one extreme are diurnal species, which are most frequently active by day when ambient light levels fall in the range of cone-mediated (i.e., photopic) vision. At the other extreme are nocturnal species, which are usually only active at night. Depending on microhabitat characteristics and the phase of the moon, nocturnal species may be active in ambient light levels that fall into the range of rod-mediated (i.e., scotopic) or dual rod-and-cone-mediated (i.e., mesopic) vision. However, any attempt to classify activity patterns along the lines of a simple nocturnal/diurnal dichotomy would ignore the fact that a large number of mammalian species are active at intervals across a 24-hr cycle (Nowak, 1991). Many such cathemeral species must function across a wide range of ambient light levels, from below starlight (scotopic) to full sunlight (photopic).

Morphological adaptations for different activity patterns are perhaps nowhere more evident than in the gross anatomy of the eye. Although some nocturnal and fossorial mammals adapt to low ambient light levels by reducing their reliance on vision in favor of other sensory modalities, all primates have highly developed visual sys-

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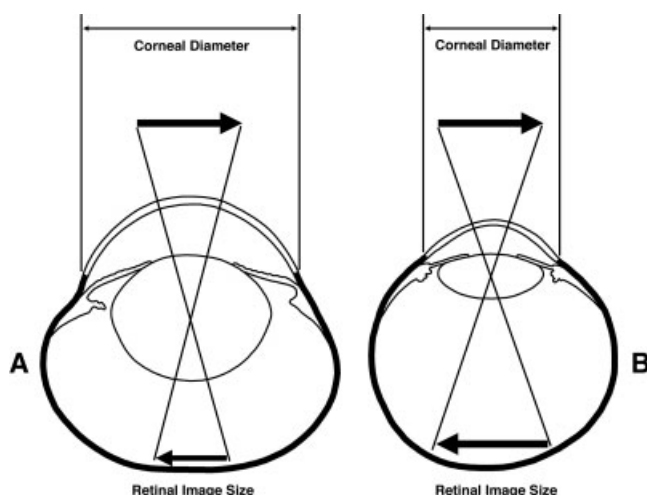


Fig. 1. Schematic comparison of eye morphology in *Galago* (A) and *Callithrix* (B). In this highly schematic view, differences in corneal diameter are shown at the top. Differences in retinal image size for identical visual targets (top arrows) that are equidistant from the two retinas are represented by arrows at the bottom. The crossing point of the lines connecting each top arrow (object of visual fixation) and bottom arrow (retinal image) represents the posterior nodal point, which typically occurs near the center of the lens (Hughes, 1977). All light rays passing through the posterior nodal point exit the optical system traveling in the same direction that they entered the optical system (McIlwain, 1996). Note, however, that the positions of the posterior nodal points are only approximate and that the paths of light rays have been simplified. Both eye cross-sections follow Detwiler (1939) and are shown at the same scale.

tems regardless of activity pattern (Walls, 1942; Lythgoe, 1979; Martin, 1990). In primates and other visually oriented mammalian groups, eye morphology typically varies with activity pattern in a highly predictable fashion (Detwiler, 1939, 1940, 1941; Walls, 1942; Prince, 1956; Duke-Elder, 1958; Tansley, 1965; Hughes, 1977). Because the size of the cornea places an upper limit on the maximum amount of light that the eye can admit at full pupillary dilation, nocturnal species typically enhance visual sensitivity by increasing the size of the cornea relative to the transverse diameter of the eye (Fig. 1A). If factors other than cornea size (e.g., eye size, corneal transmission) are held constant, an eye in which the cornea occupies a larger proportion of the anterior face of the globe can admit more light (and confer greater visual sensitivity) than an eye with a proportionally smaller cornea. Large relative cornea size is usually accompanied by the presence of a larger, more spherical lens and displacement of the posterior nodal point toward the retina (Fig. 1A). This configuration of the dioptric apparatus in nocturnal species helps to produce a smaller and brighter retinal image with the available light admitted to the eye, thereby further enhancing visual sensitivity (Walls, 1942; Prince, 1956; Duke-Elder, 1958; Tansley, 1965; Hughes, 1977).

In contrast to nocturnal species, diurnal mammals typically exhibit smaller corneas relative to the transverse diameter of the eye (Fig. 1B). The presence of relatively small corneas in diurnal species probably has little to do with limiting the amount of light that can enter the eye because the iris can easily reduce light admittance by constricting the size of the pupil. Instead, small relative

cornea size is usually accompanied by the presence of a smaller, more flattened, and anteriorly placed lens than is typically found in nocturnal species. This configuration of the dioptric apparatus results in anterior displacement of the posterior nodal point (Fig. 1B), which is probably an adaptation for enhancing visual acuity by producing a larger (albeit dimmer) retinal image that is spread over a larger number of ganglion cell receptive fields (Walls, 1942; Prince, 1956; Duke-Elder, 1958; Tansley, 1965; Hughes, 1977; Ross, 2000; Kirk and Kay, 2004).

Due to the demands of maintaining visual functionality across a wide range of ambient light levels, the eyes of cathemeral mammals are usually intermediate in morphology between those of diurnal and cathemeral species (Walls, 1942; Prince, 1956; Duke-Elder, 1958; Tansley, 1965). Accordingly, the size of the cornea relative to the transverse diameter of the eye in cathemeral species is generally smaller than in nocturnal species but larger than in diurnal species. Similarly, the lenses of cathemeral species are typically neither as large and spherical as those of nocturnal species, nor as small and flattened as those of diurnal species. This intermediate eye morphology in cathemeral mammals probably reflects an adaptive compromise between the need to enhance visual sensitivity under scotopic conditions and the need to enhance visual acuity under photopic conditions.

Eye Morphology in Primates

Given the large amount of attention that has been devoted to study of functional, adaptive, and evolutionary features of the primate visual system (Martin, 1990; Allman, 1999; Kaas and Collins, 2004; Ross and Kay, 2004), it is somewhat surprising that relatively few authors have examined the effect of activity pattern on primate eye morphology (Detwiler, 1939). Several authors have presented data on eye size in primates (Schultz, 1940; Rohen, 1962; Rohen and Castenholz, 1967; Stephan et al., 1984), but unlike relative cornea size, eye size does not vary in a predictable fashion with activity pattern (Kirk, 2003, 2004). This lack of comparative data of the relationship between eye morphology and activity pattern is problematic because some primate groups may exhibit eye morphologies that do not conform to the general trends seen in other mammalian groups.

Ross (2000) suggested that diurnal anthropoids have atypical eye morphologies relative to other mammals on the basis of data presented in a PhD thesis by Ritland (1982) on vertebrate eye allometry. Ritland's data set, which is derived primarily from measurements of preserved museum specimens, represents the largest single source of comparative data on eye and cornea size in vertebrates (including 38 species of primates). In the first published analysis of Ritland's mammalian data, Ross (2000) demonstrated that diurnal anthropoids have much smaller corneas relative to eye size than most other mammalian groups.¹ These results were interpreted as evidence that eye morphology is derived in diurnal anthropoids as an adaptation for increased visual acuity. Although Ross (2000) did not explicitly address the rela-

¹Ross (2000) actually compared corneal diameter to an estimate of the eye's posterior nodal distance. Posterior nodal distance was calculated using the formula $0.63 \times$ the axial length of the eye.

tionship between eye morphology and activity pattern in different mammalian clades, his findings suggest that diurnal anthropoids have eye morphologies that diverge from those of other diurnal mammals.

Similarly, the assumption that diurnal strepsirrhines exhibit eye morphologies comparable to other diurnal mammals is called into question by the possibility that lemuriform evolution has been influenced by exceptional historical factors. Van Schaik and Kappeler (1996) proposed that dissimilarities between the social systems of gregarious lemurs and anthropoids are the result of a recent transition from nocturnality to cathemerality or diurnality in many extant lemur species “the disequilibrium hypothesis.” This increasing trend toward diurnal activity in extant lemurs is hypothesized to be the result of anthropogenic ecological disturbances over the last 2,000 years, including the reduction of predation pressure associated with the extinction of large diurnal raptors and relaxed pressures for niche separation associated with the extinction of large-bodied lemur species. Due to the recency of this proposed transition in activity pattern, van Schaik and Kappeler (1996) suggested that extant diurnal lemurs retain many behavioral and morphological adaptations that are better suited for nocturnality than for diurnal activity.

In support of the disequilibrium hypothesis, van Schaik and Kappeler (1996) called attention to several salient differences between anthropoid and lemuriform visual systems, including, the presence of tapeta lucida and relatively low levels of antioxidant lens enzymes in some day-active lemur species. These differences led van Schaik and Kappeler to propose that “there is only a weak trend toward adaptations of the visual system of non-nocturnal [lemurs] toward high-light conditions, consistent with cathemeral activity, and no evidence for adaptations to exclusive diurnality” (van Schaik and Kappeler, 1996: p. 92).

If this hypothesis is correct, diurnal lemurs would not be expected to differ systematically from nocturnal or cathemeral lemurs in relative cornea size or any other aspect of eye morphology. Diurnal lemurs would also not be expected to have relative cornea sizes that are similar to diurnal members of other mammalian clades (which are presumably well-adapted to their current activity pattern).

Goals of Present Analysis

The primary goal of this analysis is to provide a quantitative description of the relationship between eye morphology and activity pattern in a broad comparative sample of primate species. This analysis also seeks to test comparative predictions derived from the hypotheses of Ross (2000) and van Schaik and Kappeler (1996) regarding the similarities between primates and nonprimate mammals in eye morphology. Accordingly, the specific questions addressed by this analysis include:

- 1) Do nocturnal, cathemeral, and diurnal primates exhibit systematic differences in eye morphology as predicted by qualitative studies of mammalian eyes and functional expectations?
- 2) Do diurnal anthropoids demonstrate relative cornea sizes that are smaller than those of other diurnal mammals?

- 3) Do diurnal lemurs have eye morphologies that are comparable to those of nocturnal and cathemeral lemurs (as predicted by the disequilibrium hypothesis) or other diurnal mammals (contrary to the expectations of the disequilibrium hypothesis)?

MATERIALS AND METHODS

Data were collected on eye and cornea size for 147 specimens of 55 primate species (Table 1). Specimens were obtained from the following sources: the Duke University Primate Center (DUPC); the comparative teaching collections of Duke University, SUNY Stony Brook, and the University of Chicago; the neurobiology laboratories of Columbia University; and the personal research collections of Dr. William Hylander, Dr. Pierre Lemelin, and Dr. Chris Vinyard. Measured specimens include both fixed and unfixed material. Most DUPC specimens were frozen shortly postmortem without fixative. Dissections and measurements of these specimens were performed after they had been allowed to thaw in a fume hood for 1–3 hr. However, several DUPC specimens were measured after being stored for several days in 10% formalin. Specimens obtained from all other sources were preserved for varying lengths of time in either formalin (usually 10%), ethanol, or dissection wetting solutions. Any specimens showing evidence of pathology or excess postmortem deformation were excluded from this analysis.

Primate cadavers were enucleated using standard dissection tools. Once removed from the orbit, eyes were cleaned of periorbital connective tissue using fine-tipped dissecting scissors and were examined visually for damage, pathologies, and preservational defects. In several instances, small holes were accidentally punctured in the sclera during the process of removal from the orbit. In these cases, the surface of the eye surrounding the puncture was dried with a paper towel and the hole was sealed using a fast-drying cyanoacrylate glue (Hot Stuff Special T). Because eyes generally collapse due to loss of internal fluids postmortem, each eye was refilled with 10% formalin or ethanol using a 50 cc syringe with a small-gauge needle. The needle was inserted through the optic nerve head, and the eye was reinflated until it returned to a globose shape and resisted further attempts at inflation.² With the needle still inserted and the eye maintained at full internal pressure, the following measurements were taken using Mitutoyo digital calipers to the nearest 0.1 mm: maximum and minimum transverse (equatorial) eye diameters, and maximum and minimum corneal diameters.

Because the size of the cornea relative to total eye size is closely related to both light admittance at maximum pupil dilation and retinal image size (Fig. 1), eye shape was quantified in this analysis as the ratio of mean corneal diameter to mean transverse eye diameter (henceforth the C:E ratio). The C:E ratio thus expresses actual cornea size

²Note that the sclera and cornea are relatively inelastic, and that the point of maximum inflation of the eye is not difficult to ascertain regardless of its preservational state (fixed or unfixed). In all instances, the eye reached its state of maximum inflation immediately after the external surface attained a smoothly curved shape (i.e., filling did not cause the eye to expand like a balloon with added pressure).

TABLE 1. Activity patterns and mean eye measurements for all included taxa

Taxon	AP	N	TD	SD	CD	SD	CD:TD
Primates							
<i>Alouatta</i> sp.	D	3	18.6	0.7	9.3	0.4	0.50
<i>Aotus</i> sp.	N	2	19.2	1.1	13.4	1.3	0.70
<i>Ateles</i> sp.	D	6	20.1	2.0	10.1	1.0	0.50
<i>Cacajao rubicundus</i>	D	1	19.9		9.3		0.47
<i>Callithrix jacchus</i>	D	5	11.6	0.3	6.0	0.3	0.52
<i>Cebus</i> sp.	D	1	15.1		7.3		0.48
<i>Cercopithecus albogularis</i>	D	1	18.9		9.7		0.51
<i>Cercopithecus ascanius</i>	D	2	18.8	1.0	9.8	0.9	0.52
<i>Cercopithecus diana</i>	D	1	20.2		10.7		0.53
<i>Cercopithecus neglectus</i>	D	1	20.6		10.9		0.53
<i>Cheirogaleus major</i>	N	1	12.9		10.6		0.83
<i>Cheirogaleus medius</i>	N	3	10.5	0.2	8.8	0.1	0.84
<i>Colobus polykomos</i>	D	3	19.1	0.3	10.1	0.5	0.53
<i>Daubentonia madagascariensis</i>	N	1	17.6		14.1		0.80
<i>Erythrocebus patas</i>	D	2	24.3	0.7	11.1	0.3	0.45
<i>Eulemur coronatus</i>	C	2	16.1	1.1	12.3	1.7	0.77
<i>Eulemur fulvus</i>	C	6	17.6	0.6	13.2	0.6	0.75
<i>Eulemur macaco</i>	C	4	17.4	0.8	12.1	1.0	0.70
<i>Eulemur mongoz</i>	C	3	16.4	0.5	12.6	0.7	0.77
<i>Eulemur rubriventer</i>	C	1	18.1		14.2		0.78
<i>Galago moholi</i>	N	8	13.8	0.6	11.3	0.5	0.82
<i>Galagoides demidoff</i>	N	1	9.6		8.8		0.92
<i>Hapalemur griseus</i>	D	2	14.1	0.3	9.7	0.2	0.69
<i>Hylobates</i> sp.	D	4	19.9	1.2	10.5	0.5	0.53
<i>Lagothrix lagotricha</i>	D	2	20.5	0.3	10.0	0.2	0.49
<i>Lemur catta</i>	D	3	16.2	0.4	12.0	0.5	0.74
<i>Leontopithecus rosalia</i>	D	1	12.0		6.6		0.55
<i>Loris tardigradus</i>	N	2	15.1	0.1	12.8	0.3	0.85
<i>Macaca fascicularis</i>	D	3	18.5	0.3	9.6	0.0	0.52
<i>Macaca mulatta</i>	D	3	20.5	0.4	10.8	0.6	0.53
<i>Macaca nemestrina</i>	D	2	20.5	0.2	11.4	0.7	0.56
<i>Macaca radiata</i>	D	3	18.6	0.1	9.3	0.2	0.50
<i>Macaca</i> sp.	D	1	17.9		9.7		0.54
<i>Mandrillus leucophaeus</i>	D	1	21.6		11.4		0.53
<i>Microcebus murinus</i>	N	7	9.4	0.5	8.0	0.3	0.85
<i>Mirza coquereli</i>	N	6	13.0	0.3	11.5	0.3	0.88
<i>Nycticebus coucang</i>	N	4	15.8	0.6	12.6	0.7	0.80
<i>Nycticebus pygmaeus</i>	N	1	14.9		12.3		0.83
<i>Otolemur crassicaudatus</i>	N	2	17.4	1.0	13.4	0.7	0.77
<i>Pan troglodytes</i>	D	1	23.0		10.2		0.44
<i>Papio</i> sp.	D	3	20.2	0.8	10.0	1.2	0.49
<i>Perodicticus potto</i>	N	2	12.2	0.3	10.2	0.5	0.84
<i>Pongo pygmaeus</i>	D	1	22.8		11.6		0.51
<i>Procolobus badius</i>	D	1	18.7		9.7		0.52
<i>Propithecus diadema</i>	D	1	20.3		14.9		0.73
<i>Propithecus tattersalli</i>	D	3	18.4	0.5	13.4	0.3	0.73
<i>Propithecus verreauxi</i>	D	6	17.8	0.7	13.1	0.8	0.74
<i>Saguinus fuscicollis</i>	D	3	10.5	0.4	5.9	0.4	0.56
<i>Saguinus midas</i>	D	1	12.7		6.1		0.48
<i>Saguinus</i> sp.	D	1	12.1		6.5		0.54
<i>Saimiri</i> sp.	D	10	15.1	0.4	7.8	0.3	0.51
<i>Tarsius syrichta</i>	N	2	17.9	0.4	14.1	0.1	0.79
<i>Theropithecus gelada</i>	D	1	18.4		8.6		0.47
<i>Trachypithecus cristatus</i>	D	1	19.4		11.0		0.57
<i>Varecia variegata</i>	D	5	19.4	0.3	14.2	0.3	0.73
Carnivorans							
<i>Acinonyx jubatus</i>	D	2	35.9	0.0	22.4	1.2	0.62
<i>Ailurus fulgens</i>	N	1	13.0		10.0		0.77
<i>Alopex lagopus</i>	C	2	18.8	0.1	13.3	0.3	0.71
<i>Bassariscus astutus</i>	N	1	13.2		11.8		0.89
<i>Canis lupus</i>	C	1	22.9		16.6		0.72
<i>Cerdocyon thous</i>	N	1	17.8		14.4		0.81
<i>Galidia elegans</i>	D	1	9.2		7.0		0.76
<i>Genetta genetta</i>	N	2	14.8	0.4	13.0	0.0	0.88
<i>Hemigalus derbyanus</i>	N	1	13.1		12.3		0.94
<i>Ichneumia albicauda</i>	N	1	14.0		12.0		0.86
<i>Ictailurus planiceps</i>	N	1	19.2		17.1		0.89
<i>Leopardus tigrinus</i>	C	1	20.1		17.9		0.89
<i>Leopardus wiedii</i>	C	2	22.0	0.3	19.8	0.1	0.90
<i>Lutra annectens</i>	C	1	10.6		7.3		0.68
<i>Lutra marculicollis</i>	C	1	10.7		8.6		0.80
<i>Lynx canadensis</i>	C	2	26.7	0.0	19.1	0.0	0.71

TABLE 1. Activity patterns and mean eye measurements for all included taxa (continued)

Taxon	AP	N	TD	SD	CD	SD	CD:TD
Carnivorans (continued)							
<i>Martes flavigula</i>	D	1	12.2		8.4		0.69
<i>Meles meles</i>	N	1	10.6		8.5		0.80
<i>Melursus ursinus</i>	N	1	17.0		11.2		0.66
<i>Mustela nivalis</i>	C	1	6.0		4.9		0.82
<i>Mydaus</i> sp.	C	1	7.4		6.1		0.82
<i>Otocolobus manul</i>	C	1	19.2		12.8		0.67
<i>Panthera leo</i>	C	3	36.1	2.3	25.3	0.8	0.70
<i>Panthera onca</i>	N	1	28.2		20.5		0.73
<i>Panthera tigris</i>	C	2	34.8	3.2	24.2	1.2	0.70
<i>Panthera uncia</i>	C	2	31.1	0.8	22.1	0.5	0.71
<i>Paracynictis selousi</i>	C	1	10.5		6.3		0.60
<i>Pardofelis marmorata</i>	N	1	21.6		17.0		0.79
<i>Prionailurus bengalensis</i>	C	2	20.4	0.3	16.3	1.0	0.80
<i>Prionailurus viverrinus</i>	C	1	23.6		19.6		0.83
<i>Procyon lotor</i>	N	3	14.0	1.0	11.6	0.9	0.83
<i>Salanoia concolor</i>	D	1	14.3		12.7		0.89
<i>Selenarctos thibetanus</i>	C	1	17.0		11.5		0.68
<i>Speothos venaticus</i>	D	1	17.7		10.0		0.56
<i>Suricata suricatta</i>	D	1	12.7		6.0		0.47
<i>Urocyon cinereoargenteus</i>	C	3	17.4	2.7	13.8	2.2	0.79
<i>Ursus americanus</i>	C	1	18.5		13.8		0.74
<i>Ursus arctos</i>	C	1	20.0		13.0		0.65
<i>Vormela peregusna</i>	C	1	7.6		6.6		0.87
<i>Vulpes vulpes</i>	N	3	19.8	0.5	15.9	0.5	0.80
Scandentians							
<i>Ptilocercus lowii</i>	N	1	6.7		6.2		0.93
<i>Tupaia belangeri</i>	D	1	8.8		6.6		0.74
<i>Tupaia glis</i>	D	2	9.6	0.1	7.8	0.3	0.82
<i>Tupaia minor</i>	D	1	8.0		6.6		0.82
<i>Urogale everetti</i>	D	1	9.0		6.9		0.77
Sciurids							
<i>Callosciurus notatus</i>	D	1	9.9		7.5		0.75
<i>Glaucomys volans</i>	N	1	8.6		7.8		0.91
<i>Marmota monax</i>	D	1	12.3		7.5		0.61
<i>Myosciurus pumilio</i>	D	1	5.2		4.2		0.81
<i>Sciurus carolinensis</i>	D	1	12.6		9.1		0.73
<i>Sciurus niger</i>	D	1	13.3		9.7		0.73
<i>Tamias striatus</i>	D	6	8.0	0.3	5.9	0.4	0.73
<i>Tamiasciurus</i> sp.	D	3	9.7	0.5	7.1	0.4	0.73

Measurements for primates were obtained as described in text. Measurements for nonprimates were taken from Ritland (1982). Activity patterns follow Nowak (1991) and Garbutt (1999) for nonprimates and Kay and Kirk (2000) for primates. AP, activity pattern; TD, mean transverse eye diameter in mm; SD, standard deviation; CD, mean transverse corneal diameter in mm; C:E, ratio of mean corneal diameter and mean transverse eye diameter; D, diurnal; C, cathemeral; N, nocturnal.

relative to the maximum value that could theoretically be achieved (transverse eye diameter) without increasing eye size. According to both comparative and functional expectations, nocturnal primates should exhibit relatively high C:E ratios and diurnal primates should exhibit relatively low C:E ratios (Detwiler, 1939, 1940, 1941; Walls, 1942; Prince, 1956; Duke-Elder, 1958; Tansley, 1965). However, the C:E ratio is not a measure of absolute light-gathering ability, which is determined by the absolute sizes of the cornea and pupil. It should also be noted that although transverse eye diameter is not a good estimator of posterior nodal distance or focal length per se, transverse and axial eye diameters are highly positively correlated in primates (Spearman rho = 0.98; $P < 0.0001$) (Kirk, 2003). As a result, the C:E ratio should provide comparative results very similar to other quantifications of eye shape that rely on axial length to estimate posterior nodal distance or focal length [e.g., Ross (2000)].

All data analyses were carried out using JMP version 5.0.1.2 (SAS Institute) on species means (Table 1). How-

ever, some specimens were identifiable only to genus (e.g., *Cebus*, *Saimiri*, *Alouatta*, *Ateles*, *Hylobates*, and *Papio*) and were accordingly included as generic means. Data for carnivorans (40 species), scandentians (5 species), and sciurids (8 species) were taken from Ritland (1982), whose data collection methods and measurement protocols are nearly identical to those described above. Carnivorans, scandentians, and sciurids were selected for the comparative sample because each group includes both diurnal and nocturnal species. Pairwise comparisons of C:E ratio (including statistical significance levels) in different taxa grouped by clade and activity pattern are presented in Tables 2 and 3. Because C:E ratios of included taxa are not normally distributed (Shapiro-Wilk test; $W = 0.9085$; $P < 0.001$), Wilcoxon rank-sum tests were used to compare groups rather than parametric tests of greater statistical power. As a result, statistical comparisons of some groups (e.g., nocturnal haplorhines, nocturnal scandentians, and nocturnal sciurids) are limited by small sample sizes. Because there is a strong functional expectation that noctur-

TABLE 2. Summary statistics and Wilcoxon rank-sum tests comparing C:E ratios of primates grouped by suborder and activity pattern

	Diurnal haplorhines	Nocturnal haplorhines	Diurnal strepsirrhines	Cathemeral strepsirrhines	Nocturnal strepsirrhines
Number	30	2	6	5	12
Mean C:E ratio	0.51	0.74	0.73	0.75	0.83
Standard deviation	0.03	0.06	0.02	0.03	0.04
Diurnal haplorhines		$P = 0.01$	$P < 0.001$	$P < 0.001$	$P < 0.001$
Nocturnal haplorhines			NS	NS	NS
Diurnal strepsirrhines				$P < 0.05$	$P < 0.001$
Cathemeral strepsirrhines					$P = 0.001$

TABLE 3. Summary statistics for nonprimates and Wilcoxon rank-sum tests comparing C:E ratios of primate and nonprimate groups

	Diurnal scandentians	Diurnal sciurids	Diurnal carnivorans	Cathemeral carnivorans	Nocturnal scandentian	Nocturnal sciurid	Nocturnal carnivorans
Number	4	7	6	21	1	1	13
Mean C:E ratio	0.79	0.73	0.67	0.75	0.93	0.91	0.82
Standard deviation	0.04	0.06	0.15	0.08			0.07
Diurnal haplorhines	$P < 0.01$	$P < 0.001$	$P < 0.01$	$P < 0.001$	$P = 0.05$	$P = 0.05$	$P < 0.001$
Nocturnal haplorhines	NS	NS	NS	NS	NS	NS	NS
Diurnal strepsirrhines	$P < 0.05$	NS	NS	NS	NS	NS	$P < 0.01$
Cathemeral strepsirrhines	NS	NS	NS	NS	NS	NS	$P < 0.05$
Nocturnal strepsirrhines	$P < 0.05$	$P < 0.001$	$P = 0.01$	$P < 0.01$	NS	NS	NS

nal species will have larger C:E ratios than diurnal species, statistical comparisons of groups with different activity patterns are one-tailed. Comparisons of groups with the same activity pattern are two-tailed. Statistical tests were considered significant at $P < 0.05$.

RESULTS

Comparisons Within Primates

C:E ratios differ substantially between primates of different suborders and activity patterns (Fig. 2, Table 2). Within haplorhines, diurnal anthropoids have significantly lower C:E ratios than the only two nocturnal haplorhine genera: *Tarsius* (tarsiers) and *Aotus* (owl monkeys). Similarly, diurnal strepsirrhines have significantly lower C:E ratios than nocturnal strepsirrhines. Cathemeral strepsirrhines have C:E ratios that are significantly larger than those of diurnal strepsirrhines and significantly smaller than those of nocturnal strepsirrhines. Within suborders, diurnal primates thus conform to functional expectations in having smaller relative cornea sizes than cathemeral or nocturnal close relatives. Cathemeral strepsirrhines also conform to functional expectations in exhibiting a range of relative cornea sizes that is intermediate between that of diurnal and nocturnal strepsirrhines (Fig. 2).

Across primates, however, diurnal strepsirrhines and diurnal haplorhines also demonstrate significant differences in C:E ratio. In fact, the mean value for diurnal strepsirrhines (0.73) is closer to the mean value for nocturnal haplorhines (0.74) than that of diurnal haplorhines (0.51). A bivariate plot of corneal diameter and transverse eye diameter (Fig. 3) reveals that although strepsirrhines and haplorhines span a similar range of eye sizes, all diurnal haplorhines have smaller cornea sizes than strepsirrhines or nocturnal haplorhines of comparable eye size. Thus, while diurnal haplorhines have corneas that are on

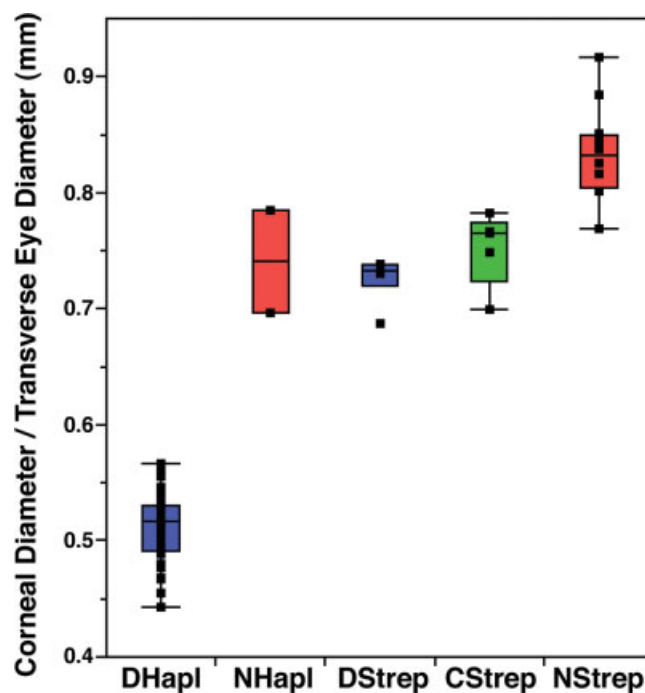


Fig. 2. Quantile box plots of C:E ratio in primates. All data points represent species means (Table 1). DHapl, diurnal haplorhines; NHapl, nocturnal haplorhines; DStrep, diurnal strepsirrhines; CStrep, cathemeral strepsirrhines; NStrep, nocturnal strepsirrhines.

average 1/2 of the total transverse diameter of the eye, corneas of diurnal and nocturnal strepsirrhines are approximately 3/4 and 4/5 of the eye's transverse diameter, respectively.

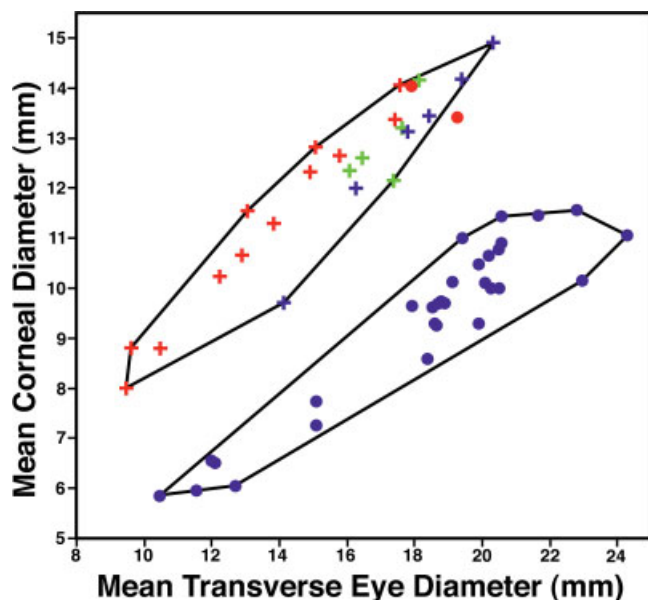


Fig. 3. Bivariate plot of transverse eye diameter and corneal diameter in primates. All data points represent species means (Table 1). Minimum-area convex polygons have been fitted around all strepsirrhines (top polygon) and diurnal haplorhines (= diurnal anthropoids; bottom polygon). Crosses, strepsirrhines; circles, haplorhines; blue, diurnal; green, cathemeral; red, nocturnal.

Comparisons of Haplorhines and Nonprimate Mammals

Comparisons of C:E ratios in haplorhines with Ritland's (1982) data for scandentians, sciurids, and carnivores are shown in Figure 4 and Table 3. These data indicate that, like diurnal strepsirrhines, diurnal scandentians and diurnal sciurids (mean ratios = 0.79 and 0.73) both have significantly larger C:E ratios than diurnal haplorhines (mean ratio = 0.51). Furthermore, the nocturnal haplorhines *Tarsius* and *Aotus* (mean ratio = 0.74) have C:E ratios that are considerably lower than those of the nocturnal scandentian *Ptilocercus* (0.93) or the nocturnal sciurid *Glaucomys* (0.91).

When haplorhines are compared to carnivores (Fig. 4, Table 3), diurnal carnivores (mean ratio = 0.67) also have significantly larger C:E ratios than diurnal haplorhines. However, unlike diurnal strepsirrhines, scandentians, or sciurids, the range of C:E ratios exhibited by diurnal carnivores partly overlaps the range of diurnal haplorhines. Among all of the nonprimate species considered in this analysis, only the diurnal carnivores *Suricata suricatta* (meerkat) and *Speothos venaticus* (bush dog) have C:E ratios (0.47 and 0.56, respectively) that fall within the diurnal haplorhine range. Furthermore, the mean C:E ratio of nocturnal haplorhines (0.74) is intermediate between the mean C:E ratios of diurnal (0.67) and nocturnal (0.82) carnivores and is nearly identical to the mean value for cathemeral carnivores (0.75).

These data thus indicate that diurnal haplorhines have corneas that are significantly smaller relative to eye size than the corneas of diurnal strepsirrhines and diurnal nonprimate mammals. Similarly, nocturnal haplorhines have relatively smaller corneas than most nocturnal members of other groups.

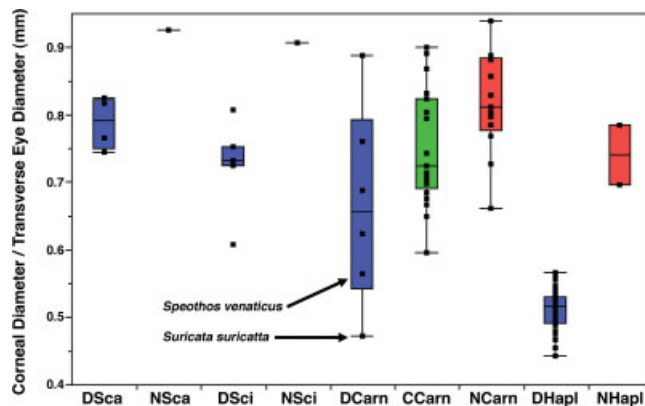


Fig. 4. Quantile box plots of C:E ratio in haplorhines and nonprimate mammals. All data points represent species means (Table 1). DSca, diurnal scandentians; NSca, nocturnal scandentian; DSci, diurnal sciurids; NSci, nocturnal sciurid; DCarn, diurnal carnivores; CCarn, cathemeral carnivores; NCarn, nocturnal carnivores; DHapl, diurnal haplorhines; NHapl, nocturnal haplorhines.

Comparisons of Strepsirrhines and Nonprimate Mammals

Unlike diurnal haplorhines, diurnal strepsirrhines (mean ratio = 0.73) have C:E ratios that are not significantly different from those of diurnal sciurids (mean ratio = 0.73) or diurnal carnivores (mean ratio = 0.67; Fig. 5, Table 3). Although diurnal strepsirrhines do have significantly smaller C:E ratios than diurnal scandentians, the mean C:E ratio for diurnal scandentians (0.79) is much closer to the mean value for diurnal strepsirrhines than diurnal haplorhines. Similarly, the C:E ratios of nocturnal strepsirrhines (mean ratio = 0.83) are not significantly different from those of nocturnal carnivores (mean ratio = 0.82), and the C:E ratios of the nocturnal scandentian *Ptilocercus* (0.93) and the nocturnal sciurid *Glaucomys* (0.91) are closer to the mean value for nocturnal strepsirrhines than nocturnal haplorhines. Cathemeral strepsirrhines likewise have C:E ratios that are not significantly different from those of cathemeral carnivores, and the mean C:E ratios of both groups are identical (0.75). These data indicate that, in strong contrast to haplorhines, strepsirrhines have relative cornea sizes that are similar to carnivores, scandentians, and sciurids of comparable activity pattern.

DISCUSSION

The data provided in this analysis demonstrate that within each primate suborder, eye morphology varies predictably with activity pattern. Within strepsirrhines, relative cornea size is largest in nocturnal species, intermediate in cathemeral species, and smallest in diurnal species. Although the ranges of C:E ratios for diurnal and nocturnal strepsirrhines do not overlap, the ranges of both groups are overlapped by species of the cathemeral genus *Eulemur*. Similar results are obtained for haplorhines, in which diurnal taxa (all of which are anthropoids) have much smaller relative cornea sizes than the nocturnal genera *Tarsius* and *Aotus*. Variation in eye morphology within haplorhines and strepsirrhines thus conforms to the functional expectation that relative cornea size (*ceteris*

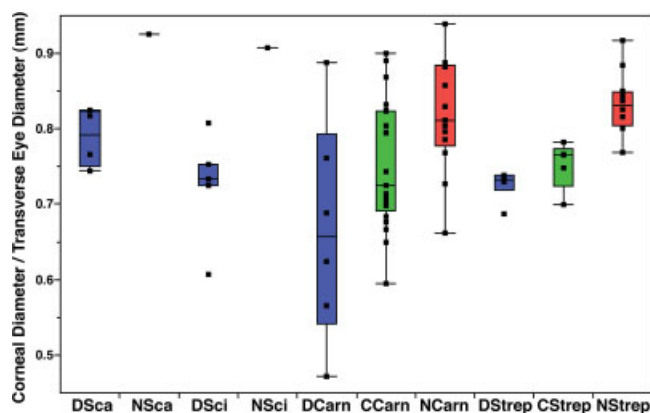


Fig. 5. Quantile box plots of C:E ratio in strepsirrhines and nonprimate mammals. All data points represent species means (Table 1). DSca, diurnal scandentians; NSca, nocturnal scandentian; DSci, diurnal sciurids; NSci, nocturnal sciurid; DCarn, diurnal carnivorans; CCarn, cathemeral carnivorans; NCarn, nocturnal carnivorans; DSrep, diurnal strepsirrhines; CSrep, cathemeral strepsirrhines; NSrep, nocturnal strepsirrhines.

paribus) should be larger in species that engage in more nocturnal activity and smaller in species that engage in more diurnal activity (Walls, 1942; Prince, 1956; Duke-Elder, 1958; Tansley, 1965; Hughes, 1977). These results support the conclusion that primates have evolved distinct eye morphologies that maximize either visual acuity or visual sensitivity according to the functional demands of their activity pattern.

This analysis also indicates, however, that haplorhines and strepsirrhines have substantially different eye morphologies. As a group, diurnal strepsirrhines have much larger relative cornea sizes (C:E range = 0.69–0.74) than diurnal haplorhines (C:E range = 0.44–0.57). Furthermore, nocturnal haplorhines have relative cornea sizes that are smaller than those of most nocturnal strepsirrhines. These results suggest that the two primate suborders have been subjected to divergent selective pressures with respect to their visual ecology.

The significant differences in relative cornea size between haplorhines and strepsirrhines beg the question of whether other mammalian groups have eye morphologies similar to those of either primate suborder. An analysis of Ritland's (1982) data for carnivorans, scandentians, and sciurids shows that diurnal members of these three clades have relative cornea sizes (mean diurnal C:E ratio: carnivorans = 0.67; scandentians = 0.79; sciurids = 0.73) that are much larger than those of diurnal haplorhines (0.51), but not substantially different from those of diurnal strepsirrhines (0.73). Accordingly, while corneal diameter appears to range between about 2/3 and 4/5 of the transverse diameter of the eye in most diurnal mammals (including strepsirrhines), the average corneal diameter of diurnal haplorhines is only about 1/2 of the transverse diameter of the eye.

Although diurnal haplorhines are not unique in having relatively small corneas, comparable eye morphologies do not appear to be common among mammals. Of the 53 nonprimate species included in this analysis, only 2 diurnal carnivorans (*Suricata suricatta* and *Speothos venaticus*) have relative cornea sizes similar to those of diurnal

haplorhines. Furthermore, most nocturnal species (e.g., *Glaucomys*, *Ptilocercus*, all nocturnal strepsirrhines, and all nocturnal carnivorans except *Melursus ursinus*) have larger relative cornea sizes than *Aotus*. By comparison, the C:E ratio of *Tarsius* (0.79) is higher than that of *Aotus* (0.70) and falls within the ranges of both nocturnal strepsirrhines and nocturnal carnivorans. These data suggest that the low mean C:E ratio of nocturnal haplorhines relative to other nocturnal groups may be primarily attributed to the fact that owl monkeys exhibit unusually small corneas for their eye size (although absolute cornea size remains exceptionally large). Tarsiers, by contrast, demonstrate eye morphologies that are more typical of other nocturnal mammals.

Implications for Anthropoid Origins

These combined data sets suggest that anthropoids are highly derived in terms of their eye morphology. Compared to most diurnal mammals, diurnal anthropoids have eyes in which the cornea occupies a much smaller proportion of the anterior face of the globe. Similarly, owl monkeys have relatively smaller corneas than all but one of the other nocturnal species included in this analysis. By contrast, strepsirrhines have relative cornea sizes that are broadly similar to those of nonprimate mammals of comparable activity pattern. Due to the functional consequences of a reduction in cornea size relative to eye size (i.e., enlargement and reduced brightness of the retinal image), the unusual eye morphology of diurnal anthropoids relative to other mammals probably represents an adaptation for increasing visual acuity under photopic conditions. This conclusion is consistent with the fact that diurnal anthropoids exhibit a number of other adaptations for extremely high visual acuity, including an all-cone retinal fovea and macula lutea (Kirk and Kay, 2004). Furthermore, behavioral and anatomical tests of visual acuity demonstrate that diurnal anthropoids have the highest acuities known for mammals (Kirk and Kay, 2004). In the case of owl monkeys, unusually small relative cornea size may provide further evidence of recent diurnal ancestry and/or adaptation for relatively acute nocturnal vision (Cartmill, 1980; Martin, 1990; Kay and Kirk, 2000; Ross, 2000).

The uniqueness of anthropoids in terms of their eye morphology, retinal anatomy, and concomitant high visual acuity provides strong *prima facie* support for the conclusion that anthropoids have been subject to selective pressures that have had a lesser or minimal effect on other mammalian groups. While it is clear that the anthropoid visual system evolved in the context of selection for very high acuity, the ecological factors associated with such a selective regime are poorly understood. Ross (1996, 2000) has suggested that high visual acuity in anthropoids originally evolved as an adaptation for visually mediated insect predation in the small diurnal ancestors of either crown anthropoids or haplorhines. According to this scenario, strepsirrhines did not evolve similar adaptations for high acuity because the ancestors of diurnal indriids and lemurids independently evolved diurnality at larger body sizes than stem anthropoids. The earliest diurnal lemurs would thus have been frugivorous or folivorous and would not require high acuity to meet the demands of visual predation under photopic conditions.

Some comparative support for Ross' hypothesized link between high acuity and diurnal visual predation is pro-

vided by the fact that the only vertebrates known to possess visual acuities comparable to or higher than diurnal anthropoids are diurnal raptors (Ross, 2000; Kirk and Kay, 2004). Furthermore, high acuity might have been maintained in later-occurring anthropoids that were frugivorous or folivorous through an expansion of the adaptive role played by vision in anthropoids. Although diurnal anthropoids and diurnal lemurs accomplish many similar visually dependent tasks (e.g., leaping between arboreal supports) despite their differences in visual acuity, high acuity in living anthropoids could be important in other contexts (e.g., social communication) in which strepsirrhines may exhibit a greater reliance on nonvisual sensory modalities (Epple and Moulton, 1978; Schilling, 1979).

Implications for Evolutionary Disequilibrium Hypothesis

The comparative data presented in this analysis demonstrate that diurnal strepsirrhines have relative cornea sizes that are significantly smaller than either cathemeral or nocturnal strepsirrhines. This result is clearly at odds with the conclusion that the visual systems of diurnal lemurs have diverged little from a nocturnal or cathemeral ancestral condition (van Schaik and Kappeler, 1996). Instead, the data presented here indicate that at least two clades of diurnal lemurs (indriids and lemurids) have evolved derived eye morphologies associated with increased visual acuity. Moreover, the finding that diurnal strepsirrhines exhibit eye morphologies that are very similar to those of diurnal nonprimate mammals is inconsistent with the hypothesis that the visual systems of diurnal strepsirrhines are poorly adapted for function under photopic conditions. Indeed, strepsirrhines of different activity patterns exhibit variation in eye morphology comparable to that seen in scandentians, sciurids, and carnivorans, and this variation is consistent with functional expectations of an inverse relationship between relative cornea size and degree of diurnal activity. These results further underscore the conclusion that it is diurnal anthropoids, rather than diurnal strepsirrhines, that demonstrate unusual visual adaptations relative to other mammals (Kay and Kirk, 2000; Heesy and Ross, 2001; Kirk and Kay, 2004).

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