



# Effects of activity pattern on eye size and orbital aperture size in primates

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## Abstract

Among primates, nocturnal species exhibit relatively larger orbital apertures than diurnal species. Most researchers have considered this disparity in orbital aperture size to reflect differences in eye size, with nocturnal primates having relatively large eyes in order to maximize visual sensitivity. Presumed changes in eye size due to shifts in activity pattern are an integral part of theoretical explanations for many derived features of anthropoids, including highly convergent orbits and a postorbital septum. Here I show that despite clear differences in relative orbital aperture size, many diurnal and nocturnal primates do not differ in relative eye size. Among nocturnal primates, relative eye size is influenced by diet. Nocturnal visual predators (e.g., *Tarsius*, *Loris*, and *Galago moholi*) tend to have larger relative eye sizes than diurnal primates. By contrast, nocturnal frugivores (e.g., *Perodicticus*, *Nycticebus*, and *Cheirogaleus*) have relative eye sizes that are comparable to those of diurnal primates. Although some variation in orbital aperture size can be attributed to variation in eye size, both cornea size and orbit orientation also exert a strong influence on orbital aperture size. These findings argue for caution in the use of relative orbital aperture size as an indicator of activity pattern in fossil primates. These findings further suggest that existing scenarios for the evolution of unique orbital morphologies in anthropoids must be modified to reflect the importance of ecological variables other than activity pattern.

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## Introduction

### *Orbit size and eye size*

Comparative studies of relative orbit size have provided one of the most valuable tools for reconstructing the paleoecology of fossil primates. Beginning with Walker's (1967) analysis of orbit size in subfossil lemurs, quantitative studies of the relative size of the orbital aperture<sup>1</sup> in primates have consistently demonstrated that nocturnal primates have larger

orbital apertures than diurnal primates of similar cranial size (Kay and Cartmill, 1977; Martin, 1990; Kay and Kirk, 2000; Heesy and Ross, 2001). The results of these analyses have typically been presented as bivariate plots of orbital aperture diameter and an anatomical proxy for cranial size (e.g., skull length). As initially noted by Kay and Cartmill (1977), the bivariate distributions of diurnal and nocturnal primate species in such plots generally show no overlap at small cranial sizes, but demonstrate progressively greater overlap as cranial size increases. More recently, it has been shown that cathemeral primates have relative orbital aperture sizes that overlap the distributions of both diurnal and nocturnal primates (Kay and Kirk, 2000).

Because relative orbital aperture size can be used to discriminate between most extant diurnal and nocturnal primate species, quantification of this variable in fossil crania has provided a basis for inferring the activity patterns of extinct primates (Walker, 1967; Kay and Cartmill, 1977; Simons,

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<sup>1</sup> Most previous analyses (e.g., Kay and Cartmill, 1977; Martin, 1990; Kay and Kirk, 2000; Heesy and Ross, 2001) have measured orbit size as the diameter of the external bony margin of the orbit. In this analysis, the term "orbital aperture" will be used in conjunction with linear measurements of orbital margin diameter in order to distinguish these dimensions from orbital volume (cf. Schultz, 1940) or internal linear dimensions of the orbit (e.g., orbit depth).

1990, 1997, 2001; Beard et al., 1991; Rasmussen and Simons, 1992; Simons and Rasmussen, 1994; Kay and Kirk, 2000; Heesy and Ross, 2001; Ni et al., 2004). Judgments regarding the probable activity patterns of extinct primates are most frequently based on the position of a fossil species relative to extant primates in a bivariate plot of orbital aperture diameter and cranial size. Generally speaking, if a fossil species plots exclusively within the bivariate distribution for either extant diurnal or nocturnal primates, the extinct species is judged to have been diurnal or nocturnal accordingly. Similarly, if a fossil species plots within the region of overlap between the extant diurnal and nocturnal primate distributions, its activity pattern is regarded as equivocal (Kay and Kirk, 2000). Some attempts have been made to infer the activity patterns of fossil taxa that fall outside the bivariate distributions of extant species (e.g., Ni et al., 2004), but the interpretive value of such extrapolation is controversial (Walker, 1967; Martin, 2004).

Although the use of relative orbital aperture size to reconstruct the activity patterns of fossil primates is now common practice, the functional implications of variation in orbital aperture size are poorly understood. The most widely accepted explanation for the observation that nocturnal primates have larger orbital apertures than diurnal primates is that the orbits of nocturnal species must be relatively large in order to accommodate larger eyes (Ross, 1995, 1996, 2000; Heesy and Ross, 2001). Indeed, larger eyes are capable of supporting higher visual sensitivity provided that they have relatively large corneas and lenses (Walls, 1942; Kirk, 2004, 2006). Nonetheless, while it may be functionally and intuitively appealing to infer that nocturnal primates have relatively larger eyes than diurnal primates, this assumption has never been tested. Several authors have provided comparative data on absolute eye dimensions in primates (e.g., Rohen, 1962; Rohen and Castenholz, 1967; Ritland, 1982; Stephan et al., 1984; Kirk, 2004), but none have specifically addressed the effect of activity pattern on eye size. Furthermore, the relationship between eye size and orbit size is poorly understood due to a dearth of published comparative data on the subject. To date, Schultz's (1940) study of eye and orbit volume in a sample of 28 species (including 6 strepsirrhines and 22 anthropoids) provides the only direct analysis of the relationship between eye size and orbit size in primates. Although Schultz did not consider the effect of activity pattern on either eye size or orbit size, his measurements indicate that variation in eye volume accounts for only about 83% of the variation in orbit volume (Schultz, 1940; Kay and Kirk, 2000). Schultz's data also reveal that while both eye volume and orbit volume are negatively allometric with respect to body mass, eye volume demonstrates greater negative allometry than orbit volume (Schultz, 1940; Kay and Kirk, 2000). Therefore, as body mass increases, orbit volume increases more rapidly than eye volume. The eyes of large primates accordingly occupy a smaller proportion of the total orbital volume than the eyes of small primates (Schultz, 1940). These findings caution that absolute orbit size may be quite different from absolute eye size, particularly at large body sizes.

### *Activity pattern and anthropoid origins*

Despite uncertainty regarding the effect of activity pattern on eye size, concomitant changes in eye size and activity pattern have been proposed to play a major role in the evolution of the unique orbital features of anthropoids. According to Cartmill (1970, 1972), mammals with moderately frontated and approximated orbits should exhibit an inverse relationship between orbital convergence and relative eye size.<sup>2</sup> This hypothesis suggests that as eye diameter increases, orbital aperture size must also increase. Such increases in orbital aperture size are hypothesized to result in displacement of the lateral orbital margin postero-laterally along the zygomatic arch, thus decreasing the angle of orbital convergence (Cartmill, 1972). This proposed relationship between orbital convergence and relative eye size has been integrated by Ross (1995, 1996) into a comprehensive scenario for anthropoid and haplorhine origins. According to Ross, haplorhines were primitively small (i.e., <1 kg) and nocturnal. When stem haplorhines became diurnal, eye size and orbital aperture size decreased in tandem. These decreases in eye and orbit size subsequently led to increased orbital convergence according to Cartmill's model (Cartmill, 1970, 1972). The combined effect of increased orbital convergence and increased frontation due to forebrain expansion caused the anterior temporalis to impinge upon the orbital contents, necessitating the evolution of a postorbital septum to prevent mechanical perturbation of the eye during mastication (cf. Cartmill, 1980).

According to Ross (1995, 1996), therefore, a decrease in eye size associated with a transition to a diurnal activity pattern played a key role in producing a distinctive suite of orbital features characteristic of anthropoids (e.g., high orbital convergence and a complete postorbital septum). Although Ross (1995, 1996) confirmed an inverse relationship between orbital aperture size and orbital convergence, his evolutionary scenario for anthropoid origins is only tenable if decreases in eye size would be expected to occur following a transition to diurnality. This expectation would be supported if nocturnal primates generally have larger relative eye sizes than diurnal primates. As noted previously, however, the relationship between eye size and activity pattern in primates has never been directly addressed.

### *Goals of the current analysis*

This analysis provides a quantitative examination of the relationship between activity pattern, eye size, and orbital aperture size in a broad comparative sample of extant primates. The primary goal of this analysis is to determine whether primates demonstrate activity-pattern-dependent variation in eye

<sup>2</sup> Cartmill originally proposed this hypothesis to explain changes in orbital convergence associated with allometric changes in eye size. However, its basic premise should apply to all changes in relative eye size (whether the result of the differential allometry between the eye and the orbit or direct selection on eye size) as well as changes in absolute eye size among smaller-bodied species.

size that mirrors known differences in orbital aperture size. Additionally, this analysis seeks to determine the degree of correspondence between orbital aperture size and eye size. Both goals are critical for understanding the functional implications of relative orbit size as a tool for inferring the activity patterns of fossil primates. This analysis also helps to assess the viability of adaptive scenarios that posit a functional link between changes in activity pattern, eye size, and orbital morphology during anthropoid origins (Ross, 1995, 1996).

## Methods

Eyes were collected from adult cadavers ( $n = 147$ ) representing 55 primate species (Table 1). Specimens were derived from the following sources: (1) the Duke University Primate Center (DUPC); (2) the comparative teaching collections of Duke University, SUNY Stony Brook, and the University of Chicago; (3) the Neurobiology Laboratories of Columbia University; and (4) 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 post mortem without fixative. Dissections and measurements of these specimens were performed after they had been allowed to thaw in a fume hood for 1–3 hours. However, several DUPC specimens were measured after 1–3 days in 10% formalin. Specimens derived from all other sources were preserved for varying lengths of time (i.e., from several weeks to more than 10 years) in formalin (usually 10%), ethanol, or dissection wetting solutions. Comparison of fixed and unfixed representatives of the same species did not reveal any systematic differences attributable to differential shrinkage of tissues from long-term fixation.

Cadavers were enucleated using standard dissection tools. Tissues surrounding the orbital rim were completely removed in order to provide an unobstructed view of the orbit. Incisions were also made over the zygomatic arches and the occipital region of the cranium. The upper lip and the skin surrounding each incision were then retracted to expose prosthion, inion, and the zygomatic arches. Measurements subsequently taken from each cranium using digital calipers include cranial length (prosthion to inion), cranial width (zygion to zygion), and orbital aperture diameter (diameter of the orbital aperture in a parasagittal plane). “Orbital aperture” is here defined as the externally visible margin of the bony orbit. In all primates, the orbital aperture constitutes a roughly circular bony rim with variable contributions from the maxilla, frontal, lacrimal, and zygomatic bones. Cranial size was calculated as the geometric mean of cranial length and width.

Once removed from the orbit, eyes were cleaned of periorbital connective tissue using fine-tipped dissecting scissors and visually inspected for damage, pathologies, and preservational defects. Any specimens showing evidence of pathology or excess post-mortem deformation were excluded from this analysis. 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 post mortem, 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 (1) the eye returned to a globose shape, (2) all creases and wrinkles on the external surface of the eye were smoothed out, and (3) the eye resisted further attempts at inflation.<sup>3</sup> With the needle still inserted and the eye maintained at full internal pressure, the following measurements were taken using digital calipers to the nearest 0.1 mm: (1) axial eye diameter, (2) maximum transverse (equatorial) eye diameter, and (3) minimum transverse (equatorial) eye diameter.

Analysis of data was carried out using JMP version 3.1.5 (SAS Institute) on species means (Table 1). However, some specimens were identifiable only to genus (e.g., *Cebus*, *Saimiri*, *Alouatta*, *Ateles*, *Hylobates*, and *Papio*), and were accordingly included as generic means. Transverse eye diameter was calculated as the mean of the maximum and minimum measured values. Relative orbital aperture size was assessed using a bivariate plot of orbital aperture diameter and cranial size. Similarly, relative eye size was assessed using a bivariate plot of transverse eye diameter and cranial size. In both plots, maximum-area convex polygons were fit around groups of species with the same activity pattern. These methods are comparable to those of previous analyses that examined relative orbital aperture size only (Kay and Cartmill, 1977; Martin, 1990; Kay and Kirk, 2000; Heesy and Ross, 2001). The relationship between transverse eye diameter and orbital aperture diameter was assessed using non-parametric (Spearman rank) correlation and LS regression of log10 transformed data, as well as bivariate comparison in raw space.

## Results

### *Orbital aperture size and activity pattern*

The data presented in this analysis confirm that the relative size of the orbital aperture may be used to discriminate between extant primates with diurnal and nocturnal activity patterns. Figure 1A is a bivariate plot of orbital aperture diameter and cranial size in which convex polygons have been fit around mean values for (1) nocturnal strepsirrhines and (2) all diurnal primates. Although the sample size is relatively small because it includes only the specimens for which eye data were also collected, Figure 1A recapitulates the well-established findings of previous analyses of the relationship

<sup>3</sup> The sclera and cornea are relatively inelastic, and 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  
Primate eye and cranial metrics

Species	<i>n</i>	AP	CL	CW	CS	OAD	TD	AD
<i>Alouatta</i> sp.	3	D	111.2	69.6	88.0	22.8	18.6	17.2
<i>Aotus</i> sp.	2	N	63.6	39.2	49.9	20.0	19.3	20.0
<i>Ateles</i> sp.	6	D	106.1	64.9	83.0	22.0	20.1	19.2
<i>Cacajao rubicundus</i>	1	D	95.8	61.8	76.9	22.7	19.9	19.2
<i>Callithrix jacchus</i>	5	D	47.4	29.8	37.6	9.9	11.6	11.3
<i>Cebus</i> sp.	1	D	64.1	40.6	51.0	13.9	15.1	14.1
<i>Cercopithecus albogularis</i>	1	D	97.0	63.5	78.5	21.1	18.9	19.0
<i>Cercopithecus ascanius</i>	2	D	88.5	58.5	71.9	20.1	18.8	18.5
<i>Cercopithecus diana</i>	1	D	100.0	59.9	77.4	22.2	20.2	19.5
<i>Cercopithecus neglectus</i>	1	D	107.7	69.8	86.7	24.0	20.6	20.7
<i>Cheirogaleus major</i>	1	N	51.4	33.6	41.6	14.3	12.9	12.2
<i>Cheirogaleus medius</i>	3	N	43.4	29.9	36.0	12.9	10.5	10.3
<i>Colobus polykomos</i>	3	D	105.8	76.0	89.6	22.3	19.1	18.2
<i>Daubentonia madagascariensis</i>	1	N	86.8	58.6	71.3	21.7	17.6	17.7
<i>Erythrocebus patas</i>	2	D	125.7	74.9	97.0	23.5	24.3	24.9
<i>Eulemur coronatus</i>	2	C	82.8	46.8	62.2	18.4	16.1	16.1
<i>Eulemur fulvus</i>	6	C	92.4	54.2	70.8	19.7	17.6	16.7
<i>Eulemur macaco</i>	4	C	93.0	53.4	70.4	19.9	17.4	15.3
<i>Eulemur mongoz</i>	3	C	83.0	48.8	63.6	19.3	16.4	15.9
<i>Eulemur rubriventer</i>	1	C	86.1	54.0	68.2	20.4	18.1	18.2
<i>Galago moholi</i>	8	N	40.1	27.6	33.3	15.0	13.8	13.4
<i>Galagoides demidoff</i>	1	N	36.0	22.8	28.6	11.6	9.6	10.1
<i>Hapalemur griseus</i>	2	D	68.1	46.5	56.2	15.4	14.1	13.8
<i>Hylobates</i> sp.	4	D	111.2	70.4	88.5	22.6	19.9	19.4
<i>Lagothrix lagotricha</i>	2	D	111.2	72.9	90.0	22.9	20.5	20.0
<i>Lemur catta</i>	3	D	87.5	52.6	67.8	17.8	16.2	15.6
<i>Leontopithecus rosalia</i>	1	D	59.5	39.8	48.7	11.3	12.0	11.2
<i>Loris tardigradus</i>	2	N	47.1	29.1	37.0	16.9	15.1	15.5
<i>Macaca fascicularis</i>	3	D	109.7	84.4	96.1	22.4	18.5	18.4
<i>Macaca mulatta</i>	3	D	115.4	86.7	100.0	22.7	20.5	20.0
<i>Macaca nemestrina</i>	2	D	127.1	78.7	100.0	24.7	20.6	20.0
<i>Macaca radiata</i>	3	D		79.0		23.9	18.6	18.6
<i>Macaca</i> sp.	1	D	104.1	70.5	85.7	19.6	17.9	18.0
<i>Mandrillus leucophaeus</i>	1	D	210.0	128.1	164.0	26.4	21.7	21.6
<i>Microcebus murinus</i>	7	N	33.2	21.9	27.0	10.4	9.4	9.2
<i>Mirza coquereli</i>	6	N	51.1	30.9	39.7	15.0	13.0	13.0
<i>Nycticebus coucang</i>	4	N	62.7	45.5	53.4	19.7	15.8	16.2
<i>Nycticebus pygmaeus</i>	1	N	52.3	35.8	43.3	17.1	14.9	15.5
<i>Otolemur crassicaudatus</i>	2	N	76.7	49.0	61.3	20.1	17.4	16.3
<i>Pan troglodytes</i>	1	D	207.0	126.4	161.8	30.8	23.0	21.8
<i>Papio</i> sp.	3	D	193.1	112.8	146.0	26.1	20.3	19.5
<i>Perodicticus potto</i>	2	N	62.8	44.8	53.0	15.8	12.2	12.1
<i>Pongo pygmaeus</i>	1	D	213.3	141.8	173.9	36.1	22.8	22.6
<i>Procolobus badius</i>	1	D	92.2	59.2	73.9	18.6	18.7	18.4
<i>Propithecus diadema</i>	1	D	97.3	64.9	79.5	22.3	20.3	20.2
<i>Propithecus tattersalli</i>	3	D	84.9	54.5	68.0	20.8	18.4	18.2
<i>Propithecus verreauxi</i>	6	D	83.9	56.3	68.7	19.5	17.8	17.7
<i>Saguinus fuscicollis</i>	3	D	45.6	27.1	35.1	9.8	10.5	10.3
<i>Saguinus midas</i>	1	D	52.8	36.8	44.1	10.4	12.7	12.2
<i>Saguinus</i> sp.	1	D	51.3	35.5	42.7	10.3	12.1	11.6
<i>Saimiri</i> sp.	10	D	63.4	39.2	49.9	14.6	15.1	15.0
<i>Tarsius syrichta</i>	2	N	39.8	29.7	34.4	18.6	17.9	17.3
<i>Theropithecus gelada</i>	1	D	156.9	104.0	127.7	24.8	18.4	19.6
<i>Trachypithecus cristatus</i>	1	D	95.3	69.6	81.4	22.6	19.4	18.6
<i>Varecia variegata</i>	5	D	106.2	60.1	79.9	22.2	19.4	18.5

All measurements (defined in text) are in mm. Abbreviations: *n* = number of individuals measured, AP = activity pattern, D = diurnal, C = cathemeral, N = nocturnal, CL = cranial length, CW = cranial width, CS = cranial size, OAD = orbital aperture diameter, TD = mean transverse eye diameter, AD = axial eye diameter.

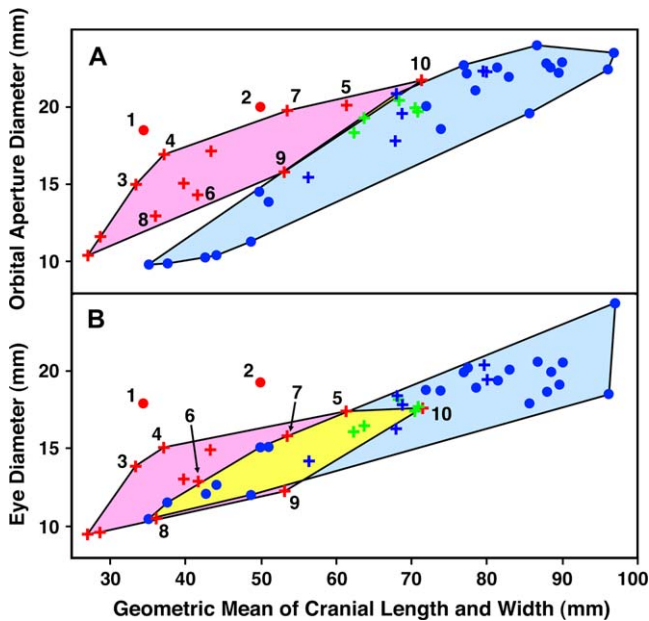


Fig. 1. Bivariate plots of orbital aperture diameter (A) and eye diameter (B) versus the geometric mean of cranial length and width. All measurements are in mm. Markers represent species means. Convex polygons have been fit around species means of nocturnal strepsirrhines (pink polygon) and all diurnal species (blue polygon) to aid visualization of different groups. Regions of overlap between the two polygons are shown in yellow. Representative nocturnal taxa are identified by numbers, including: *Tarsius syrichta* (1), *Aotus* sp. (2), *Galago moholi* (3), *Loris tardigradus* (4), *Nycticebus coucang* (5), *Cheirogaleus major* (6), *Otolemur crassicaudatus* (7), *Cheirogaleus medius* (8), *Perodicticus potto* (9), *Daubentonia madagascariensis* (10). Key to markers: blue circles = diurnal haplorhines, red circles = nocturnal haplorhines, blue crosses = diurnal strepsirrhines, green crosses = catheermal strepsirrhines, red crosses = nocturnal strepsirrhines.

between activity pattern and relative orbital aperture size in primates<sup>4</sup> (Kay and Cartmill, 1977; Kay and Kirk, 2000; Heesy and Ross, 2001). Like these studies, Figure 1A demonstrates that most nocturnal species have larger orbital apertures than similar-sized diurnal species across the entire range of cranial sizes at which direct comparisons can be made. The only taxa that do not fit this description are aye-ayes (*Daubentonia*) and pottos (*Perodicticus*), which have relatively small orbital apertures for nocturnal primates and accordingly plot near the upper limit of the diurnal primate distribution. Figure 1A further shows that diurnal haplorhines and diurnal strepsirrhines have very similar relative orbital aperture sizes. The catheermal strepsirrhines included in this analysis (all of which are species of *Eulemur*) have relative orbital aperture sizes that overlap the range of diurnal taxa. Nonetheless, most catheermal species plot along the border between the diurnal and nocturnal polygons in Figure 1A. Tarsiers (*Tarsius*) and owl monkeys (*Aotus*), by contrast, have the largest relative

orbital aperture sizes among primates, and therefore plot as outliers above the nocturnal strepsirrhine distribution in Figure 1A.

#### Eye size and activity pattern

Unlike the relative size of the orbital aperture, relative eye size cannot be used to reliably discriminate between diurnal and nocturnal primates. Figure 1B is a bivariate plot of transverse eye diameter and cranial size calculated using the same specimens as in Figure 1A. In both figures, diurnal haplorhines and diurnal strepsirrhines have very similar distributions and nocturnal haplorhines are outliers from all other species. However, in marked contrast to Figure 1A, Figure 1B clearly demonstrates a broad range of overlap in relative eye size between nocturnal strepsirrhines and diurnal primates of both suborders. Some nocturnal strepsirrhines, such as *Loris tardigradus* and *Galago moholi*, have eyes that are substantially larger than those of diurnal primates. However, other nocturnal strepsirrhines (including *Cheirogaleus major*, *Cheirogaleus medius*, *Perodicticus potto*, *Nycticebus coucang*, *Otolemur crassicaudatus*, and *Daubentonia madagascariensis*) have transverse eye diameters that are very similar to those of diurnal primates of comparable cranial size. Nearly identical results are obtained when the axial diameter of the eye is substituted for transverse eye diameter (not shown).

Figure 1B also reveals that some closely related nocturnal strepsirrhine taxa differ considerably in relative eye size. For example, *Perodicticus potto* and *Nycticebus coucang* have transverse eye diameters (12.2 mm and 15.8 mm) that differ by 23% despite the fact that both lorises have similar-sized crania. Comparable degrees of variation in relative eye size are also found among closely related diurnal species. For example, at 24.3 mm transverse diameter, *Erythrocebus patas* has the largest absolute eye size of any primate measured in this analysis. By contrast, *Macaca fascicularis* has a similar cranial size but a transverse eye diameter of only 18.5 mm (a difference of 24%).

These results indicate that eye size alone cannot account for the differences in relative orbital aperture size between diurnal and nocturnal species. Similarly, the wide range of variation in eye size among closely related species of similar body size and activity pattern (e.g., as described for *N. coucang* and *P. potto* or *E. patas* and *M. fascicularis*) suggests that selective factors unrelated to phylogenetic heritage and scaling relationships must exert a strong influence on relative eye size in primates.

#### Eye size and orbital aperture size

The measurements collected in this analysis demonstrate that orbital aperture diameter is significantly correlated with transverse eye diameter (Spearman Rho = 0.92;  $p < 0.0001$ ). The close relationship between these two variables is evident in Figure 2, which shows a least-squares regression of  $\log_{10}$  orbital aperture diameter and  $\log_{10}$  transverse eye diameter. This regression is also highly significant ( $p < 0.0001$ ), and

<sup>4</sup> In most prior studies of relative orbit size, orbit diameter was expressed as a function of cranial length. In the present study, the use of cranial size (i.e., the geometric mean of cranial length and cranial width) as a body size surrogate produces results that are very similar to those obtained using cranial length.

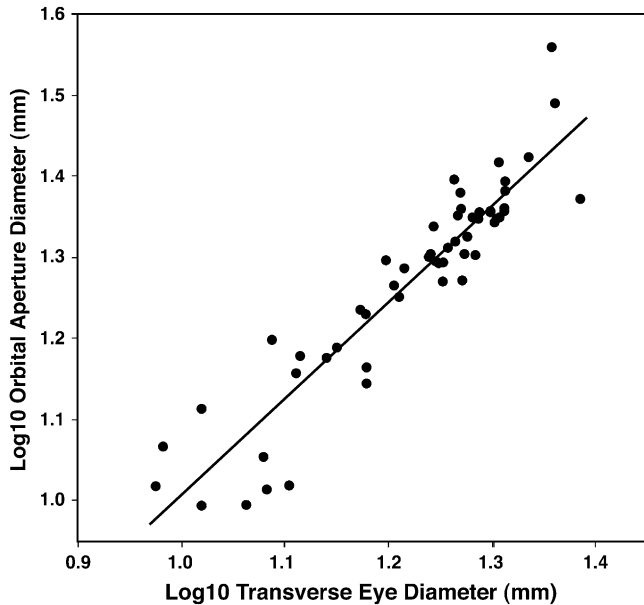


Fig. 2. Least-squares regression of log<sub>10</sub> orbital aperture diameter on log<sub>10</sub> transverse eye diameter. All measurements are in mm. Markers represent species means. Regression slope = 1.188; y-intercept = -0.181;  $p < 0.0001$ ;  $r^2 = 0.86$ .

indicates that 86% of the variation in orbital aperture size may be explained by variation in eye size alone. These results are comparable to those of previous analyses of the relationship between eye volume and orbit volume (Schultz, 1940; Kay and Kirk, 2000).

Despite the fact that eye size clearly has a significant influence on orbital aperture size, closer examination of the relationship between these two variables in raw space reveals important differences between haplorhines and strepsirrhines. Figure 3A presents a bivariate comparison of transverse eye diameter and orbital aperture diameter in haplorhines only. This figure demonstrates that several anthropoid genera (including *Callithrix*, *Saguinus*, *Leontopithecus*, *Cebus*, *Saimiri*, *Procolobus*, and *Erythrocebus*) have transverse eye diameters that are greater than the diameter of the orbital aperture. This group includes all anthropoids in the comparative sample with orbital aperture diameters less than 16 mm (Table 1) and body masses less than 1 kg (Smith and Jungers, 1997). As orbital aperture diameter increases, the disparity between orbital aperture size and eye size becomes progressively greater (Fig. 3A). This trend is responsible for the curvilinear distribution of taxa in Figure 3A, and is probably the result of differential allometry between eye size and orbit size (Schultz, 1940; Kay and Kirk, 2000). Indeed, the anthropoids with the largest body sizes in this analysis (*Pan troglodytes* and *Pongo pygmaeus*) exhibit the greatest disparity between eye size and orbital aperture size (transverse eye diameter as a percentage of orbital aperture diameter = 70% in *Pan* and 63% in *Pongo*). Among the nocturnal haplorhines shown in Figure 3A, both *Tarsius* and *Aotus* have orbital aperture diameters that exceed eye diameter.

In contrast to many haplorhines, eye size never exceeds orbital aperture size in strepsirrhines. Figure 3B presents

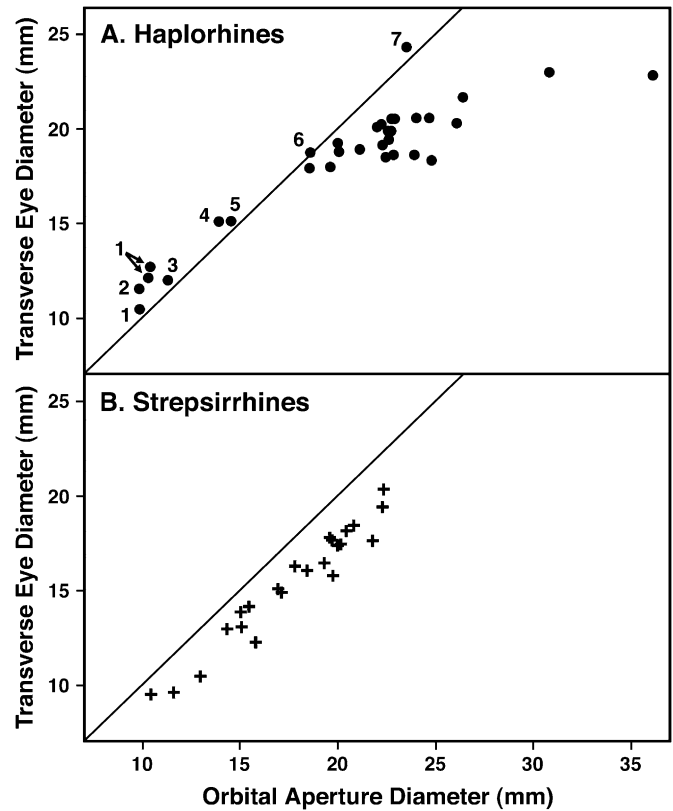


Fig. 3. Bivariate plot of transverse eye diameter versus orbital aperture diameter (OAD) in haplorhines (A) and strepsirrhines (B). All measurements are in mm. Markers represent species means. Diagonal lines represent equality of eye diameter and OAD. Anthropoid taxa with eye diameters greater than OAD are identified by numbers, including: *Saguinus* spp. (1), *Callithrix jacchus* (2), *Leontopithecus rosalia* (3), *Cebus* sp. (4), *Saimiri* sp. (5), *Procolobus badius* (6), *Erythrocebus patas* (7). Key to markers: circles = haplorhines, crosses = strepsirrhines.

a bivariate plot of transverse eye diameter and orbital aperture diameter in strepsirrhines. This figure shows that across the entire range of orbit (and body) sizes sampled, orbital aperture diameter exceeds eye diameter by approximately 1–4 mm. As a result, orbital aperture diameter always overestimates eye diameter in strepsirrhines regardless of eye size or activity pattern. This condition differs from haplorhines, in which orbital aperture diameter simultaneously underestimates eye diameter in smaller-bodied (i.e., <1 kg) anthropoids and overestimates eye diameter in *Tarsius*, *Aotus*, and most larger-bodied anthropoids.

## Discussion

### *Different effects of activity pattern on eye and orbital aperture size*

A bivariate plot of orbital aperture diameter and cranial size in primates (Fig. 1A) demonstrates that nocturnal species typically have larger orbital apertures than diurnal species across the entire range of cranial sizes at which direct

comparisons can be made. This finding is true *a fortiori* for the nocturnal haplorhines *Tarsius* and *Aotus*, which have larger orbital apertures than nocturnal strepsirrhines. These results are comparable to those of previous analyses, which show that relative orbital aperture size may be used to discriminate between extant primates with diurnal and nocturnal activity patterns (Walker, 1967; Kay and Cartmill, 1977; Martin, 1990; Kay and Kirk, 2000; Heesy and Ross, 2001). It is therefore surprising that a comparison of transverse eye diameter and cranial size in the same specimens demonstrates substantial overlap in the distributions for diurnal and nocturnal taxa (Fig. 1B). Although some nocturnal taxa, such as *Tarsius*, *Aotus*, *Loris*, and *Galago moholi*, do have larger eyes than diurnal primates of comparable cranial size, many diurnal and nocturnal primates have very similar relative eye sizes. A number of nocturnal lemuriforms (*Daubentonia*, *Cheirogaleus*) and lorisiforms (*Nycticebus*, *Pero-dicticus*, *Otolemur*) accordingly cannot be distinguished from diurnal primates on the basis of relative eye size despite the fact that these nocturnal species have relatively larger orbital apertures. These findings indicate that diurnal and nocturnal primates do not necessarily differ in relative eye size even if they differ in relative orbital aperture size. As a result, factors other than enlargement of the eye must play a role in producing the relatively large orbital apertures of many nocturnal primates (e.g., *Cheirogaleus*). These results further suggest that nocturnality *per se* is insufficient to account for the greatly enlarged eyes of some primates (e.g., *Tarsius*, *Aotus*, *Loris*, and *Galago moholi*).

A partial explanation for these findings is provided by a direct comparison of transverse eye diameter and orbital aperture diameter in the two extant primate suborders (Fig. 3A, B). These bivariate plots reveal a fundamental difference between small-bodied anthropoids and strepsirrhines in the eye/orbit relationship. Many anthropoids (including all species with orbital aperture diameters less than 16 mm) have eye diameters that are greater than orbital aperture diameter. This phenomenon had been previously described for two species of callitrichines (Martin, 1990), but the data presented here suggest that it is generally true for small-bodied diurnal anthropoids. In Figure 3A, all diurnal anthropoids with body masses less than 1 kg have transverse eye diameters that exceed orbital aperture diameter by anywhere from 4% (*Saimiri*) to 22% (*Saguinus midas*). By contrast, Figure 3B demonstrates that all strepsirrhines have transverse eye diameters that are less than the diameter of the orbital aperture, irrespective of cranial size or activity pattern. These results indicate that measurements of orbital aperture diameter simultaneously underestimate eye size in small-bodied anthropoids and overestimate eye size in strepsirrhines.

These clade-specific differences in the eye/orbit relationship help to accentuate the distinction between nocturnal and diurnal species in relative orbital aperture size. Below the body size of the smallest living diurnal strepsirrhine (*Hapalemur griseus*; ~900 g; Smith and Jungers, 1997), all diurnal primates are anthropoids and all nocturnal primates (except

the highly derived *Tarsius*) are strepsirrhines. It is precisely at such smaller body sizes that the differences between diurnal and nocturnal species in relative orbital aperture diameter are most prominent (Kay and Cartmill, 1977; Martin, 1990; Kay and Kirk, 2000). Analyses of the relationship between activity pattern and orbital aperture diameter in primates are therefore based largely on comparisons of diurnal anthropoids and nocturnal strepsirrhines. Because orbital aperture diameter underestimates eye size in small-bodied anthropoids, the distribution of small diurnal species in Figure 1A is shifted downward (e.g., away from the nocturnal distribution) relative to Figure 1B. Conversely, because orbital aperture diameter overestimates eye size in strepsirrhines, the distribution of nocturnal species in Figure 1A is shifted upward (e.g., away from the diurnal distribution) relative to Figure 1B. As a result, the bivariate distributions of orbital aperture diameter in nocturnal and diurnal species (Fig. 1A) exhibit much less overlap than the bivariate distributions of nocturnal and diurnal eye sizes (Fig. 1B).

#### *Reconciling the differences: A morphological explanation*

Differences between anthropoids and strepsirrhines in the relationship between eye size and orbital aperture size can be primarily explained as the result of clade-specific differences in corneal size and orbit orientation. Relative to eye size, corneal size is significantly smaller in diurnal anthropoids than in all other primates (Kirk, 2004, 2006). Indeed, mean corneal diameter is approximately 50% of transverse eye diameter in diurnal anthropoids, but ranges between 70–92% of transverse eye diameter in all other primates (Kirk, 2004). This highly derived eye morphology in diurnal anthropoids probably represents an adaptation for increased visual acuity associated with the formation of a larger retinal image (Ross, 2000; Kirk, 2004; Kirk and Kay, 2004). Anthropoids also exhibit a unique combination of highly convergent (i.e., forward-facing) eyes (Johnson, 1901) and orbits (Cartmill, 1970; Kay and Cartmill, 1977; Ross, 1995; Noble et al., 2000; Ravosa et al., 2000; Heesy, 2003). The combination of high ocular convergence, high orbital convergence, and relatively small corneal size in diurnal anthropoids permits the diameter of the orbital aperture to be smaller than the transverse diameter of the eye without occluding the cornea and impeding visual function (Figs. 3A, 4A). This configuration of the eye and circum-orbital region accounts for the presence of orbital apertures in some anthropoids that are smaller than the internal diameter of the orbit (Martin, 1990), although the functional benefits of such a configuration are not known. As body size increases, however, the eye occupies a smaller proportion of the orbital volume due to the effects of differential allometry (Schultz, 1940; Martin, 1990; Kay and Kirk, 2000). Accordingly, with several notable exceptions (e.g., *Erythrocebus* and *Procolobus*), eye diameter tends to be smaller than the diameter of the orbital aperture in large-bodied anthropoids (Fig. 3A).

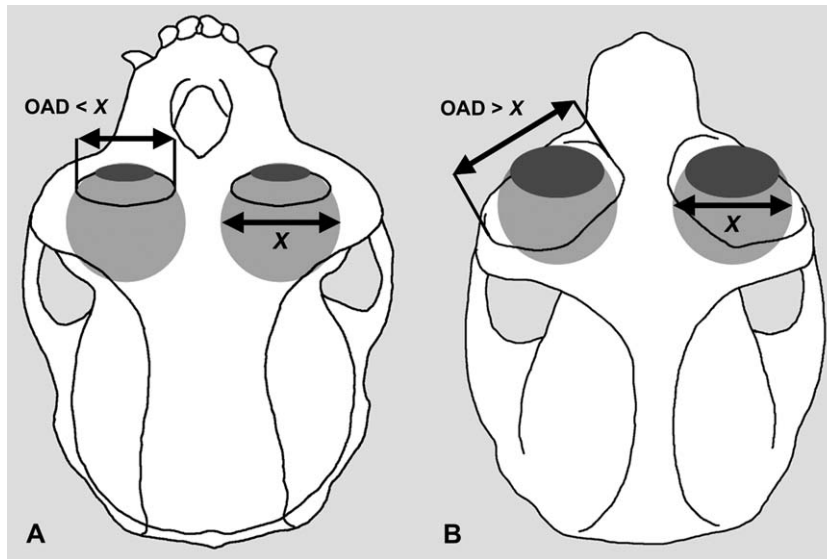


Fig. 4. Schematic diagram comparing eye diameter and orbital aperture diameter in generalized diurnal anthropoids (A) and nocturnal strepsirrhines (B). Eyes are represented as gray circles and corneas (scaled to the mean size relative to eye diameter for both groups) are represented as darkened ellipses. In both species, cranial size is similar and transverse eye diameter ( $X$ ) is identical. In the diurnal anthropoid (A), relatively small cornea size and high orbital convergence permits orbital aperture diameter to be less than eye diameter ( $OAD < X$ ). In the nocturnal strepsirrhine, relatively large cornea size and low orbital convergence constrains orbital aperture diameter to be greater than eye diameter ( $OAD > X$ ).

As is generally true for all primates, strepsirrhines resemble anthropoids in having highly convergent eyes (Johnson, 1901).<sup>5</sup> However, strepsirrhines differ from anthropoids in exhibiting larger corneas relative to eye size (Kirk, 2004, 2006) and less convergent orbits (Cartmill, 1970; Kay and Cartmill, 1977; Ross, 1995; Noble et al., 2000; Ravosa et al., 2000; Heesy, 2003). This lack of correspondence between eye orientation and orbit orientation in strepsirrhines has two important consequences. First, the position of the medial margin of the orbital aperture in strepsirrhines is constrained by corneal size because overlap of the cornea by the orbital margin would impede the light-gathering and image-forming capacity of the eye. The presence of relatively larger corneas in nocturnal strepsirrhines compared to diurnal strepsirrhines (Kirk, 2004, 2006) may thus be responsible for the observation that extant diurnal and nocturnal strepsirrhines differ in orbital aperture size despite broad similarity in eye size (Fig. 1A, B). Second, the position of the lateral margin of the orbital aperture in strepsirrhines is not constrained by corneal size because the lateral orbital margin lies posterior to the lateral corneal margin and adjacent to the lateral aspect of the eye itself (Fig. 4B). This unique combination of large relative cornea size, convergent eyes, and relatively divergent orbits constrains the diameter of the orbital aperture in strepsirrhines to always be greater than eye diameter (Figs. 3B, 4B). Indeed, at the

relatively low orbital convergence angles characteristic of most strepsirrhines (Cartmill, 1970; Ross, 1995; Ravosa et al., 2000; Heesy, 2003), orbital aperture diameter could never be smaller than eye diameter without partial occlusion of the relatively large cornea and a concomitant reduction in visual functionality.

These observations further help to explain the fact that diurnal and nocturnal primates generally differ in relative orbital aperture size (Fig. 1A), but do not necessarily differ in relative eye size (Fig. 1B). At smaller cranial sizes where differences in relative orbital aperture size between diurnal and nocturnal species are most pronounced (Kay and Cartmill, 1977; Kay and Kirk, 2000), most diurnal species are anthropoids and most nocturnal species are strepsirrhines. Smaller diurnal anthropoids have orbital aperture diameters that are less than transverse eye diameters in part because they have convergent orbits and relatively small corneas (Figs. 3A, 4A). By contrast, nocturnal strepsirrhines have orbital aperture diameters that are greater than transverse eye diameters because they have relatively divergent orbits and large corneas (Figs. 3B, 4B). These clade-specific differences in eye and orbit morphology create the potential for similar-sized diurnal anthropoids and nocturnal strepsirrhines to differ substantially in orbital aperture diameter, but have identical eye diameters (Fig. 4A, B).

#### Activity patterns of fossil primates

These results have significant implications for the use of orbital aperture size as a means of reconstructing the activity patterns of fossil primates (e.g., Walker, 1967; Kay and Cartmill, 1977; Simons, 1990, 1997, 2001; Beard et al., 1991; Rasmussen and Simons, 1992; Simons and Rasmussen,

<sup>5</sup> According to Johnson (1901), anthropoids have slightly more convergent eyes than strepsirrhines. However, among the large number of mammals studied by Johnson (182 species from 16 orders), only primates (including strepsirrhines) and some feloid carnivores have optic axes within 15 degrees of parallel. Accordingly, primates are highly derived among mammals in exhibiting pronounced convergence of the optic axes.



1994; Kay and Kirk, 2000; Heesy and Ross, 2001; Ni et al., 2004). Foremost, the data presented here clearly indicate that the differences between extant nocturnal and diurnal primates in orbital aperture size are not a simple function of activity-pattern-dependent changes in eye size. Instead, eye size, cornea size, and clade-specific differences in orbital morphology are all likely to play a complex role in determining the size of the orbital aperture. This finding urges caution in comparing orbital aperture size in living and fossil primates, particularly at smaller body sizes where the extant comparative sample is strongly influenced by anatomical differences between haplorhines and strepsirrhines.

Future analyses of activity pattern in fossil taxa must take into consideration the fact that the smallest diurnal primates are all anthropoids, which exhibit unusually small orbital apertures associated with derived reductions in corneal size and derived increases in orbital convergence (Fig. 4A). Because all diurnal and cathemeral strepsirrhines are relatively large-bodied (i.e., greater than ~900 g; Smith and Jungers, 1997), it is currently unknown what orbital aperture size should be expected for a small diurnal primate lacking the highly derived orbital features of an anthropoid. However, it is reasonable to infer that orbital aperture size in such a species would be smaller than that of extant small-bodied nocturnal strepsirrhines because cornea size partly determines orbital aperture size (see above) and is strongly influenced by activity pattern (Kirk, 2004, 2006). Furthermore, it is also reasonable to expect that orbital aperture size in a small diurnal non-anthropoid might be larger than that of a comparably-sized diurnal anthropoid due to the derived “constriction” of the orbital aperture relative to eye size seen in all anthropoids below 1 kg in body mass.

Given the lack of an adequate extant comparative sample to test these expectations, several practical considerations should be taken into account when interpreting orbital aperture size in fossil specimens. First, eye size clearly has an important influence on orbital aperture size, and all extant taxa with very large eyes and orbits (e.g., *Loris*, *Tarsius*, *Galago*, and *Aotus*) are nocturnal. As a result, one may safely conclude that fossil species with very large orbital apertures for their cranial size (e.g., *Shoshonius*; Beard et al., 1991) were nocturnal. Second, extant haplorhines exhibit large activity-pattern-dependent differences in both eye size and orbital aperture size. These differences are accentuated by derived reduction in the size of the diurnal anthropoid orbital aperture, as well as the extreme ocular and orbital hypertrophy of living nocturnal haplorhines (Kay and Cartmill, 1977; Kay and Kirk, 2000; Kirk and Kay, 2004). As a result, it is reasonable to infer that relative orbital aperture size is a good indicator of activity pattern in fossil crown haplorhines and that anthropoids with small orbital apertures (e.g., *Catopithecus*, *Apidium*, and *Proteopithecus*; Simons, 1990, 1997; Rasmussen and Simons, 1992) were diurnal. Third, among larger-bodied extant strepsirrhines, orbital aperture size is relatively smaller in diurnal species than in most nocturnal species (presumably due to differences in relative cornea size). Accordingly, non-anthropoid fossil taxa with small orbital apertures that fall within the size range

of living diurnal strepsirrhines (e.g., *Adapis* and *Notharctus*; Kay and Kirk, 2000) can safely be considered diurnal.

The primary question that remains to be addressed is how to interpret relative orbital aperture size in fossil non-anthropoids that lack clear orbital hypertrophy and have smaller crania than extant diurnal strepsirrhines (i.e., less than ~65 mm prosthion-inion length; Kay and Kirk, 2000). For example, the late Eocene adapiform *Mahgarita stevensi* and omomyiform or stem haplorhine *Rooneyia viejaensis* have been judged to be nocturnal and diurnal, respectively, on the basis of relative orbital aperture size (Kay and Kirk, 2000). This interpretation is interesting because most adapiforms are thought to have been diurnal and most omomyiforms are thought to have been nocturnal (Kay and Cartmill, 1977; Martin, 1990; Kay and Kirk, 2000; Heesy and Ross, 2001). However, both *Mahgarita* and *Rooneyia* have relatively small crania (~51 mm prosthion-inion length) and plot near the region of overlap between extant diurnal and nocturnal species in bivariate plots of skull length and orbital aperture size (Kay and Kirk, 2000). Although previous assessments of activity pattern may well be correct for these two genera, the fact remains that there are no living diurnal non-anthropoid primates of similar cranial size with which direct comparisons can be made. Accordingly, conclusions regarding the likely activity pattern of small non-anthropoid taxa such as *Mahgarita* and *Rooneyia* must be considered inherently more speculative than those made for taxa fitting the criteria outlined above.

Unfortunately, these theoretical considerations cannot help to resolve uncertainty regarding the activity pattern of very small extinct non-anthropoid primates like *Teilhardina asiatica* (Ni et al., 2004; Martin, 2004). This species falls outside the range of cranial sizes seen in living primates, and it is therefore difficult to draw any firm conclusions regarding its probable activity pattern. Ni et al. (2004) attempted to solve this problem by extrapolating separate regression lines for extant diurnal and nocturnal primates to very small body sizes in a bivariate plot of log skull length and log orbital aperture diameter. This procedure demonstrated that *T. asiatica* plots near the extrapolated least-squares regression line for diurnal primates. On this basis, Ni et al. (2004) concluded that relative orbital aperture size is relatively small in *T. asiatica* and that the species was therefore diurnal. However, the methodology employed by Ni et al. (2004) is potentially problematic for several reasons. Foremost, the choices of which extant species are included in a comparative sample and which line-fitting technique is used (e.g., least-squares or reduced major axis) will influence the slope and elevation of the regression line (Martin, 2004; Heesy and Ross, 2005). These factors will in turn influence conclusions regarding relative orbital aperture size in *T. asiatica*. Additionally, even if further analyses could convincingly demonstrate that *T. asiatica* had relatively small orbital apertures, it is not known to what degree extrapolated differences in orbital aperture size are influenced by the derived orbital morphologies shared by extant small-bodied diurnal anthropoids. This uncertainty compounds questions regarding the linearity of orbital allometry at small body sizes (Heesy and Ross, 2005) and the possibility that *T. asiatica* had

a visual bauplan unlike that of living primates (Martin, 2004). These considerations suggest that it is premature to conclude that *T. asiatica* and the last common ancestor of primates were both diurnal (Ni et al., 2004).

#### Implications for anthropoid origins

The results of this analysis are also relevant to the hypothesis that the unique features of the anthropoid orbit (e.g., high orbital convergence and the presence of a postorbital septum) are the result of a reduction in eye size that accompanied a shift from nocturnality to diurnality in the stem anthropoid or haplorhine lineage (Ross, 1995, 1996, 2000). The finding that nocturnal and diurnal primates do not necessarily differ in relative eye size (Fig. 1B) suggests that not all primate lineages undergoing a shift from nocturnality to diurnality would be expected to undergo a reduction in eye size. In order for the proposed decrease in eye size to have occurred (Ross, 1995, 1996), the hypothetical nocturnal ancestors of anthropoids would need to have possessed larger eyes than diurnal species. Because nocturnality alone is insufficient to produce enlargement of the eye beyond the condition seen in diurnal primates, other ecological factors must have played a role in the initial genesis of ocular hypertrophy in the hypothetical nocturnal haplorhine ancestor if Ross' (1995, 1996) scenario for anthropoid origins is to remain viable.

While the data presented here do not permit a comprehensive test of the selective factors favoring the evolution of ocular hypertrophy in nocturnal primates, they do suggest that diet may have an important influence on eye size. Indeed, it is striking that three of the largest-eyed nocturnal primates (*Tarsius*, *Loris*, and *Galago moholi*) have diets consisting of more than 50% animal prey (Bearder, 1987; Nekaris, 1999). By contrast, most nocturnal primates with eye sizes comparable to diurnal primates (e.g., *Cheirogaleus*, *Perodicticus*, *Nycticebus coucang*, and *Otolemur crassicaudatus*) have diets composed primarily of fruit and/or gums (Hladik, 1979; Bearder, 1987; Mittermeier et al., 1994). Among nocturnal frugivores, the closely-related lorises *Perodicticus potto* and *Nycticebus coucang* have eye diameters (12.2 mm and 15.8 mm, respectively) that differ by 23% despite the fact that both lorises have similar-sized crania. Although these two species are very similar ecologically and primarily frugivorous, *N. coucang* consumes more animal prey as a percentage of its total diet (30%) than *P. potto* (10%) (Bearder, 1987). These data point toward a close association between ocular hypertrophy and greater faunivory in nocturnal primates. Because enlargement of the eye, *ceteris paribus*, leads to enlargement of the retinal image (Ross, 2000; Kirk and Kay, 2004), increased eye size in some nocturnal species may therefore represent an adaptation for increased visual acuity in the context of visually locating and tracking prey.

These results are consistent with Ross' hypothesis (1996, 2000) that the unique features of the anthropoid orbit evolved when a lineage of small nocturnal predatory haplorhines adopted a diurnal activity pattern. The conclusion that early haplorhines were at least partly faunivorous is supported by their

very small body sizes (Gebo et al., 2000) and the presence of well-developed molar shearing crests in stem tarsiids and anthropoids (Heesy and Ross, 2004). According to the comparative data presented here, nocturnal predatory habits would have selected for large eyes in stem haplorhines relative to the condition seen in living diurnal primates. A transition to diurnality could thus have led to decreased eye size and increased orbital convergence, necessitating the evolution of a postorbital septum to isolate the orbital contents from perturbation by the muscles of mastication (Ross, 1996, 2000). Concomitant selection for the highly derived eye morphologies of diurnal anthropoids (Kirk, 2004, 2006) would in turn have permitted orbital aperture diameter to be smaller than eye diameter. As noted previously, the benefits of such "constriction" of the orbital aperture are not immediately apparent, but small cornea size relative to eye size is almost certainly an adaptation for increased visual acuity in a diurnal context (Ross, 2000; Kirk, 2004; Kirk and Kay, 2004). Small relative cornea size thus probably evolved concurrently with other anthropoid adaptations for high diurnal visual acuity, such as a fovea with densely packed cones, a macula lutea, low retinal summation, and UV lens filters (Kirk and Kay, 2004). These adaptations for very high visual acuity are consistent with the suggestion that the earliest diurnal anthropoids were visually-guided predators (Ross, 2000, 2004; Kirk and Kay, 2004). This general scenario thus supports the conclusion that the initial stages of anthropoid origins would have involved a change in activity pattern but not diet (Rasmussen and Simons, 1992; Ross, 1995, 1996; Kay et al., 1997; Kirk and Simons, 2001).

#### Additional selective pressures for increased eye size

In addition to diet, lineage-specific differences in visual anatomy are also likely to be important factors selecting for increased eye size in nocturnal primates. It has long been suggested that the extreme ocular hypertrophy of tarsiers and owl monkeys is related to the absence of a tapetum lucidum in both groups (Cartmill, 1980; Martin, 1990; Kirk and Kay, 2004). According to this hypothesis, nocturnal haplorhines had to compensate for the absence of a tapetum by evolving larger eyes (and corneas) than nocturnal strepsirrhines (Cartmill, 1980). However, tapeta have evolved convergently many times among vertebrates (Pirie, 1966; Nicol, 1981; Ollivier et al., 2004), raising the question of why tapeta have not evolved independently in tarsiers and owl monkeys. This consideration led to the suggestion that tapetal absence and large absolute eye size in nocturnal haplorhines represent an adaptation for increased nocturnal visual acuity (Kay and Kirk, 2000; Kirk, 2004; Kirk and Kay, 2004). Regardless of which adaptive scenario is correct, the absence of tapeta lucida in nocturnal haplorhines provides one line of evidence that the common ancestor of crown haplorhines was diurnal (Martin, 1990; Kirk and Kay, 2004). As a result, the parallel evolution of very large eyes in tarsiers and owl monkeys may be the product of a secondary return to a nocturnal habitus combined with selection to increase visual sensitivity while maintaining a relatively high degree of visual acuity (Kirk and Kay, 2004).

A final point worthy of comment is the observation that patas monkeys (*Erythrocebus patas*) have the largest absolute eye size (axial diameter ~25 mm) of all the taxa included in Table 1. This finding is even more striking when eye size is considered in relation to body size. Orangutans (*Pongo pygmaeus*) have the second largest absolute eye size in Table 1 (axial diameter = 22.6 mm), yet mean adult body mass in *P. pygmaeus* (~57 kg) is approximately six times that of *E. patas* (9.5 kg) (Smith and Jungers, 1997). Closely related African cercopithecines (e.g., *Cercopithecus*, *Papio*, *Mandrillus*, *Theropithecus*) also have smaller eye sizes than *E. patas*, suggesting that patas monkeys have been the subject of particularly strong selection pressures for increased eye size. In this context, it is striking that patas monkeys are capable of attaining very high speeds when running (55 km/hr; Kingdon, 1971) and that this skill allows patas monkeys to evade predators in open habitats (Isbell et al., 1998). Among vertebrates generally, there is some evidence for an association between increased speed of locomotion and increased absolute eye size (Hughes, 1977; Brooke et al., 1999; but see Hall, 2000). This relationship (“Leuckart’s Law”) has been proposed to be the result of selection for increased visual acuity in fast-moving species. Although a review of the effect of maximum locomotor speed on eye size in primates is beyond the scope of this paper, a functional association between very large eye size and the ability for rapid cursoriality in *E. patas* is plausible given the comparative evidence supporting Leuckart’s Law (Hughes, 1977; Brooke et al., 1999).

## Conclusions

This analysis demonstrates that although nocturnal and diurnal primates usually differ in relative orbital aperture size, they do not necessarily differ in relative eye size. Some nocturnal species (e.g., *Loris*, *Tarsius*) have larger relative eye sizes than diurnal primates, while others (e.g., *Perodicticus*, *Cheirogaleus*) have relative eye sizes that are essentially indistinguishable from those of diurnal primates. This discrepancy is primarily the result of clade-specific differences in orbit orientation and relative cornea size. Diurnal anthropoids, which have relatively convergent orbits and small cornea sizes, often have orbital apertures that are smaller than their transverse eye diameters. Nocturnal strepsirrhines, which have relatively less convergent orbits and larger cornea sizes, always have orbital apertures that are larger than their transverse eye diameters. As a result, small-bodied diurnal anthropoids and nocturnal strepsirrhines can have different relative orbital aperture sizes, but identical eye sizes. These results urge greater caution in the use of relative orbital aperture size to draw conclusions about the probable activity patterns of fossil taxa. Results of this analysis also suggest that nocturnality *per se* is insufficient to explain the relatively large eyes of some species (e.g., *Tarsius*, *Aotus*, *Loris*, and *Galago moholi*). Other selective factors favoring increased eye size in primates may include nocturnal predatory habits, lack of a tapetum lucidum, and rapid cursorial locomotion.

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## References

- Beard, K.C., Krishtalka, L., Stuckey, R.K., 1991. First skulls of the early Eocene primate *Shoshonius cooperi* and the anthropoid-tarsier dichotomy. *Nature* 349, 64–67.
- Bearder, S.K., 1987. Lorises, bushbabies, and tarsiers: diverse societies in solitary foragers. In: Smuts, B.B., Cheney, D.L., Seyfarth, R.M., Wrangham, R.W., Struhsaker, T.T. (Eds.), *Primate Societies*. University of Chicago Press, Chicago, pp. 11–24.
- Brooke, M.D., Hanley, S., Laughlin, S.B., 1999. The scaling of eye size with body mass in birds. *Proc. R. Soc. Lond. Biol.* 266, 405–412.
- Cartmill, M., 1970. The orbits of arboreal mammals: a reassessment of the arboreal theory of primate evolution. Ph.D. Dissertation, University of Chicago.
- Cartmill, M., 1972. Arboreal adaptations and the origin of the order primates. In: Tuttle, R. (Ed.), *The Functional and Evolutionary Biology of Primates*. Aldine-Atherton, Chicago, pp. 97–122.
- Cartmill, M., 1980. Morphology, function and evolution of the anthropoid postorbital septum. In: Ciochon, R.L., Chiarelli, A.B. (Eds.), *Evolutionary Biology of the New World Monkeys and Continental Drift*. Plenum Press, New York, pp. 243–274.
- Gebo, D.L., Dagosto, M., Beard, K.C., Qi, T., 2000. The smallest primates. *J. Hum. Evol.* 38, 585–594.
- Hall, M.J., 2000. Another look at Leuckart’s Law. *Am. Zool.* 40, 1041.
- Heesy, C.P., Ross, C.F., 2001. Evolution of activity patterns and chromatic vision in primates: morphometrics, genetics and cladistics. *J. Hum. Evol.* 40, 111–149.
- Heesy, C.P., 2003. The evolution of orbit orientation in mammals and the function of the primate postorbital bar. Ph.D. Dissertation, State University of New York at Stony Brook.
- Heesy, C.P., Ross, C.F., 2004. Mosaic evolution of activity pattern, diet, and color vision in haplorhine primates. In: Ross, C.F., Kay, R.F. (Eds.), *Anthropoid Origins: New Visions*. Kluwer Academic/Plenum Publishers, New York, pp. 665–698.
- Heesy, C.P., Ross, C.F., 2005. A re-analysis of activity pattern in *Teilhardina asiatica* and the evolution of activity pattern in early primates. *Am. J. Phys. Anthropol.* 113, 113.
- Hladik, C.M., 1979. Diet and ecology of prosimians. In: Doyle, G.A., Martin, R.D. (Eds.), *The Study of Prosimian Behavior*. Academic Press, New York, pp. 307–357.
- Hughes, A., 1977. The topography of vision in mammals of contrasting life style: comparative optics and retinal organization. In: Criscitelli, F. (Ed.), *Handbook of Sensory Physiology: The Visual System in Vertebrates*. Springer-Verlag, New York, pp. 613–756.
- Isbell, L.A., Pruetz, J.D., Lewis, M., Young, T.P., 1998. Locomotor activity differences between sympatric patas monkeys (*Erythrocebus patas*) and vervet monkeys (*Cercopithecus aethiops*): implications for the evolution of long hindlimb length in *Homo*. *Am. J. Phys. Anthropol.* 105, 199–207.
- Johnson, G.L., 1901. Contributions to the comparative anatomy of the mammalian eye, chiefly based on ophthalmoscopic examination. *Philos. Trans. R. Soc. B* 194, 1–82.

- Kay, R.F., Cartmill, M., 1977. Cranial morphology and adaptation of *Palaechthon nacimienti* and other Paraomomyidae (Plesiadapoidea? Primates), with a description of a new genus and species. *J. Hum. Evol.* 6, 19–35.
- Kay, R.F., Ross, C.F., Williams, B.A., 1997. Anthropoid origins. *Science* 275, 797–804.
- Kay, R.F., Kirk, E.C., 2000. Osteological evidence for the evolution of activity pattern and visual acuity in primates. *Am. J. Phys. Anthropol.* 113, 235–262.
- Kingdon, J., 1971. *East African Mammals*, vol. 1. Academic Press, New York.
- Kirk, E.C., 2004. Comparative morphology of the eye in primates. *Anat. Rec.* 281A, 1095–1103.
- Kirk, E.C., 2006. Eye morphology in catemeral lemurids and other mammals. *Folia Primatol.* 77, 27–49.
- Kirk, E.C., Simons, E.L., 2001. Diets of fossil primates from the Fayum depression of Egypt: a quantitative analysis of molar shearing. *J. Hum. Evol.* 40, 203–229.
- Kirk, E.C., Kay, R.F., 2004. The evolution of high visual acuity in the Anthropoidea. In: Ross, C.F., Kay, R.F. (Eds.), *Anthropoid Origins: New Visions*. Kluwer Academic/Plenum Publishers, New York, pp. 539–602.
- Martin, R.D., 1990. *Primate Origins and Evolution: A Phylogenetic Reconstruction*. Chapman and Hall, London.
- Martin, R.D., 2004. Palaeontology — Chinese lantern for early primates. *Nature* 427, 22–23.
- Mittermeier, R.A., Tattersall, I., Konstant, B., Meyers, D.M., Mast, R.B., 1994. *Lemurs of Madagascar*. Conservation International, Washington, DC.
- Nekaris, K.A.I., 1999. Diet of the slender loris (*Loris tardigradus lydekkerianus*) in Dindigul District, Tamil Nadu, India. *Am. J. Phys. Anthropol.* S28, 209.
- Ni, X., Wang, Y., Hu, Y., Li, C., 2004. A euprimate skull from the early Eocene of China. *Nature* 427, 65–68.
- Nicol, J.A.C., 1981. Tapeta lucida of vertebrates. In: Enoch, J.M., Tobey, F.L. (Eds.), *Vertebrate Photoreceptor Optics*. Springer-Verlag, Berlin, pp. 401–431.
- Noble, V.E., Kowalski, E.M., Ravosa, M.J., 2000. Orbit orientation and the function of the mammalian postorbital bar. *J. Zool. Lond.* 250, 405–418.
- Ollivier, F.J., Samuelson, D.A., Brooks, D.E., Lewis, P.A., Kallberg, M.E., Komaromy, A.M., 2004. Comparative morphology of the tapetum lucidum (among selected species). *Vet. Ophthalmol.* 7, 11–22.
- Pirie, A., 1966. The chemistry and structure of the tapetum lucidum in animals. In: Graham-Jones, O. (Ed.), *Aspects of Comparative Ophthalmology*. Pergamon, London, pp. 57–68.
- Rasmussen, D.T., Simons, E.L., 1992. Paleobiology of the oligopithecines, the earliest known anthropoid primates. *Int. J. Primatol.* 13, 477–508.
- Ravosa, M.J., Noble, V.E., Hylander, W.L., Johnson, K.R., Kowalski, E.M., 2000. Masticatory stress, orbital orientation and the evolution of the primate postorbital bar. *J. Hum. Evol.* 38, 667–693.
- Ritland, S., 1982. *The Allometry of the Vertebrate Eye*. Ph.D. Dissertation, University of Chicago.
- Rohen, J.W., 1962. Sehorgan. In: Hofer, H., Schultz, A.H., Starck, D. (Eds.), *Primatologia: Handbuch der Primatenkunde*. S. Karger, Basel, pp. 1–210.
- Rohen, J.W., Castenholz, A., 1967. Über die Zentralisation der Retina bei Primaten. *Folia Primatol.* 5, 92–147.
- Ross, C.F., 1995. Allometric and functional influences on primate orbit orientation and the origins of the Anthropoidea. *J. Hum. Evol.* 29, 201–227.
- Ross, C.F., 1996. Adaptive explanation for the origins of the Anthropoidea (Primates). *Am. J. Primatol.* 40, 205–230.
- Ross, C.F., 2000. Into the light: the origin of Anthropoidea. *Annu. Rev. Anthropol.* 29, 147–194.
- Ross, C.F., 2004. The tarsier fovea: functionless vestige or nocturnal adaptation. In: Ross, C.F., Kay, R.F. (Eds.), *Anthropoid Origins: New Visions*. Kluwer Academic/Plenum Publishers, New York, pp. 477–537.
- Schultz, A.H., 1940. The size of the orbit and of the eye in primates. *Am. J. Phys. Anthropol.* 26, 389–408.
- Simons, E.L., 1990. Discovery of the oldest known anthropoidean skull from the paleogene of Egypt. *Science* 247, 1567–1569.
- Simons, E.L., 1997. Preliminary description of the cranium of *Proteopithecus sylviae*, an Egyptian late Eocene anthropoidean primate. *Proc. Natl. Acad. Sci. U.S.A.* 94, 14970–14975.
- Simons, E.L., 2001. The cranium of *Parapithecus grangeri*, an Egyptian Oligocene anthropoidean primate. *Proc. Natl. Acad. Sci. U.S.A.* 98, 7892–7897.
- Simons, E.L., Rasmussen, D.T., 1994. A remarkable cranium of *Plesiopithecus teras* (Primates, Prosimii) from the Eocene of Egypt. *Proc. Natl. Acad. Sci. U.S.A.* 91, 9946–9950.
- Smith, R.J., Jungers, W.L., 1997. Body mass in comparative primatology. *J. Hum. Evol.* 32, 523–559.
- Stephan, H., Frahm, H.D., Baron, G., 1984. Comparison of brain structure volumes in Insectivora and Primates. IV. Non-cortical visual structures. *J. Hirnforsch.* 25, 385–403.
- Walker, A., 1967. Patterns of extinction among subfossil Madagascan lemuroids. In: Martin, P.S., Wright, H.E. (Eds.), *Pleistocene Extinctions: The Search for a Cause*. Yale University Press, New Haven, pp. 425–432.
- Walls, G.L., 1942. *The Vertebrate Eye and its Adaptive Radiation*. Hafner Publishing Company, New York.