RESEARCH ARTICLE

Visual Acuity in the Cathemeral Strepsirrhine *Eulemur macaco flavifrons*

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Studies of visual acuity in primates have shown that diurnal haplorhines have higher acuity (30–75 cycles per degree (c/deg)) than most other mammals. However, relatively little is known about visual acuity in non-haplorhine primates, and published estimates are only available for four strepsirrhine genera (*Microcebus*, *Otolemur*, *Galago*, and *Lemur*). We present here the first measurements of visual acuity in a cathemeral strepsirrhine species, the blue-eyed black lemur (*Eulemur macaco flavifrons*). Acuity in two subjects, a 3-year-old male and a 16-year-old female, was assessed behaviorally using a two-alternative forced choice discrimination task. Visual stimuli consisted of high contrast square wave gratings of seven spatial frequencies. Acuity threshold was determined using a 70% correct response criterion. Results indicate a maximum visual acuity of 5.1 c/deg for the female (1718 trials) and 3.8 c/deg for the male (846 trials). These values for *E. macaco* are slightly lower than those reported for diurnal *Lemur catta*, and are generally comparable to those reported for nocturnal *Microcebus murinus* and *Otolemur crassicaudatus*. To examine ecological sources of variation in primate visual acuity, we also calculated maximum theoretical acuity for *Cheirogaleus medius* (2.8 c/deg) and *Tarsius syrichta* (8.9 c/deg) using published data on retinal ganglion cell density and eye morphology. These data suggest that visual acuity in primates may be influenced by activity pattern, diet, and phylogenetic history. In particular, the relatively high acuity of *T. syrichta* and *Galago senegalensis* suggests that visual predation may be an important selective factor favoring high visual acuity in primates. Am. J. Primatol. 71:1–10, 2009.   © 2009 Wiley-Liss, Inc.

INTRODUCTION

Primates are characterized by higher visual acuity than most other mammals [Kirk & Kay, 2004]. The gray mouse lemur (*Microcebus murinus*), for example, has both the lowest visual acuity [4.2 c/deg; Dkhissi-Benyahya et al., 2001] and the smallest axial eye diameter [9.2 mm; Ross & Kirk, 2007] known for any primate. Nonetheless, acuity in *Microcebus* is higher than that found in many other mammals, including some taxa (e.g. *Loxodonta*, African elephant) with substantially larger eyes [Kirk & Kay, 2004; Ross & Kirk, 2007]. Within primates, diurnal haplorhines in particular have exceptionally high visual acuity [30–75 c/deg: Cowey and Ellis, 1967; De Valois et al., 1974; Spence, 1934; Troilo et al., 1993]. Compared with other vertebrates, these acuity values for diurnal haplorhines are exceeded only by those of large-eyed, diurnal birds of prey [Kirk & Kay, 2004; Ross, 2000].

Functional and comparative data suggest that the numerous visual specializations for high acuity found in living haplorhines probably evolved in a diurnal, visually predatory ancestor [Kirk & Kay, 2004; Kirk, 2006a; Ross, 1996, 2000; Ross & Kirk, 2007]. However, much less is known about the factors responsible for the evolution of enhanced

visual acuity in the stem primate lineage. It is generally believed that the visual systems of early primates were adapted for locating small food items (e.g. fruits, flowers, and insects) under nocturnal conditions [Cartmill, 1992; Rasmussen, 1990; Rasmussen & Sussman, 2007; Sussman, 1995], although the relative importance of fruits and insects in selection on early primate visual systems has been heavily debated [e.g. Cartmill, 1992; Sussman, 1995]. Recently, some authors have challenged traditional hypotheses of primate origins by arguing that comparative data on primate photopigments suggest that basal primates were diurnal or cathemeral [Lucas et al., 2007; Osorio et al., 2005; Tan et al., 2005].

Accordingly, there is currently little consensus regarding which selective pressures favored the evolution of increased visual acuity in the primate stem lineage. Because some aspects of strepsirrhine visual anatomy are more similar to non-primate mammals than to haplorhines [Kay & Kirk, 2000; Kirk, 2004, 2006b; Rohen & Castenholz, 1967; Ross, 2000], the visual systems of extant strepsirrhines may be the best living analogs for those of the earliest crown primates. Unfortunately, visual acuity has been quantified for only four strepsirrhine species: the ring-tailed lemur [*Lemur catta*: Neuringer et al., 1981], the gray mouse lemur [*M. murinus*: Dkhissi-Benyahya et al., 2001], the greater galago [*Otolemur crassicaudatus*: Langston et al., 1986], and the Senegal galago [*Galago senegalensis*: Treff, 1967]. Notably missing from this short list of strepsirrhine primates are any cathemeral species.

Cathemerality, in which a species is habitually active under both nocturnal and diurnal conditions, is a common activity pattern across Mammalia [Curtis & Rasmussen, 2006; Tattersall, 1987]. By contrast, cathemerality is relatively rare among primates, and has been fully documented in only three genera: *Eulemur, Hapalemur,* and *Aotus* [Curtis & Rasmussen, 2002, 2006]. Nonetheless, if the last common ancestor of living primates was exceptionally small bodied as hypothesized by Gebo [2004], a correspondingly high metabolic rate may have required cathemerality for frequent feeding bouts as in living shrews [Halle, 2006]. An improved understanding of cathemeral primate visual systems may therefore provide important insights into the visual ecology of the earliest crown primates. However, recognizing specific visual adaptations for cathemerality may not be straightforward [Kirk, 2006b]. Daytime and nighttime light environments impose divergent selective pressures on visual anatomy and often select for mutually exclusive visual adaptations in diurnal and nocturnal species [Kirk, 2004, 2006b; Ross & Kirk, 2007; Walls, 1942]. Because cathemeral activity occurs by day and night, cathemeral species must have flexible visual systems that can function effectively in both high and low light environments [Kirk, 2006b; Walls, 1942].

Comparative anatomical studies suggest that cathemeral strepsirrhines have adapted to activity across a 24 hour cycle by evolving eye and retinal morphologies that are intermediate between those of strictly nocturnal or diurnal species [Kirk, 2006b; Walls, 1942]. Relative cornea size, for example, affects both visual sensitivity and acuity by influencing the amount of light entering the eye and the size of the retinal image. Species of the cathemeral genus *Eulemur* exhibit a range of relative corneal sizes intermediate between those of strictly nocturnal and diurnal strepsirrhines [Kirk, 2004, 2006b]. The distribution and density of retinal photoreceptor types are also related to activity pattern [Arrese et al., 1999; Walls, 1942; Wikler & Rakic, 1990]. Rods primarily function in dim light and increase visual sensitivity, whereas cones mediate acute color vision at higher light levels. Comparative retinal studies demonstrate that peak rod and cone densities in *Eulemur* are intermediate between those of nocturnal and diurnal strepsirrhines [Peichl et al., 2001, 2004]. A third factor influenced by activity pattern is retinal summation (i.e. the relative number of photoreceptors that ''pool'' their output to increase the firing rates of ganglion cells). Retinal summation is positively correlated with sensitivity and negatively correlated with acuity [Walls, 1942]. *Eulemur fulvus* exhibits retinal summation that is intermediate between that of diurnal and nocturnal strepsirrhines [Kay & Kirk, 2000].

Based upon such ''intermediate'' visual anatomy in *Eulemur*, it is reasonable to expect that visual acuity in cathemeral strepsirrhines is lower than that of diurnal strepsirrhines, but higher than that of nocturnal strepsirrhines. However, other ecological factors, such as diet, may confound the relationship between visual acuity and activity pattern. Arrese et al. [1999] suggest that predatory mammalian species have higher acuity than herbivorous ones. Although some anatomical evidence supports this hypothesis for primates [Kirk, 2006c; Ross & Kirk, 2007; Tetreault et al., 2004], it has not been explicitly tested using comparative data on visual acuity.

Here we report the first data on visual acuity in a cathemeral strepsirrhine, the blue-eyed black lemur (*E. macaco flavifrons*). Like other *Eulemur* species [Curtis & Rasmussen, 2006], *E. macaco flavifrons* is active throughout a 24 hr cycle [Schwitzer et al., 2007]. We measured acuity directly in two individuals using a two-alternative forced choice behavioral testing paradigm. We also compare these results for *E. macaco* with data on visual acuity in other primate species to examine the possible ecological influences on visual acuity in primates.

METHODS
Subjects

Two blue-eyed black lemurs, one female and one male, were studied in our behavioral test of visual acuity. Both subjects were housed at the Animal Resource Center at the University of Texas at Austin. They were permitted free movement within a 3.05×6.5 m indoor enclosure. The 16-year-old female (Lamour) was wild-caught and loaned to the University of Texas by the Duke University Lemur Center. The 3-year-old male (Buddy) was born at the UT Animal Resource Center. An additional lemur (a 2-year-old male) was present in the group during the study period but did not take part in testing. Throughout the study period (June 2005–April 2006), the lemurs were provided continuous access

to monkey chow as well as alternate-day provision of fresh fruits and vegetables.

The testing room (2.13 m × 3.05 m) was located immediately adjacent to the habitat room. Both rooms were windowless and illuminated entirely by artificial light (typical indoor lighting: 200 lx). During testing sessions, the animals were allowed free movement between rooms. However, once one subject was engaged in a trial, the other animals were discouraged from entering the testing room. The animals were tested once per day, with each testing session lasting between 1 and 2 hr. Testing sessions were composed of 10–80 trials each, depending on the interest levels of the subjects. This study was approved by the University of Texas at Austin Institutional Subject Care and Use Committee (protocol ♯ 04093002).

Apparatus and Stimuli

A T-shaped test apparatus (Fig. 1) was designed by combining elements from a Mitchell jumping platform [Arrese et al., 1999] and a Y-maze. This apparatus consisted of a jumping platform approximately 30.5 cm in height, a runway divided on its long axis (1.53 m) by a partition, and a test wall (1.53 m × 1.2 m) on which visual stimuli and food rewards were presented. The jumping platform served as the decision area for the subjects. The runway partition (1.53 m × 0.91 m) ran from the jumping platform to the test wall, dividing both the runway and test wall into equal right and left halves. From the jumping platform, both the right and left halves of the test wall were visible on either side of the runway partition. Test stimuli consisted of laminated paper squares on which high contrast
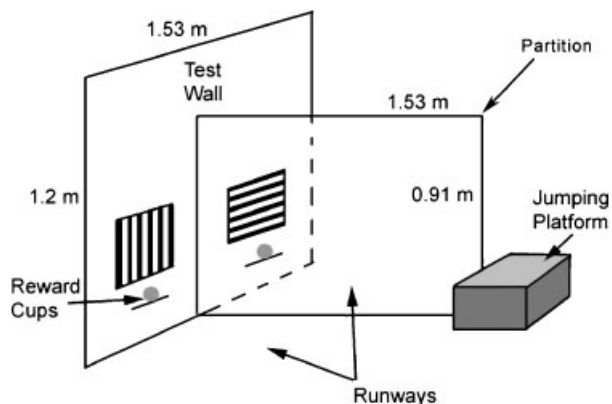

Fig. 1. Dimensions and schematic of testing apparatus used in the behavioral study. The partition was constructed of PVC pipe and opaque canvas cloth, and attached to the pegboard test wall using nylon rope. The grating stimuli hung on the test wall with dowel pegs. The reward cups sat on wooden platforms made of dowels and tongue depressors. Investigator 1 stood to the side of jumping platform, whereas Investigator 2 stood behind the test wall. Testing procedures described in text.

(100%) black and white square wave grating patterns were printed. The grating stimuli were 30.5–33.0 cm squares, subtending 12.57–13.61° of visual angle when viewed from the jumping platform. The gratings used in trials included spatial frequencies of 0.5, 1.0, 2.0, 4.0, 5.81, 6.54, and 7.47 cycles per degree (c/deg) for Lamour, and 0.5, 1.0, 2.0, 3.0, 3.5, 4.0, and 4.76 c/deg for Buddy. The stimuli were constructed in Adobe Photoshop 7.0 [Adobe Systems Incorporated, 2002] and printed on matte heavy weight paper using an HP DesignJet 5000PS printer. The stimuli were then laminated in order to facilitate cleaning between sessions. During testing, grating stimuli were hung from the test wall at the eye level of the lemurs. Small wooden shelves (5 cm by 10 cm) were attached to the test wall directly below each grating stimulus. Paper reward cups on the shelves were used to hold food rewards. Two opaque black curtains hung over the test wall were used to conceal the grating stimuli and reward cups before the initiation of each trial.

Both subjects were trained to discriminate between orthogonally oriented gratings of the same spatial frequency. In all trials, two grating stimuli were presented—one horizontally oriented and one vertically oriented. Approaches of vertically oriented gratings were reinforced with a food reward, whereas approaches of horizontally oriented gratings were not reinforced. Similar two-alternative forced choice testing paradigms based on horizontal and vertical gratings have been used previously in tests of visual acuity for ring-tailed lemurs [Neuringer et al., 1981] and galagos [Treff, 1967]. Although this type of task is unsuitable for mammals with visual streaks (i.e. elongate, linear regions of high retinal ganglion cell density), strepsirrhines have circular areae centrales [Rohen & Castenholz, 1967], and thus visual acuity is equivalent in both planes. The criterion level for successful discrimination was set at 70% correct performance following Neuringer et al. [1981].[1] This level is similar to the criterion point used for *Otolemur* [75%: Langston et al., 1986].

Procedure

Training occurred in three stages, from June to October of 2005. The initial stage involved habituating the subjects to the researchers' presence, creating an association between the presence of the reward cups and the food reward (1/2 raisin), and training the subjects to distinguish between horizontal and vertical grating stimuli. In the second stage, the subjects were habituated to the testing

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[1]Psychophysical threshold criteria are often defined as midway between chance and perfect performance (i.e. 75%). However, when maximal performance is less than 100%, the criterion should accordingly be shifted below 75% to avoid overestimation of the threshold [Langston et al., 1986]. Because maximal performance in this study was ∼93%, threshold criterion was set to 70% following Neuringer et al. [1981]

room and apparatus. Finally, in the third stage of training, the subjects were trained to discriminate between stimuli using the apparatus and testing procedures (described below). Once both subjects demonstrated performance exceeding criterion in training trials over multiple days, testing and data collection began.

Testing commenced in late October 2005 and continued until late April 2006. Although initial testing sessions involved both subjects, aggression between the subjects associated with the onset of the breeding season in early November required Buddy to be confined to a cage within the habitat room. Lamour continued testing sessions from November to mid-March, at which time she was confined and Buddy was allowed free movement within the habitat room. Buddy engaged in testing sessions from mid-March to late April. Although excluded from tests for 5 months, he immediately recalled the testing procedure and was ready for recorded trials after 2 practice days.

The testing procedure was as follows: one investigator (Investigator 1) stood adjacent to the jumping platform whereas the second investigator (Investigator 2) stood behind the test wall. On verbal command from Investigator 1 (''Box!''), the subject would approach and mount the jumping platform. At this stage, the stimuli and reward cups (with the cup beneath the vertical grating card containing a 1/2 raisin and the cup beneath the horizontal grating card remaining empty) were hidden from view by the black curtains. Once the subject oriented to face the hidden gratings, Investigator 2 would raise the curtains covering the grating cards and call the subject (''Lamour/Buddy, come!''). At this point, both test gratings and cups were visible from the jumping platform. To avoid potentially cuing the subject, Investigator 2's body was obscured behind the test wall and he/she would stare straight ahead at a fixed point on the wall with a blank face. In most trials, the subject appeared to ignore Investigator 2 and would rapidly orient toward the grating cards. In many trials, the subject would visually inspect both grating cards from the jumping platform before making a choice. A decision was recorded when the subject jumped from the platform onto one side of the divided runway. If the subject had chosen correctly (vertical grating), it would approach the reward cup and retrieve the 1/2 raisin. A correct choice was further reinforced with verbal praise from Investigator 1 (''Good girl, Lamour!/Good boy, Buddy!''). If the subject chose incorrectly (horizontal grating), it would either approach and inspect the empty reward cup or (more frequently) stop partway down the runway and return to the jumping platform. An incorrect choice resulted in a verbal reprimand from Investigator 1 (''No!''). After the completion of a trial, the subject was ushered from the testing room so that investigators could prepare

for the next trial. We discarded any trial in which a second animal was near the test apparatus in order to avoid the possibility of interference. The door between the habitat and testing rooms was adjacent to the jumping platform, and the line of sight between the two rooms precluded the possibility of seeing the test wall from the habitat room. As a further precaution to prevent the subjects from seeing the grating orientations before the beginning of a trial, the investigators would draw down the black curtains immediately following the completion of the trial and prepare the next trial hidden behind the curtains. The orientations of both stimuli were pseudo-randomly switched in order to prevent the subject from associating one side of the apparatus with the reward. After each trial, both stimuli were simultaneously rotated either 90 or 180° to further safeguard against nonacuity-based visual cues influencing the subjects' choices.

Following the initial training phase (in which a tendency to sniff test stimuli and reward cups was discouraged and subjects learned to rely on visual cues to retrieve the reward), olfactory cues appeared to have little or no influence on the results of this analysis. Reward cups were used over many testing sessions and replaced concurrently, so raisin residue was equally present on the inside of both cups. Later testing trials involving investigator error (including no reward under any grating card, rewards under both grating cards, and rewards on the incorrect side) revealed that the subjects continued to prefer vertical gratings even when the 1/2 raisin was misplaced. These findings suggest that both subjects used the visual cue of grating orientation in their decision-making process. The results also suggest that unconscious investigator cuing did not influence the subjects' decision making. Although cuing should result in similar behavior across all spatial frequencies, the subjects behaved differently at low spatial frequencies compared with high frequencies, taking longer to make decisions and peering at each stimulus several times in the high frequency trials. Furthermore, nine people (including student volunteers) served as investigators, trading between Investigator 1 and 2 roles regularly. Because these people did not share cues or threshold expectations, the fact that both test subjects performed similarly at a given spatial frequency regardless of who was the investigator is strong evidence against cuing.

Testing began at the lowest spatial frequency used for both subjects (0.5 c/deg), and stimulus spatial frequency was increased only after the subject had reached or exceeded the 70% correct criterion level on 40 nonconsecutive trials. Testing continued at each spatial frequency until approximately 150–200 complete trials had been recorded. Once the subject reached chance discrimination (approximately 50% correct performance) at a spatial frequency for over 100 trials, the experiment was

TABLE I. Performance Summary for Both *Eulemur macaco* Subjects

Subject	C/DEG	Total trials	% Correct
Lamour	0.5	112	93.57
	1	227	88.99
	2	221	88.69
	4	**307**	**76.55**
	5.81	**371**	**66.31**
	6.54	233	51.93
	7.47	120	44.17
Buddy	0.5	37	94.59
	1	117	92.31
	2	181	91.16
	3	126	87.3
	3.5	**109**	**81.65**
	4	**157**	**63.06**
	4.76	119	50.42

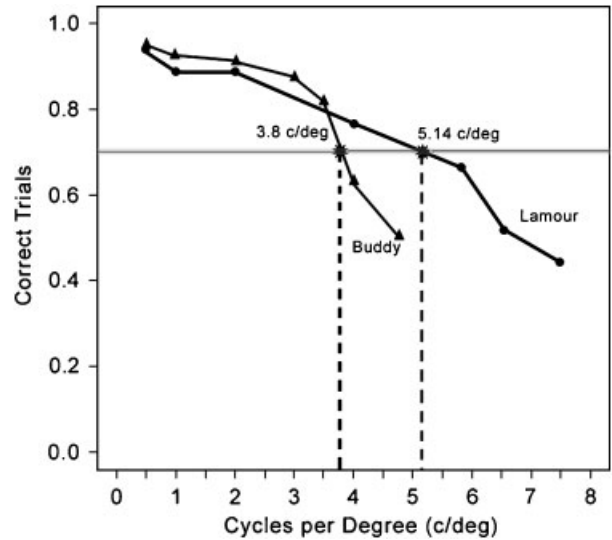Bold values indicate spatial frequencies immediately surrounding criterion threshold.

Fig. 2. Results of *Eulemur macaco flavifrons* behavioral visual acuity trials. Proportion of correct trials on y-axis, grating size (measured in cycles per degree) on x-axis. Estimated maximum visual acuity for each subject (indicated by the star) derived from the point the psychophysical function crosses the criterion level at 70% correct performance.

repeated a second time beginning at the penultimate frequency that had exceeded criterion. For Lamour, testing continued until a minimum of 200–300 trials per spatial frequency had been performed at the frequencies closest to the acuity threshold (immediately above and below 70% correct performance). Time constraints limited tests with Buddy to 100–180 trials per spatial frequency for all but the lowest spatial frequency. The number of trials completed by the subjects at each spatial frequency is summarized in Table I. Both subjects improved performance across all spatial frequencies above their thresholds as the study progressed, likely a result of prolonged exposure to the testing routine.

Comparative Primate Visual Acuity

In addition to behavioral measurements, visual acuity can be estimated anatomically using peak visual cell density and spacing [Pettigrew et al., 1988]. To facilitate interspecific comparisons of primate visual acuity, we calculated maximum visual acuity for two primate species (the nocturnal lemuriform *Cheirogaleus medius* and the nocturnal haplorhine *Tarsius syrichta*) using published estimates of peak ganglion cell density [Tetreault et al., 2004] and eye length [Ross & Kirk, 2007]. Following Pettigrew et al.'s [1988] methodology, posterior nodal distance (PND) was calculated using the constant $k = 0.52$ (the mean for nocturnal vertebrates)∗eye length. The retinal magnification factor (RMF) was then calculated: RMF = $(2\pi * PND)/360$. Visual acuity in c/deg was then calculated as: acuity = (RMF∗$\sqrt{}$peak ganglion cell density)/2.

RESULTS

In 5 months of testing, Lamour completed 1718 trials across seven spatial frequencies. In the 2

months that Buddy was involved in the study, he completed 846 trials across seven spatial frequencies. The results for both lemurs are presented in Figure 2. At the lowest spatial frequencies tested (0.5–2.0 c/deg), both subjects correctly discriminated the rewarded grating orientation (vertical) from the nonrewarded grating orientation (horizontal) about 90% of the time. These high discrimination values ultimately declined to performance near chance (50%) with increasing spatial frequency. Lamour reached chance performance at 6.5 c/deg, whereas Buddy reached chance performance at only 4.75 c/deg. The tested spatial frequencies bracketing 70% correct performance were 4.0 c/deg (77% correct) and 5.81 c/deg (66% correct) for Lamour, and 3.5 c/deg (82% correct) and 4.0 c/deg (63% correct) for Buddy. Extrapolating from the psychometric functions shown in Figure 2 and applying a threshold criterion of 70% correct, maximum visual acuity is estimated at 5.1 c/deg for Lamour and 3.8 c/deg for Buddy.[2]

Maximum theoretical visual acuity for *C. medius* was calculated using an eye length of 10.3 mm and peak retinal ganglion cell density of 3,700 [Tetreault et al., 2004; Ross & Kirk, 2007]. Using these values and Pettigrew et al.'s [1988] formula, PND = 5.36 mm, RMF = 0.093 mm per degree of visual angle, and maximum theoretical visual acuity for *Cheirogaleus* is 2.8 c/deg. For *T. syrichta*, with a 17 mm eye size and 13,300 ganglion cell

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[2]Using a 75% threshold criterion, visual acuity is estimated for Lamour at 4.28 c/deg and Buddy at 3.68 c/deg.

density, PND = 8.84 mm, RMF = 0.154 mm per degree of visual angle, and maximum visual acuity is 8.9 c/deg.

DISCUSSION

Visual Acuity in *E. macaco*

The behavioral estimates of visual acuity for *Eulemur* in this study are within the range of acuity values (2.8–6.7 c/deg) reported for other strepsirrhines (Table II). Functionally, these results indicate that in typical indoor light (200 lx) at a distance of 1.53 m, the *Eulemur* subjects were able to visually resolve individual parallel black lines spaced 2.58 and 3.49 mm apart on a white background (equivalent to 5.1 and 3.8 c/deg for Lamour and Buddy, respectively). These acuity values are slightly lower than those found for ring-tailed lemurs (*L. catta*) in a similar study [Neuringer et al., 1981], and considerably lower than visual acuity reported for diurnal haplorhines [Cowey and Ellis, 1967; De Valois et al., 1974; Spence, 1934; Troilo et al., 1993].

The observed 1.3 c/deg difference in acuity between the two *Eulemur* subjects may reflect normal inter-individual variation. Although Neuringer et al. [1981] found slightly lower variation in acuity between two *L. catta* test subjects (0.7 c/deg), more substantial inter-individual variation (>10 c/deg) has been documented in *Pan, Macaca,* and *Saimiri* [Cowey & Ellis, 1967; Spence, 1934]. Because visual acuity decreases with age in humans and rats [Blake & Sekuler, 2006; Katz & Robison, 1986], the higher acuity of the older female (Lamour: 16 years old, 5.1 c/deg) compared with the juvenile male (Buddy: 3 years old, 3.8 c/deg) is somewhat surprising. One factor that may have influenced the male's lower acuity is variation in early formative viewing environments. A large body of research on visual experience in mammals suggests that adult visual function is affected by experiences during development [Fagiolini et al., 1994; Mitchell, 1988; Nucci et al., 2003]. Although Lamour was wild-caught, and thus exposed to a more natural viewing environment during her early development, captive-born Buddy developed in a visual environment lacking natural stimuli (e.g. sunlight, long lines of sight). The artificial environments in which captive subjects are raised may limit their visual acuity [Bauer et al., 2003]. If true, effects of captivity on acuity could have important implications for comparative analyses, as most subjects of behavioral tests are captive born. The limited sample size of this study, however, does not permit differentiation between normal inter-individual variation and potential developmental effects.

Additionally, it is not known how distance from the test stimuli affects visual acuity in this species. Although pigeon acuity is maximal at 10 cm and falls to 50% of maximum acuity at 35 cm [Rounsley &

TABLE II. Non-anthropoid Primate Visual Acuity Values and Ecological Variables

Common name	Scientific name	Infraorder	Activity pattern	% Diet fauna	Method	Visual acuity	Source
Blue-eyed black lemur	*Eulemur macaco flavifrons*	Lemuriformes	Cathemeral	0.6%[a]	Behavioral—2AFC	3.8–5.1 c/deg, mean = 4.45 c/deg (n = 2)	This study
Ring-tailed lemur	*Lemur catta*	Lemuriformes	Diurnal	<0.5%[b]	Behavioral—2AFC	6.1–6.7 c/deg, mean = 6.4 c/deg (n = 2)	Neuringer et al. [1981]
Gray mouse lemur	*Microcebus murinus*	Lemuriformes	Nocturnal	~38%[c]	Anatomical—pRGC	4.2 c/deg	Dkhissi-Benyahya et al. [2001]
Fat-tailed dwarf lemur	*Cheirogaleus medius*	Lemuriformes	Nocturnal	~20%[c]	Anatomical—pRGC	2.8 c/deg	This study
Greater galago	*Otolemur crassicaudatus*	Lorisiformes	Nocturnal	5%[d]	Behavioral—2AFC	4.9 c/deg	Langston et al. [1986]
Senegal bushbaby	*Galago senegalensis*	Lorisiformes	Nocturnal	52%[d]	Behavioral – 2AFC	6.7 c/deg	Treff [1967]
Philippine tarsier	*Tarsius syrichta*	Tarsiiformes	Nocturnal	100%[d]	Anatomical—pRGC	8.9 c/deg	This study

2AFC (two-alternative forced-choice test), pRGC (peak retinal ganglion cell density).
[a]Sources for dietary data: Colquhoun [1997].
[b]Sources for dietary data: Simmen et al. [2003].
[c]Sources for dietary data: Hladik et al. [1980].
[d]Sources for dietary data: Bearder [1987].

McFadden, 2005], tree squirrel acuity does not systematically differ at distances of 30 and 50 cm [Jacobs et al., 1982]. Without an understanding of the role and degree of accommodation in strepsirrhine visual acuity, caution must be exercised in extrapolating acuity to different viewing distances.

Influences on Primate Visual Acuity

Before this study, published measurements of visual acuity were available for only four strepsirrhine species (Table II). In three of these species (*L. catta*, *G. senegalensis*, and *O. crassicaudatus*), acuity was measured behaviorally using forced choice testing paradigms. In *M. murinus*, however, visual acuity was estimated anatomically from peak retinal ganglion cell density and spacing [Dkhissi-Benyahya et al., 2001]. In this study, anatomical acuity was calculated for two additional primates: *C. medius* and *T. syrichta*. Although behavioral tests are generally considered the best means of measuring visual acuity [Arrese et al., 2000; Prusky et al., 2000], anatomical methods have the advantage of avoiding time-consuming training and testing periods, and may also be used to measure acuity in intractable test subjects. Because they calculate maximum theoretical visual acuity directly from counts of visual cells (avoiding possible acuity restrictions in higher processing areas), anatomical methods can potentially overestimate acuity compared with behavioral methods. However, the values determined by anatomical methods have been found to approximate behavioral acuity values in a number of mammalian taxa, including primates [Arrese et al., 1999, 2000; Dkhissi-Benyahya et al., 2001; Jacobs et al., 1982; Kiltie, 2000; Pettigrew et al., 1988].

With the addition of data for *E. macaco, C. medius*, and *T. syrichta*, reliable estimates of visual acuity are now available for seven non-anthropoid primate species (Table II). Although this small sample size limits the potential to conduct meaningful statistical analyses, qualitative comparisons suggest that activity pattern, diet, and phylogeny may all influence visual acuity in primates (Fig. 3). Studies of retinal anatomy and eye morphology [Kay & Kirk, 2000; Kirk, 2006b; Peichl et al., 2001] have suggested that visual acuity in primates should vary according to activity pattern. As predicted, the diurnal lemuriform *L. catta* exhibits higher mean visual acuity (6.4 c/deg) than the cathemeral (4.45 c/deg) and nocturnal (2.8–4.2 c/deg) lemuriforms sampled (Fig. 3). Surprisingly, however, the nocturnal lorisiform *G. senegalensis* exhibits slightly higher visual acuity (6.7 c/deg) than *L. catta*, and the nocturnal haplorhine *T. syrichta* exhibits much higher acuity (8.9 c/deg) than *L. catta* (Table II). Also contrary to predictions, the mean acuity for cathemeral *E. macaco* is only slightly higher than that of other nocturnal lemuriforms, and
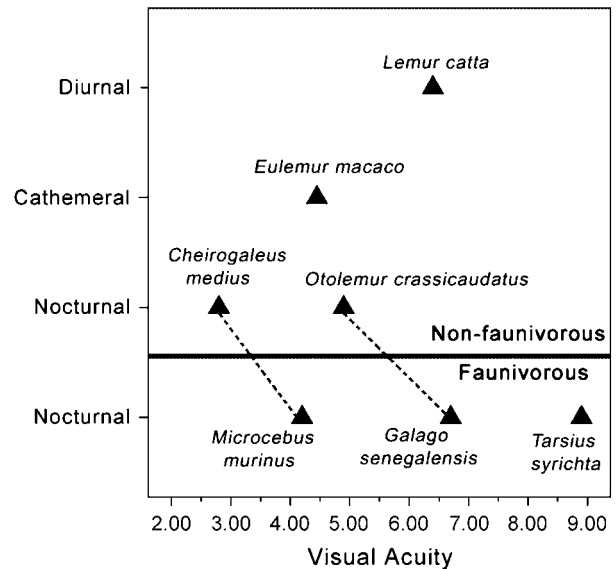

Fig. 3. Non-anthropoid primate visual acuity and ecology. Currently known prosimian visual acuity values (measured in cycles per degree), separated by activity pattern and diet. *Lemur catta* and *Eulemur macaco* points represent the means of the two measured individuals in each species, whereas the remaining points represent a single measurement per species. The bold line separates more faunivorous taxa ("Faunivorous") from less faunivorous taxa ("Nonfaunivorous"), whereas the dotted lines unite closely related pairs of nocturnal primates. Data sources from Table II.

the lower value (Buddy: 3.8 c/deg) is within the nocturnal lemuriform range. Additionally, when compared with other primates, *E. macaco* mean visual acuity is lower than that reported for the nocturnal lorisiform *O. crassicaudatus* (4.9 c/deg), *G. senegalensis*, and *T. syrichta* (Fig. 3). These data call into question whether cathemeral and nocturnal strepsirrhines consistently differ in visual acuity, as has been predicted by visual anatomy. Unfortunately, final resolution of this question awaits a larger sample size.

Together, these findings suggest that activity pattern is only one of several selective factors that influence visual acuity. Diet also appears to play an important role in determining a species' maximum acuity. Indeed, the two species with the highest acuity in Table II (*G. senegalensis* and *T. syrichta*) are also the most faunivorous taxa considered in this analysis. Furthermore, in both the cheirogaleids *Cheirogaleus* and *Microcebus*, and the galagids *Otolemur* and *Galago*, the more predatory taxon has higher visual acuity than its less predatory close relative. Additionally, *Tarsius*, as the most faunivorous taxon, has higher visual acuity than any strepsirrhine. These lines of evidence provide further support for the hypothesis that faunivory favors increased visual acuity in primates generally [Kirk, 2006c; Ross & Kirk, 2007; Tetreault et al., 2004]. In this respect, primates appear to resemble other mammals [Ross & Kirk, 2007]. Arrese et al. [1999],

for example, found that predatory marsupials generally exhibit higher acuity compared with herbivorous species. Similarly, Mass [1992] suggests that the higher acuity of predatory fur seals relative to benthic-feeding walruses may be influenced by dietary differences.

The unexpectedly high visual acuity calculated here for *T. syrichta* (Fig. 3) also supports the hypothesis that phylogeny is an important factor influencing visual acuity in primates [Kirk & Kay, 2004; Ross, 1996, 2000, 2004]. Although substantially lower than that of diurnal haplorhines, our anatomical estimate of acuity for *Tarsius* (8.9 c/deg.) is higher than that of any strepsirrhine yet measured. Maximum acuity in *T. syrichta* is also not substantially different from that reported for the only other clade of night-active haplorhines: owl monkeys (cathemeral *Aotus azarae*—8.3 c/deg [Yamada et al., 2001]; nocturnal *A. trivirgatus*—10 c/deg. [Jacobs, 1977]). Like other haplorhines, tarsiers exhibit a number of anatomical adaptations that support this high visual acuity, including large eyes, a postorbital septum, and a retinal fovea [Collins et al., 2005; Hendrickson et al., 2000; Kirk & Kay, 2004; Kirk, 2006c; Martin & Ross, 2005; Ross, 1994, 2000, 2004; Ross & Kirk, 2007]. Although the faunivorous diet of tarsiers may play an important role in selection to maintain high acuity despite a nocturnal activity pattern, the unique phylogenetic history of *Tarsius* may also be a significant variable. Tarsiers are hypothesized to have evolved from a diurnal and predatory haplorhine ancestor that already possessed a retinal fovea and relatively high acuity [Kirk & Kay, 2004; Ross, 2000, 2004]. Thus, although the selection pressures acting on tarsier visual systems (i.e. diet and activity pattern) may be similar to those acting on nocturnal strepsirrhines, the unusually high visual acuity of *Tarsius* may be the combined product of its unique evolutionary history and its highly specialized ecology.

Although the addition of data for *E. macaco*, *C. medius*, and *T. syrichta* substantially expand the number of nonanthropoid primates with known visual acuity, more measurements are needed to increase the diversity of species and sample sizes. Larger sample sizes will permit an examination of the effects of captivity on visual acuity. Data for more species with disparate activity patterns and diets will also provide a better understanding of ecological effects on visual acuity in primates. Despite the small samples currently available, the data presented here suggest that activity pattern, diet, and phylogenetic relationships all influence visual acuity in primates. In particular, the effect of activity pattern on acuity appears to be modulated by the role of vision in foraging. Within nocturnal taxa, increased faunivory is associated with higher acuity. Visual predation thus appears to exert a strong selective pressure for increased visual acuity within primates. Although the results of this analysis cannot discriminate among the validity of diurnal, cathemeral, or nocturnal hypotheses for primate origins, they do suggest that visual predation played an important role in the evolution of enhanced visual acuity in the primate stem lineage [Kirk & Kay, 2004; Ross & Kirk, 2007]. These results are thus consistent with the visual predation hypothesis of primate origins [Cartmill, 1992].

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