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Effects of Habitat Light Intensity on Mammalian Eye Shape

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ABSTRACT

Many aspects of mammalian visual anatomy vary with activity pattern, reflecting the divergent selective pressures imposed by low light and high light visual environments. However, ambient light intensity can also differ substantially between and within habitats due to differences in foliage density. We explored the effects of interhabitat and intrahabitat variation in light intensity on mammalian visual anatomy. Data on relative cornea size, activity pattern, and habitat type were collected from the literature for 209 terrestrial mammal species. In general, mammalian relative cornea size significantly varied by habitat type. In within-order and across-mammal analyses, diurnal and cathemeral mammals from forested habitats exhibited relatively larger corneas than species from more open habitats, reflecting an adaptation to increase visual sensitivity in forest species. However, in all analyses, we found no habitat-type effect in nocturnal species, suggesting that nocturnal mammals may experience selection to maximize visual sensitivity across all habitats. We also examined whether vertical strata usage affected relative cornea size in anthropoid primates. In most analyses, species occupying lower levels of forests and woodlands did not exhibit relatively larger corneas than species utilizing higher levels. Thus, unlike differences in intensity between habitat types, differences in light intensity between vertical forest strata do not appear to exert a strong selective pressure on visual morphology. These results suggest that terrestrial mammal visual systems reflect specializations for habitat variation in light intensity, and that habitat type as well as activity pattern have influenced mammalian visual evolution. Anat Rec, 294:905–914, 2011. © 2011 Wiley-Liss, Inc.

Key words: eye; cornea; ecology; light intensity; habitat type; vertical stratification

In terrestrial habitats, nocturnal and diurnal visual environments differ dramatically in the intensity and quality of ambient light (Lythgoe, 1979; Pariente, 1980; Johnsen et al., 2006). Because nocturnal mammals are active in low light levels, they are under selection to maximize sensitivity to weak light stimuli at the expense of enhanced visual acuity (Walls, 1942; Kirk, 2004; Land and Nilsson, 2006). In contrast, diurnal mammals are free to increase visual acuity, because they are active in high light environments where enhanced visual sensitivity is unnecessary (Walls, 1942; Kirk, 2004).

A number of studies have documented differences in ocular anatomy between nocturnal and diurnal mammals that support the predictions of divergent selective pressure. Nocturnal mammals are characterized by relatively larger and rounder corneas and lenses, shorter focal lengths, and larger maximum pupil areas (Walls, 1942; Hughes, 1977; Pettigrew et al., 1988; Ross, 2000;

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Kirk, 2004, 2006a,b; Ross and Kirk, 2007). These adaptations enhance visual sensitivity by increasing the amount of light admitted to the eye and by forming a brighter retinal image (Walls, 1942; Ross, 2000; Kirk, 2004). In contrast, the smaller and more flattened corneas and lenses, longer focal lengths, and smaller maximum pupil areas found in diurnal mammals increase the size and clarity of the retinal image, enhancing visual acuity (Walls, 1942; Hughes, 1977; Pettigrew et al., 1988; Kirk, 2004, 2006a,b; Ross and Kirk, 2007). Within the retina, nocturnal and diurnal mammals also significantly differ in the number of photoreceptors synapsing on a single ganglion cell (retinal summation) and the ratios of rod to cone photoreceptors (Walls, 1942; Rohen and Castenholz, 1967; Pettigrew et al., 1988; Yamada et al., 1998; Arrese et al., 1999; Ahnelt and Kolb, 2000; Kay and Kirk, 2000; Peichl et al., 2000; Yamada et al., 2001; Kirk and Kay, 2004). Measurements of visual acuity for nocturnal and diurnal mammals support the results of these anatomical studies. Namely, diurnal species generally have higher visual acuity than nocturnal species (Walls, 1942; Pettigrew et al., 1988; Arrese et al., 1999; Kiltie, 2000; Ross, 2000; Kirk and Kay, 2004; Veilleux and Kirk, 2009). Additionally, anatomical and behavioral evidence from cathemeral (arrhythmic) mammals suggest intermediate adaptations balancing sensitivity for nocturnal activity and acuity for diurnal activity (Walls, 1942; Rohen and Castenholz, 1967; Pettigrew et al., 1988; Arrese et al., 1999; Kirk, 2004, 2006a; Veilleux, 2008; Veilleux and Kirk, 2009).

Although the effects of activity pattern on visual anatomy and function are well-established, relatively little work has explored how mammalian visual systems reflect specializations for habitat differences in light environments (Hughes, 1977, Schiviz et al., 2008). As with nocturnal and diurnal light environments, light intensity can differ dramatically between and within terrestrial habitats, often due to differences in foliage density (Endler, 1993). Controlling for time of day, open habitats such as grasslands generally exhibit higher light intensities than closed forest habitats (Endler, 1993). Meanwhile, woodland habitats are intermediate between open and closed habitats in ambient light levels (Endler, 1993). Light intensity also steeply decreases downward through a forest canopy (Endler, 1993; Koop and Sterck, 1994). Indeed, in many different types of closed forest habitats, only a very small percentage of direct light (range, 0.5%–7%) is transmitted to the understory (Chazdon and Pearcy, 1991; Lieffers et al., 1999). These studies suggest that substantial differences in light intensity can exist not only between habitats but also between microhabitats within a given area. Following functional expectations (Walls, 1942; Hughes, 1977; Kirk, 2004), one would predict that mammalian visual systems may exhibit specializations for habitat/microhabitat differences in light intensity.

Much of the research on habitat effects on mammalian visual anatomy has focused on identifying substrate effects (arboreal versus terrestrial) rather than ambient light effects. Hughes's "terrain hypothesis" (1974, 1977), for example, proposes that retinal cell topography and distribution reflects arboreal and terrestrial adaptations to visual environments. Terrestrial species with predominantly two-dimensional visual environments typically exhibit a horizontally elongated region of high cell density within the retina called a "visual streak," whereas arboreal species in more three-dimensional visual environments have a concentric region of high cell called an "area centralis" (Hughes, 1977; Schiviz et al., 2008). In support of the terrain hypothesis, terrestrial artiodactyls living in open habitats and forests have cone visual streaks, whereas species from mountainous terrain (which is arboreal-like in three-dimensional visual environment) exhibit cone topography intermediate between arboreal and terrestrial mammals (Schiviz et al., 2008). Similarly, terrestrial primates have more horizontally elongated eye outlines (suggested to be an adaptation to extend the visual field for improved horizontal scanning) than arboreal and semiarboreal species (Kobayashi and Koshima, 2001).

Although microhabitat effects on mammalian visual anatomy has not been demonstrated previously, evidence from other vertebrates suggests that microhabitat light environments can influence an animal's visual anatomy, coloration, and behavior (Endler, 1992; Théry, 2001). For example, Leal and Fleishman (2002) propose that microhabitat light characteristics are responsible for variation in retinal cone spectral sensitivity and dewlap coloration in two closely related species of *Anolis* lizards. Similarly, rainforest birds often adapt their plumage color displays to the ambient light of their preferred canopy level (Endler, 1992; Théry, 2001). Because foliage preferentially absorbs shorter wavelengths, blue light availability decreases vertically downward through forest canopies (Endler, 1993). Thus, in French Guiana, canopy birds utilize brighter and bluer colors while understory birds utilize darker and redder colors (Théry, 2001). Even seasonal differences in light environments have been found to affect avian plumage displays and breeding seasons (Endler, 1992; Théry, 2006).

The goal of this study was to examine the relationship between habitat type and eye morphology in mammals to explore whether habitat/microhabitat differences in light intensity have imposed differential selective pressure on mammalian visual systems. Eye morphology was quantified using a measurement of eye shape (size of the cornea relative to eye length) known to vary by activity pattern (Fig. 1; Walls, 1942; Kirk, 2004, 2006a; Ross and Kirk, 2007). Using a large sample of mammalian taxa, we first tested the relationship between relative cornea size and habitat type (closed, woodland, and open). For a smaller sample of diurnal anthropoid primates that live in closed forest and woodland habitats, we then examined the relationship between relative cornea and forest stratum use. Following our functional expectations, we predicted that within an activity pattern, mammals endemic to closed habitats have larger corneas relative to eye size than mammals occupying more open habitats to enhance visual sensitivity. Similarly, we predicted that primates typically occupying lower strata have larger corneas relative to eye size than species that use higher forest strata.

MATERIALS AND METHODS

Visual Anatomy and Ecology Datasets

Mean cornea size, eye axial diameter, and activity pattern for 209 terrestrial mammals representing nine major clades (artiodactyls, carnivorans, metatherians, perissodactyls, anthropoid primates, strepsirrhine

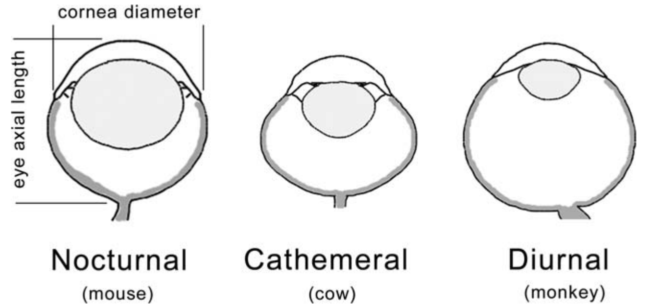

Fig. 1. Schematic comparison of mammalian eye shapes by activity pattern. Nocturnal species have relatively broad corneal diameters relative to the length of the eye, which increases the amount of light admitted to the retina (Ross, 2004; Kirk, 2004). Diurnal species have small corneal diameters relative to eye length, which enhance visual acuity by aiding in increasing the size of the retinal image and decreasing the distortions of peripheral light rays on image clarity (Ross, 2000; Kirk, 2004). Cathemeral mammals exhibit intermediate morphology (Kirk, 2006a).

primates, rodents, xenarthrans, and macroscelideans) were obtained from the literature (Ross and Kirk, 2007). Marsupial taxa were combined into a metatherian clade following Kirk (2006a). Because diurnal anthropoids have highly derived small corneas (Ross, 2000; Kirk, 2004; Ross and Kirk, 2007), the primate order was divided into anthropoid and strepsirrhine clades. Relative cornea size ($C{:}A$) was calculated by dividing cornea diameter by eye axial length following Kirk (2006a) and Ross and Kirk (2007). Habitat data were collected from the literature for each species (Supporting Information Table 1). Habitats were divided into three light-dependent categories: (1) "open," representing high light intensity environments with little to no foliage cover (including savannas, deserts, steppes, marshes, and rocky country); (2) "woodland," representing intermediate light intensity environments with some foliage cover but lacking closed canopy (including woodlands, thickets, spiny desert, and scrub); and (3) "forest," representing low light intensity environments with at least seasonal

TABLE 1. Intraclade analyses of relative cornea size and habitat in nine mammalian clades[a]

Clade	Activity Pattern	Habitat	*n*	Median–Range	Kruskal–Wallis/Mann–Whitney Statistics
Artiodactyla	**Diurnal**	**Forest**	**1**	**0.73**	**n/a**
		Open	**2**	**0.70–0.07**	
	Cathemeral	**Forest**	**5**	**0.74–0.09**	**$H = 3.05$, $P = 0.109$**
		Woodland	**7**	**0.75–0.07**	
		Open	**9**	**0.72–0.08**	
	Nocturnal	**Forest**	**2**	**0.90–0.13**	**n/a**
		Open	**1**	**0.79**	
Carnivora	**Diurnal**	**Forest**	**3**	**0.82–0.19**	**$U = 0.00$, $P = 0.10$**
		Open	**2**	**0.59–0.04**	
	Cathemeral	**Forest**	**10**	**0.77–0.23**	**$H = 2.23$, $P = 0.164$**
		Woodland	**3**	**0.69–0.23**	
		Open	**5**	**0.72–0.20**	
	Nocturnal	Forest	7	0.79–0.30	$H = 0.55$, $P = 0.380$
		Woodland	3	0.87–0.04	
		Open	3	0.86–0.21	
Metatheria	Cathemeral	Forest	2	0.81–0.01	n/a
	Nocturnal	Forest	15	0.90–0.15	$U = 27.5$, $P = 0.405$
		Woodland	4	0.88–0.07	
Perissodactyla	Cathemeral	Woodland	2	0.64–0.12	$U = 3.00$, $P = 0.400$
		Open	4	0.67–0.09	
Primates: Anthropoidea	**Diurnal**	**Forest**	**45**	**0.54–0.15**	**$H = 9.02$, $P = 0.005$***
		Woodland	**5**	**0.53–0.14**	
		Open	**2**	**0.47–0.05**	
Primates: Strepsirrhini	Diurnal	Forest	5	0.74–0.06	n/a
		Woodland	1	0.77	
	Cathemeral	**Forest**	**4**	**0.79–0.01**	**n/a**
		Woodland	**1**	**0.76**	
	Nocturnal	**Forest**	**10**	**0.84–0.11**	**$U = 11.5$, $P = 0.228$**
		Woodland	**3**	**0.82–0.07**	
Rodentia	**Diurnal**	**Forest**	**5**	**0.81–0.11**	**$U = 2.50$, $P = 0.072$**
		Woodland	**1**	**0.83**	
		Open	**3**	**0.65–0.19**	
	Cathemeral	**Forest**	**5**	**0.92–0.06**	**$H = 3.46$, $P = 0.09$**
		Woodland	**2**	**0.95–0.03**	
		Open	**4**	**0.88–0.06**	
	Nocturnal	Forest	4	0.93–0.12	$H = 0.907$, $P = 0.318$
		Woodland	3	0.90–0.09	
		Open	3	0.93–0.06	
Xenarthra	Cathemeral	Forest	2	0.68–0.02	$U = 0.00$, $P = 0.067$
		Open	4	0.75–0.07	
	Nocturnal	Forest	2	0.79–0.10	n/a
		Open	2	0.85–0.21	
Macroscelidea	Diurnal	Forest	1	0.86	n/a
		Woodland	2	0.92–0.09	

[a] Subgroups in bold reflect the predicted direction of the relationship.

*Indicates a significant result.

TABLE 2. The relative cornea size (*C*:A) of congeneric mammalian pairs inhabiting different habitat light environments[a]

Genus	Activity Pattern	Relative Light Intensity: Lower	Relative Light Intensity: Higher
Strepsiceros	Cathemeral	0.75	0.79
Taurotragus	**Cathemeral**	**0.81**	**0.72**
Tragulus	**Nocturnal**	**0.96**	**0.83**
Ursus	**Cathemeral**	**0.75**	**0.72**
Didelphis	**Nocturnal**	**0.91**	**0.88**
Callithrix	**Diurnal**	**0.56**	**0.52**
Eulemur	Cathemeral	0.79	0.78
Panthera	Cathemeral	0.69	0.70
Tolypeutes	Cathemeral	0.69	0.77

[a]Genera in bold reflect the predicted relationship.

Note: *Tragulus* species are both "forest" but inhabit different types of forest habitats with differing light intensities. We averaged *C*:*A* values for *Eulemur* species; "lower intensity" is the mean of three forest species and "higher intensity" is the mean of two woodland species.

closed canopies (including deciduous forests, rainforests, and humid forests). Further, for diurnal anthropoids from forest and woodland habitats ($n = 35$ species), vertical stratum usage (defined as "upper," "middle," or "lower") was collected from the literature (Supporting Information Table 2). Species were assigned to strata categories based on the authors' own descriptions. Species inhabiting the canopy were considered to use the "upper" strata. We excluded strepsirrhine primates from these canopy analyses because they are not directly comparable with diurnal anthropoids in their eye morphology (Kirk, 2004), and we did not have sufficient sample sizes to compare strata effects within strepsirrhines.

Whether species adapt to the resources or environments they utilize most frequently or to the ones they utilize in selectively critical periods is debated. A number of studies have suggested that anatomical features are often adaptations to exploit "fallback" resources rather than preferred or primary resources (Kay, 1975; Terborgh, 1983; van Schaik et al., 1993; Lambert et al., 2004). Following this theoretical framework, when a species was described as utilizing habitats (or strata) from multiple light intensity categories that species was assigned to the lowest light intensity category listed. Similarly, species from seasonal dry forests, which can have dry season woodland light environments (Endler, 1992), were classified as "forest." This procedure makes the assumption that decreased visual sensitivity in low light environments is more detrimental than having increased sensitivity in relatively higher light environments. This assumption is supported anatomically, as species with large corneas adapted to lower light environments can opportunistically decrease their pupil size in brighter light intensities (Walls, 1942).

Statistical Analyses

We used multiple approaches to test our predictions. When sample sizes were particularly small (i.e., <9), analyses resulting in *p*-values of less than or equal to 0.1 were considered to be a trend. Tests were one-tailed when we had an *a priori* hypothesis. All statistical tests were performed in SPSS 15.0.

Habitat type. Kirk (2006a) found substantial variation in relative cornea sizes across higher mammalian clades in addition to the significant variation between activity patterns. Therefore, to control for possible phylogenetic effects on mammalian relative cornea size, we conducted several different analyses.

Relative cornea index. We developed a clade-adjusted *C*:*A* value for each species, the relative cornea index (RCI). To determine RCI, each clade was divided into subgroups by activity pattern. We tested each subgroup with χ^2 tests to verify that each habitat category had similar numbers of species. Three subgroups (diurnal anthropoids, cathemeral metatherians, and nocturnal metatherians) had significantly uneven numbers of species among habitat types and were excluded from the RCI analysis. The RCI value for each species was then calculated as (subgroup mean—observed *C*:*A*)/(subgroup standard deviation). Thus, RCI represents a *z*-score to compare relative cornea size between habitats across all mammals of the same activity pattern. This method allows us to compare relative cornea size across clades with differing "baseline" eye morphology. We compared RCI values among habitat types using one-tailed Kruskal–Wallis tests and *post hoc* Mann–Whitney *U* tests.

Intraclade analysis. We also directly tested *C*:*A* variation by habitat type among species of the same activity pattern within clades (i.e., cathemeral artiodactyls) using nonparametric one-tailed Kruskal–Wallis tests with *post hoc* Mann–Whitney *U* tests.

Matched-pairs analysis. Finally, we utilized matched congeneric pair analysis from different habitat types (but the same activity pattern) as a further control for possible phylogenetic effects on relative cornea size (Møller and Birkhead, 1993; Thomas et al., 2006). We classified each member of a pair as either "relatively lower light intensity" or "relatively higher light intensity" based on habitat preference. We only considered *C*:*A* differences between congeners greater than 0.02 as truly different, because *C*:*A* ratios less than 0.02 could reflect simple measuring error in the original anatomical collecting methods. We used a one-tailed sign test to compare relative light intensity and *C*:*A*. If multiple congeners inhabited the same light habitat, their average *C*:*A* was used to represent that light intensity.

Vertical strata usage. We used three analyses to test for vertical strata effects on relative cornea size in diurnal anthropoid primates.

Direct strata analysis. We directly compared *C*:*A* between diurnal anthropoids from upper, middle, and lower canopy levels in forest and woodland habitats with one-tailed Mann–Whitney U tests.

Sympatric species. Data on vertical habitat stratification in sympatric diurnal anthropoid primates were collected from the literature for 10 research sites: Lomako Reserve, Democratic Republic of Congo (McGraw, 1994); Urucu River, Brazil (Peres, 1993); Maraca Island, Brazil (Mendes Pontes, 1997); Río Curaray, Peru (Heymann et al., 2002); Ituri Forest, Zaire (Thomas, 1991); Peru (Warner, 2002); Sumatra (Ungar, 1996); East Kalimantan, Indonesia (Rodman, 1991); San Sebastian, Bolivia

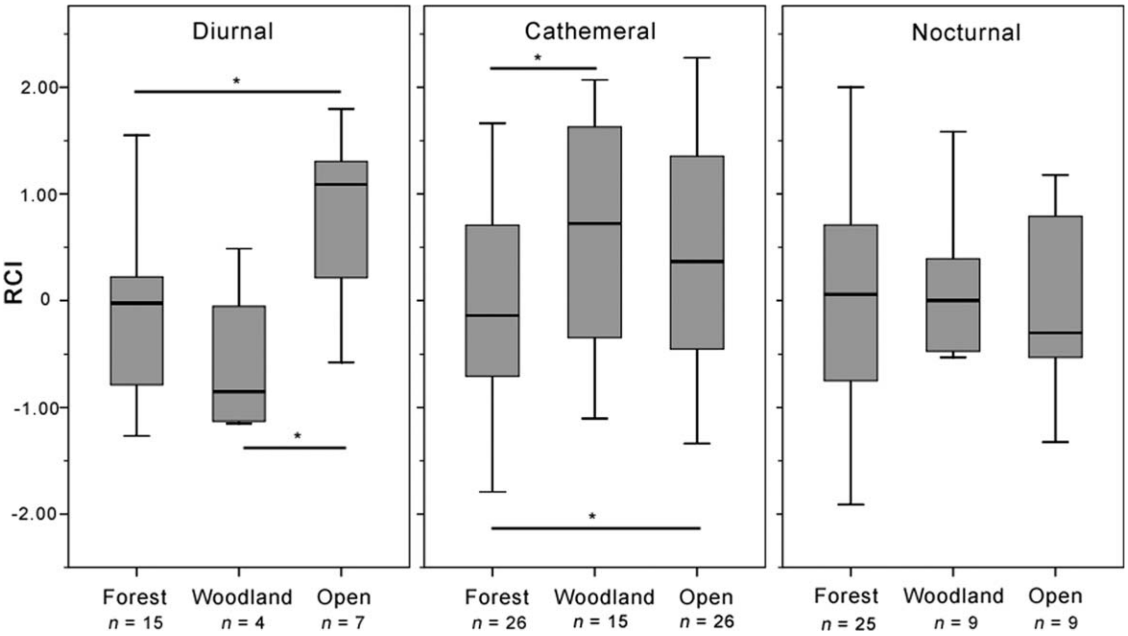

Fig. 2. Quartile box-plots for mammalian relative cornea index (RCI) by habitat type. Higher RCI values signify smaller relative cornea sizes. Diurnal anthropoids, cathemeral metatherians, and nocturnal metatherians were excluded (see Methods). Whiskers represent the highest and lowest values.

(Porter, 2004); and Noel Kempff Mercado National Park, Bolivia (Wallace et al., 1998). For each site, we compared *C:A* among sympatric primates and used a binomial test to determine whether the primates exhibited the predicted relationship (lower strata > middle strata > upper strata) at a significant proportion of the sites.

Matched-pairs analysis. Congeneric pairs were assigned to either “higher strata” or “lower strata” categories depending on their vertical strata usage. To be conservative, we excluded middle strata species from this analysis except where we could directly compare them with sympatric upper/lower species. Because many species were used in multiple comparisons (e.g., five species of *Saguinus*, four species of *Macaca*), the data are not independent. Thus, statistical analyses could not be used.

RESULTS

Eye Shape and Habitat Type

Relative cornea index. After excluding diurnal anthropoids, cathemeral metatherians, and nocturnal metatherians (see Methods), we calculated RCI values for 136 mammalian species. Our results suggest that RCI varies among mammals by habitat (Fig. 2). However, this relationship was influenced by activity pattern. Among diurnal mammals, RCI varied significantly by habitat type (Kruskal–Wallis $H = 6.655$, $df = 2$, $P = 0.018$). *Post hoc* tests indicate that diurnal species living in open habitats had significantly higher RCI (thus smaller relative cornea sizes) than forest (Mann–Whitney $U = 22.00$, $n_{\mathrm{open}} = 7$, $n_{\mathrm{forest}} = 15$, $P = 0.016$) and woodland species (Mann–Whitney $U = 2.00$, $n_{\mathrm{woodland}} = 4$, $P = 0.012$). Diurnal woodland and forest species did not significantly differ in RCI (Mann–Whitney $U = 22.5$, $P = 0.235$). Cathemeral mammals also exhibited a significant relationship between RCI and habitat type (Kruskal–Wallis $H = 4.939$, $df = 2$, $P = 0.043$). Among cathemeral mammals, open and woodland species had significantly higher RCI than forest dwelling species (Mann–Whitney open vs. forest: $U = 236.50$, $n_{\mathrm{open}} = 26$, $n_{\mathrm{forest}} = 26$, $P = 0.032$; woodland vs. forest: $U = 125.5$, $n_{\mathrm{woodland}} = 15$, $P = 0.03$). However, cathemeral open and woodland species did not differ significantly in RCI (Mann–Whitney $U = 183.50$, $P = 0.378$). Unlike diurnal and cathemeral mammals, nocturnal mammals did not vary in RCI by habitat type (Kruskal–Wallis $H = 0.355$, $df = 2$, $P = 0.419$).

Intraclade comparisons. Table 1 summarizes the descriptive and statistical results for the relationship between *C:A* and habitat type in nine mammalian clades. Seven groups were too small for statistical comparisons (diurnal and nocturnal artiodactyls, cathemeral metatherians, diurnal and cathemeral strepsirrhines, nocturnal xenarthrans, and diurnal macroscelideans). Even with relatively small sample sizes, several groups showed significant results or strong trends for a relationship between *C:A* and habitat usage (Fig. 3). Among diurnal anthropoids, *C:A* differs significantly between species from different habitats (Kruskal–Wallis $H = 9.02$, $df = 2$, $P = 0.005$). The *post hoc* tests indicate that open habitat species had significantly smaller *C:A* than forest species (Mann–Whitney $U = 1.00$, $n_{\mathrm{open}} = 2$, $n_{\mathrm{forest}} = 45$, $P = 0.01$) and a trend for smaller *C:A* than woodland species (Mann–Whitney $U = 1.50$, $n_{\mathrm{woodland}} = 5$, $P = 0.085$). Woodland species had significantly smaller *C:A* than forest species (Mann–Whitney $U = 51.00$, $P = 0.023$).

Five additional groups (diurnal rodents, cathemeral rodents, diurnal carnivorans, cathemeral artiodactyls,

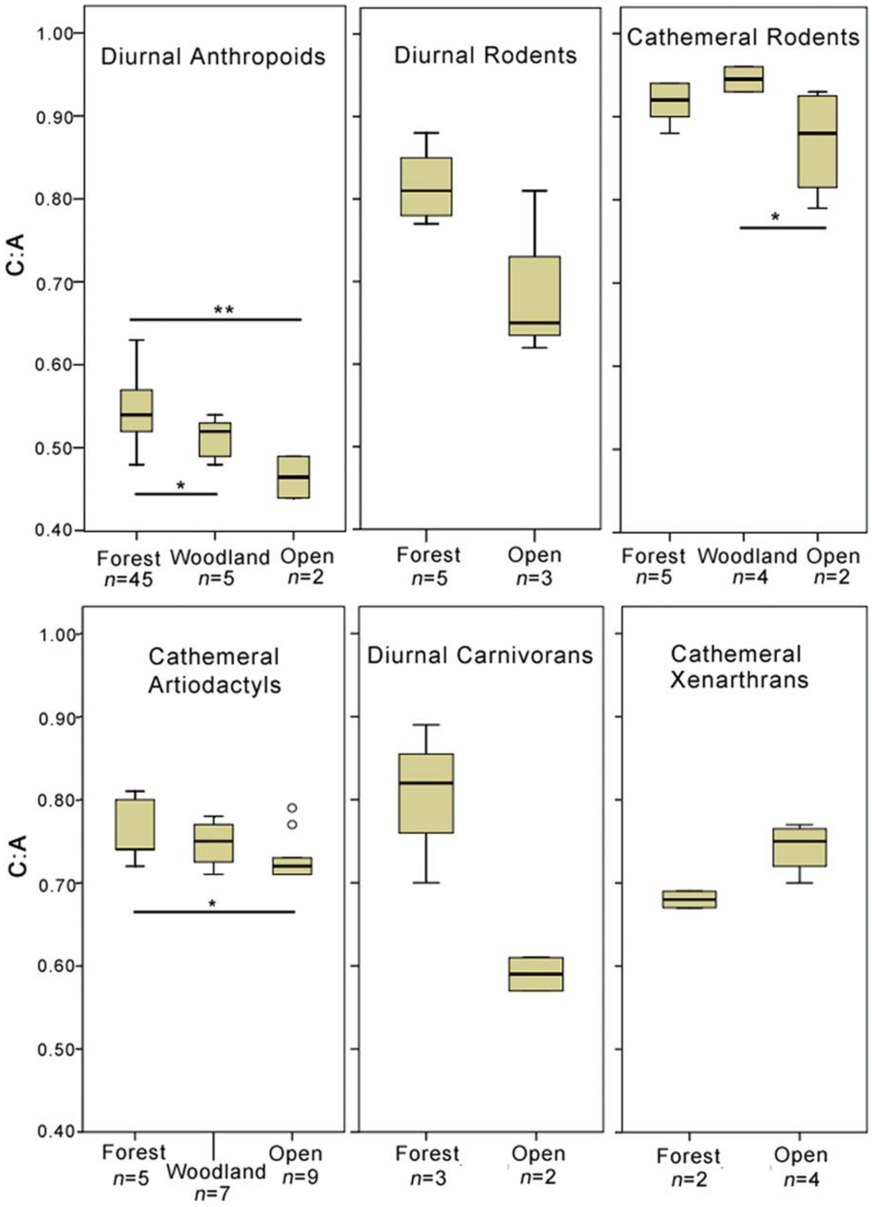

Fig. 3. Quartile box plots for significant or near significant intraclade comparisons of relative cornea size (*C*:*A*) and habitat type. Whiskers represent the highest and lowest values that are not outliers (open circles: between 1.5 and 3 times the interquartile range).

and cathemeral xenarthrans) exhibited trends for *C*:*A* variation by habitat type despite small sample sizes. Among diurnal rodents, open habitat species had smaller *C*:*A* than forest species, although this relationship did not reach significance (Mann–Whitney $U = 2.50$, $n_{\text{open}} = 3$, $n_{\text{forest}} = 5$, $P = 0.072$). Similarly, cathemeral rodents exhibited a trend for *C*:*A* to vary across habitats (Kruskal–Wallis $H = 3.46$, $df = 2$, $P = 0.09$). *Post hoc* tests found that open habitat species exhibited a strong trend to have smaller *C*:*A* than woodland species (Mann–Whitney $U = 0.50$, $n_{\text{open}} = 4$, $n_{\text{forest}} = 2$, $P = 0.05$) but not forest species (Mann–Whitney $U = 5.5$, $n_{\text{forest}} = 5$, $P = 0.133$). Cathemeral woodland and forest rodents did not differ in *C*:*A* (Mann–Whitney $U = 2.0$, $P = 0.121$). Open habitat diurnal carnivorans also exhibited a trend of smaller *C*:*A* compared with forest carnivorans (Mann–Whitney $U = 0.00$, $n_{\text{open}} = 2$, $n_{\text{forest}} = 3$, $P = 0.10$). An analysis of cathemeral artiodactyls was not statistically significant (Kruskal–Wallis $H = 3.05$, $df = 2$, $P = 0.109$). *Post hoc* tests, however, indicate that open habitat cathemeral artiodactyls had significantly smaller *C*:*A* than forest species (Mann–Whitney $U = 9.00$, $n_{\text{open}} = 9$, $n_{\text{forest}} = 5$, $P = 0.042$). Both open habitat versus woodland and woodland versus forest comparisons for cathemeral artiodactyls were not statistically significant (Mann–Whitney open versus woodland: $U = 23.00$, $n_{\text{woodland}} = 7$, $P = 0.204$; woodland versus forest: $U = 14.00$, $P = 0.320$). Although open habitat species exhibited smaller

C:*A* compared with forest species in the rodent, carnivoran, and artiodactyl groups, cathemeral xenarthrans, exhibited the opposite trend. Contrary to predictions, forest dwelling cathemeral xenarthrans had smaller *C*:*A* than open dwelling species (Mann–Whitney $U = 0.00$, $n_{\text{open}} = 4$, $n_{\text{forest}} = 2$, $P = 0.067$). Of the remaining 14 groups with nonsignificant results or sample sizes too small for analysis, five exhibited the predicted relationship of more open-dwelling (open, woodland) species having smaller median *C*:*A* than forest dwelling species (diurnal artiodactyls, nocturnal artiodactyls, cathemeral carnivorans, cathemeral strepsirrhines, nocturnal strepsirrhines).

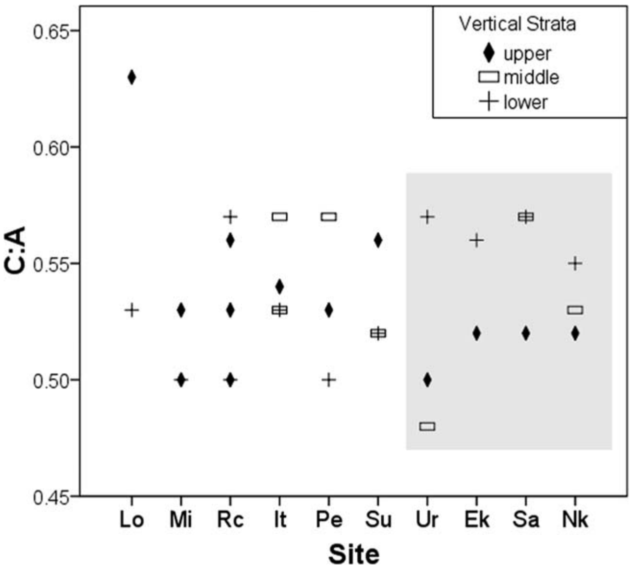

Fig. 4. The relative cornea size (*C*:*A*) of sympatric diurnal anthropoids at 10 field sites. At only four sites (shaded box) do species occupying lower strata exhibit relatively larger corneas than species occupying higher strata. Lo, Lomako Reserve; Mi, Maraca Island; Rc, Río Curaray; It, Ituri Forest; Pe, Peru; Su, Sumatra; Ur, Urucu River; Ek, East Kalimantan; Sa, San Sebastian; Nk, Noel Kempff Mercado National Park.

Matched-pairs analysis. We identified nine congeneric pairs that inhabit different relative light environments (Table 2). A sign test revealed no significant differences in *C*:*A* between congeners from lower and higher light intensity habitats ($P = 0.145$). Of the nine pairs, five exhibited the predicted difference of lower *C*:*A* in the lower light intensity congener, whereas two exhibited the opposite and two showed no difference (≤ 0.02) between congeners from different habitats.

Eye Shape and Vertical Strata Usage

Direct strata analysis. We directly compared *C*:*A* in diurnal anthropoids from forest ($n = 32$) and woodland ($n = 3$) habitats. Among forest anthropoids, *C*:*A* did not significantly differ among upper ($n = 13$, median = 0.53, range = 0.09), middle ($n = 8$, median = 0.55, range = 0.07), and lower strata species ($n = 11$, median = 0.53, range = 0.10; Kruskal–Wallis $H = 1.223$, $df = 2$, $P = 0.271$). Although the relationship between *C*:*A* and strata in woodland species followed predictions (upper *C*:*A* = 0.48; middle *C*:*A* = 0.53; lower *C*:*A* = 0.57), samples size did not permit statistical analysis.

Sympatric species. The vertical distributions of *C*:*A* for sympatric species at the 10 sites is summarized in Fig. 4. Only four of the ten sites followed the predicted relationship of lower strata *C*:*A* > middle strata *C*:*A* > upper strata *C*:*A*, which was not significant in a binomial test ($P = 0.377$).

Matched-pairs analysis. Our sample included 12 congeneric pairs using different vertical strata (Fig. 5). Of these pairs, eight followed predictions of lower *C*:*A* in

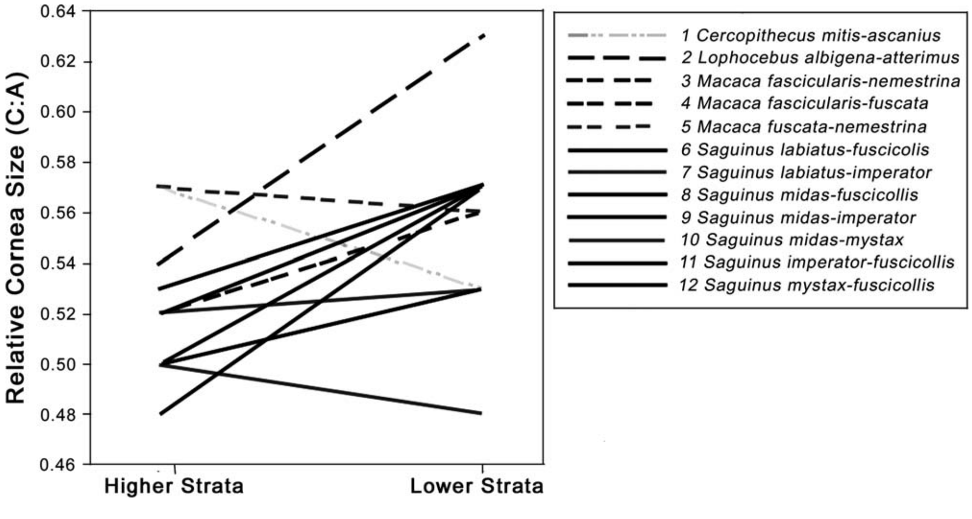

Fig. 5. The relative cornea size (*C*:*A*) of congeneric diurnal anthropoid pairs utilizing different vertical strata. Line shade reflects *C*:*A*-stratum relationship: black lines indicate pairs following the predicted relationship (larger *C*:*A* in lower stratum species); light grey lines indicate pairs following the opposite relationship (larger *C*:*A* in higher stratum species); dark grey lines indicate no difference (≤0.02 differences). Line pattern reflects genera: solid lines indicate *Saguinus* species; small dashed lines indicate *Macaca* species, large dashed lines indicate other taxa.

the higher strata congener, whereas three showed no difference in $C{:}A$ (≤ 0.02) and one exhibited the opposite relationship (higher $C{:}A$ in the higher strata congener). Seven of the pairs are combinations of *Saguinus* species and three are combinations of *Macaca* species. For the *Saguinus* pairs, five (71.4%) followed the predicted relationship and two (28.6%) showed no difference. For the *Macaca* pairs, two showed the predicted relationship while one did not differ in $C{:}A$ by strata.

DISCUSSION

The amount of light available during the day versus the night has long been known to influence mammalian visual anatomy, especially the anatomy related to acuity and sensitivity (Walls, 1942; Hughes, 1977; Pettigrew et al., 1988; Ross, 2000; Kay and Kirk, 2000; Kirk, 2004, 2006a,b; Ross and Kirk, 2007). In particular, activity pattern significantly influences relative cornea size in mammals, with nocturnal species having larger corneas relative to eye size to enhance visual sensitivity at low light levels (Ross, 2000; Kirk 2004, 2006a; Ross and Kirk, 2007). Because ambient light intensity varies within and between habitats (Endler, 1993), we tested whether mammalian relative cornea size also varies by habitat and microhabitat. We used multiple approaches to examine the effect of habitat type and vertical stratification on relative cornea size while controlling for possible phylogenetic effects. Our results suggest that differences in habitat light intensity do influence relative cornea size, but this effect is influenced by activity pattern. Very little data were available to test for a microhabitat effect, even for the well-studied primate clade. Nevertheless, our preliminary analysis suggests that vertical strata differences in light intensity do not influence relative cornea size in diurnal anthropoid primates.

Habitat Type

In our RCI analysis, we found that habitat type significantly influences relative cornea size within diurnal and cathemeral but not nocturnal, mammals. As expected, diurnal and cathemeral mammals from forests exhibited larger relative cornea sizes compared with species from more open habitats. Among nocturnal species, we found no relationship between relative cornea size and habitat type. Thus, just as activity pattern influences mammalian visual anatomy, habitat variation in light intensity also appears to influence eye morphology in day-active or partially day-active mammals. Diurnal and cathemeral forest-dwelling species, which encounter lower light intensities than diurnal/cathemeral species in open habitats (Endler, 1993), exhibit larger corneas relative to eye size, presumably as an adaptation for enhancing visual sensitivity.

The results for some of our intraclade analyses support the RCI results. Although sample size was small, in several clades (cathemeral artiodactyls, diurnal carnivorans, diurnal anthropoids, and diurnal rodents), relative cornea size significantly varied with habitat type as predicted or it approached significance. As in the RCI analysis, we found no significant relationship between relative cornea size and habitat in nocturnal subgroups. These results suggest that habitat differences in nocturnal light intensity do not affect nocturnal mammal visual anatomy for enhancing sensitivity. Because nocturnal light intensity also varies significantly by lunar phase (Lythgoe, 1979; Johnsen et al., 2006), nocturnal mammals may be maximizing their visual sensitivity across all habitat types to manage the very low light levels available by starlight alone. Many nocturnal mammals also have other adaptations to maximize sensitivity, such as specialized rod cell morphology (Solovei et al., 2009; Perry and Pickrell, 2010) and tapeta lucida (Walls, 1942; Nicol, 1981; Ollivier et al., 2004).

The relative lack of significant results in our intraclade comparisons suggests several confounding factors that may be influencing our analyses. First, contrary to predictions, cathemeral xenarthrans exhibited a trend for forest species to have smaller $C{:}A$ than open habitat species. This result may be influenced by the classification system and limits of the dataset used in this study. For example, one of the cathemeral xenarthrans classified as "forest" (*Myrmecophaga tridactyla*) inhabits a range of environments, including savanna and humid forests (Nowak, 1999). In some vertebrates, habitat variation can result in intraspecific populational differences in sensory systems (Wilczynski and Ryan, 1999). If similar intraspecific variation is present in mammalian visual systems, it could obscure habitat–cornea size relationships. Alternatively, some species may exhibit adaptations for a "habitat generalist" niche (McPeek, 1996).

A second factor that may have confounded our intraclade analyses is that mammalian clades rely on vision to different extents (Hughes, 1977; Barton et al., 1995; Arrese et al., 1999; Kirk and Kay, 2004; Kirk, 2006b). Anthropoid primates, for example, are more visually oriented and have significantly higher visual acuity than other mammal groups (Ross, 2000; Kirk and Kay, 2004; Veilleux, 2008; Veilleux and Kirk, 2009). This increased emphasis on vision may account (with large sample size) for why the habitat-cornea size relationship is strongest in anthropoids. In contrast, other mammal groups (such as murid rodents or xenarthrans), which are not as visually oriented, may not experience as strong selection for habitat light visual specialization. Additionally, these confounding factors, as well as very small sample size, may explain why the analysis of matched pairs was inconclusive and inconsistent with our RCI and intraclade analyses, which demonstrated significant habitat effects on relative cornea size.

Vertical Stratification

We hypothesized that microhabitat differences in light intensity also affect mammal relative cornea size, but this prediction was not supported. First, contrary to our predictions, we found that anthropoid primates utilizing lower strata in forests did not exhibit relatively larger corneas than species occupying higher strata. The woodland comparisons followed expectations, but sample size was too small for any conclusions. Second, our analysis of species vertically stratified in the same forest found that cornea size consistently decreased in size as the primates spent more time in the upper strata for only 40% of the sites examined. Third, although the analysis of congeneric pairs used nonindependent data and are thus difficult to interpret, over 70% of the *Saguinus* pairs and two-thirds of the *Macaca* pairs followed the expected direction with species inhabiting the lower strata having relatively larger corneas. Although more data are obviously needed before the effects of microhabitat light levels can be conclusively determined, the current lack of relationship between vertical strata usage and relative cornea size in primates is not particularly surprising. As a group, primates exhibit great behavioral plasticity (Campbell et al., 2007). Although primates often prefer certain strata, they utilize many levels of the forest (e.g., *Saguinus* spp., Buchanan-Smith, 1999). Thus, morphological specializations for one particular microhabitat may not be advantageous for behaviorally plastic species.

CONCLUSIONS

Using a broad comparative approach, we provide evidence that eye morphology in mammals is adapted to habitat variation in light intensity. Controlling for activity pattern and clade-level differences in eye morphology, we found that cathemeral and diurnal mammals from closed habitats tend to have larger corneas relative to eye size than mammalian species from open habitats. These differences probably reflect an adaptation to increase sensitivity in the darker forest light environments. Although the influence of microhabitat light levels on relative cornea size in primates was inconclusive, preliminary results suggest that vertical strata usage differences in light intensity are not as selectively important as habitat type. A more detailed analysis with more strata usage data for primates as well as other mammals may help resolve the influence of microhabitat light environments on visual anatomy.

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