

The Influence of Maximum Running Speed on Eye Size: A Test of Leuckart's Law in Mammals

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ABSTRACT

Vertebrate eye size is influenced by many factors, including body or head size, diet, and activity pattern. Locomotor speed has also been suggested to influence eye size in a relationship known as Leuckart's Law. Leuckart's Law proposes that animals capable of achieving fast locomotor speeds require large eyes to enhance visual acuity and avoid collisions with environmental obstacles. The selective influence of rapid flight has been invoked to explain the relatively large eyes of birds, but Leuckart's Law remains untested in nonavian vertebrates. This study investigates the relationship between eye size and maximum running speed in a diverse sample of mammals. Measures of axial eye diameter, maximum running speed, and body mass were collected from the published literature for 50 species from 10 mammalian orders. This analysis reveals that absolute eye size is significantly positively correlated with maximum running speed in mammals. Moreover, the relationship between eye size and running speed remains significant when the potentially confounding effects of body mass and phylogeny are statistically controlled. The results of this analysis are therefore consistent with the expectations of Leuckart's Law and demonstrate that faster-moving mammals have larger eyes than their slower-moving close relatives. Accordingly, we conclude that maximum running speed is one of several key selective factors that have influenced the evolution of eye size in mammals. *Anat Rec*, 295:1053–1062, 2012. © 2012 Wiley Periodicals, Inc.

Key words: eye size; visual acuity; Leuckart's law; locomotion; cursoriality; mammalia

INTRODUCTION

The evolution of eye size in vertebrates has been influenced by multiple adaptive or constraining factors (Walls, 1942; Hughes, 1977). Key influences on vertebrate eye size include body or head size (Schultz, 1940; Kay and Kirk, 2000; Kiltie, 2000; Howland et al., 2004; Burton, 2006, 2008), activity pattern (Garamszegi et al., 2002; Kirk, 2006a,b; Thomas et al., 2006; Werner and Seifan, 2006; Hall and Ross, 2007; Hall, 2008; Ockendon et al., 2009), and diet (Garamszegi et al., 2002; Kirk, 2006b; Lisney and Collin, 2007). In birds, locomotor speed has also been suggested to influence eye size via a relationship known as Leuckart's Law (Walls, 1942; Hughes, 1977; Brooke et al., 1999; Hall and Heesy, 2011). According to Leuckart's Law, animals capable of achieving fast speeds require large eyes to enhance vis-

ual acuity¹ and avoid collisions with obstacles in their environment (Hughes, 1977). Absolutely large eyes have long focal lengths,² allowing the projection of a large image onto the retinal surface. A large retinal image is

¹Visual acuity refers to an animal's ability to discern the fine spatial details of visual stimuli (Walls, 1942).

²In addition to eye size, the configurations of the cornea and lens also influence focal length (Hughes, 1977).

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sampled by a greater number of photoreceptors than a small image, leading to increased visual acuity if other factors (e.g., photoreceptor and ganglion cell density, retinal summation) remain constant (Walls, 1942; Land and Nilsson, 2002). Accordingly, Leuckart's Law predicts that the maximum speed of locomotion should be positively correlated with absolute eye size in vertebrates. In comparative analyses, fast-moving species are therefore expected to have absolutely larger eyes than their slower-moving close relatives.

Leuckart's Law has been invoked to explain why most birds have large eyes compared to other vertebrates of similar body size (Walls, 1942; Hughes, 1977). According to this scenario, the relatively large eyes of birds first evolved as an adaptation for rapid flight (Walls, 1942; Hughes, 1977; Martin, 1985). However, despite its long persistence in the published literature, this hypothesis has received only limited support from comparative studies. Brooke et al. (1999) estimated eye mass for 104 species of flying birds and calculated that visual acuity scales with positive allometry relative to expected flight speed. Accordingly, these authors concluded that faster-moving avian species are able to resolve visual details at a greater time to contact than slower-moving species (Brooke et al., 1999, p. 410). Brooke et al. (1999) further observed that their sample of flightless birds (including kiwis, penguins, and ratites) exhibited smaller eyes relative to body mass than was typical for their sample of flying birds. Both of these findings are consistent with the expectations of Leuckart's Law (Brooke et al., 1999). By comparison, Hall and Heesy (2011) examined axial eye diameter and migratory flight speed in 88 avian species and failed to find a significant relationship between these two variables. Interestingly, Hall and Heesy (2011) did report a statistically significant relationship between relative eye size and migratory flight speed, but in the opposite direction of that predicted by Leuckart's Law. In other words, species with fast migratory speeds actually had relatively smaller eyes than species with slower migratory flight speeds. Based on these results, Hall and Heesy (2011) concluded that variation in avian eye size is primarily driven by factors other than flight speed, such as diet, activity pattern, or energetic constraints associated with long distance flight.

Although quantitative tests of Leuckart's Law have heretofore been restricted to birds (Brooke et al., 1999; Hall and Heesy, 2011), comparative studies of eye size in mammals have yielded some support for the predictions of Leuckart's Law. Ritland (1982) found that cheetahs (*Acinonyx jubatus*, the fastest living terrestrial mammal; Table 1) have the second largest absolute eye size (36.7 mm axial diameter) in a sample of 40 carnivorous species. Eye size in cheetahs is thus substantially larger than in felid carnivores of similar body mass (e.g., *Panthera onca*, *Panthera uncia*) and is most comparable to felids that are about three to five times larger in body mass (e.g., *Panthera leo* and *Panthera tigris*; Ritland, 1982; Table 1). Similarly, Kirk (2006b) found that patas monkeys (*Erythrocebus patas*) have the largest absolute eye size (24.9 mm axial diameter) in a sample of 55 primate species. This finding is significant because patas monkeys have the fastest recorded running speed of any living primate (Table 1). Although other sources report somewhat smaller axial eye diameters for patas monkeys (i.e., 21 mm, Rohen, 1962; 20 mm, Ritland, 1982; 23 mm, Ste-

phan et al., 1984), it is nevertheless clear that patas monkeys have very large eyes for their body mass. Indeed, patas monkeys have eye sizes that are most comparable to other catarrhines (e.g., *Papio*, *Mandrillus*, *Pan*, and *Gorilla*) that are 3 to 25 times larger in body mass (Smith and Jungers, 1997). Eye size in patas monkeys is also about 25% larger than cercopithecoids of similar body mass (e.g., *Macaca nemestrina* and *Colobus polykomos*; Kirk 2006b), suggesting that the need for enhanced visual acuity during fast running bouts may be driving selection for large eyes in *Erythrocebus*.

Although these observations regarding eye size in cheetahs and patas monkeys are suggestive, a more comprehensive analysis is required to assess the validity of Leuckart's Law as a functional explanation for variation in mammalian eye size. The goal of this study is to investigate the relationship between maximum running speed and eye size in a diverse sample of mammals. If Leuckart's Law is applicable to mammals generally, then we expect absolute eye size to be positively correlated with maximum running speed. After controlling for the potentially confounding effects of body mass and phylogeny, we further expect fast-moving animals to have larger eyes than their slower-moving close relatives. Alternatively, if Leuckart's Law does not explain some proportion of the observed interspecific variation in mammalian eye size, then we expect to find no relationship between eye size and maximum running speed.

MATERIALS AND METHODS

We collected measurements of axial eye diameter (AD), maximum running speed (MRS), and body mass from the published literature for 50 species from 10 mammalian orders (Table 1). This sample includes 13 artiodactyls, 11 carnivores, 1 dasyuromorph, 2 didelphimorphs, 1 diprotodont, 2 lagomorphs, 4 perissodactyls, 3 primates, 2 proboscideans, and 11 rodents. To avoid comparing species that are fundamentally different in their visual or locomotor ecology, we excluded humans as well as volant, gliding, aquatic, and primarily fossorial species from this analysis. Direct measurements of AD (i.e., the linear distance from the anterior-most point of the cornea to the posterior-most point of the sclera) were reported by Calderone et al. (2003) and Ross and Kirk (2007). However, Schiviz et al. (2008) only report the posterior nodal distance (PND) of the eye, which they obtained by multiplying axial eye diameter by 0.57. PND values from Schiviz et al. (2008) were therefore divided by 0.57 to recalculate AD.

Measurements of MRS reflect the maximum speed achieved by an animal during a locomotor bout. The MRS data used in this analysis were collected using a variety of methods, which we have identified in Table 1 using five categories: (s) vehicle speedometer readings taken while pacing or chasing an animal, (f) calculations derived from filming animals in the field, (t) measurements of maximum speed on a treadmill, (w) timing an animal moving over a known distance in the wild, and (l) timing an animal moving over a known distance in the laboratory. A sixth category (i) identifies MRS data for which the author provides insufficient information to determine the specific methods of data collection. For example, Spector (1956, p.350) states that the red fox can attain speeds of 42 km/hr for an "average maximum,

TABLE 1. Body mass (BM), axial eye diameter (AD), maximum running speed (MRS), and activity pattern (ACT) for included taxa

Taxon	BM (kg)	AD (mm)	MRS (km/h) ^a	ACT ^b	Sources ^c
Artiodactyla					
Bovidae					
<i>Aepyceros melampus</i>	50.0	27.4	47 (f)	c	1, 2, 3, 4
<i>Alcelaphus buselaphus</i>	170.0	32.8	80 (s)	c	1, 2, 5, 4
<i>Antilope cervicapra</i>	37.0	28.0	105 (i)	c	1, 6, 7, 6
<i>Bison bison</i>	865.0	36.8	56 (s)	c	8, 2, 9, 4
<i>Connochaetes gnou</i>	300.0	26.5	90 (i)	c	1, 6, 10, 7
<i>Hippotragus equines</i>	250	21.6	56 (s)	c ^d	1, 2, 1, 11
<i>Taurotragus oryx</i>	900.0	47.7	70 (i)	c	1, 6, 5, 6
Cervidae					
<i>Alces alces</i>	450	36.6	56 (s)	c	1, 6, 12, 6
<i>Cervus elaphus</i>	300	34.4	72 (s)	c	1, 2, 12, 13
<i>Dama dama</i>	80	34.0	65 (s)	c	1, 6, 14, 6
<i>Odocoileus hemionus</i>	120	26.8	61 (s)	c	1, 6, 15, 6
<i>Odocoileus virginianus</i>	100	27.0	64 (i)	c	1, 6, 15, 6
Giraffidae					
<i>Giraffa camelopardalis</i>	1000.0	42.0	60 (s)	c	1, 2, 10, 16
Carnivora					
Canidae					
<i>Canis lupus</i>	40	22.5	64 (s)	c	1, 6, 17, 6
<i>Urocyon cinereoargenteus</i>	5.0	17.4	64 (s)	c	1, 6, 1, 6
<i>Vulpes vulpes</i>	5.1	20.1	42 (i)	n	18, 6, 18, 4
Felidae					
<i>Acinonyx jubatus</i>	55	36.7	110 (i)	d	1, 6, 19, 4
<i>Panthera leo</i>	155.8	36.9	59 (i)	c	9, 6, 5, 6
<i>Panthera tigris</i>	230	35.0	56 (i)	c	1, 6, 5, 6
Hyaenidae					
<i>Crocuta crocuta</i>	65	25.4	65 (i)	n	1, 20, 1, 21
Mustelidae					
<i>Meles meles</i>	11	8.9	30 (s)	n	1, 6, 22, 6
Procyonidae					
<i>Procyon lotor</i>	12	13.4	24 (i)	n	1, 6, 23, 24
Ursidae					
<i>Ursus americanus</i>	135	18.5	48 (i)	c	1, 6, 25, 6
<i>Ursus arctos</i>	251.3	18.0	47 (s)	c	26, 6, 8, 6
Dasyuromorphia					
Dasyuridae					
<i>Dasyurus viverrinus</i>	1.12	10.6	16 (t)	n	27, 6, 27, 6
Didelphimorphia					
Didelphidae					
<i>Didelphis marsupialis</i>	5.0	8.7	7.4 (l)	n	1, 6, 28, 4
<i>Didelphis virginiana</i>	3.75	9.7	10.2 (l)	n	4, 6, 27, 4
Diprotodontia					
Potoroidae					
<i>Bettongia penicillata</i>	1.1	13.7	20.9 (t)	n	1, 6, 29, 4
Lagomorpha					
Leporidae					
<i>Lepus californicus</i>	2.0	18.7	64 (i)	c	1, 6, 30, 6
<i>Sylvilagus</i> sp. ^e	1.5	14.9	40 (i)	c	1, 6, 1, 6
Perissodactyla					
Equidae					
<i>Diceros bicornis</i>	1400	27.6	45 (i)	c	1, 6, 1, 31
<i>Equus burchelli</i>	400	42.0	70 (i)	c	1, 6, 1, 4
<i>Equus caballus</i>	350	41.3	70 (w)	c	1, 6, 1, 4
<i>Equus zebra</i>	300	41.5	64 (s)	c	1, 6, 5, 4
Primates					
Cebidae					
<i>Cebus capucinus</i>	3.34	16.0	9 (t) ^f	d	32, 6, 32, 6
Cercopithecidae					
<i>Erythrocebus patas</i>	9.5	22.5	55 (i)	d	33, 6, 34, 6
Hominidae					
<i>Gorilla gorilla</i>	127	23.0	32 (i)	d	1, 6, 1, 6
Proboscidea					
Elephantidae					
<i>Elephas maximus</i>	4000	30.0	26 (i)	c	1, 6, 1, 4
<i>Loxodonta africana</i>	6000	39.6	35 (w) ^g	c	1, 6, 1, 4

TABLE 1. Body mass (BM), axial eye diameter (AD), maximum running speed (MRS), and activity pattern (ACT) for included taxa (*continued*)

Taxon	BM (kg)	AD (mm)	MRS (km/h) ^a	ACT ^b	Sources ^c
Rodentia					
Cricetidae					
<i>Microtus</i> sp. ^h	0.05	3.4	11 (l)	c	1, 6, 35, 6
<i>Peromyscus maniculatus</i>	0.03	4.9	9.1 (l)	n	1, 6, 35, 4
Dipodidae					
<i>Zapus hudsonicus</i>	0.018	3.4	8.9 (l)	c	1, 6, 35, 36
Erethizontidae					
<i>Erethizon dorsatum</i>	9	10.3	3.2 (s)	c	1, 6, 13, 4
Gliridae					
<i>Myoxus glis</i>	0.09	7.3	10 (i)	c	37, 6, 37, 4
Muridae					
<i>Rattus rattus</i>	0.25	6.3	9.7 (i)	n	1, 6, 30, 6
Sciuridae					
<i>Marmota monax</i>	4.0	12.1	16 (i)	d	1, 6, 1, 6
<i>Sciurus carolinensis</i>	0.55	11.8	27 (w)	d	1, 6, 34, 6
<i>Sciurus niger</i>	1.1	12.0	24 (s)	d	27, 6, 38, 6
<i>Tamias striatus</i>	0.1	7.1	17 (w)	d	1, 6, 34, 6
<i>Tamiasciurus</i> sp. ⁱ	0.22	8.7	15 (w)	d	1, 6, 34, 6

^aMRS, maximum running speed code: s = vehicle speedometer in wild; f = calculated from field film; i = speed reported, but insufficient information provided regarding methods; t = maximum treadmill speed in laboratory; w = timed over known distance in wild; l = timed over known distance in laboratory.

^bACT, activity pattern code: c = cathemeral, d = diurnal, n = nocturnal.

^cSources listed in order of (a) BM, (b) AD, (c) MRS, and (d) ACT. 1, Garland (1983); 2, Schiviz et al. (2008); 3, Alexander et al. (1977); 4, Nowak (1991); 5, Schaller (1972); 6, Ross and Kirk (2007); 7, Maloney et al. (2005); 8, Breland (1963); 9, Garland and Janis (1993); 10, Gambaryan (1974); 11, Sahar and Owen-Smith (2007); 12, Cottam and Williams (1943); 13, Kamler et al. (2007); 14, Chapman and Chapman (1975); 15, Rue (1978); 16, Tobler and Schwierin (1996); 17, Mech (1970); 18, Spector (1956); 19, Walker (1976); 20, Calderone et al. (2003); 21, Stratford and Stratford (2011); 22, Neal (1977); 23, MacClintock (1981); 24, Carver et al. (2011); 25, Burt and Grossenheider (1976); 26, Iriarte-Díaz (2002); 27, Garland et al. (1988); 28, McManus (1970); 29, Seeherman et al. (1981); 30, Wood (1972); 31, Hillman-Smith and Groves (1994); 32, Taylor and Rowntree (1973); 33, Smith and Jungers (1997); 34, Kingdon (1971); 35, Layne and Benton (1954); 36, Whitaker (1972); 37, Ruf et al. (2006); 38, Moore (1957).

^dBased on observations for *Hippotragus niger*.

^eAD measurement is for *Sylvilagus audubonii*.

^fTaylor and Rowntree (1973) plot the relationship between oxygen consumption and running speed for *Cebus capucinus*. In this plot, the animals' maximum speed is between 9 and 10 km/h.

^gBreland (1963) reports that *Loxodonta africana* was timed with a stopwatch traveling 24 mph (~40 km/h) for 120 yards. Garland (1983) reports a speed of 35 km/h for *Loxodonta*, however, doubting the accuracy of Breland's high figure.

^hMRS measurement is for *Microtus pennsylvanicus*.

ⁱMRS measurement is for *Tamiasciurus hudsonicus*.

1 mile", while Kingdon (1971, p. 264) describes that *Erythrocebus patas* has been "clocked" at 55 km/hr. While it is impossible to be certain based on the published information, it is likely that most such reports of MRS were generated by chasing or pacing the animal with a vehicle in the wild (Garland, 1983). Garland and colleagues (e.g., Garland, 1983; Garland et al., 1988; Garland and Janis, 1993; also Iriarte-Díaz, 2002) have acknowledged and discussed the limitations of the available comparative data on MRS for mammals, including the problems of small sample size (e.g., Alexander et al., 1977), and uncertainty about whether or not the animal was running at its top speed. While it is necessary to be mindful of the inherent limitations of the comparative literature on mammalian locomotion, we are confident that the data provided in Table 1 represent the best estimates of mammalian MRS that are currently available for species with known eye sizes.

We used multiple methods to examine the relationship between AD, MRS, and body mass. All statistical operations were performed in R using the ape and nlme packages (Paradis et al., 2004; Pinheiro et al., 2011; R Development Core Team, 2011), and all continuous vari-

ables were log10 transformed prior to analysis. First, the Spearman rank correlations of AD and MRS, AD and body mass, and MRS and body mass were calculated. Second, the ordinary least-squares (OLS) regression of AD on MRS, AD on body mass, and MRS on body mass were calculated. Third, because phylogenetic relationships between taxa may violate the assumptions of non-independence required by traditional OLS models (Felsenstein, 1985; Harvey and Pagel, 1991), we calculated phylogenetic generalized least-squares (PGLS) regressions of AD on MRS, AD on body mass, and MRS on body mass. In the present study, PGLS models are used to account for the fact that closely related taxa are likely to have more similar eye sizes, running speeds, and body masses than distantly related taxa. PGLS models control for phylogenetic non-independence by adding an error term to the standard OLS regression equation (Pagel, 1997, 1999; Freckleton et al., 2002). This error term is derived from a variance-covariance matrix describing the phylogenetic relationships of the species in the comparative sample. Tree topology and branch lengths in our analyses follow Bininda-Emonds et al. (2007, 2008). In all PGLS

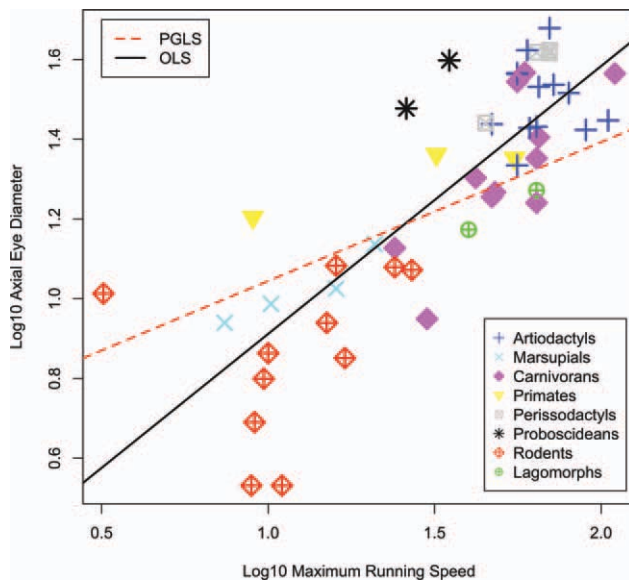


Fig. 1. Bivariate plot of log maximum running speed (km/hr) and log axial eye diameter (mm) for 50 mammalian species.

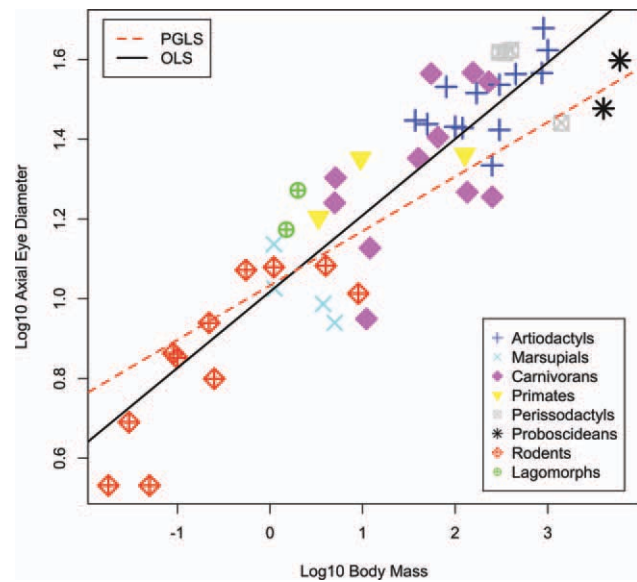


Fig. 2. Bivariate plot of log body mass (kg) and log axial eye diameter (mm) for 50 mammalian species.

regressions, Pagel's λ (Pagel, 1999) was simultaneously estimated to use as a multiplier of the off-diagonal elements in the phylogenetic variance-covariance matrix (Freckleton et al., 2002; Revell, 2010). According to Freckleton et al., "...a value of $\lambda = 0$ indicates evolution of traits, that is, independent of phylogeny, while a value of $\lambda = 1$ indicates that traits are evolving according to Brownian motion on the given phylogeny. Intermediate values of λ indicate that traits have evolved according to a process in which the effect of phylogeny is weaker than in the Brownian model" (Freckleton et al., 2002, p. 714). Both OLS and PGLS results are reported here because the questions addressed by the two methods are slightly different and the results of both methods may be informative for understanding adaptation (see Westoby et al., 1995; Garland et al., 1999; Freckleton et al., 2002). Indeed, while an OLS model simply addresses the question of whether two continuous traits covary, a PGLS model asks "whether a trait covaries with evolutionary divergence itself" (Pagel, 1997, p. 337).

In addition to examining the bivariate linear relationships between pairs of variables, we also assessed the relationship between eye size and running speed while controlling for differences in body size. This step is necessary because both AD and MRS are known to be independently correlated with body mass across mammals (Hughes, 1977; Garland, 1983; Kiltie, 2000; Howland et al., 2004). To control for the influence of body mass, we used two complementary methods. First, we examined the combined effects of body mass and running speed on eye size using multiple regression models. Both OLS and PGLS multiple regressions were calculated, with body mass and MRS as predictor variables and AD as the response variable. Second, we calculated the PGLS partial regression of eye size and running speed while holding body mass constant. Residuals were first calculated from separate PGLS regressions of (1) AD on body mass and (2) MRS on body mass. We then calculated the PGLS regression of residual AD on resid-

ual MRS. Although these methods are necessary to ensure that our results are independent of the influence of body mass, we emphasize that absolute (not relative) eye size is the most biologically relevant variable for assessing the validity of Leuckart's Law (Walls, 1942; Hughes, 1977). If all other ocular and retinal variables are held constant, an animal with an absolutely larger eye will have greater image resolution than an animal with a smaller eye, regardless of body size. Nevertheless, if two species of equal body mass are compared, Leuckart's Law predicts that the faster-moving species should have larger eyes than the slower-moving species. Accordingly, if Leuckart's Law is valid for mammals, we expect MRS to be positively correlated with (1) absolute eye size and (2) relative eye size when the effects of body mass are statistically controlled.

Finally, because activity pattern may influence eye size in mammals (Kirk, 2006a,b; Ross and Kirk, 2007), we assessed the relationship between body mass, eye size, and activity pattern in our comparative sample. The taxa analyzed here include 9 diurnal, 31 cathemeral, and 10 nocturnal species (Table 1). First, we examined the difference in body mass and AD between activity pattern groups using Wilcoxon rank-sums tests. Second, we used an OLS regression of log AD on log body mass to calculate residual AD for all species. A Kruskal-Wallis test was then used to compare residual AD between the three activity pattern groups.

RESULTS

Spearman correlations demonstrate that AD, MRS, and body mass are all significantly positively correlated (AD vs. MRS, $\rho = 0.790$, $P < 0.001$; AD vs. body mass, $\rho = 0.877$, $P < 0.001$; MRS vs. body mass, $\rho = 0.627$, $P < 0.001$). The relationships between these three variables are also evident in bivariate linear regressions (Figs. 1–3, Table 2). Figure 1 shows the effect of MRS on AD. Both the OLS and PGLS regressions are highly

significant ($P < 0.001$), with MRS alone explaining about 66% of the total variance in AD (Table 2). Because AD tends to increase as MRS increases, the fastest species in our sample (i.e., artiodactyls, canids, felids, and *Crocuta*) also have the largest eyes, while slower species (mainly rodents and marsupials) tend to have substantially smaller eyes (Fig. 1, Table 1). Figure 2 shows the effect of body mass on AD. As in Fig. 1, both the OLS and PGLS regressions are highly significant ($P < 0.0001$). However, body mass alone explains a larger proportion of the total variance in AD (81%) than does MRS alone (Table 2). Because eye size tends to increase as body mass increases, the smallest-bodied species in this analysis (rodents) also have the smallest eyes. Similarly, large-bodied species (including artiodactyls, perissodactyls, proboscideans, and some carnivorans) also have the largest eyes in our sample (Fig. 2, Table 1). Figure 3 shows the effect of body mass on MRS. In this case, the OLS regression is significant, suggesting that (across clades) body mass alone explains about 44% of the total variance in MRS (Table 2). By contrast, the PGLS regression is not significant, indicating that the signifi-

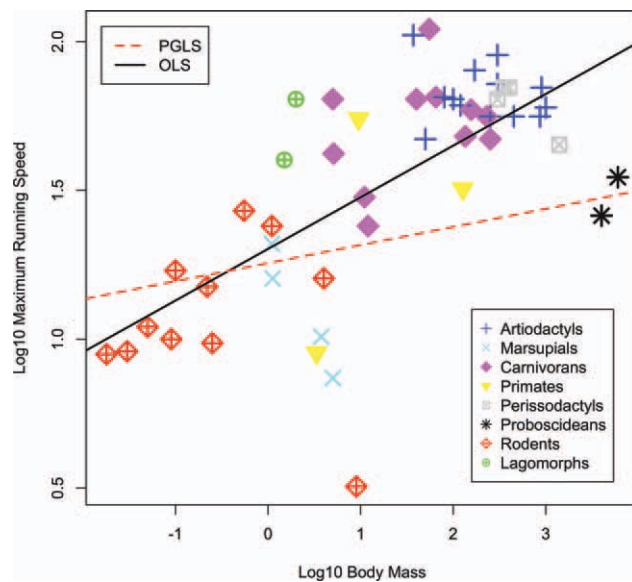


Fig. 3. Bivariate plot of log body mass (kg) and log maximum running speed (km/hr) for 50 mammalian species.

cant OLS result does not exist independent of phylogenetic influences. Indeed, in all PGLS regressions (Table 2), Pagel's λ is equal to 1.0, indicating that there is a large phylogenetic influence on character state distributions and that the evolution of all traits is consistent with a Brownian Motion model of evolution.

OLS and PGLS multiple regression models confirm that both body mass and MRS have a significant effect on AD (Table 2). The OLS multiple regression of AD on body mass and MRS has a higher r^2 value (0.89) than any bivariate OLS regression, with body mass explaining a larger proportion of the variance in AD (partial $r^2 = 0.58$) than does MRS (partial $r^2 = 0.31$). Similarly, the PGLS multiple regression of AD on body mass and MRS has a lower AIC value (-77.4) than any bivariate PGLS regression, indicating that the multiple regression model is a better fit for the data (Table 2). These multiple regression models demonstrate that the effect of MRS on AD is independent of both body mass and phylogeny. This result is also evident in Fig. 4, which presents the PGLS partial regression of residual AD on residual MRS (slope = 0.259, y-intercept = 0.000, $\lambda = 1.0$, $P < 0.001$). Figure 4 shows that when the independent correlations of both AD and MRS with body mass are statistically controlled by holding body mass constant, AD still tends to increase with MRS.

Wilcoxon rank-sums tests reveal that the nocturnal and diurnal species in our sample do not differ significantly in AD, but that the cathemeral species have significantly larger ADs than both the nocturnal and diurnal species combined ($P < 0.001$, $Z = -3.65$). This result is probably attributable to the fact that the nocturnal and diurnal species considered here do not differ significantly in body mass. By comparison, the cathemeral species in our sample are significantly larger in body mass than the nocturnal and diurnal species combined ($P < 0.001$, $Z = -3.87$). When residual AD is compared for all taxa, a Kruskal-Wallis test shows no significant difference in relative eye size between the three activity pattern groups.

DISCUSSION

The results of this analysis clearly demonstrate that eye size, maximum running speed, and body mass are significantly inter-related in mammals. When the bivariate linear relationships of these three variables are assessed, the strongest effect is clearly that of body mass on eye size. Nonparametric correlation, OLS regression,

TABLE 2. Ordinary least-squares (OLS) and phylogenetic generalized least-squares (PGLS) regression statistics

Variables	Slope	y-intercept	P-value	r^2 (adjusted) or λ	AIC
OLS					
\log_{10} AD (y), \log_{10} MRS (x)	0.672	0.240	<0.0001	$r^2 = 0.66$	—
\log_{10} AD (y), \log_{10} body mass (x)	0.191	1.018	<0.0001	$r^2 = 0.81$	—
\log_{10} MRS (y), \log_{10} body mass (x)	0.174	1.303	<0.0001	$r^2 = 0.44$	—
\log_{10} AD (y), \log_{10} body mass (x_1), \log_{10} MRS (x_2)	—	—	(x_1) <0.0001 (x_2) <0.0001	$r^2 = 0.89$	—
PGLS					
\log_{10} AD (y), \log_{10} MRS (x)	0.348	0.696	<0.001	$\lambda = 1.0$	-51.97
\log_{10} AD (y), \log_{10} body mass (x)	0.136	1.033	<0.0001	$\lambda = 1.0$	-69.89
\log_{10} MRS (y), \log_{10} body mass (x)	0.061	1.255	NS	$\lambda = 1.0$	-8.97
\log_{10} AD (y), \log_{10} body mass (x_1), \log_{10} MRS (x_2)	—	—	(x_1) <0.0001 (x_2) <0.001	$\lambda = 1.0$	-77.38

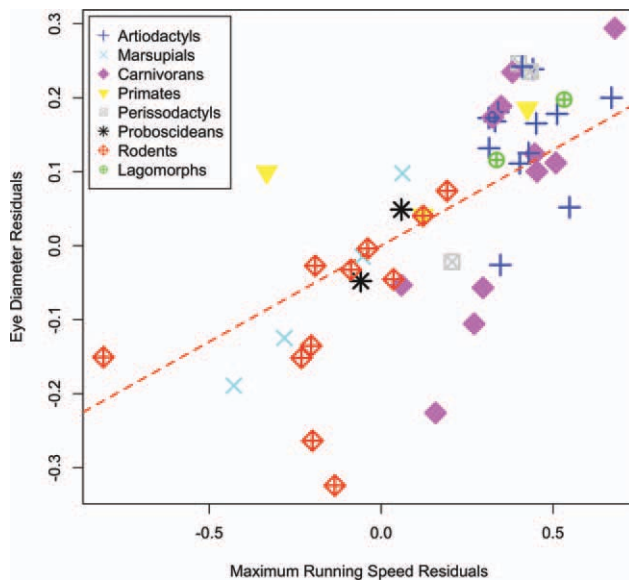


Fig. 4. Partial-regression plot of the PGLS residuals of log maximum running speed (km/hr) and log axial eye diameter (mm) on body mass (kg).

and PGLS regression all indicate that as body mass increases, eye size also increases (Fig. 2; Table 2). This result is not surprising given the findings of prior comparative studies, and it supports the hypothesis that small body and/or head size may constrain eye size (Schultz, 1940; Walls, 1942; Hughes, 1977; Brooke et al., 1999; Kay and Kirk, 2000; Kiltie, 2000; Howland et al., 2004; Burton, 2006, 2008). The weakest effect observed in this analysis is that of body mass on maximum running speed. Nonparametric correlation and OLS regression indicate that as body mass increases, maximum running speed also tends to increase (Fig. 3; Table 2). However, there are clearly many individual exceptions to this larger-scale relationship observed across taxa. For example, North American porcupines (*Erethizon*) have the largest body mass but the slowest maximum running speed of any rodent in our sample (Table 1). Similarly, African and Asian elephants have the largest body masses in our comparative sample, but they only exhibit moderate maximum running speeds (Fig. 3; Table 1). Indeed, the correlation between body mass and maximum running speed observed across all taxa is not clearly evident within orders (Fig. 3), and as a result the PGLS regression of the two variables is not significant. In other words, while it is true that locomotor speed is correlated with body mass in a large and diverse mammalian sample, this effect does not exist independent of phylogeny. This finding closely matches that of Garland (1983), who reported a significant relationship between body mass and maximum running speed across mammals ($N = 106$ species) but found no such relationship within most orders.

The results of this analysis also provide strong support for Leuckart's Law as a causal explanation for interspecific variation in mammalian eye size. Nonparametric correlation, OLS regression, and PGLS regression all indicate that as maximum running speed increases, eye size also increases (Fig. 1; Table 2). In isolation,

maximum running speed explains 66% of the variance in eye size in our sample, although this value is clearly influenced by phylogeny. Furthermore, the relationship between eye size and maximum running speed is complicated by the independent positive correlations of these two variables with body mass. However, when body mass and maximum running speed are both used as predictor variables in OLS and PGLS multiple regression models, the relationship between eye size and maximum running speed remains significant. Similarly, when the influence of body mass is statistically controlled using a PGLS partial regression, residual maximum running speed still has a significant effect on residual eye size (Fig. 4). Accordingly, the observed effect of maximum running speed on eye size (Fig. 1) is independent of the potentially confounding influences of body mass and phylogenetic non-independence. These results are consistent with the expectations of Leuckart's Law and suggest that locomotor speed is one of several factors influencing the evolution of eye size in mammals.

Because factors other than speed of locomotion are known to influence the evolution of mammalian eye size (Schultz, 1940; Kirk, 2006a,b; Ross and Kirk, 2007), it is important to note that activity pattern has little influence on eye size in the comparative sample analyzed here. Indeed, differences between our three activity pattern groups in absolute eye size are largely attributable to differences in body mass. Cathemeral species in our sample have significantly larger eyes than nocturnal and diurnal species, but the cathemeral species are also significantly larger in body mass. These results closely match those of Kirk (2006a), who found that absolute eye size was greatest for cathemeral species in a much larger mammalian comparative sample. Indeed, when residual eye size is compared for the species used in our analysis, there were no significant differences among the three activity pattern groups. This finding is well in accord with evidence that the great majority of diurnal, cathemeral, and nocturnal primates have broadly similar eye sizes relative to head size (Kirk, 2006b), and that non-primate mammals demonstrate a comparatively weak relationship between activity pattern and relative eye size (Ross and Kirk, 2007).

Interestingly, the results of this analysis differ from those of Hall and Heesy (2011), who examined the relationship between eye size and migratory flight speed in 88 avian species. Contrary to the expectations of Leuckart's Law, these authors did not find a significant positive relationship between absolute eye size and flight speed. Moreover, Hall and Heesy (2011) found a significant negative correlation between relative eye size and flight speed—a finding that is opposite of the relationship predicted by Leuckart's Law. These differing results regarding the relationship between eye size and locomotor speed within Mammalia and Aves could indicate that the selective factors influencing eye size are not uniform across vertebrates. However, it is also possible that speed of locomotion may influence eye size in birds even if migratory flight speed has little effect on eye size. For example, Hall and Heesy (2011) note that while hawks have large eyes and are relatively slow migratory fliers, hawks often use bouts of very rapid flight when diving for prey. In other words, it is possible that migratory flight speed is less important as a selective influence on eye size than maximum flight speed and ecological

context (e.g., flying at altitude vs. flying in a forest with multiple potential obstacles). While an analysis of maximum flight speed and eye size is outside the scope of this paper, further tests of Leuckart's Law in birds may help to resolve these questions.

Moreover, it is worth noting that Leuckart's Law may help to explain some interspecific variation in eye size within other vertebrate classes. Among reptiles, Werner and Seifan (2006) found that cursorial geckos have relatively larger eyes than scansorial and "intermediate" (i.e., between scansorial and cursorial) geckos. However, although the relative eye size of cursorial geckos is significantly larger than those of both scansorial and intermediate species, there was no significant difference in absolute eye size among the three locomotor classes (Werner and Seifan, 2006). A more detailed investigation into the relationship between eye size and locomotor speed among various groups of reptiles would also enhance our ability to assess the merits of Leuckart's Law as it applies to vertebrates more generally.

Finally, although we did not include humans in our comparative analysis, a comment on the relationship between eye size and running speed in humans is warranted given the fact that selective pressures related to running may have played an important role in human evolution (Carrier, 1984; Bramble and Lieberman, 2004). The Endurance Running Hypothesis posits that endurance running, instead of long-distance walking, played a significant role in human evolution and is responsible for shaping many aspects of the modern human body form (Carrier, 1984; Bramble and Lieberman, 2004; Rolian et al., 2009). Endurance running involves running many kilometers over an extended period to time. Unlike sprinting, endurance running does not necessitate that a runner achieves his/her maximum running speed. Human endurance runners typically travel at speeds between 9.36 and 23.4 km/hr, while elite sprinters are capable of reaching speeds of 36.7 km/hr (though they are unable to sustain these speeds for more than ~15 secs; Bramble and Lieberman, 2004). Our OLS regression of axial eye diameter on maximum running speed predicts that a mammal whose maximum running speeds are between 9.36 and 23.4 km/hr is expected to have eyes with an axial diameter of 8.2 and 14.8 mm, respectively. A mammal that achieves speeds of 36.7 km/hr, such as human elite sprinters, is predicted to have an axial eye diameter of approximately 19.89 mm. These values are well below the size of human emmetropic eyes, which average ~23.3 mm in axial diameter³ (± 0.1 mm standard deviation; Oliveira et al., 2006; Moriyama et al., 2011). Therefore, humans have larger than expected eyes given their endurance and sprinting (maximum) running speeds. Human eye size is similar to that of *Canis lupus* (22.5 mm), *Erythrocebus patas* (22.5 mm) and *Gorilla gorilla* (23 mm), which are reported to have a maximum running speed of 64 km/hr, 55 km/hr, and 32 km/hr, respectively. Hence, with the exception of the gorilla, humans achieve maximum running speeds (~37 km/hr) that are much slower than most other spe-

cies with comparable eye size. These data suggest that Leuckart's Law cannot account for the large eyes of humans compared to other primates. While it is possible that factors related to locomotion comprise one component of the selective regime contributing to the large eyes (Ross and Kirk, 2007; Oliveira et al., 2006; Moriyama et al., 2011) and very high visual acuity (Kirk and Kay, 2004) of humans, maximum running speed clearly does not explain why humans have very large eyes. Other selective factors, such as the need to interpret subtle facial expressions as a means of mediating social interactions (Dobson, 2009), appear to play a more significant role in the evolution of large eye size and high visual acuity in humans.

CONCLUSIONS

Maximum running speed has a significant effect on mammalian eye size that is independent of body mass and phylogeny. This finding that faster-moving mammalian species have larger eyes than slower-moving species is consistent with the expectations of Leuckart's Law, which proposes that rapid locomotion selects for large eyes to enhance visual acuity and avoid collisions (Walls, 1942; Hughes, 1977). We conclude that maximum running speed is one of several selective factors (e.g., activity pattern, diet) that have influenced the evolution of eye size in mammals. Additional comparative studies are required to determine whether Leuckart's Law is valid for other major vertebrate clades.

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³This mean value for humans is larger than the mean axial eye diameter reported for any other primate species by Ross and Kirk (2007), although both *Gorilla* (AD = 23 mm), *Mandrillus* (AD = 23.2) approach the human value.

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