Eye shape and activity pattern in birds

M. I. Hall[1] & C. F. Ross[2]

1 Department of Biomedical Sciences, College of Health Sciences, Midwestern University, Glendale, AZ, USA
2 Organismal Biology & Anatomy, University of Chicago, Chicago, IL, USA

Abstract

Many aspects of an animal's ecology are associated with activity pattern, the time of day when that animal is awake and active. There are two major activity patterns: *diurnal*, active during the day in a light-rich, or photopic, environment, and *nocturnal*, active after sunset in a light-limited, or scotopic, environment. Birds are also *cathemeral*, or equally likely to be awake at any time of day, or *crepuscular*, awake and active at dawn and dusk. Each of these activity patterns is associated with different levels of ambient light. This study examines how the morphology (size and shape) of the eye varies according to these different light environments for birds in a phylogenetic context. Activity pattern has a significant influence on eye shape and size in birds. Birds that are adapted for scotopic vision have eye shapes that are optimized for visual sensitivity, with larger corneal diameters relative to axial lengths. Birds that are adapted for photopic vision have eye shapes that are optimized for visual acuity, with larger axial lengths relative to corneal diameters. Birds adapted for scotopic vision also exhibit absolutely larger corneal diameters and axial lengths than do photopic birds. The results indicate that the light level under which the bird functions has a more significant influence on eye shape than phylogeny.

Introduction

It is very likely that the vertebrate eye arose only once, because throughout the entire group the same basic design of the eye is retained (e.g. Walls, 1942; Duke-Elder, 1958; Salwini-Plawen & Mayr, 1977; Charman, 1991). Yet, vertebrates have radiated into a variety of ecological niches that place diverse demands on the visual system. Evolutionary adaptive responses of the visual system to these differing demands might be expected to be accentuated in clades of vertebrates that are highly dependent on the visual sense for survival. Birds as a class are highly visually dependent; it is often asserted that birds have the largest eyes, both absolutely and relative to body size, of any of the terrestrial vertebrate classes, reflecting the role of vision as these animals' main sensory interface with their environments (Walls, 1942; Rochon-Duvigneaud, 1943; Meyer, 1977, 1986; Ritland, 1982; Martin, 1985; Zeigler & Bischof, 1993; Brooke, Hanley & Laughlin, 1999; Kiltie, 2000; Husband & Shimizu, 2001; Garamszegi, Moller & Erritzoe, 2002; Gaffney & Hodos, 2003; Howland, Merola & Basarab, 2004; Hall, 2005; Ross, Hall & Heesy, 2006).

Vision is made possible by the presence of light, which behaves under different conditions in ways that are both well known and predictable. Birds, like other vertebrates, have a simple eye where light enters anteriorly and is refracted by the cornea and lens to project an image onto the retina lining the back of the eyeball. The morphology and optical properties of these parts of the eye determine both the exact pathway of light through the eye and the size and quality of the resultant image (e.g. Hughes, 1977; Lythgoe, 1979; Ali & Klyne, 1985; Martin, 1985, 1993, 1999; Charman, 1991). It is therefore reasonable to hypothesize that both the sizes and shapes of bird eyes will reflect the visual ecology of their hosts. This study evaluates this hypothesis by specifically examining how the size and shape of bird eyes vary with one aspect of that animal's visual ecology, activity pattern, defined here as the time of day when an animal is awake and active. Activity pattern is directly related to how much light is available to create an image and is expected to have a relationship with both eye *size*, absolute measurements of the eye, and eye *shape*, the relative magnitudes of those measurements.

Eye size

The eye has been shown to scale with negative allometry against body size across a broad range of vertebrate groups, although at very small body sizes eye size appears to be positively allometric (Ritland, 1982; Brooke *et al.*, 1999; Kiltie, 2000; Howland *et al.*, 2004; Ross *et al.*, 2006). This suggests that lineages of visually dependent small animals take every opportunity to increase eye size as much as possible. Nevertheless, all visually dependent animals potentially benefit from eye enlargement and eye size increases with body size at all body sizes. Larger eyes can have more photoreceptors, larger image sizes and can collect more light (Walls, 1942; Duke-Elder, 1958; Hughes, 1977; Meyer, 1977;

Lythgoe, 1979; Land, 1980; Martin, 1982, 1985, 1990, 1993; Charman, 1991; Garamszegi *et al.*, 2002; Land & Nilsson, 2002; Gaffney & Hodos, 2003; Howland *et al.*, 2004). This study focuses on two functionally relevant measurements of gross eye size: the corneal diameter (CD) and the axial length of the eye (AL) (Fig. 1).

Corneal diameter is associated with visual sensitivity, or the light-gathering ability of the eye. Under low light conditions, the probability that an individual photoreceptor cell will capture a photon of light is described by a Poisson distribution (Lythgoe, 1979; Land, 1980; Land & Nilsson, 2002), where the probability (P) of capturing p photons if the average number of photons arriving at the retina is n is equal to $P(pn)$ (Land, 1980). An enlarged cornea allows for an enlarged pupil, which increases the probability of light entering the eye (Walls, 1942; Martin & Gordon, 1974*a*; Martin, 1982, 1985, 1990, 1993, 1999).

Axial length of the eye should be associated with visual acuity, the ability to resolve two discrete objects (Walls, 1942; Fite, 1973; Martin & Gordon, 1974*b*; Green, Powers & Banks, 1980; Land, 1980; Land & Nilsson, 2002). A larger axial length is associated with a larger posterior nodal distance (PND), which is the distance from the posterior nodal point of the lens to the point at which the image is focused on the retina (see Fig. 1). Across vertebrates, PND is about 0.6 of the axial length of the eye (Hughes, 1977; Martin, 1982, 1999). The longer the axial length of the eye and PND, the larger the image projected onto the retina. Since bird photoreceptors are a near-constant size and are packed into the retina in a regular and conservative way, in general a larger retina contains more photoreceptor cells (Snyder & Miller, 1977; Land, 1980; Ali & Klyne, 1985; Rostgaard & Qvortrup, 1999; Land & Nilsson, 2002). An eye with a larger image projected over more photoreceptor cells is capable of perceiving more detail in that image, or heightened visual acuity, because each photoreceptor processes a smaller portion of the image.
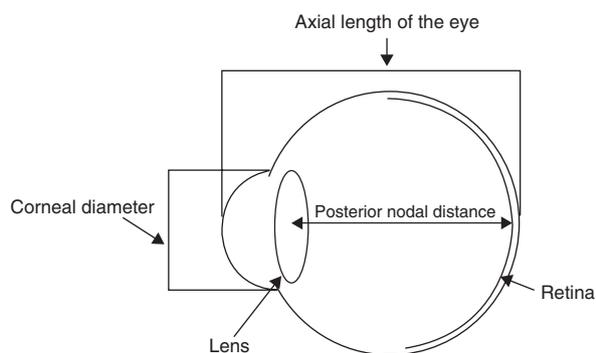

Figure 1 Measurements taken for this study depicted on a general schematic of the vertebrate eye. Posterior nodal distance is the distance between the posterior nodal point of the lens and the point on the retina where the image is projected. The posterior nodal point is an idealized point where the angle of light exiting the lens is the same as the angle of light entering the lens in a schematic eye model. This distance determines how large an image will be, and therefore indicates the animal's visual acuity.

Eye shape

In addition to looking at absolute measures of the eye, this study also examines eye shape. *Shape* can be defined as the relationship, or ratio, between two size measurements (Mosimann, 1970; Mosimann & James, 1979). This study examines the relationship between corneal diameter and axial length of the eye with the effects of both eye size and body size removed by looking at the $\log_{10}$ ratio of corneal diameter:axial length of the eye (see Results below). Larger animals with absolutely larger eyes have the potential for more acute and sensitive vision than smaller animals with smaller eyes. However, there is no ideal eye design for all conditions. The demands of imaging under plentiful and limited light levels have been hypothesized to require different eye shapes (Walls, 1942; Lythgoe, 1979; Land, 1980; Martin, 1982, 1985, 1999; Ali & Klyne, 1985; Charman, 1991; Land & Nilsson, 2002). Hence, animals of different body and eye sizes are expected to optimize eye shape for the specific needs of their light-level adaptation, which is highly correlated with that animal's activity pattern (Ross, 2000; Kirk, 2003, 2004; Hall, 2005; Ross *et al.*, 2006).

Activity pattern

Diurnal animals, for which there is plenty of light, are free to increase visual acuity by maintaining a small corneal diameter while lengthening the eye to maximize image size. Nocturnal animals also benefit from the increased acuity that accompanies increased eye size. However, because they function in environments with lower ambient light levels, the main challenge to nocturnal animals is increasing the ratio of signal to noise in their visual fields or, in other words, maximizing their chances of capturing enough photons of light to create a usable image on their retinae (Pirenne, 1967; Land & Nilsson, 2002). Because isometric increases in eye size are not accompanied by changes in image brightness, nocturnal animals are expected to have eyes shaped differently than those of diurnal animals. In order to increase image brightness, nocturnal animals must increase the size of the cornea *relative* to the axial length of the eye, whether by increasing corneal diameter or by decreasing axial length. Therefore, diurnal birds are expected to have smaller corneas relative to axial lengths, nocturnal birds are expected to have larger corneas relative to axial lengths, and cathemeral and crepuscular birds are expected to have intermediate states.

Materials and methods

Study animals

Data were collected on corneal diameters and axial lengths of the eye for 682 specimens of 459 non-passerine bird species (see Supplementary Material Table S1). Study groups included Strigiformes (barn owls and true owls), Psittaciformes (parrots), Columbiformes (pigeons), Pterocliformes (sandgrouse), Apodiformes (swifts),

Falconiformes (falcons), Accipidrae (hawks), Cathartidae (New World vultures) Charadriiformes (shorebirds), Caprimulgidae (nightjars), Aegothelidae (owlet-nightjars), Nyctibidae (potoos), Podargidae (frogmouths) and five groups of ratites (ostriches, rheas, cassowaries, kiwis and tinamous). Groups were chosen to include all activity patterns and a broad array of diets and feeding techniques. The majority of these data were collected by Ritland (1982), but that dataset was culled to eliminate non-adult specimens and was supplemented by the addition of 75 specimens of 60 species for the current study (see Supplementary Material Table S1). Specimens collected for this study were obtained from the Departments of Ornithology of the American Museum of Natural History (New York, NY), the Field Museum of Natural History (Chicago, IL) and the British Natural History Museum (Tring, UK). One frozen ostrich specimen was obtained from the Witmer Lab at Ohio University (Athens, OH). All of the museum specimens were preserved in ethanol, and individuals exhibiting any pathology or unusual preservational deformation were excluded from this study.

Measurements

In order to allow for analysis of the two datasets together, eye measurement procedures were according to Ritland (1982) as follows. In order to gain access to the eyeball, the eyelid was reflected or removed, and fascia and extraocular muscles were separated from the eyeball using blunt dissection with closed, curved scissors and forceps to preserve the eyeball from accidental puncture. When the eye was partially removed from the orbit and the optic nerve was seen, the nerve was cut with scissors. After complete removal from the orbit, the eyeball was cleaned of all remaining fascia and extraocular muscles and inflated using a small amount of preservative injected using a syringe with a small-gauge needle inserted at an angle into the sclera just inferior to the outer edge of the sclerotic ring. Preservative was injected until the eye was fully inflated and would not accept any more liquid. For many of the larger specimens, this required several injections, in which case care was taken to utilize the same puncture hole each time. Any eye that could not be fully inflated was not measured. Maximum corneal diameter and maximum axial length of the eye were measured to the closest 0.01 mm using digital calipers (see Supplementary Material Table S1 for raw data). In order to have a consistently measured body-size measurement, head-body length was taken on all specimens from the top of the crown to the rump; beak and tail length were not included, but neck length was included. While there may be some drawbacks in including neck length for birds that have long necks, no other body-size measurement was available for all the animals in this study. While some long-necked birds are represented in this study, such as ostriches, in general very long-necked clades, such as the different groups of waterbirds, were not represented, and most included birds, such as owls, have relatively short necks.

Activity pattern coding

Animals were coded into three different activity pattern categories: (1) *diurnal*, defined as active during the day in a photopic, or light-rich, environment; (2) *crepuscular*, active during the dawn and dusk, and *cathemeral,* equally likely to be active at any time of day; and (3) *nocturnal*, active at night in a scotopic, or relatively light-limited, environment.

Activity pattern is defined by that time of day when the animal conducts its normal visually directed activities, and excludes occasional activities that take place at other times of day. For example, swifts are day-active, and as such are coded as diurnal. However, during some parts of their life cycle swifts literally do not come to the ground for several months at a time, even sleeping in the air (Martin, 1990; Chantler & Driessens, 1995). Therefore, they are also active at night. However, their nighttime activities are fundamentally different from those during the day; flight ascends to an altitude where the animal is unlikely to meet any obstacles, and feeding and social interactions generally do not take place (Martin, 1990; Chantler & Driessens, 1995). Therefore, even though the animal is technically also active at night, visually directed behaviors take place only during the day in light-rich environments and the animal is coded as diurnal.

Statistical analysis

The purpose of this study is to examine how activity pattern correlates with both the size and shape of the eye. All analyses are computed using $\log_{10}$ data. Corneal diameter and axial length of the eye are both size variables, whereas the logged ratio between the two of them is the shape variable. In order to investigate the possible negative effects of using a ratio, the Kolmogorov–Smirnov test with the Lilliefors transformation was conducted for the shape ratio ($\log_{10}$ CD–$\log_{10}$ AL) to determine if it is log-normally distributed without homoscedasticity, skewness or kurtosis (Sokal & Rohlf, 1995). The test for normality was repeated for each of the three activity pattern groups.

To investigate whether the means of eye size and shape were significantly different between the animals coded into the different activity pattern categories, three one-way ANOVAs were performed for $\log_{10}$ absolute corneal diameter, $\log_{10}$ absolute axial length of the eye and the shape ratio ($\log_{10}$ CD–$\log_{10}$ AL). A scatter plot was generated to allow for visual inspection of data distribution (see Results; Fig. 2). For those groups not normally distributed, the Kruskal–Wallis non-parametric alternative to ANOVA was performed.

In order to see if there is a similar allometric relationship between eye size and head body length, as has been previously shown for eye mass and body mass (Ritland, 1982; Brooke et al., 1999; Howland et al., 2004), $\log_{10}$ axial length of the eye was regressed against $\log_{10}$ head-body length. In order to determine if the ratio of axial length/corneal diameter changes with either body size or eye size, the logged ratio of axial length/corneal diameter was regressed against both head-body length and axial length alone as a measure
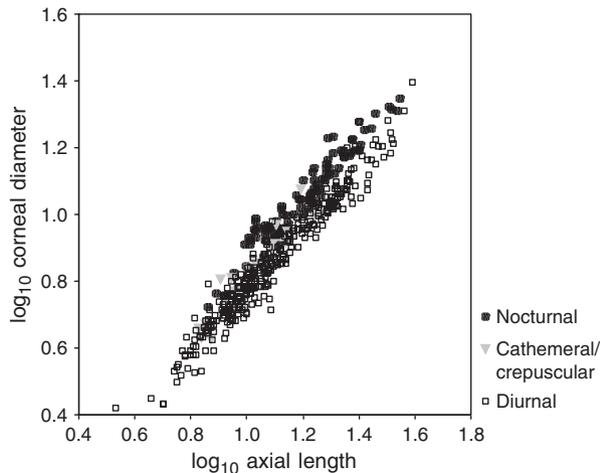
Figure 2 Scatter plot of birds coded for activity pattern with $\log_{10}$ axial length on the *x*-axis and $\log_{10}$ corneal diameter on the *y*-axis. There is good separation between nocturnal and diurnal animals. Nocturnal: $r^2 = 0.93$, ordinary least squares (OLS) slope $= 0.869$, reduced major axis (RMA) slope $= 0.90$; confidence intervals do not include 1, excluding isometry. Diurnal: $r^2 = 0.948$, OLS slope $= 0.895$, RMA slope $= 0.92$; confidence intervals do not include 1, excluding isometry. Cathemeral/crepuscular: $r^2 = 0.87$, OLS slope $= 0.903$, RMA slope $= 0.97$; confidence intervals include 1, including the possibility of isometry. ANCOVA analysis indicates significant elevational differences between nocturnal and diurnal lines, but the cathemeral/crepuscular line cannot be statistically differentiated from the diurnal line.

of eye size. Because measurement error and natural variation affect both dependent and independent variables, reduced major axis (RMA) was the Model II line-fitting technique utilized in this study; this method does not assume that variance in either variable is more significant or that one is influencing the other (Ricker, 1984; Rayner, 1985; Sokal & Rohlf, 1995).

Phylogenetic comparative methods

The tree utilized in this study is a composite of the individual lower taxonomic level phylogenies compiled from molecular phylogenies by Iwaniuk (2003), updated by several more recent lower taxonomic level molecular phylogenies (Dumbacher, Pratt & Fleischer, 2003; Garcia-Moreno, Sorenson & Mindell, 2003; Paton *et al.*, 2003; Thimassen *et al.*, 2003; Poe & Chubb, 2004; Thomas, Willis & Szekely, 2004). These individual composite lower-level group phylogenies were then assembled into a large-scale composite phylogeny that reflects inter-ordinal relationships from Cracraft *et al.* (2004). Of the total of 459 species included in the standard statistical analysis, it was possible to find group phylogenies that included 202. However, even utilizing the best-resolved trees available, polytomies in the final tree were unavoidable (see Supplementary Material Fig. S1). Branch lengths were set as equal because there is contradictory evidence for branch lengths from biogeography, the fossil record and

molecular clock studies (reviewed in Cracraft, 2001; see also Graur & Martin, 2004).

This study combines continuous (measurements of eye size and shape) and discrete (ecological categories) variables. Phylogenetic independent contrasts for this study were performed in CAIC (v.2.6.9) (Purvis & Rambaut, 1995) because this program does not require a fully resolved tree and it is able to analyze a combination of continuous and discrete variables utilizing the BRUNCH algorithm (Purvis & Rambaut, 1995; Nunn & Barton, 2001). Because the activity pattern categories are unordered, and independent contrasts can only be performed on dichotomous discrete variables, independent-contrast analysis was only performed on nocturnal and diurnal activity pattern data. The null hypothesis tested by BRUNCH is that the dependent continuous variables (corneal diameter, axial length and the shape ratio of corneal diameter/axial length) are not related to the independent discrete variable (activity pattern). BRUNCH calculates contrasts only at those nodes where the discrete variable changes, in this case, where there is a transition between nocturnal and diurnal activity patterns (Purvis & Rambaut, 1995). The sign of the contrast depends on the direction of the discrete variable change; if zero, there is no change and the null hypothesis of no relationship between the morphological and discrete variables is not rejected.

Results

The regression of axial length on head-body length reveals a negatively allometric relationship between eye size and body size [$r^2 = 0.42$; ordinary least squares (OLS) slope $= 0.536$, RMA slope $= 0.827$; phylogenetic independent-contrast OLS slope $= 0.54$, phylogenetic independent-contrast RMA slope $= 0.57$; no confidence intervals include 1, excluding isometry]. The regression of corneal diameter on head-body length also reveals a negatively allometric relationship between eye size and body size ($r^2 = 0.32$; OLS slope $= 0.461$, RMA slope $= 0.816$; phylogenetic independent-contrast OLS slope $= 0.45$, phylogenetic independent-contrast RMA slope $= 0.48$; no confidence intervals include 1, excluding isometry). These are shallower but similar slopes to the relationship between eye mass and body mass found in previous studies of avians (standard OLS slope $= 0.682$, phylogenetic independent-contrast OLS slope $= 0.696$; Brooke *et al.*, 1999). Regressions showed that there was no discernable relationship between the logged ratio of axial length to corneal diameter on the *y*-axis and head-body length on the *x*-axis ($r^2 = 0.135$), with axial length of the eye on the *x*-axis ($r^2 = 0.041$) or with corneal diameter on the *x*-axis ($r^2 = 0.008$), indicating that the ratio is a measurement of shape that is uncorrelated with size.

Shape analysis ($\log_{10}$ CD–$\log_{10}$ AL)

One-way ANOVA results were significant ($P < 0.001$). The Kolmogorov–Smirnoff test showed that the shape ratio was not log-normally distributed for either nocturnal or diurnal

birds, but is normally distributed for cathemeral/crepuscular birds. Therefore, the Kruskal–Wallis non-parametric alternative to ANOVA was performed to test for differences between the groups, and the result was significant (asymptotic significance <0.001). Levene's test for homogeneity of variances was significant, and Games–Howell *post hoc* tests were performed to investigate differences between the three activity patterns. The results of the *post hoc* tests revealed that all three activity patterns were significantly different from one another, with diurnal animals exhibiting longer axial lengths of the eye relative to the corneal diameters, nocturnal animals exhibiting larger corneal diameters relative to the axial lengths of the eye, and cathemeral/crepuscular animals exhibiting an intermediate state (see Fig. 3).

Size analysis

The Kolmogorov–Smirnoff test showed that axial length of the eye and corneal diameter were not log-normally distributed for diurnal birds but are normally distributed for cathemeral/crepuscular birds and nocturnal birds. Therefore, the Kruskal–Wallis non-parametric alternative to ANOVA was performed in addition to ANOVA to test for differences between the groups, and the result was significant (asymptotic significance <0.001). One-way ANOVA results were also significant for both axial length of the eye and corneal diamater ($P<0.001$). In both cases, Levene's test for homogeneity of variances was significant; therefore, Games–Howell *post hoc* tests were performed. Nocturnal birds showed significantly larger axial lengths and corneal diameters than both diurnal and cathemeral/crepuscular birds. However, the axial lengths and corneal diameters of diurnal and cathemeral/crepuscular birds were not significantly different from one another.
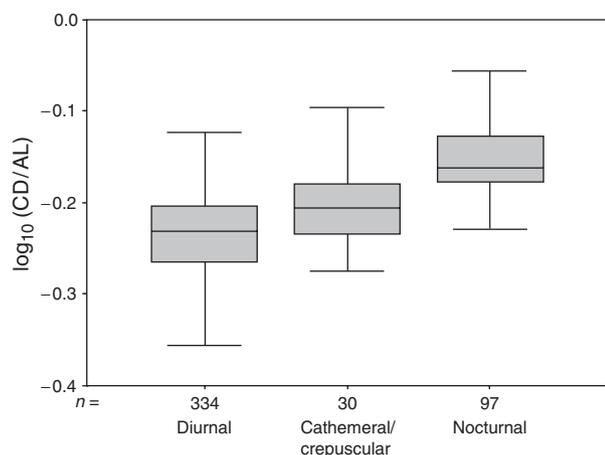

Figure 3 Box-and-whiskers plot of the shape ratio $\log_{10}(CD/AL)$, showing the differences between diurnal, cathemeral/crepuscular and nocturnal activity patterns. The solid line contained within the box represents the grand mean, and ANOVA analysis found the differences between the means to be statistically significant ($P<0.001$). CD, corneal diameter; AL, axial length of the eye.

Regression analysis

Regression analysis of corneal diameter versus axial length confirms ANOVA results (see Fig. 2). Regression results for the different activity patterns are as follows: nocturnal: $r^2 = 0.93$, OLS slope = 0.869, RMA slope = 0.90; confidence intervals do not include 1, excluding isometry; diurnal: $r^2 = 0.948$, OLS slope = 0.895, RMA slope = 0.92; confidence intervals do not include 1, excluding isometry; cathemeral/crepuscular: $r^2 = 0.87$, OLS slope = 0.903; RMA slope = 0.97; confidence intervals include 1, including the possibility of isometry. ANCOVA results indicate significant elevational differences between nocturnal and diurnal lines, but the cathemeral/crepuscular line cannot be statistically differentiated from the diurnal line.

Phylogenetic analysis

The BRUNCH algorithm calculated phylogenetic independent contrasts at 13 nodes where there was a change between activity patterns. Shape, the $\log_{10}$ ratio of corneal diameter to axial length, was found to be highly significantly related to changes in activity pattern ($P = 0.009$, F-ratio = 9.426, $r^2 = 0.44$). In contrast, neither of the two size variables, corneal diameter and axial length, were significantly related to changes in activity pattern at these nodes.

Discussion and conclusions

Activity pattern, the time of day when an animal is active, is the main determinant of how much light is available to birds. The principles of dioptrics predict that visually dependent animals in a light-limited environment will have large corneal diameters in order to maximize the chances of capturing quanta of light. Likewise, dioptrics predict that animals in light-rich environments will have eyes with large axial lengths in order to maximize visual acuity (see Introduction). Analysis of the shape ratio data yields the expected relationship between axial length and corneal diameters based on the principles of dioptrics: nocturnal birds, visually active in light-limited environments, have larger corneal diameters relative to their axial lengths. Diurnal birds, for which light is plentiful, have larger axial lengths of the eye relative to their corneal diameters. This can be seen in the scatter plot shown in Fig. 2; at any given axial length of the eye, a nocturnal bird has a larger corneal diameter than a diurnal bird.

Conventional statistical methods assume that data observations are independent (e.g. Sokal & Rohlf, 1995). However, data observations in closely related animals are inherently not independent (Felsenstein, 1985), requiring specialized statistical methods. Here independent-contrast analysis (Felsenstein, 1985; Harvey & Pagel, 1991) is used to analyze the relationship between eye size and shape and ecology in a phylogenetic context. Currently, avian systematics is still highly controversial and there is no commonly accepted phylogeny that includes all the animals in this study. Nunn & Barton (2001) argue that while incorrect topology or branch lengths tend to increase type I error

rates, ignoring phylogeny completely produces a greater increase in type I error. Therefore, it is preferable to use the best tree available rather than ignore phylogeny, even if it contains some relationships that may be reassessed in the future. Some systematists argue that one reason why avian phylogeny remains so unresolved may be because the initial bird radiation was so rapid and explosive that most modern bird groups do in fact have similar branch lengths (Cracraft, 2001; Poe & Chubb, 2004). However, even though only 13 contrasts could be calculated because of the unresolved state of bird phylogenetics, phylogenetic independent contrast data also showed that the shape ratios were significantly different between nocturnal and diurnal activity patterns, Therefore, when taking phylogeny into account, bird eyes are shaped as expected on the basis of dioptric principles.

It was also predicted that analysis of the absolute size measurements would yield similar results, and nocturnal birds would have absolutely larger corneal diameters than diurnal birds, diurnal birds would have absolutely larger axial lengths than nocturnal birds, and cathemeral birds would display intermediate size measurements of both variables. However, the results show that nocturnal birds have not only larger corneal diameters but also larger axial lengths than either diurnal or cathemeral birds. These longer axial lengths in nocturnal birds must decrease image brightness relative to a shorter axial length. Thus, although nocturnal birds do exhibit eye shapes that are optimized for increased image brightness, with larger corneal diameters relative to the axial lengths of the eye, they also exhibit longer absolute axial lengths than diurnal animals. We hypothesize that the increased axial lengths in nocturnal birds reflect selection for heightened visual acuity in animals with absolutely large effective photoreceptor pools. The high degree of pooling or summation of photoreceptors to ganglion cells in nocturnal animals means that the size of the effective photoreceptors is larger than that in diurnal animals (Walls, 1942; Hughes, 1977; Land, 1980; Martin, 1982, 1990, 1999; Ali & Klyne, 1985; Dowling, 1987; Kandel, Schwartz & Jessel, 1991; Land & Nilsson, 2002). Having larger effective photoreceptor areas means that larger eyes would be needed to achieve the same acuity, and, depending on the amount of photoreceptor pooling, larger eyes may be needed to achieve even less acuity. This indicates the importance of absolute eye size to nocturnal birds for both visual sensitivity and acuity. Figure 2 demonstrates that below a log corneal diameter of about 0.7 and a log axial length of about 0.9, there are no sampled nocturnal birds. It is possible that these eye dimensions represent a lower limit, below which the light available at night is not sufficient to support occupation of a visually dependent aerial, nocturnal niche.

Summary

Activity pattern has a significant influence on eye shape and size in birds. Nocturnal birds have eye shapes that are maximized for visual sensitivity, with larger corneal diameters relative to axial lengths. Diurnal birds have eye shapes that are maximized for visual acuity, with larger axial lengths relative to corneal diameters. Cathemeral and crepuscular animals exhibit intermediate states. However, nocturnal birds exhibit absolutely larger corneal diameters and axial lengths than diurnal birds, and below a minimum eye size there are no nocturnal birds present in this sample. This may indicate a minimum eye size, below which nocturnality is difficult or impossible in birds.

Acknowledgements

References

Ali, M.A. & Klyne, M.A. (1985). *Vision in vertebrates*. New York: Plenum Press.

Brooke, M.L., Hanley, S. & Laughlin, S.B. (1999). The scaling of eye size and body mass in birds. *Proc. Roy. Soc. Lond. B* **266**, 405–412.

Chantler, P. & Driessens, G. (1995). *Swifts: a guide to the swifts and treeswifts of the world*. East Sussex, South Africa: Russel Friedman Books CC.

Charman, W.N. (1991). The vertebrate dioptric apparatus. In *Evolution of the eye and visual system. Vol 2: Vision and visual disfunction*: 82–117. Cronly-Dillon, J.R. & Gregory, R.L. (Eds). Ann Arbor: CRC Press.

Cracraft, J. (2001). Avian evolution, Gondwana biogeography and the Cretaceous–Tertiary mass extinction event. *Proc. Roy. Soc. Lond. B* **1466**, 459–469.

Cracraft, J., Barker, F.K., Braun, M., Harshman, J., Dyke, G.J., Feinstein, J., Stanley, S., Cibois, A., Schikler, P., Beresford, P., Garcia-Moreno, J., Sorenson, M.D., Yuri, T. & Mindell, D.P. (2004). Phylogenetic relationships among modern birds (Neornithes). In *Assembling the tree of life*: 468–489. Cracraft, J. & Donoghue, M.J. (Eds). Oxford and New York: Oxford University Press.

Dowling, J.E. (1987). *The retina*. Cambridge: Harvard Belknap Press.

Duke-Elder, S. (1958). *System of opthalmology: the eye in evolution*. Chicago: University of Chicago Press.

Dumbacher, J.P., Pratt, T.K. & Fleischer, R.C. (2003). Phylogeny of the owlet-nightjars (Aves: Aeothelidae) based on mitochondrial DNA sequence. *Mol. Phyl. Evol.* **29**, 540–549.

Felsenstein, J. (1985). Phylogenies and the comparative method. *Am. Nat.* **125**, 1–15.

Fite, K.V. (1973). Anatomical and behavioral correlates of visual acuity in the great horned owl. *Vision Res.* **13**, 219–230.

Gaffney, M.F. & Hodos, W. (2003). The visual acuity and refractive state of the American kestrel (*Falco sparverius*). *Vision Res.* **43**, 2053–2059.

Garamszegi, L.Z., Moller, A.P. & Erritzoe, J. (2002). Coevolving avian eye size and brain size in relation to prey capture and nocturnality. *Proc. Roy. Soc. Lond. B* **269**, 961–967.

Garcia-Moreno, J., Sorenson, M.D. & Mindell, D.P. (2003). Congruent avian phylogenies inferred from mitochondrial and nuclear DNA sequences. *J. Mol. Evol.* **57**, 27–37.

Graur, D. & Martin, W. (2004). Reading the entrails of chickens: molecular timescales of evolution and the illusion of precision. *Trends Genet.* **20**, 80–86.

Green, D.G., Powers, M.K. & Banks, M.S. (1980). Depth of focus, eye size and visual acuity. *Vision Res.* **20**, 827–835.

Hall, M.I. (2005). *The roles of function and phylogeny in the morphology of the diapsid visual system*. PhD thesis, Stony Brook University, NY.

Harvey, P.H. & Pagel, M.D. (1991). *The comparative method in evolutionary biology*. Oxford: Oxford University Press.

Howland, H.C., Merola, S. & Basarab, J.R. (2004). The allometry and scaling of the size of vertebrate eyes. *Vision Res.* **44**, 2043–2065.

Hughes, A. (1977). The topography of vision in mammals of contrasting life style: comparative optics and retinal organization. In *The visual system in vertebrates*: 613–756. Crescitelli, F. (Ed.). Berlin: Springer Verlag.

Husband, S. & Shimizu, T. (2001). Evolution of the avian visual system. In *Avian visual cognition*. Cook, R.G. (Ed.). Available at: www.pigeon.psy.tufts.edu/avc/husband/

Iwaniuk, A.N. (2003). *The evolution of brain size and structure in birds*. PhD thesis, Monash University, Clayton, Victoria, Australia.

Kandel, E.R., Schwartz, J.H. & Jessel, T.M. (1991). *Principles of neural science*. Norwalk, CT: Appleton and Lange.

Kiltie, R.A. (2000). Scaling of visual acuity with body size in mammals and birds. *Funct. Ecol.* **14**, 226–234.

Kirk, E.C. (2003). *Evolution of the primate visual system*. PhD thesis, Duke University.

Kirk, E.C. (2004). Comparative morphology of the eye in Primates. *Anat. Rec.* **281A**, 1095–1103.

Land, M.F. (1980). Optics and vision in invertebrates. In *Handbook of sensory physiology VII/6B*: 471–592. Antrum, H. (Ed.). Berlin: Springer-Verlag.

Land, M.F. & Nilsson, D.-E. (2002). *Animal eyes*. New York: Oxford University Press.

Lythgoe, J.N. (1979). *The ecology of vision*. Oxford: Clarendon Press.

Martin, G. (1999). Optical structure and visual fields in birds: their relationship with foraging behaviour and ecology. In *Adaptive mechanisms in the ecology of vision*: 485–508. Archer, S.N., Djamgoz, M.B.A., Loew, E.R., Partridge, J.C. & Vallerga, S. (Eds). London: Kluwer Academic Publishers.

Martin, G.R. (1982). An owl's eye: schematic optics and visual performance in *Strix aluco*. *J. Comp. Physiol.* **145**, 341–349.

Martin, G.R. (1985). Eye. In *Form and function in birds*, Vol. 3: 311–373. King, S.A.S. & McLelland, J. (Eds). New York: Academic Press.

Martin, G.R. (1990). *Birds by night*. San Diego: Academic Press.

Martin, G.R. (1993). Producing the image. In *Vision, brain, and behavior in birds*: 5–24. Zeigler, H.P. & Bischof, H.-J. (Eds). Cambridge, MA: MIT Press.

Martin, G.R. & Gordon, I.E. (1974a). Increment-threshold spectral sensitivity in the tawny owl *Strix aluco*. *Vision Res.* **14**, 615–621.

Martin, G.R. & Gordon, I.E. (1974b). Visual acuity in the tawny owl *Strix aluco*. *Vision Res.* **14**, 1393–1397.

Meyer, D.B. (1977). The avian eye and its adaptations. In *Handbook of sensory physiology*, Vol. VII/5: 549–611. Crescitelli, F. (Ed.). New York: Springer-Verlag.

Meyer, D.B. (1986). The avian eye and vision. In *Avian physiology*, 4th edn: 38–48. Sturkie, P.D. (Ed.). New York: Springer.

Mosimann, J.E. (1970). Size allometry: size and shape variables with characterizations of the log-normal and gamma distributions. *J. Am. Stat. Assoc.* **56**, 930–945.

Mosimann, J.E. & James, F.C. (1979). New statistical methods for allometry with application to Florida red-winged blackbirds. *Evolution* **33**, 444–459.

Nunn, C.L. & Barton, R.A. (2001). Comparative methods for studying primate adaptation and allometry. *Evol. Anthrop.* **10**, 81–98.

Paton, T.A., Baker, A.J., Groth, J.G. & Barrowclough, G.F. (2003). RAG-1 sequences resolve phylogenetic relationships within Charadriiform birds. *Mol. Phylog. Evol.* **29**, 268–278.

Pirenne, M.H. (1967). *Vision and the eye*. London: Chapman & Hall.

Poe, S. & Chubb, A.L. (2004). Birds in a bush: five genes indicate explosive evolution of avian orders. *Evolution* **58**, 404–415.

Purvis, A. & Rambaut, A. (1995). Comparative analysis by independent contrasts (CAIC): an Apple Macintosh application for analysing comparative data. *Comp. Appl. Biosci.* **11**, 247–251.

Rayner, J.M.V. (1985). Linear relations in biomechanics: the statistics of scaling functions. *J. Zool. (Lond.)* **206**, 415–439.

Ricker, W.E. (1984). Computation and uses of central trend lines. *Can. J. Zool.* **62**, 1897–1905.

Ritland, S. (1982). *The allometry of the vertebrate eye*. PhD thesis, University of Chicago, Chicago.

Rochon-Duvigneaud, A. (1943). *Les yeux et la vision des vertebres*. Paris: Masson.

Ross, C.F. (2000). Into the light: the origin of Anthropoidea. *Annu. Rev. Anthropol.* **29**, 147–194.

Ross, C.F., Hall, M.I. & Heesy, C.P. (2006). Were basal primates nocturnal? Evidence from eye and orbit shape. In *Primate origins and adaptations*: 233–256. Ravosa, M. & Dagosto, M. (Eds). New York: Kluwer Academic/Plenum Publishers.

Rostgaard, J. & Qvortrup, K. (1999). A note about retinal structure and visual acuity. A light microscopic study of the cones in fovea centralis. *Acta Opthalmol. Scand.* **77**, 45–49.

Salwini-Plawen, L. & Mayr, E. (1977). On the evolution of photoreceptors and eyes. In *Evolutionary biology*, Vol. 10. Hecht, M.K., Steere, W.C. & Wallace, B. (Eds). New York: Plenum Press.

Snyder, A.W. & Miller, W.H. (1977). Photoreceptor diameter and spacing for highest resolving power. *J. Opt. Soc. Am.* **67**, 696–698.

Sokal, R.R. & Rohlf, F.J. (1995). *Biometry*. 3rd edn. New York: W. H. Freeman and Co.

Thimassen, H.A., Wiersema, A.T., de Bakker, M.A.G., de Knijff, P., Hetebrij, E. & Povel, G.D.E. (2003). A new phylogeny of swiftlets (Aves: Apodidae) based on cytochrome-*b* DNA. *Mol. Phylog. Evol.* **29**, 86–93.

Thomas, G.H., Willis, M.A. & Szekely, T. (2004). A supertree approach to shorebird phylogeny. *BMC Evol. Biol.* **4**, article 28, 18 pp.

Walls, G.L. (1942). *The vertebrate eye and its adaptive radiation*. New York: Hafner.

Zeigler, H.P. & Bischof, H.-J. (Eds) (1993). *Vision, brain, and behavior in birds*. Cambridge, MA: MIT Press.

Supplementary material

The following material is available for this article online:

Figure S1a and b This is a composite cladogram of bird taxa compiled for the phylogenetic analysis utilized in this study. Inter-ordinal bird relationships are after Cracraft *et al.* (2004). Lower taxonomic level cladograms included in this tree follow the composite tree compiled by Iwaniuk (2003), and updated by several more recent molecular phylogenies including Dumbacher, Pratt & Fleischer (2003), Garcia-Moreno, Sorenson & Mindell (2003), Paton *et al.* (2003), Thimassen *et al.* (2003), Poe & Chubb (2004) and Thomas, Willis & Szekely (2004).

Table S1 Species means raw data

This material is available as part of the online article from http://www.blackwell-synergy.com/doi/abs/10.1111/j.1469-7998.2006.00227.x

Please note: Blackwell Publishing are not responsible for the content or functionality of any supplementary materials supplied by the authors. Any queries (other than missing material) should be directed to the corresponding author for the article.