



## Flight Distance and Eye Size in Birds

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### Abstract

Larger eyes capture more information from the environment than small eyes, but also require more brain space for information processing. Therefore, individuals have to optimize the size of their eyes, leading to the prediction that larger eyes should have evolved in species with greater benefits from large eyes, such as species subject to intense predation risk. In a comparative analysis of 97 bird species, we found that species that fled at longer distances from an approaching potential predator indeed had relatively large eyes for their body size. In contrast, there was no indication that large eyes had evolved in species living in secluded habitats, or in species eating mobile prey. These findings are consistent with the assumption that eye size is labile and can evolve in response to changing predator environments. They also suggest that eye size may act as a constraint on optimal anti-predator behavior, if the predator community changes as a consequence of introductions or invasions.

### Introduction

Eye size determines the capacity of eyes in handling information visually extracted from the environment through the overall abundance of photoreceptors and/or their density (e.g. Land & Nilsson 2002). Eye size increases with body size with an allometry coefficient  $< 1$ , except for very small animals that show positive allometry (e.g. Kiltie 2000; Ross et al. 2006). Larger eyes have a larger overall abundance of photoreceptors and larger image sizes, and larger eyes can together with the size of the cornea, and hence eye shape, collect more light than small eyes (e.g. Walls 1942; Martin 1985, 2007). Birds have relatively large eyes compared to other classes of vertebrates, reflecting the unique importance of vision in their life (Walls 1942; Tansley 1965; Martin 1985, 2007; Garamszegi et al. 2002; Hall & Ross 2006). The ways in which this occurs mainly relates to specialization of eyes as adaptations to foraging. Blumstein et al. (2004) analyzed the relationship between eye size and flight initiation distance using

a small sample of species recorded by Garamszegi et al. (2002), but did not find any significant association between flight distance and relative eye size. It is surprising that there have been so few successful attempts to relate relative eye size to other aspects of ecology or general life history (but see Land & Nilsson 2002; Walls 1942; Tansley 1965; Martin 1985, 2007; Garamszegi et al. 2002; Hall & Ross 2006 for a discussion of vision and nocturnal activity).

Vision has evolved and is maintained due to interactions with conspecifics, heterospecifics and the environment. Selection arising from (1) social communication among conspecifics; (2) foraging and food; and (3) anti-predator behavior and predators may all contribute to determine among other factors the size of eyes and hence the ability to perceive the environment including conspecifics and heterospecifics. First, social communication associated with competition for limiting resources such as shelter, food and roosting sites and competition for mates may affect the size and the position of eyes in the head, but also the structure of visual fields

(e.g. Martin 1985, 2007; Fernández-Juricic et al. 2004). Second, foraging and food may be important determinants of eye size because mobile food items may more readily be detected, captured and subdued when binocular vision allows potential prey items to be located independently by the two eyes. Binocular vision provisions each eye with an optic flow-field that encompasses the object (such as a prey item) or the surface toward which a given animals' head is moving, allowing the animal to continuously integrate information from the two eyes to achieve a view of the target object (Martin & Katzir 1999). Third, predation and anti-predator behavior are key factors determining the behavior of all animals including birds (review in Caro 2005). Martin (2007) suggested that there is a trade-off between the need to visually locate a food item and guide the bill toward it and the cyclopean vision (the total angular width of the visual field in a particular plane). Thus, birds that do not need to see where their bill is located may evolve lateral eyes that allow comprehensive vision all around the head (Martin 2007). Wide lateral fields of vision in ground-foraging passerines allow detection of approaching predators while simultaneously allowing them to forage efficiently (Fernández-Juricic et al. 2008), although not as efficiently as when attention is not diverted away by food items difficult to detect (Dukas 1998). This suggests that predation risk in addition to precise pecking for food on the ground may independently affect the position of eyes, increase the cyclopean field of vision, and reduce the blind area where objects cannot be seen (Fernández-Juricic et al. 2004). Similarly, we suggest that eye size may have evolved as a means of avoiding or reducing risk of predation because larger eyes may more readily allow early detection of an approaching predator.

The objectives of this study were to test a number of predictions relating to the evolution of relative eye size in birds. First, we hypothesized that anti-predator behavior has coevolved with the size of eyes. Larger eyes may equate with the early detection of an approaching predator, hence flight initiation distance as a measure of anti-predator behavior can be predicted to be positively related to eye size relative to body size of prey. We have previously shown that flight distance by birds to human approach is positively correlated with risk of predation by a common species of diurnal raptor, the sparrowhawk *Accipiter nisus*, across species of birds (Møller et al. 2008). Blumstein et al. (2004) investigated the relationship between eye size and flight

distance in birds, but did not find a significant relationship. Here, we used a larger sample of species, a wider range of eye sizes, and better statistical techniques to control for the confounding effects of body size. Second, we hypothesized that species living in more complex habitats that included vegetation in three dimensions had larger eyes than species living in open habitats. The underlying assumption is that three-dimensional habitats would make detection of predators, but also conspecifics and competitors more difficult than in two-dimensional habitats. Thus, we predicted that relative eye size should increase from open grassland over shrub to forest. Finally, we hypothesized that bird species relying on a diet of mobile prey had evolved larger eyes than species that entirely rely on immobile food such as plant material. If larger eyes are more sensitive and have higher resolution, species feeding on mobile food that may escape if detected late by an avian predator should select for relatively larger eyes. This hypothesis is not at conflict with the first hypothesis because bird species that are commonly preyed upon by avian predators would enjoy a selective advantage if being able to detect an approaching predator early, independent of their diet.

## Methods

### Eye Size

JE received fresh dead birds of more than 500 species from the public during 1960–2009 and measured by post-mortem examination the equatorial diameter and the axial length of the eye (to the nearest 0.1 mm with a caliper). Because information on anti-predator behavior was only available for a limited sample of 97 species, the remaining species were discarded from the subsequent analyses. Although eye shape varies among species (Zeigler & Bischof 1993; Hall & Ross 2006), we assumed in the following that eyes had a spheroid shape and calculated the volume of an eye by using the equation

$$\text{Eye volume (cm}^3\text{)} = 1.33a^2(\text{cm}^2)b(\text{cm})$$

where  $a$  is the equatorial radius and  $b$  is the axial radius of the eye (Garamszegi et al. 2002). This definition of eye size takes into account the fact that axial length is important for acuity and resolution of eyes, and eye size estimated in this way is similar to that used in previous comparative studies (e.g. Garamszegi et al. 2002; Kiltie 2000; Ross et al. 2006).

### Habitat

Species living in more closed habitats will experience different light levels (Endler 1993) and may experience more problems of monitoring the environment for potential predators than species living in open habitats, where approaching predators can be readily detected. Therefore, we classified species on a three point scale as living in (1) grassland or similar open habitats, (2) habitats with scattered or continuous shrub, or (3) habitats with scattered or continuous trees, relying on descriptions of breeding habitats in Cramp & Perrins (1977–1994). If a species inhabited two or three of these habitat categories, it was scored as having the highest level because that would be the habitat that imposed the greatest challenge on vision.

### Food Mobility

Mobile food items can be considered to be more difficult to catch than immobile food because mobile food items captured by use of eye sight will require binocular vision that allows motion detection and potential food to be located independently by the two eyes to determine location. Furthermore, mobile prey may escape and hence defy predation, putting a premium on fast detection and capture of prey. We classified food as being mobile (given a score of 1) or immobile (given a score of 0) based on descriptions of the main food in Cramp & Perrins (1977–1994). All bird species feeding on mobile invertebrates or on vertebrates were classified as having mobile food, while all species feeding on sessile invertebrates or plants were classified as having immobile food.

### Flight Distance

Regularly during Feb.–Sep. 2006–2008 APM estimated flight distances for birds, using a standardized technique in Ile-de-France, France and Northern Jutland, Denmark. In brief, when an individual bird had been located with a pair of binoculars, APM moved at a normal walking speed toward the individual, while recording the number of steps [which approximately equals the number of meters measured with a laser-based hypsometer (Møller et al. 2008)]. The distance at which the individual took flight was recorded as the flight initiation distance, while the starting distance was the distance from where the observer started walking up to the position of the bird. If the individual was positioned in the vegetation, the height above ground was

recorded to the nearest meter. Flight initiation distance was estimated as the Euclidian distance, which equals the square root of the sum of the squared horizontal distance and the squared height above ground level (Blumstein 2006). If an individual of a specific species had been recorded in a particular site, no further individuals were recorded in that specific site during the remainder of the study to avoid inclusion of the same individual more than once (i.e., to avoid pseudo-replication).

All recordings were made during the breeding season, when most individuals are sedentary, thus preventing the same individual from being recorded in different sites. The number of flight initiation distances recorded during different months was 387 in Feb., 220 in Mar., 1054 in Apr., 1970 in May, 411 in Jun., 428 in Jul., 390 in Aug. and 94 in Sep. For the present study APM recorded a total of 4347 flight initiation distances for 151 species.

Flight initiation distance was consistent for the same species in different studies, as shown by three different cross-validations (Møller 2008a–c). Møller (2008a–c) has also shown statistically significant consistency in estimates among observers, among study sites, and among seasons. Previous studies have shown that starting distance is positively correlated with flight initiation distance (e.g. Blumstein 2003, 2006; Cooper 2005, 2008), thereby causing a problem of collinearity. We eliminated this problem of collinearity by searching habitats for birds with a pair of binoculars when choosing an individual for estimating flight initiation distance. In this way we assured that almost all individuals were approached from a distance of at least 30 m, thereby keeping starting distances constant across species. Flight initiation distance was negatively related to starting distance in a model that included species, age (juvenile or adult), habitat, country and body mass as predictors ( $F_{1,4188} = 37.97$ ,  $p < 0.0001$ ), only explaining 1% of the variance. None of the results presented in this paper changed statistically when including starting distance as an additional variable.

### Body Mass

We included body mass as a control variable because body mass has previously been shown to correlate with flight initiation distance (e.g. Møller 2008a–c) and eye size (e.g. Kiltie 2000; Garamszegi et al. 2002; Hall & Ross 2006). Body mass was recorded as the mean mass of males and females from the breeding season, as reported by Cramp & Perrins (1977–1994). If more than a single estimate was reported

in that source, we used the one with the largest sample size.

The entire data set is reported in Appendix S1.

### Comparative Analyses

Flight initiation distance, eye size and body mass were  $\log_{10}$ -transformed to ensure that variables were normally distributed, while all other variables were untransformed.

Analyses of comparative data from different species as statistically independent observations may result in misleading conclusions if sister taxa are more similar than randomly chosen species. Therefore, we analyzed statistically independent, standardized linear contrasts (Felsenstein 1985), which controls for similarity in phenotype among species due to common descent, using the software of Purvis & Rambaut (1995). All regressions were forced through the origin (Felsenstein 1985), because the dependent variable is not assumed to have changed, when the predictor variable has not evolved. Standardization of contrast values were checked by examination of absolute values of standardized contrasts vs. their standard deviations (Garland & Ives 2000; Garland et al. 1992). Plotting the resulting contrasts against the variances of the corresponding nodes revealed that these transformations made the variables suitable for regression analyses. In order to reduce the consequent problem of heterogeneity of variance: (1) outliers (contrasts with Studentized residuals  $> 3$ ) were excluded from subsequent analyses (Jones & Purvis 1997) (the presented analyses included these outliers), and (2) analyses were repeated with the independent variable expressed in ranks (Møller & Birkhead 1994). However, these analyses all produced statistically similar conclusions and thus we present the results with the outliers included based on the unranked data.

A common underlying assumption of statistical analyses is that each data point provides equally precise information about the deterministic part of total process variation, i.e. the standard deviation of the error term is constant over all values of the predictor variable(s) (Sokal & Rohlf 1995). The standard solution to violations of this assumption is to weight each observation by sampling effort to make optimal use of all data, by giving each datum a weight that reflects its degree of precision due to sampling effort (Draper & Smith 1981; Neter et al. 1996). Comparative analyses may be confounded by sample size if sampling effort is important, and if sample size varies considerably among taxa. Therefore, we weighted

regression by sample size. In order to weight regressions by sample size in the analysis of contrasts, we calculated weights for each contrast by calculating the mean sample size for the taxa immediately subtended by that node (Møller & Nielsen 2007).

We estimated phylogenetically adjusted relative eye size of birds by first estimating the phylogenetically adjusted allometric relationship between  $\log_{10}$ -transformed eye size and  $\log_{10}$ -transformed body mass. Subtracting expected eye size from the observed value provides an estimate of relative eye size that takes the phylogenetic relationships among species into account.

The comparative analyses relied on composite phylogenies created by using information in Hackett et al. (2008) and Sibley & Ahlquist (1990), supplemented with information in Jønsson & Fjeldså (2006) to resolve relationships between some species. The phylogeny is reported in Appendix S2.

### Results

Eye size scaled negatively to body mass in a model based on contrasts ( $F_{1,91} = 99.60$ ,  $r^2 = 0.50$ ,  $p < 0.0001$ , slope [SE] = 0.579 [0.058]), with an allometry coefficient that differed significantly from one ( $t_{91} = 7.26$ ,  $p < 0.0001$ ). This was similar to the scaling coefficient of 0.54 reported by Hall & Ross (2006) for least squares models based on contrasts, and the scaling coefficient of paired eye size of 1.089 reported by Garamszegi et al. (2002). The scaling coefficient of 1.089 should be divided by 2 ( $1.089/2 = 0.545$ ) to provide an estimate comparable to those listed above. Differences between observed and predicted eye size based on this phylogenetic relationship (phylogenetically corrected residuals) were used in all subsequent analyses. The residuals were normally distributed (Shapiro-Wilk  $W$ -test,  $W = 0.96$ ,  $p = 0.051$ ).

A full model based on species-specific data explained 48% of the variance in relative eye size (Table 1). Residual eye size increased significantly with flight initiation distance (Fig. 1a) and body mass, but decreased with increasing habitat complexity (Table 1). Finally, birds eating mobile prey had relatively larger eyes (Table 1). Effect size for residual eye size estimated as Pearson's product-moment correlation coefficient was intermediate at 0.34.

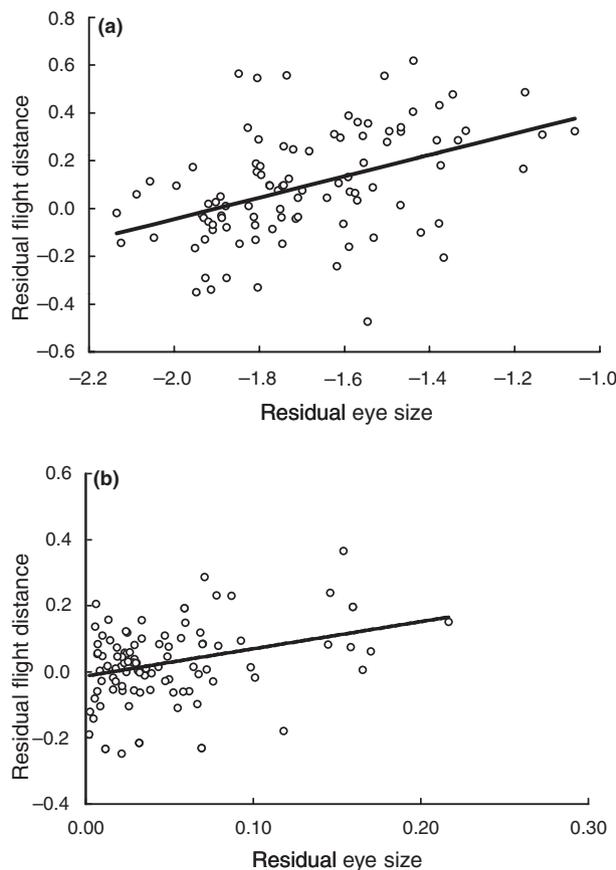
Analysis of linear contrasts only showed a significant effect of flight distance (Fig. 1b), with an intermediate effect size of 0.25. In contrast, there was no significant effect of body mass, habitat, or prey

**Table 1:** Residual eye size in relation to flight initiation distance, body mass, habitat and mobile food. The models had the statistics  $F_{4,92} = 21.41$ ,  $r^2 = 0.48$ ,  $p < 0.0001$  for species-specific data and  $F_{4,92} = 2.20$ ,  $r^2 = 0.03$ ,  $p = 0.025$  for contrasts

Variable	Sum of squares	df	F	p	Slope (SE)
<b>Species</b>					
Flight initiation distance	9.98	1	11.63	0.0010	0.239 (0.070)
Body mass	4.29	1	6.26	0.014	0.082 (0.033)
Habitat	2.78	1	4.05	0.047	-0.032 (0.016)
Mobile food	14.99	1	21.87	< 0.0001	0.068 (0.015)
Error	63.09	92			
<b>Contrasts</b>					
Flight initiation distance	0.61	1	5.93	0.017	0.127 (0.052)
Body mass	0.10	1	1.00	0.32	0.043 (0.043)
Habitat	0.00	1	0.01	0.93	-0.002 (0.019)
Mobile food	0.03	1	0.26	0.61	0.019 (0.038)
Error	9.52	92			

**Table 2:** Absolute eye size in relation to flight initiation distance, body mass, habitat and mobile food. The model had the statistics  $F_{4,92} = 222.45$ ,  $r^2 = 0.91$ ,  $p < 0.0001$

Variable	Sum of squares	df	F	p	Slope (SE)
Flight initiation distance	0.39	1	15.23	<0.0001	0.313 (0.080)
Body mass	6.16	1	243.42	<0.0001	0.616 (0.039)
Habitat	0.12	1	4.59	0.035	0.041 (0.019)
Mobile food	0.52	1	20.51	<0.0001	0.087 (0.019)
Error	2.33	92			



**Fig. 1:** Residual flight initiation distance (after controlling for body mass) in relation to residual eye size (after controlling for body mass) for (a) species and (b) independent linear contrasts. The lines are the linear regression lines.

mobility (Table 1), showing that the effects of these variables in the species-specific analyses were due to a few clades having specific trait values. A reduced model that only included mean flight initiation distance as a predictor of residual eye size had the statistics  $F = 7.77$ ,  $df = 1$ ,  $95$ ,  $r^2 = 0.08$ ,  $p = 0.0064$ , slope (SE) = 0.140 (0.050). The results were not confounded by nocturnal behavior (Garamszegi et al. 2002; Hall & Ross 2006) because none of the species included in the analyses were nocturnal.

Finally, we tested the possibility that the use of residuals could have caused bias in estimates due to errors in parameter estimation for residuals (García-Berthou 2001; Freckleton 2002). However, a model based on eye size as the response variable and body mass as a predictor variable did not change any of the conclusions (Table 2).

**Discussion**

Relative eye size in birds was positively related to anti-predator behavior measured as flight initiation distance. This positive association was independent of the potentially confounding effects of habitat, diet, nocturnal activity, body size and similarity in phenotype among taxa due to common phylogenetic descent. Blumstein et al. (2004) investigated the relationship between relative eye size and relative flight distance for 23 species of birds, but did not find a significant relationship. We consider the difference in results between our study and that of Blumstein et al. (2004) to be due to three different factors. First, their number of species was a quarter of ours, and hence the statistical power of their test was lower. Second, they included both eye size and body mass as predictors into the same statistical model, an approach that may provide misleading conclusions due to collinearity between the two variables. Third, we included a wider range of eye sizes than did Blumstein et al. (2004), and this may

have facilitated detection of the positive relationship between flight distance and relative eye size.

Flight initiation distance comprises an estimate of the optimal risk taking behavior of animals (Ydenberg & Dill 1986; Blumstein 2006; Cooper & Frederick 2007). Because early flight from a potential predator reduces food intake, while delayed flight is associated with increased food intake, but at an elevated risk of death, individuals are assumed to optimize their risk taking behavior. Therefore, if the risk of mortality is increased, this should reduce flight distances. Consistent with this body of theory birds with higher levels of infection with blood parasites have shorter flight distances than less infected species (Møller 2008a), species taking greater risks have higher probability of being eaten by a sparrowhawk (Møller et al. 2008), urban populations of birds have shorter flight initiation distances than rural populations, as expected from the lower abundance of predators in urban environments (Møller 2008b), and species with long flight initiation distances have declining breeding populations, apparently because they are particularly susceptible to increasing levels of human disturbance (Møller 2008c). Clearly, flight initiation distances must depend on acquisition and processing of visual (and acoustic) information, and we predicted that bird species with larger eyes should have longer flight distances for their body mass if larger eye size allows early detection of predators. This was indeed the pattern that we found. We were unable to find any additional variable such as habitat, food mobility or body mass that could account for this finding. This does not exclude the possibility such as social behavior may constitute yet another confounding variable, although we consider that unlikely.

Habitats differ in the degree to which they allow early detection of predators (e.g. Caro 2005; Giraldeau & Caraco 2000), but also in their light regime that can have important implications for vision (e.g. Endler 1993). While we found evidence of relative eye size differing among habitats in analyses of species-specific data, we could not replicate this finding in analyses of statistically independent linear contrasts. This suggests that the effect observed at the species level was due to specific eye sizes being present in certain clades that also happened to have specific habitat requirements, while this relationship between eye size and habitat had not evolved repeatedly in different clades. We also suggested that mobile prey might affect the evolution of relative eye size if bird species that rely on a diet of mobile prey have evolved larger eyes than species that entirely rely on immobile food such as plant mate-

rial. However, we found no evidence consistent with this explanation, although we consider a test based on a larger diversity of species to be required before any firm conclusions can be reached.

These findings reported here have several implications. First, they imply that eye size is labile and can evolve in response to changing predator environments. Therefore, we can predict that eye size has changed in response to an absence of predators on oceanic islands. Second, the findings also suggest that eye size may act as a constraint on optimal anti-predator behavior, if the predator communities change due to introductions or invasions. Third, we might expect that vision and hence relative eye size have coevolved between predators and their prey, with specialist predators in particular having selected for relative larger eyes in their prey.

In conclusion, the relative size of eyes of birds is related to predation risk as reflected by flight distance when approached by a potential predator. This finding provides evidence consistent with the hypothesis that the visual system of birds and potentially also other organisms constitutes adaptations to risk of predation.

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### Supporting Information

Additional Supporting Information may be found in the online version of this article:

**Appendix S1.** Summary information on eye size (cc), flight initiation distance (m), sample size for flight distance, body mass (g), habitat (0, grassland; 1, bushes and shrub; 2, trees and forest); and mobile food (0, immobile food; 1, mobile food)

**Appendix S2.** Phylogenetic relationships among bird species. See Methods for sources

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