Coevolving avian eye size and brain size in relation to prey capture and nocturnality

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Behavioural adaptation to ecological conditions can lead to brain size evolution. Structures involved in behavioural visual information processing are expected to coevolve with enlargement of the brain. Because birds are mainly vision-oriented animals, we tested the predictions that adaptation to different foraging constraints can result in eye size evolution, and that species with large eyes have evolved large brains to cope with the increased amount of visual input. Using a comparative approach, we investigated the relationship between eye size and brain size, and the effect of prey capture technique and nocturnality on these traits. After controlling for allometric effects, there was a significant, positive correlation between relative brain size and relative eye size. Variation in relative eye and brain size were significantly and positively related to prey capture technique and nocturnality when a potentially confounding variable, aquatic feeding, was controlled statistically in multiple regression of independent linear contrasts. Applying a less robust, brunching approach, these patterns also emerged, with the exception that relative brain size did not vary with prey capture technique. Our findings suggest that relative eye size and brain size have coevolved in birds in response to nocturnal activity and, at least partly, to capture of mobile prey.

Keywords: adaptation; behaviour; brain size; coevolution; eye size; vision

1. INTRODUCTION

The relative size of an organ may reflect its functional significance, adaptations to the environment, or constraints to adaptation caused by genetic correlations with other characters, or recent changes in the environment (Harvey & Krebs 1990; Møller 1991; Møller *et al.* 1998). For example, it is often assumed that brain size is associated with increased information processing or computing power (Jerison 1973; Clutton-Brock & Harvey 1980). Among mammalian and avian species relative brain size reflects differences in ecology, life history, diet, parental care, behavioural flexibility, habitat and foraging technique (Harvey & Krebs 1990; Gittleman 1994; Barton 1996; Lefebvre *et al.* 1997; Pagel & Harvey 1998).

Birds are known to have relatively large eyes for their body size, suggesting that vision is an important sensory modality in this class of animals, and that eye size is subject to selection and evolutionary change (Martin 1985, 1993). Although the resolution power of the eye depends on the structure and concentration of rods and cones on the retina, eye size is also an important property of this sensory organ (Martin 1993). Larger eyes hold more retinal photoreceptive cells, and receive more light per solid angle of image, determining their spatial resolution power. The most important parameter associated with eye size is the focal length, since this affects the size of the retinal area over which the image is spread.

Once vision has become an important sensory modality in a group of species, it could be expected that neural pathways, neural connections and eye structures that enhance behaviourally related visual information processing will evolve, leading to the evolution of a large brain. Alternatively, interspecific differences in brain size can be the result of visual specialization associated with ecological and social conditions, as shown in primates (Barton 1996, 1998). These evolutionary mechanisms suggest that brain size and visual structures can coevolve leading to complex co-adaptation of the sensory system, and the central nervous system, to ecological conditions, thereby enhancing adaptive behavioural performance.

Eye size and brain size scale with body size (Martin & Harvey 1985; Harvey & Krebs 1990; Brooke *et al.* 1999; but see also Deaner & Nunn 1999; figure 1). In an allometric analysis of birds Brooke *et al.* (1999) showed that eye size scales with body mass, to increase spatial resolution in proportion to flight speed. The authors suggested that eye size and brain size scale with similar exponents, since they are both subject to selection pressures arising from the same sensory information (Jerison 1973). Larger eyes would require larger brain areas for processing the projected visual information. Surprisingly, according to our knowledge, this predicted correlation between the size of these two types of organs related to ecological factors has not yet been analysed.

We determined the relationship between eye size and brain size in birds with a comparative approach. (i) We calculated the allometric relationships for eye size and brain size. (ii) We used this information to obtain estimates of eye size and brain size adjusted for allometry. (iii) We tested whether selection pressures arising from the capture of actively moving prey, and nocturnal activity, have contributed to the evolution of eye and brain size
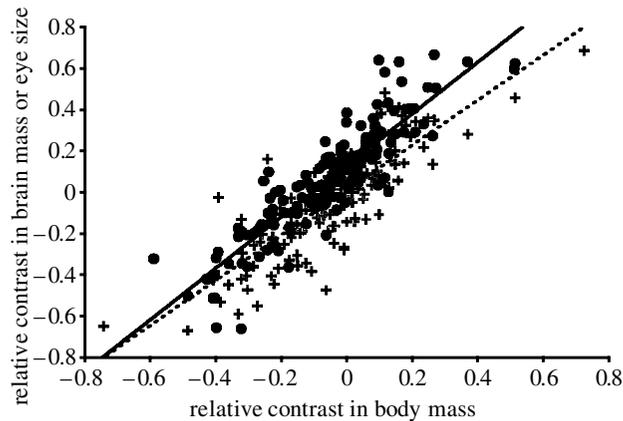
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Figure 1. Regression of eye size and brain size on body mass using statistically independent linear contrasts ($N = 141$ for eye size, $N = 159$ for brain size). The lines are based on the following equations: solid line, [$\log_{10}$(eye volume) contrast] $= 0.011 + 1.089$ [$\log_{10}$(body mass) contrast]; dashed line, [$\log_{10}$(brain mass) contrast] $= 0.001 + 1.017$ [$\log_{10}$(body mass) contrast]. Circles represent eye size, plus signs represent brain size.

while controlling for a potentially confounding factor, aquatic feeding.

2. MATERIAL AND METHODS

The following variables were measured by post-mortem examination of dead birds: the smallest and the largest diameter of the eye (to the nearest 0.1 mm with a calliper), brain mass (weighed on a balance to the nearest 0.001 g) and body mass (weighed on a balance to the nearest 0.001 g). A total of 2716 individuals were measured by J.E., blindly with respect to the predictions under test. Although eye shape varies among species (Martin 1993), we assumed in the following that eyes had a spheroid shape, and calculated their volume by using the equation

eye size (cm³) $= 2 \times 1.33\pi a^2$(cm²)b(cm),

where a is the largest and b the smallest radius of the eyes (we found highly significant correlations among different eye volume estimates if we used other formulae).

Information on eye size was available for 771 individuals of 238 bird species, while brain size data were available for 1072 individuals belonging to 344 bird species. In total, 167 species with a resolved phylogeny were used in the present study with 141 species with information on eye size and 159 with information on brain size. These variables were $\log_{10}$ transformed before performing any analysis.

One-way ANOVAs showed that there was significantly larger variance among, than within species in eye size and brain size (eye volume: $F_{218,354} = 30.47$, $p < 0.001$; brain mass: $F_{270,982} = 300.88$, $p < 0.001$; body mass: $F_{270,1026} = 355.55$, $p < 0.001$), which is required for a comparative analysis to be feasible. All measurements were significantly repeatable (eye volume: $R = 0.786$, s.e. = 0.092; brain mass: $R = 0.974$, s.e. = 0.017; body mass: $R = 0.978$, s.e. = 0.030).

We obtained information on prey capture technique, nocturnality and aquatic foraging from handbooks and field guides. For prey capture technique, species feeding on plant material were given a score of 1; omnivorous and insectivorous species applying simple capturing techniques, such as probing or glean-

ing from the vegetation, a score of 2; whereas birds hunting for actively moving prey in air or water were scored as 3.

Daily activity was also scored on a three-value scale by giving diurnal species a score of 1; crepuscular species (or species that show significant nocturnal activity beside their daylight activity) a score of 2; and strictly nocturnal species a score of 3.

As amphibious feeding can lead to eye structure adaptation (Sivak 1978; Martin & Young 1984; Martin 1998) that could be a potentially confounding factor in eye size evolution, we included this variable in our analyses. To express the increasing importance of water-connected foraging, species feeding in the air, on vegetation, or on the ground were represented by a score of 1; species that feed from the water surface (or their diet partly consists of aquatic prey that are caught without diving) a score of 2; and diving birds a score of 3.

The scores for each variable represent the increasing order of complexity of prey capture technique, nocturnality and water-dependent foraging, respectively. Because we intended to control for confounding effects by applying a multivariate approach based on independent linear contrasts (Harvey & Pagel 1991), we treated these variables as continuous variables, because intermediate states between character states are biologically meaningful (see also Møller & Cuervo 2000). The whole dataset is given in electronic Appendix A, available on The Royal Society's Publications Web site.

Species are not statistically independent in respect of observations, and associations between biologically important variables may be confounded by common ancestry. Hence a comparative method should be applied to distinguish between the effects of common descent and convergent evolution (Felsenstein 1985; Harvey & Pagel 1991). We controlled for similarity among species, due to common descent, by linear regression analysis based on statistically independent linear contrasts (Harvey & Pagel 1991) using Phenotypic Diversity Analysis Programs (Garland *et al.* 1993), and by the *Brunch* procedure of the software CAIC (Purvis & Rambaut 1995).

We constructed a composite phylogeny based on Sibley & Ahlquist (1990), combined with information for Carduelinae (Björklund 1991), Paridae (Sheldon *et al.* 1992), Sylviidae (Blondel *et al.* 1996), Corvidae (Cibois & Pasquet 1999) and Charadriidae and Scolopacidae (Székely *et al.* 2000). We assumed that branch lengths were equal in the calculations of contrasts.

We first calculated the allometric relationships for eye and brain size using standardized linear contrasts. We used these allometric relationships to calculate relative organ size, and to investigate the covariation between relative eye size and relative brain size.

Applying multiple regression we tested whether increase in relative eye or brain size was associated with changes in prey capture technique, nocturnality and aquatic foraging as independent variables. Owing to the large number of zero values (indicating no evolutionary changes between closely related taxa), the distributions of contrasts for the independent variables were not normally distributed. Since we intended to test if evolutionary transitions of these variables were accompanied by brain and/or eye enlargement, we calculated regressions based on the ranks of the contrasts. Using this approach, we obtained normality, and we simultaneously reduced the importance of extreme data points (see also Møller & Birkhead 1994).

Because the dependent variables can be viewed as categorical variables, one might question the use of standard independent contrasts in parametric regression. Thus, in a second approach,
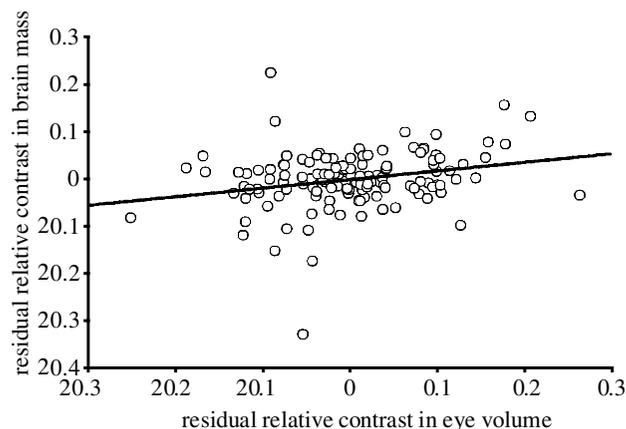
Figure 2. Regression of relative brain size on relative eye size, after removing allometric effects, by using residuals from the relevant organ size–body size regressions, based on statistically independent linear contrasts ($N = 133$).
$Y = -0.002 + 0.182X$.

we investigated our predictions by using the *Brunch* algorithm of CAIC software based on bivariate categorical states of predictor variables (Purvis & Rambaut 1995). However, collapsing three-way categories into two-way categories might reduce the power of the analysis, owing to loss of information.

When we applied this approach, we compared mean values for residual eye and brain size contrasts with the null expectation of no consistent change in organ size, with the evolution of capture of actively moving prey, nocturnality and amphibious feeding.

3. RESULTS

After controlling for the effects due to common ancestry by using statistically independent contrasts, eye size and brain size increased significantly with body mass (figure 1; eye volume: $F_{1,138} = 298.28$, $R^2 = 0.684$, $p < 0.001$, [$\log_{10}$(eye volume) contrast] $= 0.011$(s.e. $= 0.012$) $+ 1.089$(s.e. $= 0.063$)[$\log_{10}$(body mass) contrast]; brain mass: $F_{1,156} = 573.58$, $R^2 = 0.786$, $p < 0.001$, [$\log_{10}$(brain mass) contrast] $= 0.001$(s.e. $= 0.009$) $+ 1.017$(s.e. $= 0.042$)[$\log_{10}$(body mass) contrast]. Residuals from these regressions, hereafter called relative brain or eye size, were used in the subsequent analyses.

After adjusting organ size for effects due to allometry, there was a significant positive relationship between relative eye size and relative brain size linear contrasts (figure 2; $F_{1,130} = 8.74$, $R^2 = 0.063$, $p = 0.004$, (relative eye size contrast) $= 0.001$(s.e. $= 0.007$) $+ 0.346$(s.e. $= 0.117$) (relative brain size contrast)).

Analysing phylogenetically independent linear contrasts, we found a significant positive correlation between prey capture technique and relative eye size (Kendall $T = 0.170$, $p = 0.003$, $N = 140$; figure 3), and a similar, but non-significant, tendency for relative eye size and nocturnality (Kendall $T = 0.090$, $p = 0.113$, $N = 140$; figure 3). These patterns also appeared when we generated contrasts by the *Brunch* procedure, using binary states of predictor variables. Transitions towards capturing for actively moving prey were significantly linked to relative eye size variation (mean contrast $= 0.025$, $t_{26} = 2.211$, $p = 0.034$, species with 1 or 2 prey capture scores were pooled).
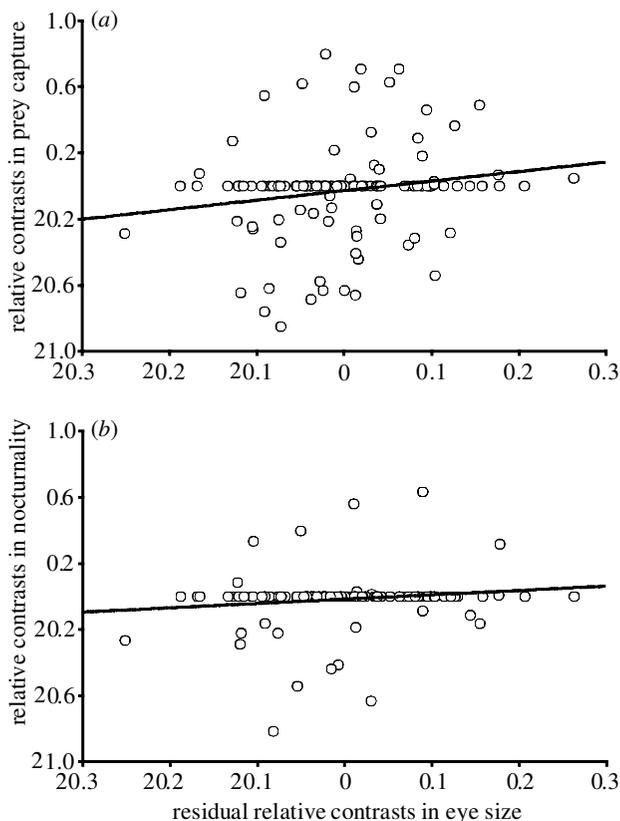

Figure 3. Correlation between (*a*) prey capture technique ($Y = -0.028 + 0.576X$), (*b*) nocturnality ($Y = -0.016 + 0.262X$) and relative eye size. Data points are linear contrasts ($N = 140$).

There was also a positive, nearly significant, effect between nocturnality and relative eye size (mean contrast $= 0.022$, $t_{17} = 1.953$, $p = 0.068$, nocturnal and crepuscular species were pooled).

In a multivariate comparative approach, when ranks of independent contrast were used as independent data points, relative eye size was positively, and significantly, associated with prey capture technique and nocturnality while controlling for water-related feeding statistically (table 1).

To achieve similar statistical control for covarying independent variables by using the *Brunch* procedure, we calculated the contrasts for different subsets of species data. To test if prey capture technique affects eye size evolution independently from nocturnality, we analysed strictly diurnal species by *Brunch*. A positive, but non-significant, relationship emerged between eye size and prey capture technique (mean contrast $= 0.021$, $t_{26} = 1.936$, $p = 0.064$, species with 1 or 2 prey capture scores were pooled). We also found a positive and significant relationship within nocturnal species (mean contrast $= 0.095$, $t_2 = 36.776$, $p = 0.001$, species with 1 or 2 prey capture scores were pooled). Combined probability from independent tests of significance revealed a significant overall effect between relative eye size and prey capture technique, independently of nocturnality ($\chi^2_4 = 19.313$, $p < 0.001$).

Nocturnality among species capturing for actively moving prey positively and significantly affected relative eye size, indicating that nocturnal activity can also play a role in relative eye size determination independently of prey

Table 1. Relationship between relative organ size (eye size and brain size) among birds, and ranks of contrasts in prey capture technique, nocturnality and aquatic feeding, respectively.
(Regression coefficients are coefficients from a regression forced through the origin. The overall regression models are statistically significant (relative eye size: $F_{3,136} = 93.61$, $R^2 = 0.642$, $p < 0.001$; relative brain size: $F_{3,155} = 92.90$, $R^2 = 0.642$, $p < 0.001$).)

dependent variable	independent variable	d.f.	mean square	F	b	p
eye size	prey capture	1	55 320.08	24.98	0.396	< 0.001
	nocturnality	1	27 289.58	12.32	0.307	< 0.001
	aquatic feeding	1	231.11	0.10	0.030	0.747
	residual	136	2 214.9			
brain size	prey capture	1	16 956.98	5.54	0.207	0.020
	nocturnality	1	90 764.19	29.66	0.496	< 0.001
	aquatic feeding	1	3 236.58	1.06	0.101	0.305
	residual	155	3 060.28			

capture (mean contrast = 0.032, $t_5 = 2.901$, $p < 0.034$, nocturnal and crepuscular species were pooled). Because only a few, closely related, crepuscular species were represented within the complement prey capture group (with score 1 or 2), we did not test for significant effects for nocturnality within this group.

In a pairwise comparison of linear contrasts, there was no significant correlation between relative brain size and capture technique, but nocturnality was significantly related to brain size (capture technique: Kendall $T = -0.050$, $p = 0.348$, $N = 158$; nocturnality: Kendall $T = 0.124$, $p = 0.020$, $N = 158$; figure 4). Using the *Brunch* approach, no significant relationship emerged between relative brain size and prey capture technique, or between relative brain size and nocturnality (prey capture technique: mean contrast = -0.001, $t_{30} = -0.048$, $p = 0.962$, species with 1 or 2 prey capture scores were pooled; nocturnality: mean contrast = 0.013, $t_{21} = 1.122$, $p = 0.275$, nocturnal and crepuscular species were pooled).

However, in a multiple regression, forced through the origin, which reduced the importance of extreme data points (figure 4) by using ranks, we found that nocturnality and prey capture technique significantly determined relative brain size (table 1).

Using the *Brunch* algorithm we also detected a significant, and positive relationship between relative brain size and nocturnality within bird species capturing actively moving prey (mean contrast = 0.020, $t_{12} = 2.186$, $p = 0.049$, nocturnal and crepuscular species were pooled). We did not test for significant effects for nocturnality within the complement prey capture group.

Applying this approach, prey capture technique was not related to relative brain size, either in diurnal or in nocturnal species, probably due to the reduced power of these tests and the extreme data points (diurnal species: mean contrast = -0.003, $t_{30} = -0.290$, $p = 0.774$, nocturnal species: mean contrast = 0.028, $t_1 = 1.260$, $p = 0.427$, combined probability: $\chi^2_4 = 2.214$, $p = 0.696$, species with 1 or 2 prey capture scores were pooled).

On the basis of amphibious feeding, brunching relative eye size and brain size in different prey capture subgroups did not result in any significant effect (combined probabilities: relative eye size, $\chi^2_2 = 4.080$, $p = 0.130$; relative brain size, $\chi^2_4 = 3.988$, $p = 0.407$, species with 1 or 2 aquatic feeding scores were pooled).

4. DISCUSSION

In this comparative study of birds we found that relative brain size was significantly and positively related to relative eye size. This can be viewed as a result of coevolution, caused by the same selective pressures on the sensory system and the central nervous system in order to achieve behavioural adaptation, for example to prey capture technique and/or nocturnal activity. However, selection arising from prey capture may be stronger on eye size, since their covariation appeared to be more robust than between relative brain size and prey capture. Significant patterns were detected for relative eye size independently of the method used, while only the more vigorous approach indicated that prey capture may affect the evolution of relative brain size. The effect of nocturnality on relative brain size emerged to be as strong as the effect on relative eye size.

The avian eye is an optical device in the visual system. Its primary function is image reproduction on the retina, in order to provide an accessible code of the image for further visual information processing. The larger the eye, the longer the focal length that determines the size of the retinal area over which the image of an object spreads (Miller 1979; Martin 1993). If the focal length is increased, spreading the image over more photoreceptors, then the amount of detail that can be resolved at a given receptor density will increase. Hence, selection for improved resolution power, for example in birds capturing actively moving prey, may lead to eye size enlargement through focal length. It has already been shown in raptors that the deep foveal pit functions as a telephoto lens system, providing an effective and large focal length, which leads to excellent detection ability, necessary during hunting (Walls 1942; Snyder & Miller 1978). In general, improved visual acuity may be correlated with the presence of well-developed areas and foveas (Meyer 1986).

Because movement is a fundamental property of the visual stimuli (Hodos *et al.* 1975; Hodos 1993), velocity detection might also be particularly important in birds capturing moving prey, thereby determining their eye structure. Maldonado *et al.* (1988) reported that pigeons adopt frontal viewing for slow-moving stimuli, and lateral viewing for fast-moving stimuli, and they considered the possibility that different retinal regions may be specialized for frontal and lateral, i.e. static or dynamic, acuity. In
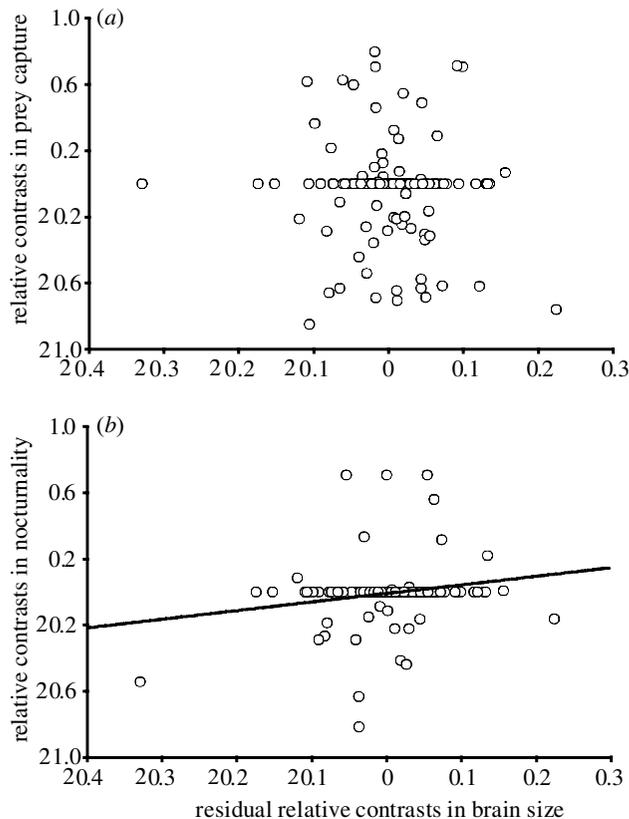
Figure 4. Correlation between (*a*) prey capture technique, (*b*) nocturnality ($Y = -0.008 + 0.519X$) and relative brain size. Data points are linear contrasts ($N = 158$).

order to cope with the increased velocity of actively moving prey, well-developed, frontal-viewing-related retinal areas may be expected to lead to an increase in eye size in species applying a complex capture technique. The pecten and fovea, for example, have been implicated as possible mechanisms in movement detection (Meyer 1986).

The focal length is also associated with the ability to function adequately during different levels of luminance (Martin 1982, 1990, 1993). At lower light levels large, widely spaced receptors become necessary in order to maximize the gathered information from the retinal image. That would explain why large eye size is associated with nocturnality. However, the large eyes of owls cannot be regarded simply as a result of selection for enlarged retinal areas, since nocturnal species may evolve larger eyes in order to provide a wide pupil to enhance sensitivity during night (Martin 1985; Brooke *et al.* 1999).

Thus, eye size may vary for at least two reasons. First, it varies according to the number of photoreceptors and the size of the retinal area involved in image reproduction, which relates to resolution power. Second, it varies according to the need for light gathering, which may influence the size of the retina, and also the pupil. Nocturnal species foraging at low light are therefore expected to evolve large eyes independently of their capturing technique. In this study we have shown that both mechanisms may play an important role in the determination of eye size, as we found that prey capture technique and timing of daily activity independently affected eye volume.

In amniote vertebrates, visual information arriving from the retina is conveyed to the telencephalon by two distinct major pathways (Pearson 1972; Shimizu & Karten 1991; Husband & Shimizu 2001). In birds, the thalamofugal route terminates in a noticeable protuberance on the surface of the dorsal telencephalon, called the visual 'Wulst'. The optic tectum, an important projection target of both visual pathways, is often well developed, and can easily be identified on the surface of the avian brain. This large anatomical structure of the visual system in birds suggests that visual information processing is an important function of the avian central nervous system. Probably, visual areas occupy a large portion of the total volume of the brain, and brain mass may thus be strongly determined by the development of these areas.

This is not surprising, since birds are particularly visually oriented animals and they rely heavily on vision to function in their environment (Zeigler & Bischof 1993; Husband & Shimizu 2001). Owing to the three-dimensional navigation demands, adaptation to rapid flight is known to be an important factor underlying the enhancement of visual information processing (Walls 1942; Martin 1985; Husband & Shimizu 2001). Additionally, birds exhibit an impressive range of visually guided behaviours other than flight, and ecological and behavioural patterns may also relate to a highly sensitive visual system (Brooke *et al.* 1999; Husband & Shimizu 2001).

For example, actively hunting species, with larger eyes, are expected to evolve increased visual information processing ability in order to cope with the increased amount of information that the eye projects. The effect of foraging on brain size in birds has already been proposed (Bennett & Harvey 1985*a*; Lefebvre *et al.* 1997), and here we provided at least some support that foraging technique might be related to brain size, probably through visual specialization.

Anatomical evidence is also available regarding how visual brain size can be affected by capturing technique. Predatory birds have a highly developed dorsal thalamus and visual 'Wulst', where binocular processing occurs, since these birds tend to have more frontally placed eyes and presumably a larger binocular visual field used for stereoscopic vision (Karten *et al.* 1973; Pettigrew 1979).

We have demonstrated that the timing of activity was also associated with brain size in birds. This is an interesting observation, because nocturnal mammals have larger eyes (Hughes 1977), but not larger brains (Barton *et al.* 1995). In these animals, olfactory and, probably, acoustic modalities become important, while visual orientation is less developed. Larger olfactory structures in the brain seem to counteract the smaller size of vision-related structures, and timing of activity is therefore not consistently associated with differences in overall brain size (Barton *et al.* 1995; Barton 1999). Nocturnal birds are known not to use olfactory stimuli during their activity at night, and therefore optical sensory mechanisms remain important. Hence, besides the adaptation of eye structure, nocturnal activity of birds can be expected to enhance visual specialization in the central nervous system and therefore also brain size evolution.

We assessed the significance of visualization in birds by measuring eye size. However, the real importance of visual specialization is underestimated using such an approach, and a direct analysis of the volume of visual areas of the brain will obviously provide more convincing tests. In

spite of this shortcoming, our results suggest that a relatively large brain has evolved in birds, at least partly through selection on visual mechanisms, that can be related to ecology and behaviour.

Eye size and brain size may be linked through metabolic rate, since the maintenance of a large brain and large eyes is energetically expensive, and the size of these organs scales with body mass in a similar manner to metabolic rate (Bennett & Harvey 1985*b*). The size of the skull may also influence the evolution of eye size and brain size, as mechanical, aerodynamic and physiological constraints arising from the size of the skull could affect the level of co-adaptation of the brain and the eye (Brooke *et al.* 1999). However, we found clear evidence of co-adaptation of relative eye size and relative brain size despite such potential constraints. To better understand the evolution of eye size and brain size in birds we need to uncover the contribution of adaptation and constraint. Furthermore, a detailed and more precise analysis within, and among, taxonomic groups is required to determine the behavioural consequences related to the evolution of relatively large eyes and brains.

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