

EYE DESIGN IN BIRDS AND VISUAL CONSTRAINTS ON BEHAVIOR

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Resumo. – Projeto do olho nos pássaros e em confinamentos visuais no comportamento. – Aves de olhos grandes podem atingir maiores diâmetros de pupila e portanto, mantendo-se todo o resto igual, maior sensibilidade e resolução visuais em relação às aves de olhos mais pequenos. Existem contudo custos associados aos olhos grandes, prevendo-se, por isso, que esta característica possa reflectir adaptações à ecologia visual. Os nossos estudos testam a hipótese de que o tamanho dos olhos está relacionado com a utilização e incidência de determinados comportamentos. Nomeadamente o tamanho dos olhos está relacionado com o momento a que diferentes espécies de aves canoras começam a cantar e a forragear de madrugada, e com o encerramento destes comportamentos ao fim do dia. Luzes artificiais podem assim alterar as rotinas comportamentais diárias de algumas espécies (sobretudo as de olhos grandes), apesar desses efeitos poderem variar entre populações. Analisamos também as relações entre tamanho do olho, técnica de busca de alimento (técnicas visual/táctil) e o padrão diário desta actividade (diurna/nocturna) em aves costeiras. Fornecemos alguns resultados preliminares acerca de um novo método fotográfico para estimar o valor mínimo de F-, e portanto o máximo brilho de imagem da retina, em olhos de aves vivas. Relacionando medidas das características do olho, tais como tamanho e valor de F-, com o comportamento, demonstramos como as limitações visuais a baixos níveis de luminosidade podem impor limitações importantes na incidência dos comportamentos.

Abstract. – Birds with large eyes can achieve greater pupil diameters and hence, all other things being equal, greater visual sensitivity and resolution than birds with small eyes. However, there are costs of having large eyes, so eye size is predicted to reflect adaptations to visual ecology. Our studies test hypotheses about how eye size and visual performance are related to the use and timing of different behaviors. Eye size is related to the times at which different species of songbirds start to sing and forage at dawn, and the cessation of these behaviors at dusk. Artificial light can alter the daily behavioral routines of some (mainly large-eyed) species, though such effects may vary between populations. We also examine the relationships between eye size, foraging technique (visual/tactile techniques) and the daily pattern of foraging activity (diurnal/nocturnal) in shorebirds. We provide some preliminary results of a new photographic method for estimating minimum F-number, and hence maximum retinal image brightness, from the eyes of live birds. By relating measurements of eye design such as eye size and F-number to behavior, we show how visual constraints at low light levels can impose important constraints on the timing of behavior. *Accepted 15 October 2003.*

Key words: Eye size, visual constraints, behavior, pupil aperture, F-number.

INTRODUCTION

Birds are highly visually guided animals. A bird's ability to carry out its various behaviors therefore depends strongly on its visual capabilities, which in turn depend on features of its eye design. In this symposium contribution, we discuss some of the trade-offs influencing eye design (particularly eye size) in birds, and highlight some of the relationships between eye design and aspects of behavior.

In comparison with most other animals, the eyes of birds are very large in relation to their body size. Indeed, a bird's eyes occupy a major part of the volume of its skull, and together weigh almost as much as the brain (Tansley & Erichsen 1985). The large eyes of birds appear to reflect the importance of vision in guiding their behavior. For example, the very large eyes of owls Tytonidae and Strigidae, nightjars Caprimulgidae and other nocturnal birds are thought to be necessary for visually guided activities (e.g., foraging) under nighttime light conditions (Martin 1990).

To form an image, light enters the eye through the pupil and is captured by the photoreceptors in the retina. Larger eyes allow a larger maximum pupil aperture, and therefore allow more light to enter the eye. Large eyes are advantageous for visually guided animals, because two key aspects of visual capability depend on maximum pupil aperture, and hence on overall eye size: (i) visual sensitivity (the ability to detect light of low intensity), and (ii) visual resolution (the ability to distinguish detail at a given light intensity).

Visual sensitivity depends on pupil aperture, and on the size of the photoreceptors. Sensitivity can be increased without a loss of visual resolution by increasing pupil aperture, up to a certain limit (reached when pupil aperture is 0.5 of the focal length of the eye). Above this limit, sensitivity can be further increased without a loss of resolution by cou-

pling an increase in pupil diameter with an increase in focal length and photoreceptor diameter (Miller 1979, Land 1981, Land & Nilsson 2002).

Visual resolution depends on the focal length of the eye, and on the diameter of the photoreceptors. Resolution can be increased without a loss of sensitivity by coupling an increase in focal length with an increase in pupil aperture (Land 1981, Land & Nilsson 2002).

Both sensitivity and resolution are likely to be important for visually guided behavior, particularly at low light intensities, though it should be emphasized that the relative importance of sensitivity and resolution for vision in different light conditions or for different purposes (e.g., detecting daybreak, versus detecting an approaching predator) is currently unknown. Nevertheless, it is clear that the evolution of eyes in the direction of greater sensitivity without a loss of resolution, or in the direction of greater resolution without a loss of sensitivity, requires an increase in maximum pupil aperture, and hence an increase in the overall size of the eye (Land & Nilsson 2002).

Larger eyes provide the benefits of better vision but they also incur significant costs, particularly for relatively small flying animals such as most birds. Larger eyes mean a larger payload that must be carried in flight, with a high energetic cost (Witter & Cuthill 1993). This is partly due to the weight of the eyes themselves, but also due to the mass of the associated neural apparatus (Laughlin 1995). As well as energetic costs, there may be other types of costs (e.g., increased predation risk) associated with increased body mass (Witter & Cuthill 1993). Further costs of increasing eye size include the energetic costs of building and maintaining the extra nerve cells and larger eye structures (Laughlin *et al.* 1988), and perhaps also an increased risk of damage to the exposed surfaces of the eyes.

The trade-offs between the costs and benefits of increasing eye size will differ between species with different behaviors and lifestyles, so eye size is predicted to reflect adaptations to visual ecology. We present a series of case studies illustrating how interspecific differences in eye size are associated with different aspects of bird behavior. Specifically, we have tested the following hypotheses: (1) eye size is associated with interspecific variation in the onset of singing at dawn, and with the cessation of singing at dusk [this hypothesis was originally suggested by E. A. Armstrong (1963)]; (2) manipulations of light intensity using artificial illumination can be used to change the visual constraints on behavior, and hence influence birds' decisions about when to sing and forage; and (3) eye size is associated with the timing of foraging (nocturnal/diurnal) and foraging methods (visual/tactile) in shorebirds.

To date, most of our own research on eye design and visual constraints on behavior has focused on eye size as a measure of visual capability, and overall "investment" in vision (in the sense that eye size is the outcome of the trade-off between the relative costs and benefits of having large eyes). The theoretical considerations outlined above, and our own empirical results (see below) indicate that overall eye size is an important correlate of a bird's visual capability and the overall importance of vision in the bird's behavior. However, further information about vision can be obtained from other measurements of the eyes of live birds. For example, the maximum brightness of an image falling on the bird's retina, relative to that of other eye designs at an equivalent light intensity, is inversely proportional to the square of the minimum F-number of the eye: Relative maximum image brightness = $1/F_{\min}^2$ (equation 1), where F_{\min} = Focal length (f)/Maximum pupil aperture (d) (equation 2).

In our ongoing research, we are currently using a new photographic method suggested by Prof. Graham Martin of Birmingham University, UK, to obtain direct measurements of maximum pupil aperture, and estimates of focal length, for a range of species. These two values can be used to calculate estimates of minimum F-number and relative retinal image brightness. We present some preliminary results of this method below.

METHODOLOGY

Measuring eye size

We have used several non-invasive methods of measuring eye size (and hence estimating maximum pupil aperture) in live birds and from museum skeletons.

Calliper measurements of the exposed eye surface. A bird's pupil aperture obviously cannot usefully be wider than the area of the exposed eye surface. Maximum pupil aperture can be estimated by using callipers to measure (± 0.1 mm) the maximum diameter of the exposed corneal surface, between the eyelids and mucous membrane surrounding the eye. Care must be taken not to touch the eye surface with the calipers. Measurements made using this method are very highly repeatable within species (Thomas *et al.* 2002).

Measurements from skulls. Other researchers (Brooke *et al.* 1999) have estimated eye volume from skulls by fitting balls of Plasticine® modeling clay into the eye sockets of bird skulls to find the diameter of ball, which provides the best fit. We have adapted this method to avoid measurement error in obtaining the size of the ball of best fit, by using a range of different sized steel ball bearings of known diameters. Measurements made using this method are very highly repeatable within species (Thomas *et al.* in prep.).

Measurements of eye socket diameters can also be made from scale photographs of eye sockets of museum skulls. This method is useful for studies of skulls that are too small or delicate to apply the ball bearing method.

Measuring behavior

Hypothesis 1. To test the hypothesis that eye size is associated with interspecific variation in the onset of singing at dawn, and with the cessation of singing at dusk, we measured the times of the first songs at dawn of the different species of songbirds present in seven different bird communities, and the light intensities at these times for two of these communities. We also measured the times of the last songs at dusk in two of these communities.

Hypothesis 2. We carried out two tests of the hypothesis that manipulations of light intensity using artificial illumination can be used to change the visual constraints on behavior, and hence influence birds' decisions about when to sing and forage.

We used floodlights to carry out an experimental manipulation of the light intensities experienced at dawn by aviary-held European Robins (*Erithacus rubecula*), and compared the times at which these birds started to sing and forage on treatment days when light levels at dawn were artificially high, with the times of onset of those behaviors under natural dawn light intensities on control days (Thomas & Cuthill in prep.).

We also tested the daytime (dawn) and nighttime (midnight) responses of European Robins to simulated territorial intrusions by rival conspecifics, by using acoustic playbacks of conspecific songs. We compared the responses of individuals whose territories were illuminated by streetlights, with the responses of individuals whose territories received only natural levels of illumination (Thomas in prep.). We also tested for differ-

ences in such responses between populations (Thomas *et al.* 2003).

Hypothesis 3. To test the hypotheses that eye size is associated with the timing of foraging (nocturnal/diurnal) and foraging methods (visual/tactile) in shorebirds, we carried out a literature search to extract descriptions for shorebird species on both the foraging technique, and the time of day that foraging occurs. These species descriptions were independently scored by four people, blind to the species names.

Diel foraging patterns were classified according to the following scale: daylight only (1), daylight and twilight (2), no obvious bias between day and night (3), night and twilight (4), and night only (5).

Foraging methods were classified as follows: visual techniques (1), mainly visual techniques but some tactile (2), mixture of visual and tactile techniques, no obvious bias (3), mainly tactile techniques but some visual techniques (4), and tactile techniques (5). This classification of each species used records of foraging techniques made at any time of day, so that species which use different foraging methods in different circumstances (e.g., visual methods by day and tactile methods by night, McNeil *et al.* 2004) would be scored as using both visual and tactile methods. The repeatability of the scores between the four scorers was high, both for the timing of foraging, and for foraging methods.

Estimating retinal image brightness

The minimum F-number of an eye, and hence its maximum relative retinal image brightness, can be calculated from maximum pupil aperture and focal length, using equations 1 & 2, above.

Maximum pupil aperture (d) can be measured directly from the dark-adapted eyes of live birds, by photographing the bird's eye in a dark-room or dark box, using a camera

with an infra-red light source. In our studies to date, we have used a Sony digital “Handycam” DCR-TRV25 (Sony Corporation) with infra-red “Nightshot” facility. Pupil aperture can be measured against the scale of a ruler held adjacent to the surface of the bird’s eye.

Focal length (f) is known to be approximately equal to $0.6 \times$ the axial length of the eye across a range of species (G.R. Martin pers. com.): Focal length $\approx 0.6 \times$ axial length (equation 3), where axial length = (cornea to cornea distance – 1 mm septum)/2 (equation 4).

In birds with laterally oriented eyes (i.e., most avian orders), the two eyes almost touch each other in the centre of the head, with only a thin bony septum (approx. 1mm) between them (Tansley & Erichsen 1985). An estimate of the axial length can therefore be obtained from a photograph taken from vertically above the bird’s head, such that the distal corneal surfaces of both eyes are visible in the photograph. The distance between the most distal points of the two corneas can be measured against the scale of a ruler held adjacent to the bird’s head in line with the centres of the two eyes, and axial length calculated as above.

RESULTS & DISCUSSION

Hypothesis 1. According to this hypothesis, eye size is associated with interspecific variation in the onset of singing at dawn, and with the cessation of singing at dusk.

We found that birds with larger eyes tend to start singing earlier (i.e., at lower light intensities) at dawn than those with smaller eyes (Thomas *et al.* 2002). Body mass also has a significant, and independent, effect on the onset of singing at dawn, with smaller bodied birds starting to sing earlier at dawn than larger bodied birds of equivalent eye size. The results of analyses controlling statistically for

phylogeny are consistent with the species-level analyses (Thomas *et al.* 2002). These results are repeatable across a range of latitudes and habitat types within Europe (Thomas *et al.* 2002) and on other continents (Thomas *et al.* in prep.). Furthermore, birds with larger eyes stop singing later (i.e., at lower light intensities) at dusk (Thomas 1997), and those species that start earlier at dawn are the same species that stop later at dusk (Thomas 1997).

Visual performance may affect the timing of song directly, e.g., birds might only begin to sing once they can see well enough to interact visually with conspecifics, or to detect predators. Alternatively, the association may be mediated by visual constraints on other behaviors, e.g., birds might normally sing for a set time until it is light enough to begin foraging efficiently (Kacelnik 1979, Kacelnik & Krebs 1982).

Further research on this topic could shed more light on the mechanisms by which such relationships are mediated. For example, current research on the timing of song at dawn and dusk in a range of bird communities from around the world is investigating how the rate of change in light intensity during twilight (which varies with latitude and season) influences the rate at which different species join the dawn chorus (Thomas *et al.* in prep.). Another as yet unexplained aspect of these relationships is that the light intensities at which birds begin singing at dawn are far lower than those at which they end singing at dusk (Thomas 1997).

Hypothesis 2. According to this hypothesis, manipulations of light intensity using artificial illumination can be used to change the visual constraints on behavior, and hence influence birds’ decisions about when to sing and forage.

Evidence supporting this hypothesis comes from our studies of the timing of

behavior of birds under different levels of artificial illumination. For example: (i) Onset of singing and foraging at dawn are influenced by light intensity. This study will be described in detail in a separate publication (Thomas & Cuthill in prep.). We found that the time of the start of singing at dawn was significantly earlier on days when the aviary was floodlit from approx. 1 h before the normal (unmanipulated) time of the first song. Birds also started feeding significantly earlier at dawn on days when their aviary was floodlit than on control days. The time difference between the start of singing and the start of foraging did not differ between treatment (floodlit) and control (unmanipulated) days. These results support the view that light intensity at dawn, in that it affects foraging success and other visually mediated behaviors, affects the timing of the dawn chorus (Kacelnik 1979, Kacelnik & Krebs 1982). (ii) Response to conspecific song at night is affected by street lighting, and may vary between populations (Thomas *et al.* 2003). At one of our study sites (in Cardiff, Wales, UK), European Robins inhabiting territories illuminated by streetlights were significantly more likely to respond at night to acoustic playback of conspecific songs than were individuals whose territories were not illuminated artificially by streetlights (Thomas in prep.). Surprisingly, we found that this effect was not consistent between two populations: while most robins inhabiting territories illuminated by streetlights in Wales responded to playbacks at night, those experiencing equivalent levels of artificial illumination at a second study site (in Dublin, Ireland) rarely responded. In contrast, both populations responded equally during daylight (Thomas *et al.* 2003). The reasons for these differences between populations are unclear, but may relate to differences in the level of predation risk for songbirds singing at night at the two study sites.

Hypothesis 3. According to this hypothesis, eye size is associated with the timing of foraging (nocturnal/diurnal) and foraging methods (visual/tactile) in shorebirds.

The results of this study will be presented in detail in a separate publication (Thomas *et al.* in prep.). We found that nocturnal foragers have larger eyes than daytime foragers, but we found no significant relationship between eye size and foraging strategies. That is, while nocturnally foraging shorebirds tend to have larger eyes than daytime foragers, those that tend to use visual foraging techniques do not have significantly larger eyes than those using mainly tactile methods to detect their prey. The results of analyses controlling statistically for phylogeny are consistent with our species-level analyses.

Retinal image brightness and time of song. We have so far estimated minimum F-number and maximum retinal image brightness for a small number of species, whose timing of song at dawn is known. For example, the House Sparrow (*Passer domesticus*), which starts to sing late at dawn, has a relatively high F_{\min} of 1.85 (and hence a relatively dim retinal image). This value is comparable with the previously published value of $F_{\min} = 1.98$ for the Domestic Pigeon (*Columba livia*) (Marshall *et al.* 1973). In contrast, the European Blackbird (*Turdus merula*), which starts to sing very early at dawn, has a relatively low F_{\min} of 1.22 (and hence a relatively bright retinal image). Thus, the contrast in minimum F-number between the House Sparrow and the European Blackbird is consistent with the observed differences in the timing of their song at dawn. Surprisingly though, the F-number of European Blackbird is lower even than the previously published value of $F_{\min} = 1.30$ for the Tawny Owl (*Strix aluco*) – an exclusively nocturnal predator (Martin 1982). This suggests that songbirds that are active at low light intensities at dawn and dusk, but which are otherwise diurnal,

may have eyes that are well adapted for vision at low light intensities.

CONCLUSIONS

Our results indicate that visual performance at low light levels imposes important constraints on the timing of different behaviors, including singing and foraging. We have also shown that artificial lights, such as street lighting, can significantly advance the onset of singing and foraging at dawn, and may therefore have a major effect on daily behavioral routines. These results imply that the effects of light pollution on the behavior and ecology of birds and other animals may be considerable, and this certainly merits further investigation. In addition to overall eye size, other aspects of eye design can be related to behavior. For example, F-number and retinal image brightness has previously been measured using invasive methods. We have presented a new way to measure image brightness in dark adapted eyes of live birds using a non-invasive infra-red photographic method. The preliminary results of our investigation appear to relate well to behavioral observations on the timing of dawn song. This method is readily applicable to a wide range of species in field conditions, and will be used in ongoing research to investigate further the associations between eye design and visual constraints on behavior.

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