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The eye of a passeriform bird, the European starling (*Sturnus vulgaris*): eye movement amplitude, visual fields and schematic optics

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Summary. The European starling, *Sturnus vulgaris*, is a diurnal, ground feeding bird of the order Passeriformes. Aspects of its visual fields, eye movements and the optical structure of its eye are described.

1. The magnitude of eye movements as a function of elevation in the median sagittal plane of the head was measured (Fig. 1). Maximum eye movement amplitude (32°) occurs in a plane which passes 50°–60° below the closed bill while the minimum amplitude (11°) occurs in a plane approximately orthogonal to this.

2. The ways in which eye movements can alter the binocular and cyclopean retinal visual fields are described (Figs. 3 and 5). When the eyes are fully converged maximum binocular overlap equals 43° and this occurs approximately 40° below the bill. The bill intrudes into the visual field and when the bill is fully open, maximum binocular field width occurs between the mandibles. The eyes can also be swung backwards and upwards so that the margins of the monocular fields just coincide behind the head to give extensive visual coverage of the celestial hemisphere. When the eyes are in this position the frontal binocular field is almost abolished.

3. The monocular retinal field is asymmetric about the optic axis and this can be attributed to asymmetry in the gross structure of the eye rather than asymmetry in the optical system (Figs. 4 and 9). From purely optical considerations the starling could have a maximum binocular field width twice that actually found.

4. A schematic model of the starling eye optical system (Fig. 4 and Table 2) shows that optically this 'flat-diurnal' eye is a small scaled version of the larger 'tubular-nocturnal' eye of an owl (Figs. 6 and 7). In addition the calculated optical fields of these two eyes are very similar (Fig. 8), and these eyes differ in their maximum retinal image brightness by only 0.33 $\log_{10}$ (Table 4). However, although the rat and starling eyes are of similar total dioptric power they are found to be of quite different optical design (Fig. 7). It is concluded that no particular 'diurnal' feature can be discerned in the optical structure of the starling eye.

5. The starling feeds mainly on the ground where it is known to employ vision to locate prey at short range. However, when foraging it is vulnerable to aerial predators. The visual problems which this presents are considered. How the bird's visual fields and eye movements may cope with these problems are discussed. There is evidence that the starling eye may embody a 'ramp' retina as a static accommodatory device which could facilitate the simultaneous detection of both close prey and distant predators (Fig. 9 and Table 5).

Introduction

The avian eye is often regarded as embodying structural adaptations which are the culmination of phylogenetic development towards diurnal vision (see for example Rochon-Duvigneaud 1943; Pumphrey 1948; Duke-Elder 1958; Meyer 1977). More than half of all extant species of bird are found within a single order, the Passeriformes, all of which may be regarded as diurnal in that they forage only during daylight hours and normally roost at night.

Although the eyes of some passeriform species have been the subject of anatomical descriptions [for example, the house sparrow, *Passer domesticus* (Slonaker 1918); the dipper, *Cinculus mexicanus* (Goodge 1960) and various species in Rochon-Duvigneaud (1943) and Donner (1951)], there have been no descriptions of the optical properties, visual fields or eye movements in any passeriform eye.

The European starling, *Sturnus vulgaris*, is a passeriform species (family Sturnidae) which is now one of the most numerous and widely distributed bird species in the world (Feare 1984). Starlings are strongly diurnal, in that they normally roost between dusk and dawn. However, they may migrate by both day [when they are thought to use the sun as a compasss (Kramer 1952)] and by night (Baker 1978). They are omnivorous and mainly forage on the ground where they employ the specialized technique of 'open-bill probing' or 'prying' to extract invertebrates from within the upper soil surface or turf. The anterior part of the skull in *S. vulgaris* is narrower than in fruit-eating starlings and it has been proposed that this permits the eyes to move forward and enable the bird to see between its opened mandibles when prying (Beecher 1978).

This paper presents data on the optical structure of the starling eye, its visual fields and its eye movements. These are examined in relation to the visual problems faced by the birds whilst foraging. Eye structure is also compared with that of a nocturnal bird, the tawny owl, *Strix aluco*. It is shown that apart from absolute size the optical structure of the owl and starling eyes are very similar.

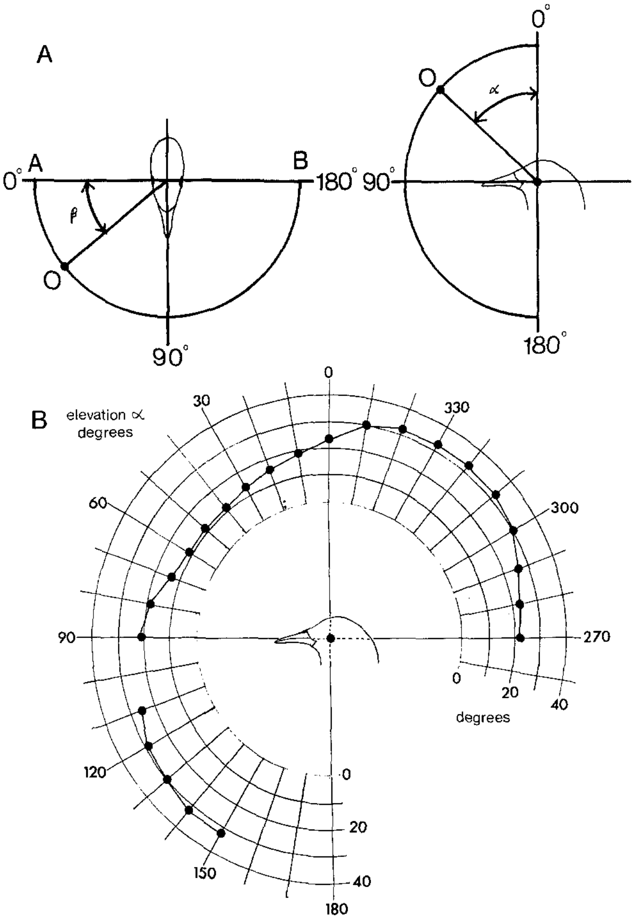

Fig. 1. A The convention used for referring to the position of the ophthalmoscope and to the visual projections of the retinal fields, pectens and optic axes. The perimeter arm pivoted about the axis A–B and the ophthalmoscope (*O*) moved along the perimeter arm. Thus points A and B can be considered the poles of an imaginary sphere surrounding the bird's head and the arm itself describes lines of longitude defined by the angle α while the angle β defines lines of latitude. The angles α and β can therefore be translated directly to the visual projections used in Fig. 3. **B** mean amplitude of eye movements as a function of elevation (α) in the median sagittal plane. Drawing of bird's head from a photograph and shown in correct orientation

Methods

Subjects. Four wild caught specimens of *S. vulgaris* were used. They were obtained from the Agricultural Science Service of the U.K. Ministry of Agriculture, Fisheries and Food (Guildford, England). Two birds were used in the investigation of visual fields and two in the study of the eye's optical structure.

Eye movements and visual fields. The procedure followed that described previously for measuring retinal visual fields in other (non-passerine) bird species (Martin 1984, 1985; Martin and Young 1983, 1984). This consisted in determining the visual projection (angular subtense measured with respect to an hypothetical cyclopean projection centre) of the limits of the ophthalmoscopically observed retinal reflex. No anaesthesia was used. A foam rubber cradle held the bird's body while the closed bill was held firmly in place by taping it to a specially designed metal holder. This arrangement permitted the visual field to be determined at all elevations about the bird except where the retinal margin was obscured by the bird's own body and at the elevation of the bill where the holder obscured the retinal margin. In the darkened conditions of the laboratory and mounted in this manner the birds remained immobile and quiescent but with eyes fully open.

The bird was placed at the centre of the visual perimeter and positioned so that when the bill was closed the lower edge of the upper mandible (which is practically straight for 20 mm) was aligned to the horizontal and the estimated mid-point between the eye's pupils positioned at the centre of the perimeter. This point defined the cyclopean projection centre and the position of the retinal field boundaries, pecten and optic axes are described by reference to that point. The co-ordinate system used is described in Fig. 1. The measured values of these features were corrected to those that would be determined at an hypothetical infinite viewing distance (Martin 1984). However, because of the relatively small separation of the eye's nodal points (approximately 10 mm) compared with the radius of the perimeter arm (320 mm) such corrections were small (<0.5°) and so were ignored for perimeter readings which lay close to the bird's median sagittal plane. The position of the ophthalmoscope on the perimeter arm could be read to an accuracy of ±0.5°.

Since the birds were not anaesthetized eye movements were present throughout the procedure. The starling has highly mobile eyes and eye movements often appeared to be non-conjugate. It therefore seemed to be of little value to attempt to determine a mean limit to the bird's visual fields. Rather it was considered of more value to determine the maximum and minimum limits of the visual fields produced by the eye movements. The maximum amplitude of the eye movements at each elevation about the head was determined by measuring the two extreme positions at which the retinal margins could be detected at each elevation of the perimeter arm.

The elevation of the perimeter arm was changed in steps of 10°. At each elevation the eyes were induced to take up their extreme positions in the same plane as the perimeter arm by intermittently flashing a small light bulb, and/or gently tapping the perimeter arm, at various locations along the arm in the periphery of the eye's visual field. The procedure was to determine initially a resting position for the retinal margin, then to move the ophthalmoscope in small steps (approximately 1°) along the perimeter arm while attempting to elicit eye movements. The bird would not readily follow the movement of the lamp when it was steadily illuminated but an intermittant flashing of the lamp at different positions and often tapping sounds from the same locus were efficient at eliciting eye movements. If the retina could still be seen (either steadily or fleetingly) at the new position of the ophthalmoscope its position was changed and the procedure repeated until a position was found at which the margin could not be detected. The final position at which the retina was seen then defined either the 'maximum' or 'minimum' limit of the visual field depending upon the direction in which the eye was being stimulated to move.

Thus at each elevation of the perimeter arm two values, the 'maximum' and the 'minimum' limit of the retinal field margins were recorded. The difference between these readings was defined as the maximum amplitude of eye movements at that elevation. Because the eyes were so mobile no attempt was made to determine the position of the optic axes or pectens.

Because of these eye movements it was decided that the visual fields should also be determined when the eyes had adopted their resting positions. However, it was not found possible to sedate the starlings satisfactorily using an injectable anaesthetic because sedation was too brief (rarely more than 2 min). A gas anaesthetic could not be used since the necessary apparatus would have obscured the ophthalmoscopic view of the fundus. Hence the birds were injected with a lethal dose of Nembutal anaesthetic and the dead birds were mounted in the perimeter as before but this time with the bill placed on a thin wire support rather than taped to the holder. With the bill held in this way it was possible to determine the limits of the retinal field at the elevation of the bill as well as at all other elevations. The eye lids were held open with adhesive tape and the position of the limits to the retinal visual fields, pectens and optic axes determined. Only one quick judgement of these positions in each eye was possible since the optical quality of the eye began to deteriorate within 15 min of death. It was possible to determine the position of the retinal field margin in only the frontal portion of the visual field because of this deterioration.

Schematic eye. A schematic eye model for the starling was constructed using data from a single eye of each of two birds. The procedure adopted was similar to that described previously (Hughes 1972; Martin 1982, 1983; Martin and Young 1984). The technique involved taking scaled photographs which were analysed by taking tracings of enlarged projections (approximately ×35) of the negatives. Photographs of the intact enucleated eye gave gross dimensions. The eye was then mounted in a holder which held the eye around the scleral ossicles. Slight pressure was applied to the rear of the globe with a blunt probe and this pressure was made just sufficient to cause the cornea to curve smoothly. Thus mounted the eye was photographed in air and under Ringer solution and the following parameters determined: radius of corneal curvature, diameter of cornea at the corneo-scleral junction, corneal thickness, entrance pupil diameter and depth of anterior chamber.

The eye was hemisected about the equator and samples of the aqueous and vitreous humours collected and their refractive index measured with a sugar refractometer. The lens was mounted on a cradle of Plasticine placed in a bath of cooled avian Ringer solution. Photographs of the lens thus mounted were used to determine lens thickness, equatorial diameter, and the radii of curvature of the two surfaces. The anterior and posterior lens vertex distances were determined by illuminating the lens with a 1 mm diameter beam from a HeNe laser centred along the presumed optical axis of the lens.

A section cut through the eye cup near to the eye's posterior pole was used to determine the thickness of the sclera. The refractive index of the cornea could not be determined with the refractometer that was available and so a value of 1.376 has been adopted in the schematic eye model. This value is the same as that adopted in the schematic models of other vertebrate eyes (e.g. Gullstrand 1909; Vakkur and Bishop 1963; Martin 1982).

Results

Eye movements and visual fields

Figure 2 shows (i) the mean maximum and minimum binocular field widths, (ii) eye movement amplitude and, (iii) the mean binocular field width of the dead birds all as a function of elevation (α) in the median sagittal plane of the bird. Eye movement amplitude as a function of elevation is also shown in Fig. 1 where the bird's head is depicted in the correct orientation relative to the co-ordinate system. Figure 3 presents equatorial orthographic projections of the visual field data.

In all of these projections the bird is at the centre. In A (maximum), B (minimum) and C (dead) the bird is facing the reader, and in D (maximum) the reader is looking from above onto the bird's head with the bill pointing towards the foot of the page. It should be noted that the maximum and minimum data cannot be considered as describing the actual total binocular field that is achieved by the starling on any one occasion, but rather it describes the maximum degree of overlap or divergence which *can* be achieved at any particular elevation. For example, the projections of Fig. 3A and D indicate the maximum limit of visual space which can be scanned by each eye and the resultant maximum limit of the cyclopean field. Hence, at $\alpha = 90°$ the retinal fields can be brought to overlap and produce a binocular field 36° wide (Fig. 3A) or they can be diverged to give no overlap with their margins 6° apart (Fig. 3B). Therefore each eye has a mean maximum amplitude of

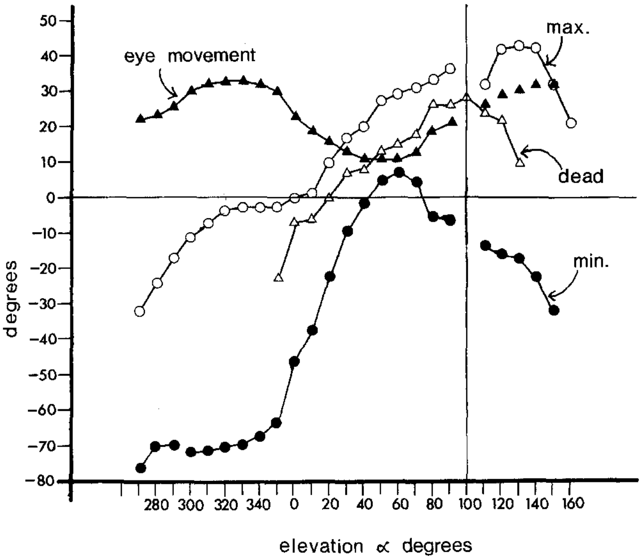

Fig. 2. Mean eye movement amplitude, maximum and minimum retinal binocular field widths, and mean retinal binocular field width in the dead starling, as a function of elevation (α) in the median sagittal plane. Positive values indicate degree of overlap of the visual projections of retinal margins while negative values indicate degree of divergence of the retinal margins. (See text for the definition of maximum and minimum binocular fields.) At α = 100° measurements were possible only in the dead bird (see text)

movement of 18° at this elevation. However, this data does not imply that while an overlap of 36° is achieved at α = 90° an overlap of (for example) 29° is simultaneously achieved at α = 60° (Fig 3A). This is because the exact position adopted by the retinal margins at α = 60° was not measured while the eyes were induced to converge maximally at α = 90°. However, data for the visual fields of the dead birds (Fig. 3C) does describe the actual binocular field (together with the visual projections of the pectens and the optic axes) of the starling when the eyes are brought to their resting position.

The eye

Table 1 presents the measurements (mean of two eyes) taken to describe eye shape and to construct a schematic model of the optical system.

Shape and size of the eye

The starling eye is of the 'flat' type (Fig. 4), typical of passerine birds (Walls 1942, p 643), with an equatorial diameter approximately 2 mm greater than the axial length (approximately 8 mm) and

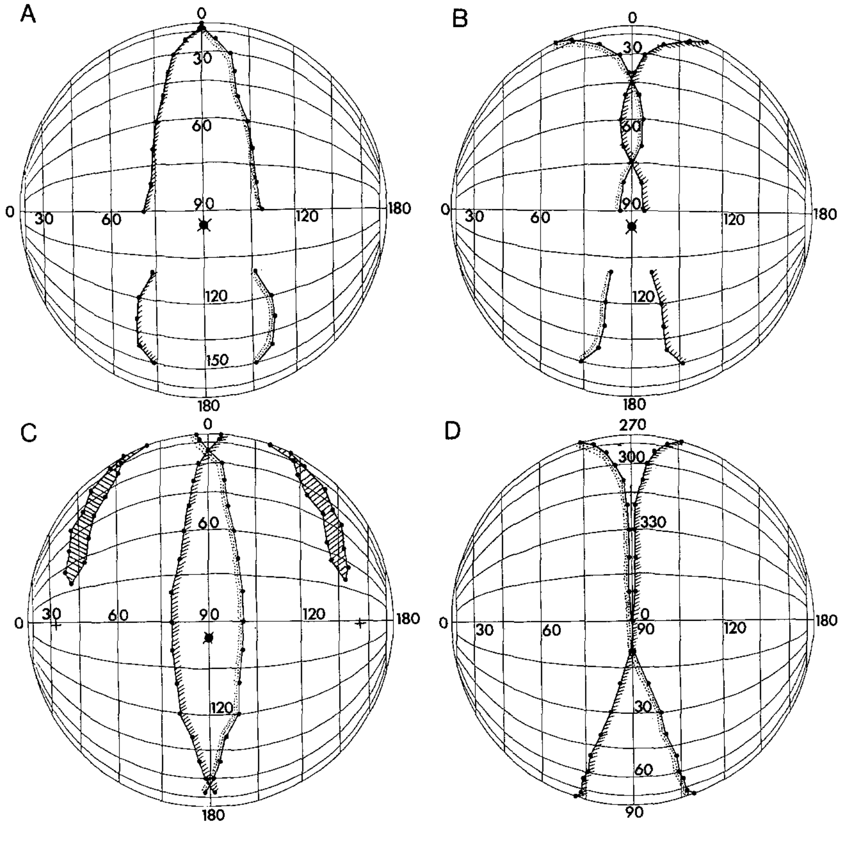

Fig. 3A–D. Equatorial zenithal orthographic projection of retinal visual fields of the starling. **A** and **D** maximum; **B** minimum, **C** dead bird (see text for definition of maximum and minimum binocular fields). In **A**, **B** and **C** the bird may be imagined to be facing the reader from the centre of the projection while in **D** the reader is looking down onto the bird's head with the bill pointing towards the foot of the page. ●, projection of the bill tip when closed; ▼, projection of the tip of the lower mandible when the bill is opened to its maximum extent; ▥ and ░, projection of the left and right eye retinal margins respectively; +, projection of optic axes; hatched area is the projection of the pectens

Table 1. Measurements for the schematic eye of the starling *Sturnus vulgaris*; the symbols refer to Fig. 4

	mm
Axial length (A_1A_6)	7.92
Equatorial diameter (R_1R_2)	10.05
Eye cup thickness	0.20
Corneo-scleral junction-eye equator	
nasal side (CS_1R_1)	3.13
temporal side (CS_2R_2)	4.54
Corneo-scleral junction dia. (CS_1CS_2)	4.70
Corneal height	1.404
Corneal thickness (A_1A_2)	0.162
Corneal radius, anterior	2.690
Corneal radius, posterior	2.530
Corneal vertex-lens vertex (A_1A_3)	1.192
Lens, equatorial dia.	4.101
Lens, thickness (A_3A_4)	2.606
Lens, anterior radius (r_a)	4.196
Lens, posterior radius (r_p)	−2.593
Lens, anterior vertex distance (v_a)	10.288
Lens, posterior vertex distance (v_p)	11.022
Lens, separation of vertex points (z)	23.196
Pupil, maximum entrance dia.	2.513
Aqueous and vitreous humours, refractive index (n_3,n_5)	1.337

only slight convexity of the scleral ossicles. The eye is asymmetric (measured in terms of the distance between the corneo-scleral junction and the equator) about its presumed optic axis. Due to the complexity of this asymmetry it was not possible to determine the exact position of the pole of the eye cup from photographs of the whole eye and hence the axial length of the eye (Table 1,A_1A_6) could not be determined with an accuracy equal to that of other eye dimensions.

The greatest degree of asymmetry occurred in a plane that in the dead bird was slightly above the horizontal from the temporal-dorsal quadrant to the nasal-ventral quadrant of the retina. Thus the starling eye exhibits the same kind of 'nasad asymmetry' reported in other avian (and some mammalian) species (Walls 1942; Martin 1984), in which the eye is shorter on the nasal side compared with the temporal side. However, the exact location of the plane of greatest asymmetry in vivo could not be determined accurately because of the possible rotation of the eye about its axis and in a bird with highly mobile eyes and head, an exactly

Table 2. The schematic eye of the starling, *Sturnus vulgaris*; symbols refer to Fig. 4

		Cornea		Lens		Whole eye	
Powers (dioptres)	anterior surface	FCA	139.777	FLA	45.138		–
	posterior surface	FCP	−15.415	FLP	73.043		–
	total	FC	124.613	FL	112.541	FE	209.095
Positions (mm from A1)	anterior principal point		–	P2	2.675	P	1.077
	posterior principal point		–	P2′	2.799	P′	1.205
	anterior focal point		–		–	F	−3.706
	posterior focal point		–		–	F′	7.599
	anterior nodal point		–		–	N	2.688
	posterior nodal point		–		–	N′	2.816
Distances (mm)	Lens, anterior vertex distance (V_a)				10.372		
	Lens, posterior vertex distance (V_p)				10.938		
	Lens, separation of vertex points (z)				23.917		
	Whole eye, posterior nodal distance (PND)				4.783		
	Whole eye, anterior focal length (f)				4.783		
	Whole eye, posterior focal length (f')				6.394		

Surface		Position (mm)	Radius (mm)	Refractive index	
Cornea, anterior	A_1	0.00	2.69	cornea n_2	1.376
Cornea, posterior	A_2	0.16	2.53	aqueous n_3	1.337
Lens, anterior	A_3	1.19	4.196	vitreous n_5	1.337
Lens, posterior	A_4	3.79	−2.593	lens bulk n_4	1.5234
Retina	A_5	7.599	–		
Posterior sclera	A_6	7.799	–		

Pupil	maximum dia. mm	mm from A_1
entrance	2.51	1.20
real	2.19	1.40
exit	2.47	1.42

horizontal plane is impossible to specify. The eye was not symmetrical in a vertical plane, the distance between the corneo-scleral junction and the equator was greater dorsally than ventrally, but this asymmetry was not recorded in detail.

Schematic eye

The schematic eye model for the starling is presented in Table 2. A scaled diagram of the model together with the overall shape of the eye in the plane of greatest asymmetry is shown in Fig. 4. Because of the difficulty of measuring exactly the axial length of the eye (see above) the refractive state of the schematic model has not been determined. However, in view of the close coincidence of the posterior focal point and the retinal surface it would seem safe to assume that the eye is approximately emmetropic about the optic axis.

In constructing the model use is made of the conventional assumptions (Martin 1983) that the corneal and lens surfaces are spherical within the paraxial region and that they are well centred about a common axis. In this case the former assumption is supported by observation of all surfaces although it is clear that as in the case of the human eye the corneal surface (Bonnet 1964) became flatter and the lens surface (Howcroft and Parker 1977) became more curved away from the optic axis i.e. outside of the paraxial region. The latter assumption was supported by photographs which indicate that when viewed laterally the anterior lens surface appears to be symmetrically placed with respect to the cornea. However, other photographs showed the pupil to be not exactly centred with respect to the cornea-scleral junction, but it is not clear whether this indicates that the lens is also eccentrically placed with respect to the cornea. However, within the assumptions of paraxial optics (which are employed in constructing schematic eye models) the further assumptions that refractive surfaces are spherical and well centred does provide a good approximation to actual average optical performance given the intraspecific variability of eye structures (Helmholtz 1909, p 95; Sorsby et al. 1957, 1961).

Thick lens theory was used to determine an equivalent bulk refractive index (n_4) for an homogeneous lens having the same refractive power as the real lens. This was achieved by using the successive approximation procedure (Vakkur and Bishop 1963) which substituted values of n_4 until the calculated separation of the vertex points of the schematic lens equalled the measured separation of these points (cf. the vertex distance v_a, v_p and the separation of the vertex points, z, in Tables 1 and 2). The equivalent bulk refractive index equalled 1.5234 which is within the range of calculated equivalent bulk refractive indices in other vertebrate schematic eye models (Hughes 1977; Martin 1982).

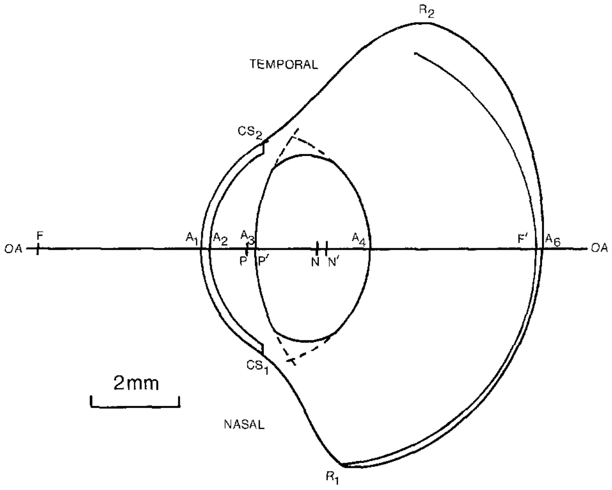

Fig. 4. Scaled diagram of the schematic eye of the starling in an approximately horizontal plane. See Table 2 for explanation of symbols

Discussion

Eye Movements

Previous measures of eye movements in birds have concentrated principally on the temporal characteristics of monocular eye movements, usually within an horizontal plane, and little attention has been devoted to the maximum amplitude of eye movements (Nye 1969; Steinbach and Money 1973; Bloch et al. 1984; Martinoya et al. 1984; Wallman and Pettigrew 1985). The procedure adopted here permitted measurement of the maximum amplitude of monocular eye movements as a function of elevation about the head and hence enables examination of the ways in which eye movements can alter the cyclopean and binocular visual fields of the bird.

It should be noted that the monocular eye movements reported here refer to the total angular excursion of an eye and not to the movement of an eye from an actual or hypothetical resting position. That eye movements are not exactly symmetrical in their amplitude about the resting position is apparent from the data of Fig. 2. Had this been the case then the plot of binocular field width in the dead bird should have been placed midway between the plots of the maximum and minimum binocular field widths.

Figures 1 and 2 show clearly that in the starling, eye movement amplitude is a function of elevation about the head. Amplitude varies between a maximum of 32° and a minimum of 11°. The two planes in which these maximum and minimum eye movements occur are approximately orthogonal. Maximum eye movements occur in a plane which passes through the eye and lies approximately 30°–50° below the closed bill, while minimum eye movement amplitude occurs between 30°–50° above the bill.

The binocular field

The maximum retinal binocular field width recorded in the starling was 43° at an elevation approximately 30°–40° below the bill (Fig. 3A). (It is of interest to note that this maximum width is only 5° less than the maximum binocular field width of the tawny owl (Martin 1984), a species often noted for its wide binocular field.) However, in the dead bird when the eyes had presumably taken up their resting position, maximum binocular field width was reduced to 26° and occurred approximately 10° above the bill (Fig. 3C). These differences in both the elevation and maximum width of the binocular fields in the bird when alert and when dead parallels that found in the pigeon (Martinoya et al. 1981; Martin and Young 1983) and suggests that eye movements may play an important role in altering the visual fields in this species also (Bloch et al. 1984; Martinoya et al. 1984; MacFadden and Reymond 1985).

Vertically the binocular field extends through 130° when the eyes are in their resting position (Fig. 3C) but the total vertical range over which binocularity can be achieved as the result of eye movements is at least 160° (Fig. 3A). However, the minimum limit to the binocular field, produced when the eyes are moved backwards and upwards, is very small being only 20° in vertical extent and 7° wide (Fig. 3B). How this variation in the extent of binocular overlap is coped with neurologically is clearly of interest.

The binocular field and foraging

Figures 3A and D show that the bill is positioned well within the binocular field. This is similar to the situation in the pigeon (Martinoya et al. 1981; Martin and Young 1983) and in the penguin, *Spheniscus humboldti* (Martin and Young 1984) but unlike the situation in the tawny owl (Martin 1984), or in the mallard duck *Anas platyrhynchos* (Martin 1986), where the bill falls below the visual field. This positioning of the bill well within the binocular field presumably reflects a role for binocular vision in the control of bill position during foraging. When the eyes are brought forward the bill limits the binocular field (Fig. 3A) thus indicating that given a sufficient degree of accommodation (see below) the starling may be able to see the tip of its own bill.

The starling is a ground feeding bird and Beecher (1978) has argued that eye movements play an important role in the starling's foraging technique of 'prying'. In prying the closed bill enters the soil surface and the mandibles are then spread widely. Beecher has further described how when the bill is fully opened within the soil the eyes are swung forward to apparently look between the mandibles and examine possible prey items.

In the present study photographs of a starling showed that the tips of the open bill could be separated by a maximum of 46° with respect to the articulation of the lower mandible. This bill opening corresponds to the tip of the lower mandible falling at $\alpha = 144°$ in the co-ordinate system used here. Thus, Fig. 3A shows that with the bill open to this maximum extent maximum binocularity would occur between the tips of the mandibles. However, observations of feeding starlings showed that the birds rarely opened their bills to this maximum extent, but even with the bill half-opened the tip of the lower mandible would fall at about $\alpha = 120°$, i.e. still in the region of maximum binocularity. Since the musculature controlling eye movements in birds is independent of the jaw musculature (Slonaker 1918) it is unlikely that bill opening would alter in any appreciable way the eye movements, and hence visual fields, recorded here.

It is noteworthy that with the bill pointing downwards when prying, the eyes can not only be converged to give a large binocular field about and between the mandibles but the eyes can also be readily swung backwards and upwards to give wide visual coverage of the celestial hemisphere (Fig. 3D) which would presumably function in the detection of predators.

In the dead birds it was possible to determine the divergence of the optic axes and the total extent of the monocular fields in the plane of the bill ($\alpha = 90°$). Thus in this plane it is possible to examine the asymmetry of the nasal and temporal portions of the monocular retinal field about the optic axis. The monocular field equalled 161° and this width is similar to that found in a similar plane

Table 3. Comparison of monocular retinal field widths (degrees) in an approximately horizontal plane in four species of bird. (Data for owl and pigeon from Martin 1982, data for duck from Martin 1986)

Species	Total	Nasal	Temporal
Pigeon (*Columba livia*)	169	77	92
Mallard duck (*Anas platyrhynchos*)	191	92	99
Owl (*Strix aluco*)	124	51	73
Starling (*Sturnus vulgaris*)	161	70	91

in the pigeon but 30° narrower than the monocular field of the mallard duck eye (Table 3). As in other vertebrate eyes (Martin 1984) the asymmetry of the monocular field is correlated with the nasad asymmetry in eye structure (see below). The way in which this asymmetry and the eye movements combine to alter the extent of the cyclopean and binocular fields at an elevation of $\alpha = 90°$ is illustrated in Fig. 5. Here it can be seen that optic axis divergence can vary between 146° and 104°. Thus the extent of the blind sector to the rear of the head and the width of the frontal binocular field can be altered by up to 42°.

The schematic eye

The starling may be regarded as an essentially diurnal animal. It would therefore seem reasonable to expect that the optical structure, as revealed by the schematic eye model, might exhibit features that are best interpreted as adaptations towards diurnal vision.

Figure 6 presents the ratio of the refractive powers of the lens and cornea of the eye as a function of anterior focal length, in those terrestrial vertebrate species for which the refractive power of the lens and cornea have been determined independently. The difference in optical structure between the rat and starling eye is readily apparent. Both eyes have similar total refractive power and hence similar anterior focal lengths. However, in the rat most of this refraction is achieved by the lens while in the starling the refractive contributions of the lens and cornea are approximately equal. Since the rat is essentially nocturnal in its habit (Barnett 1963), this difference between the rat and starling eyes could perhaps be attributed to the nocturnal and diurnal nature of these two eyes. An alternative interpretation, however, is that this difference in optical design is attributable to a difference between mammalian and avian eyes. Thus Fig. 6 shows that the ratio $F_L : F_C$ in the starling is very similar to that in the tawny owl, indicat-

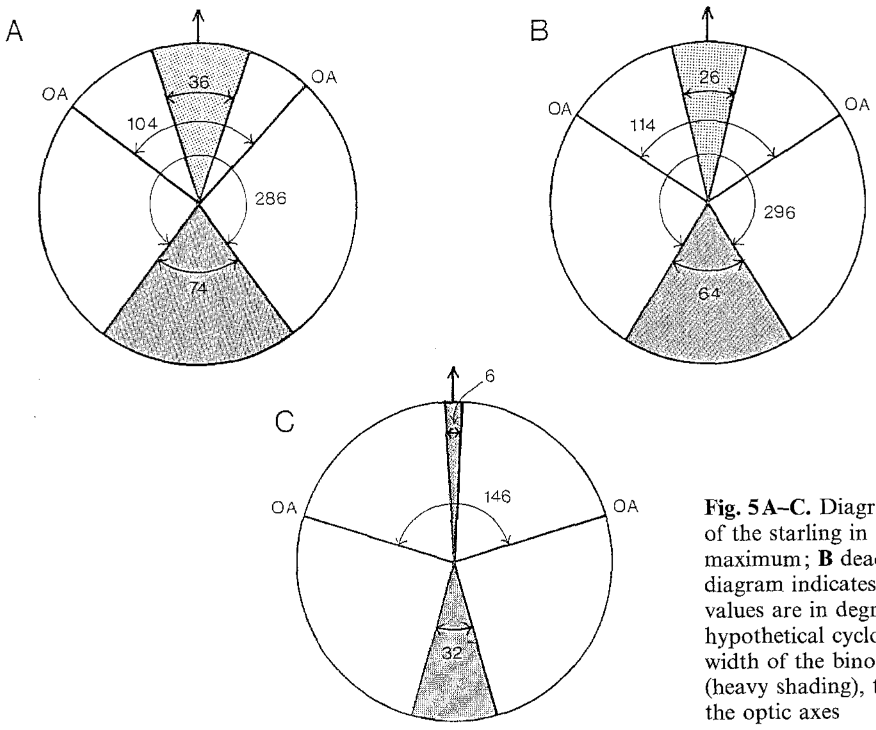

Fig. 5A–C. Diagrammatic representation of retinal fields of the starling in a horizontal plane ($\alpha = 90°$). **A** maximum; **B** dead; **C** minimum. Arrow at the top of each diagram indicates direction of the bill. All numerical values are in degrees (expressed with reference to an hypothetical cyclopean projection centre) and show the width of the binocular field (light shading), the blind area (heavy shading), the cyclopean field and the divergence of the optic axes

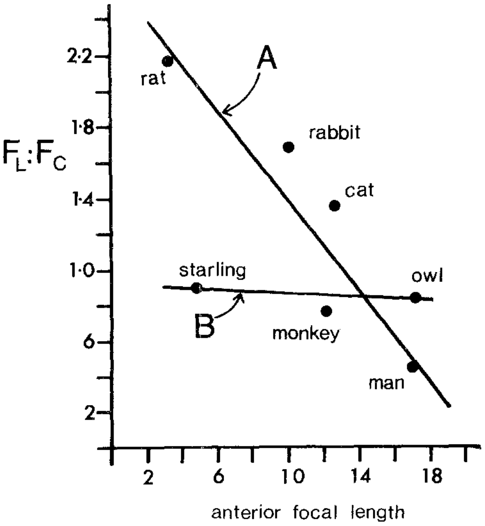

Fig. 6. Ratio of the lens: cornea refractive powers ($F_L:F_C$) as a function of anterior focal length in the schematic eyes of six species of mammal and three species of bird. Line A is the linear regression of the data points for the mammalian species, line B joints the data points for the starling and owl. Data for the mammals from Hughes (1977, Table 1) data for the owl from Martin (1982)

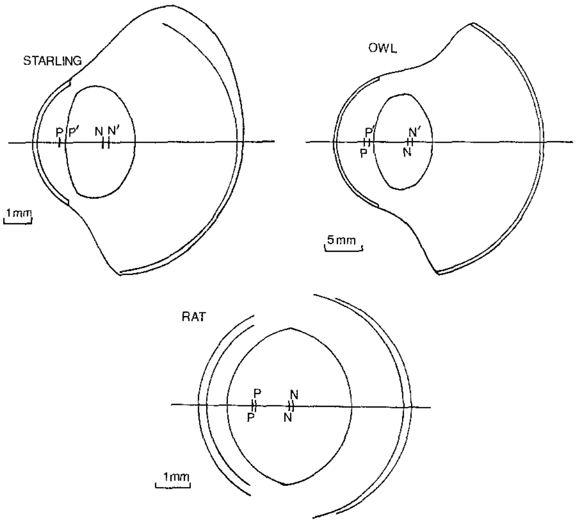

Fig. 7. Diagrams of schematic eyes for starling, owl and rat scaled to the axial length of the starling eye. P, P′ and N, N′ anterior and posterior principal and nodal points, respectively. Data for owl from Martin (1982) and for rat from Hughes (1979)

ing that in terms of its fundamental optical components the starling eye is in effect a smaller but scaled version of the owl eye. These differences and similarities in the optical structure of the owl, rat and starling eyes are apparent in Fig. 7 which presents the schematic eye models of these three species scaled to the axial length of the starling eye. Thus, despite being of similar absolute size the starling and rat eyes are of quite different optical design, while although the owl and starling eyes are quite different in size they are clearly of similar optical design.

Table 4. Comparison of the maximum retinal image illuminances produced in the eyes of man and in three species of bird, when viewing the same extended light source. (Data for owl and pigeon from Martin 1982)

Species	*f*-Number	(*f*-Number)^2	Retinal image illumination relative to man; $\log_{10}$
Man	2.13	4.54	
Owl (*Strix aluco*)	1.3	1.69	+0.43
Pigeon (*C. livia*)	1.98	3.92	+0.06
Starling	1.90	3.62	+0.098

Retinal image brigthness

In the vertebrate eye the relative brightness of the image of an extended light source is indicated by comparison of 1/(f-number)^2. The minimum f-number (maximum image brightness) of the starling eye approximately equals that of both the pigeon and man and is about $\times 0.46$ (0.33 $\log_{10}$) that of the owl (Table 4). This small difference in image brightness between the owl and starling eyes also attests to the general similarity of eye structure in these two avian species. Such a small difference in retinal image brightness between apparently nocturnal and diurnal forms has also been noted previously in mammalian and avian eyes (Hughes 1977, p 659; Pettigrew 1983). However, these measures of image brightness were mainly derived from values of posterior nodal distances and maximum pupil diameters estimated from gross eye dimensions rather than from data derived from schematic eye models.

Asymmetry of the eye and monocular visual fields

As noted above the monocular retinal field of the starling eye is not symmetrical about the optic axis. In an approximately horizontal plane the temporal portion of the retinal field exceeds that of the nasal portion by 21°.

Figure 8A shows the usual construction employed to determine the likely maximum and minimum limits of the optical field in a vertebrate eye (Vakkur and Bishop 1963). This construction is based only upon the dimensions of the cornea and

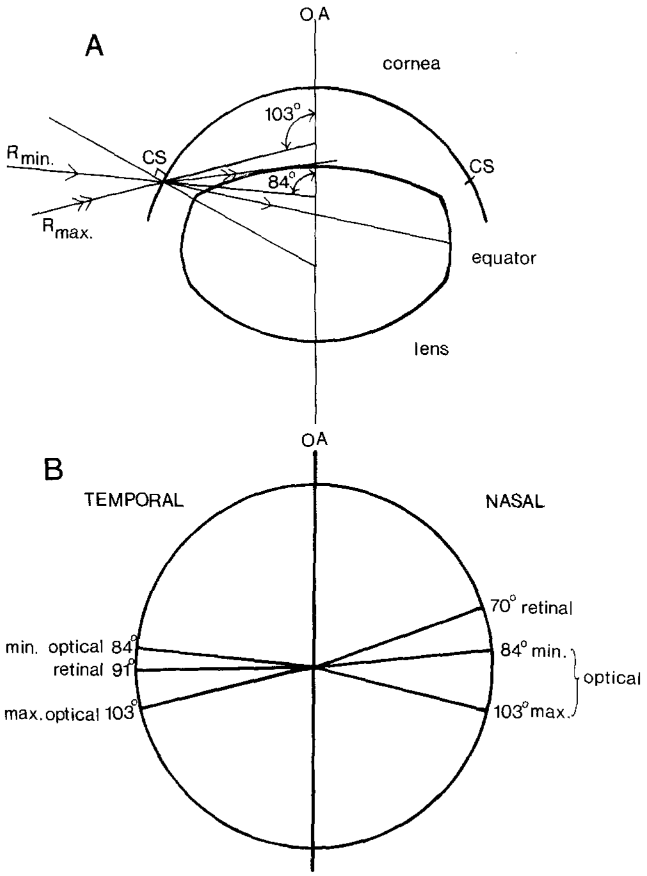

Fig. 8. A construction based upon the schematic model of the starling eye to estimate the likely minimum (Rmin) and maximum (Rmax) limits of the optical monocular field. *CS* corneoscleral junction; *OA* optic axis. **B** comparison between estimated maximum and minimum optical fields and observed limits of nasal and temporal retinal visual fields in an approximately horizontal plane ($\alpha = 90°$)

the relative positions of the corneal margin, anterior lens surface and lens equator, and hence does not employ any of the assumptions and approximations of paraxial optics used to construct the eye model.

The calculated limits to the starling's optical fields and the observed limits of the retinal fields are shown in Fig. 8 B. It can be seen that the observed temporal limit of the retinal field falls between the calculated maximum and minimum limits of the optical field. However, in the nasal field it is apparent that full use is not made of the available optical field. Since the nasal field serves binocular vision it is clear that from consideration of the optical characteristics of the eye the starling could have a considerably larger binocular field than actually found. Thus, if the angular width of the nasal field equalled that of the temporal field the starling's maximum binocular field could be double the width actually observed. Based upon the posterior nodal point of the schematic eye the retinal margins on the nasal and temporal sides of the eye subtend an angle of 85° and 66° with respect to the optic axis (Fig. 9). These two values are similar to the observed differences in the temporal and nasal retinal fields (Fig. 8 B). (Exact correspondence would not be expected because the schematic eye model is being used outside the assumptions of paraxial optics and it is likely that the retinal magnification factor will change with increased eccentricity from the optic axis.) Thus the asymmetry in retinal visual field width about the optic axis can be attributed to the nasad asymmetry of the eye rather than to any asymmetry of the optical system.

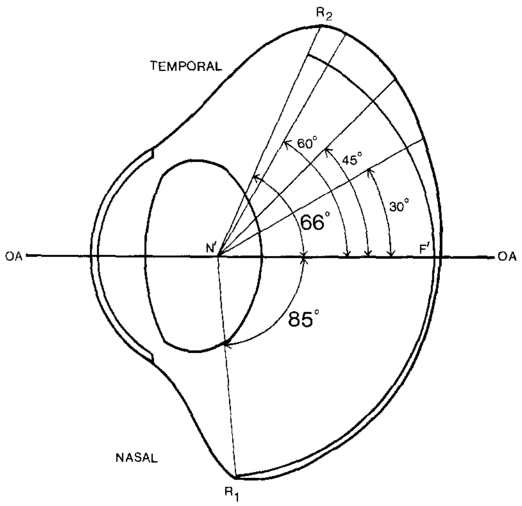

Fig. 9. Diagram of the schematic eye of the starling showing directions from the posterior nodal point (N') (defined by the angles 30°, 45° and 60° from the optic axis (OA)), along which distances to the retina given in Table 5 were estimated. Also shown are angles subtended at N′ by the approximate positions of the retinal margins (R_1 and R_2) with respect to the optic axis

Why equal use is not made of the available optical field on both sides of the optic axis is not clear but similar results have also been found in the following species: tawny owl (Martin 1984), pigeon (Martin 1984), mallard duck (Martin 1986), Humboldt penguin (Martin and Young 1984), cat (Hughes 1976), and man (Emsley 1948). Thus this asymmetry in the width of the monocular retinal hemifields may be a property which is common to many vertebrates eyes.

Nasad asymmetry in eye structure was interpreted by Walls (1942, p 299) as a structural adaptation which serves to increase binocular field size. However, it has been argued that this is unlikely to be the case (Martin 1984). The results of the starling eye would seem to support this.

Further evidence of the similarity of optical structure in the starling and owl eye is provided by comparison of the calculated maximum and minimum limits of the optical fields (Fig. 8A). Measured with respect to the optic axis the minimum and maximum optical fields of the starling equal 84° and 103°, respectively, while in the tawny owl these limits are at 82° and 101°, respectively (Martin 1984). However, due to the tubular shape of the owl eye the retinal fields are restricted and less use is made of the available optical field than in the starling. Thus, the temporal and nasal retinal hemifields in the owl's tubular shaped eye are 73° and 51° wide, respectively, compared with 91° and 70° in the 'flat' eye of the starling.

Asymmetry of the eye and accommodation

The starling eye is also asymmetric in another respect (Fig. 9). In the nasal half of the retina the scleral surface and the image surface for an object at infinity are approximately parallel. Since the schematic eye is emmetropic along the optic axis this implies that the eye is also probably emmetropic throughout much of the nasal hemifield. However, in the temporal half of the eye the scleral surface falls increasingly behind the image surface. This suggests that the eye may become increasingly myopic with greater eccentricity in the temporal-dorsal quadrant, i.e. that the eye may embody a 'ramp retina' as a static accommodatory device (Sivak and Allen 1975; Sivak 1976). Asymmetry in refractive state within the visual field of the pigeon, has been described but the basis of this asymmetry is not known (Catania 1964; Millodot and Blough 1971). Although the schematic eye model does not accurately predict the positions of the cardinal points and image surfaces outside of the paraxial region it is of interest to examine the apparent asymmetry of the starling's retinal surface in the context of the refractive problems which the starling may face whilst foraging.

Single frame analysis of cine film has shown that when foraging on the ground, a starling first detects visually a conspicuous prey item at a distance of about three bill lengths from the eye, approximately 70–90 mm (Lawrence, personal communication). In addition, as discussed above, vision would seem to play a crucial role in foraging in that birds may examine prey items close to, or between the tips of their bills when 'prying'. Personal measurement of two starlings gave a mean bill length of 26 mm, and photographs showed the bill tip to lie 35 mm from the centre of the pupil.

Table 5. Variation of distance between the posterior nodal point of the schematic eye and the retinal surface at different degrees of eccentricity with respect to the optic axis (as defined in Fig. 9) and the equivalent degree of myopia

Eccentricity (degrees)	Distance (mm)	Equivalent myopia (dioptres)
0	4.78	0
30	5.15	14.8
45	5.35	22.0
60	5.40	24.0

It seems unlikely that objects as close as the bill tip (35mm) or even three times the bill length from the eye (78 mm) could be brought into an acceptable degree of focus in the starling by the use of a small pupil. The hyperfocal distance of an eye (x) is the distance from the eye to the nearest object whose image is considered to be in focus on the retina. This distance is given approximately by the expression $x=f \cdot A/2z$ (Land 1981) where f is the anterior focal length of the eye, A, the entrance pupil diameter and z, the diameter of the blur circle of the retinal image that is permissable before it is detected as out of focus. If z is taken to equal 2 μm (the approximate diameter of a cone photoreceptor outersegment in a passeriform eye (Donner 1951; Bowmaker 1979)) it can be shown that for the hyperfocal distance of the starling eye to equal 35 mm and 78 mm respectively, it would be necessary to have entrance pupils whose diameters equalled 29 μm and 65 μm respectively, i.e. the pupil would need to be a 'pin-hole' aperture.

To bring an object at the starling's bill tip into focus using an accommodatory mechanism would require accommodation of approximately +28.6 dioptres (D), and in order to focus on objects at 78 mm would require +12.8 D of accommodation. These are relatively large degrees of accommodation and although accommodation of up to +50 D has been recorded in some aquatic diving birds, accommodation in the pigeon equals only +4 D (Levy and Sivak 1980). It is of interest to note therefore that in a small eye of high refractive power, such as that of the starling, large accommodatory changes can be achieved by relatively small increases in the length of the distance between the retinal surface and the posterior nodal point of the eye. Table 5 gives the measured lengths of this distance at 30°, 45° and 60° to the optic axis in the temporal-dorsal quadrant of the starling eye as shown in Fig. 9. (It has been assumed that the sclera is of uniform thickness at all points on the posterior of the globe.) Also shown is the shift towards myopia which these increased distances are equivalent to. It can be seen that the asymmetry of the starling eye may be sufficient to introduce equivalent accommodatory changes that would bring into focus objects which are close to the bill tip.

Such an arrangement would seem to have adaptive advantage for the starling. Thus while the temporal visual field (subserved by the nasal-ventral portion of the retina) will be focused at infinity (and hence could be used to observe objects at some distance away), the eyes may be converged to examine objects close to the bill and these would appear well focused on the temporal-dorsal retina.

However, it should be noted that while a high degree of myopia would have adaptive value in the lower half of the frontal field where it could function in foraging, such myopia would seem to be disadvantageous in the upper part of the frontal field. It is likely that this upper portion of the frontal visual field is used to guide the bird in flight when it would be necessary to detect objects at a distance from the bird. Personal observation of starlings in free horizontal flight indicates that the bill is usually held in an approximately horizontal position. However, flash photographs of starlings on short (approximately 1.5 m) flights between perches in a cage, showed that the bill was consistently held above the horizontal at an angle of approximately 10°–20° as the birds prepared to land. The reason for this difference in head position is not clear but it may be correlated with a difference in refractive state in the upper and lower portions of the frontal visual field.

Clearly further work is required in order to examine in more detail the asymmetry of the starling eye and the way in which the eyes are used during foraging and in flight. However, it is worth noting the relatively small degree of asymmetry in an eye the size of a starling's that is necessary in order to produce a static accommodatory mechanism which is equivalent to a change in refractive power of large amplitude.

The diurnal nature of the starling eye

The nocturnal-diurnal dichotomy has often been used as an explanatory device as regards the diversity of vertebrate eye structures (Walls 1942, pp 143–246; Tansley 1965, pp 39–57; Hughes 1977, p 660). However, only recently has attention focused in any detail on the luminance differences associated with day- and night-time. There would seem little doubt that the starling eye can be described as that of a diurnal animal and that the average luminance levels at which this bird chooses to be active exceed the luminance levels at which an obligate nocturnal bird is active by up to a millionfold (Martin 1982). However, the data presented here indicates that in its optical structure the starling eye differs only in one significant respect, absolute size, from the structure of the eye of one such obligate nocturnal bird, the tawny owl.

It has been possible to interpret the absolutely large size of the owl eye as associated with the nocturnal habit. However, it is less clear that the smaller size of the starling eye can be linked directly with the diurnal habit. Thus the absolutely large size of the owl eye can be seen as a necessary, though not sufficient, basis for optimizing the extraction of information from its retinal image *throughout* the million-fold luminance range which can be experienced by the tawny owl in its woodland habitat during night time (Martin 1982). For adequate visual functioning within the nocturnal luminance range there is also a requirement for flexibility in the way that the retinal mechanisms sample the large retinal image as luminance levels change (Snyder et al. 1977).

On the other hand, large eye size in diurnal, as opposed to nocturnal birds, may have more to do with the requirements of maximizing spatial resolution within a relatively fixed range of naturally occurring high luminance levels, rather than providing a basis for flexibility in the way that an image is sampled over a wide luminance range (Martin 1983). Evidence in support of this is provided by the recent findings that spatial resolution in a falcon, *Falco sparverius* (Hirsch 1982), and in an eagle, *Aquila audax* (Reymond 1985), decreases rapidly with a fall in luminance.

In a relatively small eye, however, such as that of the starling, functioning seems likely to be restricted to a relatively narrow range of luminance regardless of the absolute level of this range. This is because in such an eye there is less scope for flexibility in the way that the retinal mechanisms can sample the image as luminance levels vary (Martin 1983). Thus while there may be no particular 'diurnal' feature to be discerned in the optical structure of the starling eye, its small size is possibly one factor which restricts the bird's pattern vision to a relatively narrow luminance range and so prohibits it from being regularly active after sunset.

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