

Multifocal optical systems and pupil dynamics in birds

Olle E. Lind*, Almut Kelber and Ronald H. H. Kröger

¹Department of Cell and Organism Biology, Lund University, Helgonavägen 3, 223 62 Lund, Sweden

*Author for correspondence (e-mail: Olle.Lind@cob.lu.se)

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SUMMARY

In animal eyes of the camera type longitudinal chromatic aberration causes defocus that is particularly severe in species with short depth of focus. In a variety of vertebrates, multifocal optical systems compensate for longitudinal chromatic aberration by concentric zones of different refractive powers. Since a constricting circular pupil blocks peripheral zones, eyes with multifocal optical systems often have slit pupils that allow light to pass through all zones, irrespective of the state of pupil constriction. Birds have circular pupils and were therefore assumed to have monofocal optical systems. We examined the eyes of 45 species (12 orders) of bird using videorefractometry, and the results are surprising: 29 species (10 orders) have multifocal systems, and only five species (five orders) have monofocal systems. The results from 11 species (four orders) are inconclusive. We propose that pupils 'switching' between being fully opened (multifocal principle) to maximally closed (pinhole principle) can make multifocal optical systems useful for animals with circular pupils. Previous results indicate that mice have both multifocal optical systems and switching pupils. Our results suggest that parrots may use a similar mechanism. By contrast, owl pupils responded weakly to changes in illumination and stayed remarkably wide even in full daylight. Moreover, the parrots opened their pupils at higher light levels than owls, which correlates with the differences in sensitivity between diurnal and nocturnal eyes.

Key words: longitudinal chromatic aberration, multifocal, lens, pupil dynamics, color vision, bird.

INTRODUCTION

Color vision is used by most vertebrates to discriminate between and identify objects in changing illumination because spectral information is much more robust than intensity cues (Campenhausen, 1986; Maximov, 2000). However, color vision faces an optical challenge caused by longitudinal chromatic aberration (LCA). LCA arises because the refractive index of ocular media is a function of wavelength (Sivak and Mandelman, 1982; Kröger, 1992). Light of short wavelengths is refracted more strongly than light of long wavelengths, and the resulting chromatic defocus cannot be corrected for by accommodation if the image contains a wide range of wavelengths.

Various vertebrates compensate for LCA with multifocal optical systems (Kröger et al., 1999; Malkki and Kröger, 2005; Malmström and Kröger, 2006; Karpestam et al., 2007; Gustafsson et al., 2008). In multifocal systems, the crystalline lens has concentric zones of different refractive powers created by a complex gradient of refractive index. Each zone focuses light of a narrow band of wavelengths such that a well-focused color image is created on a background of defocused light that has passed through 'wrong' zones of the lens with unsuitable focal lengths (Fig. 1). Therefore, this is not a perfect solution, and the gain in image quality across the visual spectrum comes at the cost of lower spatial resolution at a single wavelength. A similar trade-off has also been observed in the human eye (with a monofocal system), which may utilize imperfect optics to reduce chromatic blur (McLellan et al., 2002).

Eyes with short focal lengths relative to the apertures, i.e. with low f-numbers (Land and Nilsson, 2002), suffer most from chromatic defocus because they have short depths of focus (Smith and Atchison, 1997) and gain the most from multifocal optical systems. By contrast, eyes of the same size but with higher f-numbers usually have longer depths of focus and thus a higher tolerance to defocus. Indeed, multifocal optical systems are primarily present in eyes of

aquatic, crepuscular and nocturnal vertebrates that often have low minimum f-numbers (the f-number depends on the pupil size, and the minimum f-numbers refer to the eye with a maximally opened pupil). Diurnal terrestrial animals with high minimum f-numbers commonly have monofocal systems (Kröger et al., 1999; Malmström and Kröger, 2006), i.e. no distinct zones in the lens and one single focal point for monochromatic light of a certain wavelength (Fig. 1).

In eyes with multifocal optical systems, circular pupils with a pronounced pupillary light reflex are problematic because the iris shades the outer zones of the lens as the pupil constricts (Fig. 2). In these cases, a circular pupil is only adaptive when it is either fully dilated or strongly constricted, i.e. if the multifocal system or a long depth of focus, respectively, reduces the defocusing effect of LCA. At intermediate states of pupil constriction, chromatic blur may degrade image quality since the iris shades part of the multifocal optical system and the depth of focus decreases with increasing pupil size. Slit pupils, by contrast, allow light to pass through all zones of the lens irrespective of the state of pupil constriction (Fig. 2). In terrestrial vertebrates, multifocal optical systems are therefore usually correlated with slit pupils (Malmström and Kröger, 2006).

Birds, in general, strongly rely on vision and especially on color cues, but it is unknown whether or not any species of bird has a multifocal optical system. Most birds are diurnal with eyes of relatively high minimum f-numbers (Marshall et al., 1973; Martin, 1982; Martin and Young, 1984; Martin, 1986; Martin et al., 2001), and all birds (except for skimmers, *Rynchops* spp.) have circular pupils (Walls, 1942; Zusi and Bridge, 1981). These characters are strongly correlated with monofocal optical systems in other tetrapods (Malmström and Kröger, 2006). It has therefore been assumed that birds have monofocal optical systems, with the possible exceptions of owls and other nocturnal birds that have eyes with low minimum f-numbers (Martin, 1982; Schaeffel and Wagner, 1996).

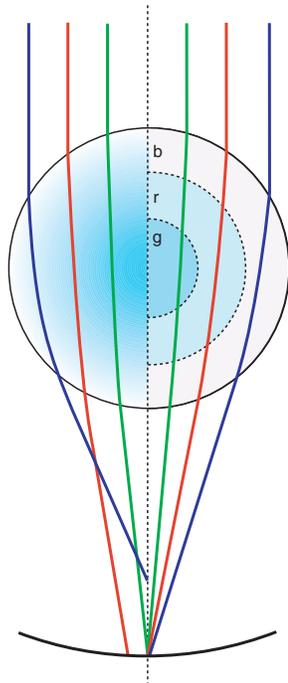


Fig. 1. Modes of operation of monofocal and multifocal lenses. The left side of the dotted line represents a chromatically uncorrected, monofocal lens and the right side a multifocal lens. The monofocal lens focuses green light properly on the retina, but blue and red light are focused in front and behind the retina, respectively, because of longitudinal chromatic aberration. The multifocal lens is, in this example, divided into three zones, each having the correct focal length for a narrow band of wavelengths ('colors'). The outer zone (b) is adjusted for blue, the intermediate zone (r) for red, and the inner zone (g) for green light. Blue, red and green are therefore all in focus, and a sharp color image is created. However, red light, for example, also passes through the outer B zone of the lens and is severely defocused. Such light that has passed through zones not suited to focus its particular wavelength generates a contrast-reducing background. In a terrestrial eye, the cornea and crystalline lens may together constitute an optical system that operates according to the same principle.

However, some animals, such as the house mouse (*Mus musculus*), have the unusual combination of circular pupils and multifocal optical systems (Malmström and Kröger, 2006). These animals may have evolved 'switching' pupils. The pupil changes ('switches') between being fully opened and strongly constricted within a narrow range of intensities and thus avoids intermediate states of pupil constriction. The results of earlier studies support such a mechanism; mice have multifocal optical systems (Malmström and Kröger, 2006), keep their pupils open even at rather high light intensities, and close them almost fully within about one log unit of intensity change (Pennesi et al., 1998; Grozdanic et al., 2003).

In the present study we examined the optical properties of the eyes of birds from 12 orders using eccentric slope-based infrared (IR) videorefractometry. In addition, we examined the pupil dynamics in two groups, parrots (Psittaciformes) and owls (Strigiformes), in order to study possible interactions between the function of the pupil and the optical system.

MATERIALS AND METHODS

Birds

Song birds (Passeriformes) that were captured for ringing were examined at Falsterbo Bird Observatory (Falsterbo, Sweden). Other

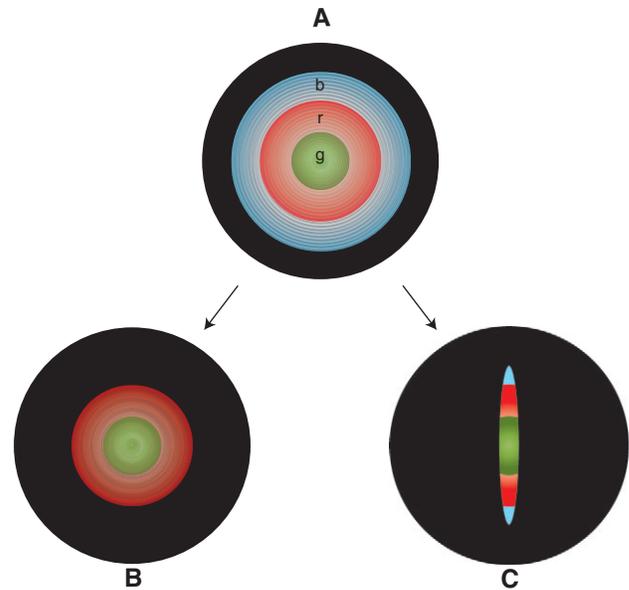


Fig. 2. The advantage of a slit pupil in an eye with a multifocal optical system. (A) The eye has three zones of different refractive powers. The zones focus light in the blue (b), red (r) and green (g) ranges of the spectrum, represented by the same colors in the figure. The iris is the black outermost region. (B) The pupil constricts circularly and the iris shades the blue-focusing zone. (C) A slit pupil allows light to pass through all zones of the optical system irrespective of the state of pupil constriction.

wild birds, as well as the domestic goose (*Anser anser*) and the domestic chicken (*Gallus gallus*) were kept and studied in zoological gardens (Skånes djurpark, Höör, Sweden; Ystad djurpark, Ystad, Sweden; Chula Vista Nature Center, San Diego, CA, USA; SeaWorld, San Diego, CA, USA). The lilac-breasted roller (*Coracias caudatus*), the homing pigeon (*Columba livia*), the budgerigar (*Melopsittacus undulatus*), the blue-fronted parrot (*Amazona aestiva*) and the grey parrot (*Psittacus erithacus*) were private pet birds. Only mature and healthy animals were chosen. The birds were investigated without being restrained from distances exceeding 1 m.

Optical properties of the eye

Eccentric slope-based IR videorefractometry was used to discriminate between monofocal and multifocal optical systems. With this technique, the refractive state of non-cooperative subjects can be determined from a distance. The details of this method are described elsewhere (Schaeffel et al., 1987; Roorda et al., 1997; Malkki and Kröger, 2005). In our setup (Fig. 3), we used a digital IR-sensitive video camera (DCR-TRV 730E; Sony, Tokyo, Japan) mounted to a custom-made IR-retinoscope. IR light-emitting diodes (LEDs) were arranged in four rows at eccentricities from 5 to 23 mm and adjustable in intensity. An IR transmissive filter, attached to the camera objective enhanced contrast by reducing visible light.

If the eye has a monofocal optical system, the fundus reflex is smooth with a brightness gradient depending on the refractive state; a hyperopic eye has a bright upper side (Fig. 4A), and a myopic eye has a bright lower side. Multifocal optical systems are detected by concentric ring-like markings in the reflex (Fig. 4B) that originate from intensity contrasts between zones of different refractive powers for monochromatic light (Kröger et al., 1999; Malkki and Kröger, 2005). Zones with bright upper sides have relatively less refractive

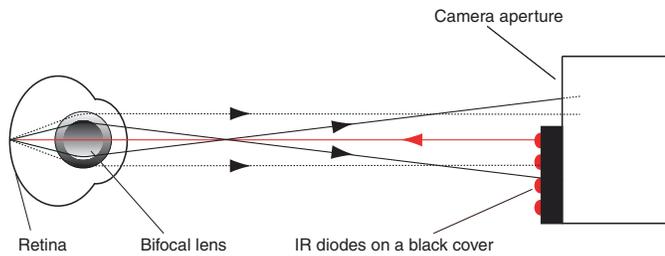


Fig. 3. Ray-tracing diagram showing the principle behind eccentric infrared slope-based videorefractometry. The ocular lens is bifocal with an outer zone of smaller refractive power than the centre. The lens is illustrated as it appears on the image taken by the camera. Reflected light that passes through the upper part of the outer zone enters the camera lens while the cover blocks light from the lower part. The opposite is true for the inner zone. This leads to ring-like patterns in the pupillary reflex captured by the camera.

power, i.e. they are hyperopic relative to the zones with bright lower sides.

We videotaped the animals as they looked into the camera under dim-light conditions (darker than 10^{-2} cd m^{-2}) usually from a distance of 1.5 to 2 m. However, some animals had to be investigated from larger distances and were videotaped with a telephoto conversion lens ($\times 2.0$; Sony). The video recordings were transferred to a computer, and single frames of reflexes were saved as still images using Adobe Premiere Pro software (Adobe Systems; Mountain View, CA, USA). Only images taken along, or close to, the optical axis were chosen in order to avoid oblique aberrations.

Pupil shapes

Photographs of the closed pupils were taken with a digital camera (DSC-F828; Sony) under daylight or equivalent lighting conditions (brighter than 400cd m^{-2}). Images from birds with black or dark brown irises were contrast-enhanced with Adobe Photoshop CS2 until the shapes of the pupils could be determined.

Pupil dynamics

One female and one male each of Ural owl (*Strix uralensis*), snowy owl (*Bubo scandiacus*), blue-fronted parrot (*A. aestiva*) and grey parrot (*P. erithacus*) were chosen to study pupil dynamics. The owls were held outdoors in zoological gardens and the observations were made under natural light. The parrots were observed indoors in the light from four fluorescent lights (36 W, TL-D 90 delux pro, Philips) and two tungsten lamps (15 W and 7 W, Philips; Eindhoven, The Netherlands) that were adjusted from 82.4 to 3.7×10^{-5} cd m^{-2} . In addition, observations of the blue-fronted parrot were made under natural light outdoors at two higher levels of illumination. The subjects were alerted by the investigator and all recordings from each bird were made with the same background in order to minimize fluctuations in pupil size due to variation in the scenery or the direction of gaze. The birds were neither drugged nor stressed and were allowed to behave normally.

At each intensity level, the pupils were recorded with a video camera (same as above) for 1–2 min. Measurements started in the afternoon at the brightest light level, and recordings were then made at 5–15 min intervals until the full range of illumination levels was covered. As the light faded, the camera was equipped with adjustable IR-LEDs that made the pupil visible without eliciting the pupillary constriction reflex. A radiometer (IL 1700 with detector–SHD 033; International Light, Newburyport, MA, USA) was used to measure

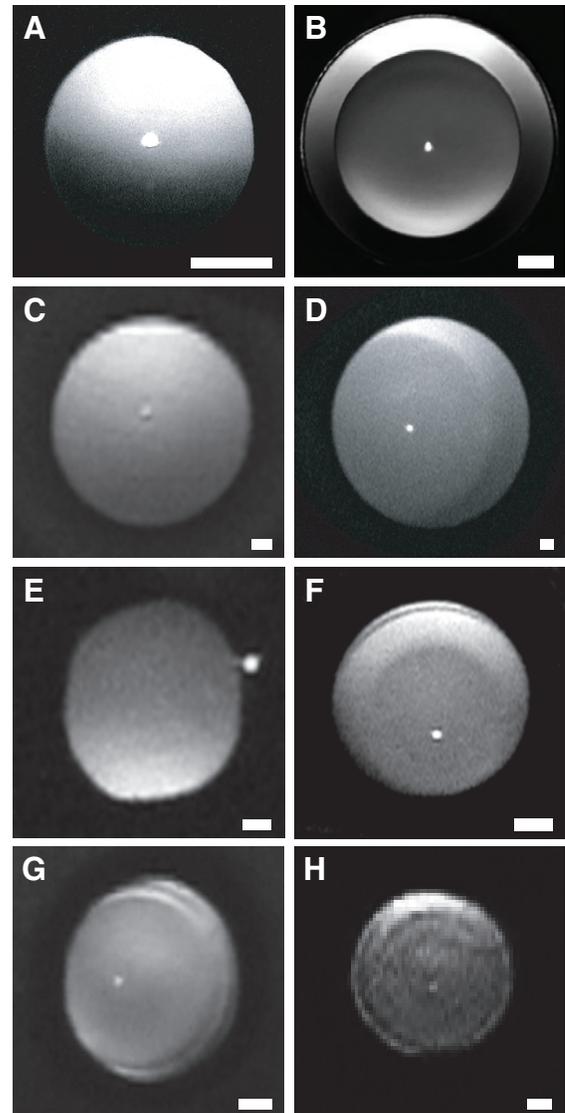


Fig. 4. Videorefractive images from bird eyes and manufactured lenses. (A) The reflex from a manufactured monofocal lens is smooth as is the reflex from (C) emu (*Dromaius novaehollandiae*; Struthioniformes) and (E) emperor penguin (*Aptenodytes forsteri*; Sphenisciformes). (A,C) Eyes in hyperopic refractive states relative to the camera have bright upper sides. (E) The eye of the emperor penguin is myopic and therefore has a bright lower side. (B) The reflex from an artificial bifocal lens with an outer zone of smaller refractive power than the inner zone. There is high similarity between the reflexes from the custom-made bifocal lens and the eyes of (D) the great horned owl (*Bubo virginianus*; Strigiformes) and (F) the lilac-breasted roller (*Coracias caudatus*; Coraciiformes). The reflexes from the eyes of the Psittaciformes (G) Tanimbar cockatoo (*Cacatua goffiniana*) and (H) grey parrot (*Psittacus erithacus*) are more complex, suggesting that the optical systems of these species consist of more than two zones of different refractive powers. Scale bars: 1 cm (A,B); 1 mm (CH).

the level of illumination as the reflection at 45° from a white card in cd m^{-2} . A ruler at the same distance from the camera as the pupils was videotaped as an absolute scale reference.

For analysis, the recordings were transferred to a computer, and single frames were extracted (4–5 for each bird and illumination level) using Adobe Premiere Pro software. The entrance pupil sizes were determined after calibrating the images to the scale reference using Image J v.1.37 software (<http://rsbweb.nih.gov/ij/index.html>).

Table 1. Multifocality, cone pigment and pupil size

Order	Species	English common name	Pupil diameter (mm)	Multifocal optics	Cone pigment	Reference (pigment)
Struthioniformes	<i>Struthio camelus</i> Linnaeus 1758	Ostrich	11	Yes	U, S, M, L	(Wright and Bowmaker, 2001)
	<i>Dromaius novaehollandiae</i> Latham 1790	Emu	10	No	L	(Sillman et al., 1981)
	<i>Rhea americana</i> Linnaeus 1758	Rhea	10	?	S, M, L	(Wright and Bowmaker, 2001)
Sphenisciformes	<i>Spheniscus humboldti</i> Meyen 1834	Humboldt penguin	5	Yes	U, S, L	(Bowmaker and Martin, 1985)
	<i>Spheniscus magellanicus</i> Forster 1781	Magellanic penguin	4.5	?	–	–
	<i>Pygoscelis adeliae</i> Hombron and Jacquinot 1841	Adelie penguin	4.5	?	–	–
	<i>Pygoscelis papua</i> Forster 1781	Gentoo penguin	5	?	–	–
	<i>Pygoscelis antarcticus</i> Forster 1781	Chinstrap penguin	5	?	–	–
	<i>Aptenodytes patagonicus</i> Miller 1778	King penguin	7	?	–	–
	<i>Aptenodytes forsteri</i> Gray 1844	Emperor penguin	7	No	–	–
	<i>Eudyptes chrysolophus</i> Brandt 1837	Macaroni penguin	5	?	–	–
Strigiformes	<i>Athene cunicularia</i> Molina 1782	Burrowing owl	13	Yes	–	–
	<i>Bubo virginianus</i> Gmelin 1788	Great horned owl	15	Yes	–	–
	<i>Bubo scandiacus</i> Linnaeus 1758	Snowy owl	14	Yes	–	–
	<i>Asio flammeus</i> Pontoppidan 1763	Short-eared owl	13	Yes	–	–
	<i>Strix nebulosa</i> Forster 1772	Great grey owl	14	Yes	–	–
	<i>Strix uralensis</i> Pallas 1771	Ural owl	12.5	Yes	–	–
	<i>Aegolius funereus</i> Linnaeus 1758	Boreal owl	12	Yes	–	–
	Falconiformes	<i>Buteo lineatus</i> Gmelin 1788	Red-shouldered hawk	8	Yes	–
<i>Haliaeetus leucocephalus</i> Linnaeus 1766		Bald eagle	9	Yes	–	–
Anseriformes	<i>Lophodytes cucullatus</i> Linnaeus 1758	Hooded merganser	5	Yes	–	–
	<i>Anser anser</i> Linnaeus 1758	Domestic goose	7	No	–	–
Passeriformes	<i>Phylloscopus trochilus</i> Linnaeus 1758	Willow warbler	2	?	–	–
	<i>Phylloscopus collybita</i> Vieillot 1817	Chiffchaff	2	Yes	–	–
	<i>Fringilla montifringilla</i> Linnaeus 1758	Brambling	3	Yes	–	–
	<i>Fringilla coelebs</i> Linnaeus 1758	Chaffinch	3	Yes	–	–
	<i>Erithacus rubecula</i> Linnaeus 1758	European robin	2.5	Yes	–	–
	<i>Emberiza schoeniclus</i> Linnaeus 1758	Reed bunting	2.5	?	–	–
	<i>Troglodytes troglodytes</i> Linnaeus 1758	Winter wren	2	?	–	–
	<i>Cyanistes caeruleus</i> Linnaeus 1758	Blue tit	2	Yes	U, S, M, L	(Hart et al., 2000)
	<i>Prunella modularis</i> Linnaeus 1758	Hedge accentor	1.5	Yes	–	–
	<i>Phoenicurus ochruros</i> Gmelin 1774	Black redstart	2.5	Yes	–	–
Coraciiformes	<i>Coracias caudatus</i> Linnaeus 1766	Lilac-breasted roller	5	Yes	–	–
Psittaciformes	<i>Cacatua goffiniana</i> Finsch 1863	Tanimbar cockatoo	6	Yes	–	–
	<i>Cacatua sulphurea</i> Gmelin 1788	Yellow-crested cockatoo	6	Yes	–	–
	<i>Melopsittacus undulatus</i> Shaw 1805	Budgerigar	3	Yes	U, S, M, L	(Bowmaker et al., 1997)
	<i>Poicephalus senegalus</i> Linnaeus 1766	Senegal parrot	6	Yes	–	–
	<i>Amazona aestiva</i> Linnaeus 1758	Blue-fronted parrot	6	Yes	–	–
	<i>Neopsephotus bourkii</i> Gould 1841	Bourke's parrot	3	Yes	–	–
	<i>Psittacus erithacus</i> Linnaeus 1758	Grey parrot	7	Yes	–	–
Galliformes	<i>Tetrao urogallus</i> Linnaeus 1758	Western capercaillie	6	Yes	–	–
	<i>Gallus gallus</i> Linnaeus 1758	Domestic chicken	6	No	U, S, M, L	(Bowmaker et al., 1997)
Ciconiiformes	<i>Ciconia ciconia</i> Linnaeus 1758	White stork	7	No	–	–
Pelecaniformes	<i>Phalacrocorax carbo</i> Linnaeus 1758	Great cormorant	7	?	–	–
Columbiformes	<i>Columba livia</i> Gmelin 1789	Homing pigeon	5.5	Yes	U, S, M, L	(Bowmaker et al., 1997)

Visual pigments are classified after their spectral absorbance maximums: U, ultraviolet/violet sensitive; S, short wavelength sensitive; M, medium wavelength sensitive; L, long wavelength sensitive. Question marks indicate ambiguous optical characters. Pupil diameters are rough estimations.

We selected only images where the birds calmly had their gaze fixed on the camera. The mean pupil area for each species and illumination level was calculated and sigmoid curves were fitted to the pupil sizes as functions of log light intensity using a curve-fitting tool (MATLAB R2007a; The Mathworks Inc., Natick, MA, USA). The negative minimum first derivatives of these curves were used as measures of the gain of changes in pupil area in response to changing light intensity.

RESULTS

Optical properties

Both monofocal and multifocal optical systems were found in birds (Table 1). Multifocality was more common and was

detected in 29 species in 10 out of 12 examined orders. Only five species in five orders had monofocal optical systems (Table 1, Fig. 4C,E).

Species in the orders of Strigiformes, Falconiformes, Passeriformes, Coraciiformes, Columbiformes and Psittaciformes had reflexes with clear multifocal characteristics (Fig. 4D,F–H). The rings that indicate multifocality were less obvious, but present, in birds from the orders of Struthioniformes, Sphenisciformes, Anseriformes and Galliformes. Furthermore, both monofocal and multifocal optical systems were found in these orders (Table 1, Fig. 4C,E). Among the domesticated birds, monofocal optical systems were present in domestic goose (*A. anser*) and domestic chicken (*G. gallus*). By contrast, the homing pigeons (*C. livia*) had

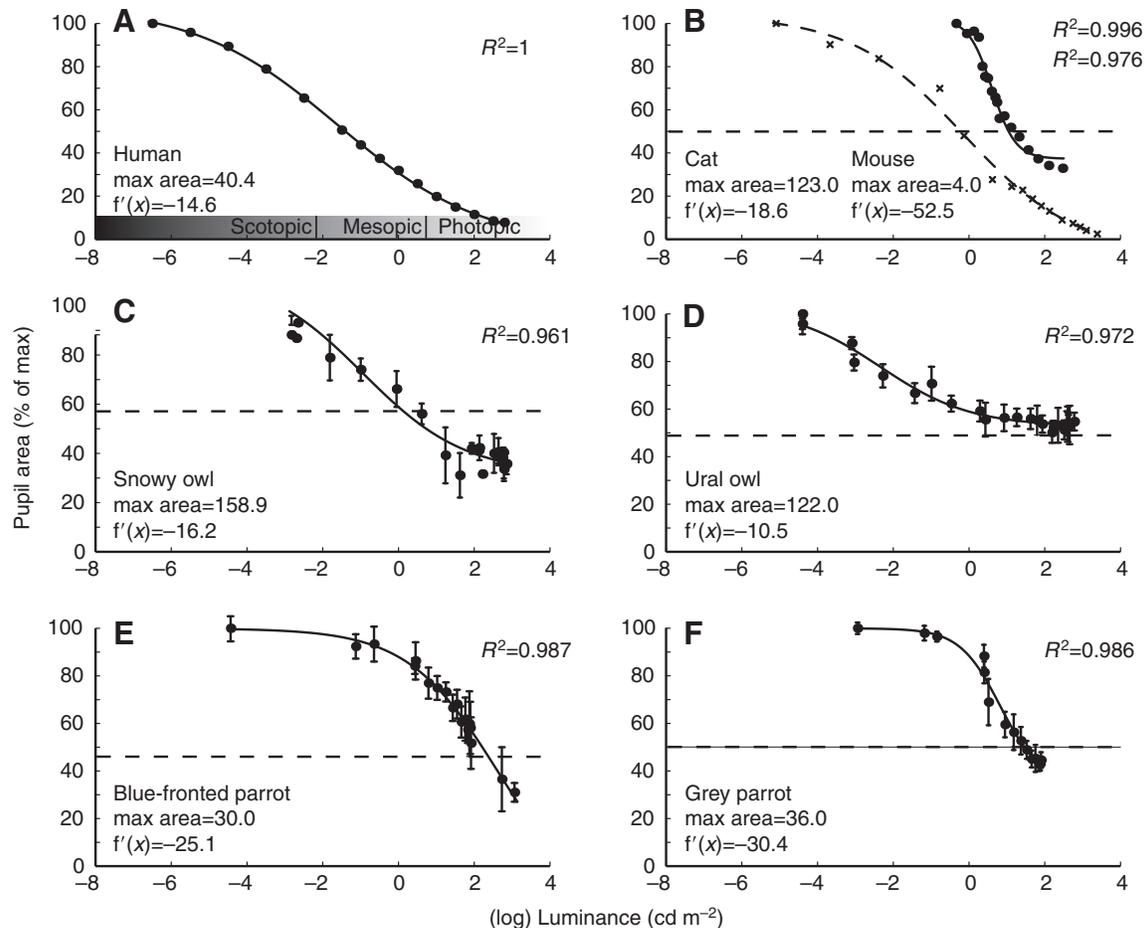


Fig. 5. Pupil dynamics in (A) humans [*Homo sapiens sapiens*, data from De Groot and Gebhard (De Groot and Gebhard, 1952)], (B) cats [*Felis sylvestris*; broken line; data from Wilcox and Barlow (Wilcox and Barlow, 1975)] and mice [*Mus musculus*; solid line; data from Grozdanic et al. (Grozdanic et al., 2003)], (C) snowy owls (*Bubo scandiacus*, $N=2$), (D) Ural owls (*Strix uralensis*, $N=2$), (E) blue-fronted parrots (*Amazona aestiva*, $N=2$), and (F) grey parrots (*Psittacus erithacus*, $N=2$). Pupil size is given as percentage area of the fully opened pupil. No systematic differences between individuals of the same species of bird were observed, and pupil sizes were averaged over both individuals, 8–10 samples/intensity level. The gradient bar in A illustrates rod (scotopic)-, rod and cone (mesopic)- and cone (photopic)-based vision in humans. The steepest portions of the curves were compared by their first derivatives [$f'(x)$]. The responsiveness of the pupillary light reflex is very high in mice and similar tendencies are present in parrots. Humans, cats and owls have pupil dynamics of lower gain. Furthermore, the parrot pupils open fully at illumination levels comparable to human mesopic conditions while the owl pupils reach this state in dimmer, human scotopic illumination. The horizontal broken line marks the relative size of the innermost zone of the multifocal optics (the line in B applies to the mice eyes only). The lens system can be regarded as multifocal for pupil sizes that exceed this level. Error bars are standard deviations.

multifocal systems. In several species, the reflexes had intermediate characteristics with indistinct rings.

Most of the observed multifocal systems were bifocal, i.e. there were only two zones of different refractive powers (Fig. 4D,E). In all of these eyes, the outer zone of the bifocal system had bright upper sides, indicating hyperopic refractive state relative to the central zone (Fig. 4D,E). Most of the parrots – the grey parrot (*P. erithacus*), Tanimbar cockatoo (*Cacatua goffiniana*), yellow-crested cockatoo (*Cacatua sulphurea*) and blue-fronted parrot (*A. aestiva*) had more complex multifocal systems with several zones of different refractive powers (Fig. 4G,H).

Pupil shapes and dynamics

All of the birds studied had circular pupils, except for the emperor penguins (*Aptenodytes forsteri*), which had diamond-shaped pupils when they were strongly constricted, and some of the homing pigeons (*C. livia*), which had slightly oval pupils.

The parrots reached maximum pupil sizes at higher intensities than the owls (Fig. 5C–F). The parrots also had a more active pupillary light reflex (higher gain), thus opening their pupils within narrower ranges of intensities than the owls (blue-fronted parrot, gain=25.1; grey parrot, gain=30.4; snowy owl, gain=16.2; Ural owl, gain=10.5). The results from the birds were compared with data from humans (diurnal, circular pupil, monofocal; gain=14.6), cats (nocturnal, slit pupil, multifocal; gain=18.6) and mice (nocturnal, switching circular pupil, multifocal; gain=52.5) (Fig. 5A,B). The owls had gains in a similar range to those in humans and cats. The parrots had higher gains, but not as high as mice (Fig. 5A–F).

In all studied birds, the border between the inner and outer refractive zones of the optical system was at about 50% of the maximum pupil area (Fig. 5B–F). The Ural owls did not close their pupils to fully block the outer refractive zone of the optical system. Within the illumination ranges used in the study, no bird closed the

pupils to less than 30% of maximum pupil size and neither did the mouse (Fig. 5B–F).

DISCUSSION

Experimental considerations

While most studied bird species clearly possessed monofocal or multifocal optical systems, the videorefractometric reflexes were difficult to interpret in some species (shown as question marks in Table 1) because of inconclusive characteristics such as very faint ring-like markings. Noisy, light environments during examination may have caused this uncertainty. Furthermore, it has been shown that the eyes of several bird species are emmetropic while, at the same time, myopic in certain parts of the visual field (Millidot and Blough, 1971; Nye, 1973; Martin, 1986; Hodos and Erichsen, 1990). This adaptation gives these birds the possibility to keep objects at different distances in focus simultaneously. The mechanisms behind this phenomenon might be the result of asymmetries in the cornea, lens or retina about the optical axis. It is possible that such features further decrease the contrast in the images from the videorefractometer.

Structure of the optical system

The nature of an optical system can, to some degree, be analyzed from the reflexes captured with eccentric slope-based IR videorefractometry, although detailed interpretations should be carried out with caution (Roorda et al., 1997). In all birds with multifocal systems, except for most of the parrots (Psittaciformes) there were only two refractive zones, with the outer one having less refractive power. This is clear from the similarities between reflexes obtained from the bird eyes and a man-made bifocal lens (Fig. 4B,D,F). In the latter, the central zone had higher refractive power than the outer zone. Most multifocal optical systems of birds are thus adapted to focus light of short wavelengths with the outer zone and longer wavelengths with the central zone.

Optical adaptations to UV-vision

The results of this study indicate that multifocality is widespread among birds. Surprisingly, diurnal birds use this optical principle even though they have circular pupils (Walls, 1942; Duke-Elder, 1958) and eyes of relatively high minimum f-numbers (Marshall et al., 1973; Martin, 1982; Martin and Young, 1984; Martin, 1986; Martin et al., 2001). Such features are strongly correlated with monofocal optical systems in other terrestrial vertebrates (Malmström and Kröger, 2006).

However, most birds are tetrachromats and see UV-light (Hart, 2001). The use of UV-light broadens the visual spectrum and this alone causes more LCA. More importantly, the relationship between refractive index and wavelength in ocular media is not linear but is close to exponential. As the wavelength of light decreases, focal length decreases at an increasing rate (Hecht, 2002). The differences in focal length that are caused by LCA are therefore particularly large when UV-light is included. This seems to cause chromatic defocus exceeding the depth of focus even in diurnal birds that have eyes of high f-numbers.

The hypothesized role of UV-vision is, except for the chicken, in agreement with our data. Song birds (Passeriformes), parrots (Psittaciformes) and the homing pigeon (*C. livia*) have UV-sensitivity (Bennett and Cuthill, 1994; Bowmaker et al., 1997; Hart, 2001; Hart and Hunt, 2007) and multifocal optical systems. This is probably true also for raptors (Falconiformes) (Ödeen and Håstad, 2003). The ostrich (*Struthio camelus*) has four spectral cone types (Wright and Bowmaker, 2001) and bifocal optics. Another

paleognath, the emu (*Dromaius novaehollandiae*), may be color blind since there is only one cone type described (Sillman et al., 1981) and the species has a monofocal optical system.

Owls have three kinds of cone visual pigment (Bowmaker and Martin, 1978) and color vision (Meyknecht, 1941; Ferens, 1947; Martin, 1974). No visual pigments with maximum absorptions in the violet–UV range have yet been found in owls. The reason for the presence of multifocal optical systems in owls may therefore not be their sensitivity to UV-light but the relatively low minimum f-number of their eyes. As is the case in other nocturnal vertebrates (Malmström and Kröger, 2006), increased chromatic blur because of short depth of focus seems to make multifocal systems advantageous for owls.

Function of the avian pupil

The combination of multifocality with a circular pupil that is typical for many birds is in contrast with results from other terrestrial vertebrates (Malmström and Kröger, 2006). In the current study, we present one possible solution to this problem: the switching pupil model. The mouse pupil – from which our idea has arisen – has a pupillary light reflex of high gain, i.e. the pupil closes and opens within a narrow range of light intensities (Fig. 5B). This minimizes the detrimental effects of intermediate states of pupil constriction in eyes with circular pupils and multifocal optical systems. The pupil dynamics of both parrot species studied show similar tendencies although they do not reach the extreme gain of the mouse pupil.

No such properties could be observed in owls. On the contrary, the Ural owls had surprisingly inactive pupils and the snowy owls had pupil dynamics comparable to those of humans and cats, although with a reduced dynamic range. In fact, the pupillary light reflex of Ural owls is so weak that the pupil does not even close enough to entirely block the outer refractive zone of the optical system (Fig. 5D). Whether this reflects a functional relationship between the maximum amount of pupil closure and the position of the border between the inner and outer refractive zones in Ural owls remains to be investigated.

All bird pupils included in the pupil dynamics study remained remarkably large in bright light. While cats and humans readily constrict their pupils to less than 15% of maximum pupil size, no bird constricted to less than 30% (Fig. 5A–F). Also, birds observed during the optical investigation had pupils that remained large even under bright conditions. However, some of the diving birds, the hooded merganser (*Lophodytes cucullatus*) and the penguins, constricted their pupils to ‘pinholes’ in bright daylight, possibly to pre-adapt to the low light levels encountered as these birds submerge for hunting (Martin, 1999).

Large pupils cause little diffraction (Land and Nilsson, 2002), and this might be valuable since the optical systems of bird eyes are excellent with low levels of refractive error and aberrations (Shlaer, 1972; Murphy and Howland, 1983; Harmening et al., 2007). Pigment migration in the bird retina has been described (Arey, 1915; Walls, 1942), which could explain how the photopigments are protected from bleaching.

Parrots opened their pupils maximally at illumination levels comparable to human mesopic conditions (Fig. 5). The owl pupils reached maximum size only under scotopic illumination levels. This is an expected result because parrots have eyes that are probably less sensitive than owl eyes, such that parrots have to maximize photon flux at higher light levels than owls. Similar correlations have been observed among butterflies (Jonson et al., 1998) but to our knowledge not previously observed among vertebrates.

Non-circular avian pupils

As expected from the literature (Walls, 1942; Duke-Elder, 1958), circular pupils were present in almost all birds studied. There were only two exceptions: the oval pupils of some homing pigeons and the diamond-shaped pupil of the emperor penguin. The functions of these non-circular shapes are unclear, but probably of minor optical importance. The oval pupils of homing pigeons are hardly an important trait since circular pupils were also found in the same species. The pupil of the emperor penguin becomes diamond-shaped only when strongly constricted. Although not observed in this investigation, earlier studies have reported a similar shape for the constricted king penguin pupil (Walls, 1942; Martin, 1999). The king penguin can change the area of its pupil 300-fold, and the non-circular shapes of these penguin pupils might be the consequence of the mechanical arrangement needed to obtain such a flexible pupil.

Conclusions

The majority of the examined birds have multifocal optical systems. The need for such systems might arise from the sensitivity to UV-light or relatively short depth of focus. Most birds have eyes of high minimum f-numbers with multifocal optical systems and circular pupils; a combination of features that has not been observed in other vertebrates. Circular pupils and multifocal optical systems do not function well together at intermediate states of pupil constriction. Our study demonstrates 'switching' pupil dynamics among parrots, which may be an adaptation to ease this conflict.

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