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## Visual fields and their functions in birds

Graham R. Martin

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**Abstract** Among birds there are considerable interspecific differences in all aspects of visual fields. However, it is hypothesised that the topography of the frontal binocular portion of fields are of only three main types, and their principal functions lie in the degree to which vision is used in the guidance of the bill (or feet) towards food objects or for the provisioning of chicks. In the majority of birds, the width of the frontal binocular field is narrow (20°–30° maximum). It shows a high degree of similarity across species and appears to be independent of phylogeny or ecology. Binocularity appears not to be concerned with higher level visual processing involving the combination of information from the two eyes (as in, for example, stereoscopic vision). Binocularity is concerned with gaining independently, in each eye, information which is derived from the symmetrically expanding optic flow-field, which specifies the direction of travel of the head and its time to contact an object, as in pecking or lunging at food items. Species which do not provision their chicks, and whose foraging is guided by tactile cues or which filter feed, have much smaller binocular overlap (10°) and this seems sufficient to control flight. These birds gain comprehensive visual coverage of the celestial hemisphere and show reduced vigilance behaviour. The visual fields of owls, which combine more extensive binocular overlap (50°) with a large blind area behind the head, may not be primarily associated with nocturnal activity. Visual fields of

this type are not found in other nocturnally active birds such as Oilbirds, nightjars and kiwis. The type of visual field found in owls may be a result of large eyes combined with elaborate outer ear structures that are placed within a relatively small skull. Eye movements of significant amplitude do not occur in all birds. However, eye movements of between 14° and 18° occur in species such as herons, hornbills and cormorants and can result in the spontaneous abolition of binocularity. These eye movements are non-conjugate and can produce markedly asymmetric visual fields. The width of any blind area above the head is a function of eye size, with the largest eyes associated with optical adnexa, (eye lashes, brows). These may be associated with avoiding imaging the sun on the retina. However, many small-eyed birds have no optical adnexa and cannot avoid seeing the sun.

**Keywords** Vision · Binocular · Eye movements · Foraging · Nocturnal behaviour

### Introduction

It has long been recognised that among vertebrates eyes are positioned in many different locations in the skull (Walls 1942). “Frontal eyes”, as in humans, describe the situation in which the axes of the eyes’ optical systems are approximately parallel, and in this case we say colloquially that the eyes “look” in the same direction. The result of parallel optic axes is that the two eyes simultaneously gain very similar views of the same objects that lie “in front” of the head. However, in the great majority of vertebrates the axes of the eyes’ optical systems are not parallel and each eye views a quite different part of the space that surrounds the head with various degrees of overlap of view between the two eyes.

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The result of this is that the visual fields of different animals exhibit considerable diversity. There are marked differences in the size and positions of the areas of binocular overlap, and in the extent of the space about the head from which visual information can be received and influence behaviour at any instant. These differences are likely to have important consequences for the way in which visual information can control behaviour in different species.

This paper reviews what is known about the topography of visual fields in birds and discusses ideas about their functions. It is based upon data determined using the same “ophthalmoscopic reflex technique” in a wide range of species, which differ in their phylogeny and ecology. This technique is described in “[Appendix 1](#)”. Details of its application in different species are described in the papers cited. Use of this technique allows visual field topography to be determined in alert birds and thus represents visual field topography as it may function in nature. In addition, because the technique can be applied across a wide range of species, it allows interspecific comparisons to be conducted with some confidence. The aim has been to determine general principles as well as provide insights into the use of vision in particular species. “[Appendix 1](#)” also provides brief definitions of various parts of the visual field which can be determined with the technique. “[Appendix 2](#)” lists species in which visual fields have been determined using the ophthalmoscopic reflex technique and also gives the source references. If a species is mentioned below without citation the specific source will be found in “[Appendix 2](#)”, as will be their scientific names.

## Describing visual fields

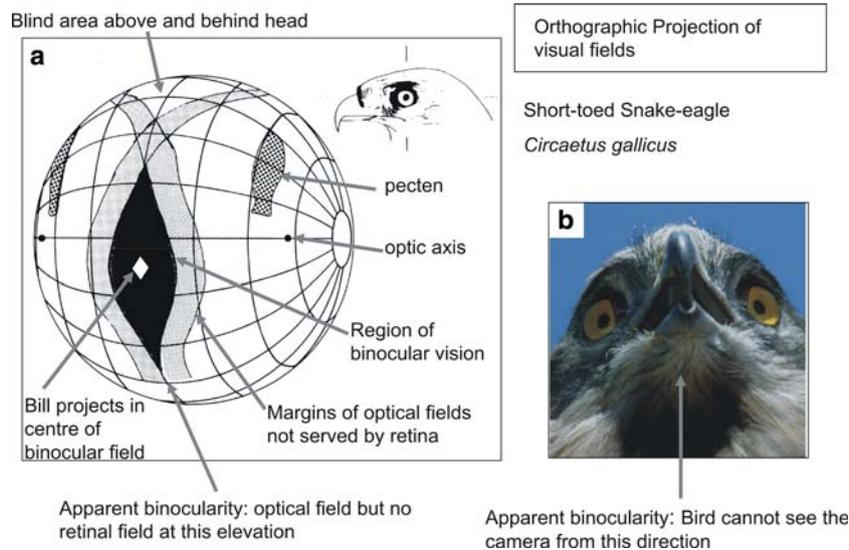
Visual fields describe the three-dimensional space about the head within which a bird can receive visual information at any one instant. Descriptions of the field, therefore, face the same problems as encountered by cartographers who work at a global scale. This problem was solved by the development of a grid system using an angular co-ordinate system based upon the centre of the earth (Snyder 1993). It must also be recognised that any attempt to map the three-dimensional structure of visual fields on a flat (two-dimensional) surface necessarily results in relative distortions (Bugayevskiy 1995). To deal with these problems in describing visual fields an angular co-ordinate system based upon conventional latitude and longitude centred on the head is employed. The equator is aligned in the median sagittal plane of the bird. Strictly, the centre of the coordinate systems is the intersection of the bird’s median sagittal plane with the midpoint of a line joining the centre of each eye’s optical system (the nodal points). In practice, such a point is impossible to determine with accuracy in an

intact animal and so the co-ordinate system is usually based upon the intersection of a line that joins the tips of the corneas (something which can usually be estimated when looking down onto the birds’ head) and its intersection with the sagittal plane as defined by the direction of the bill. The visual field can then be visualised by assuming that it is drawn onto the surface of a sphere that is centred on the bird’s head, and this drawing can be viewed from different directions in much the same way that a globe can be viewed from various directions to build up an understanding of the spatial relationships of the world’s topographical features (see example in Fig. 1). Sections through the visual fields in different planes that pass through the centre of the projection (approximately the centre of the bird’s head) can permit straightforward quantitative comparisons of visual field dimensions: for example, the angular width of the binocular field in the plane of the bill or at the horizontal, the angular width of the blind area above or behind the head, the total angular width of the visual field in a particular plane (the cyclopean field) (see example in Fig. 2).

## Appearances are deceptive

Estimation of visual field parameters, especially the size of the frontal binocular field, based upon casual examination can be seriously erroneous. In particular, the width of frontal field binocularity is likely to be considerably overestimated. This is exemplified in Figs. 1 and 2. The photograph (Fig. 1b) suggests that the bird is looking binocularly at the camera. However, the visual field characteristics determined using the ophthalmoscopic technique (Fig. 1a) shows that at this angle of view although it is possible to see into the eye (and hence the black pupil is visible), there is no retina serving vision. Thus, the eagle eye optical systems produce a binocular field in the horizontal plane that is 40° wide, but functionally the field is only half that width (Fig. 2). Figure 1 shows that there are elevations where there appears to be binocular vision (because it is possible to see into the eye), but in fact the bird is blind because there is no retina to serve vision. This, situation is not unique to this eagle and has been found in other species including Ostrich, herons and owls, and suggests that frontal binocular field width is not maximised within the constraints of the optical system. Many birds seem to forego maximising binocularity and the reasons for this are discussed below in the section on the function of binocularity in birds.

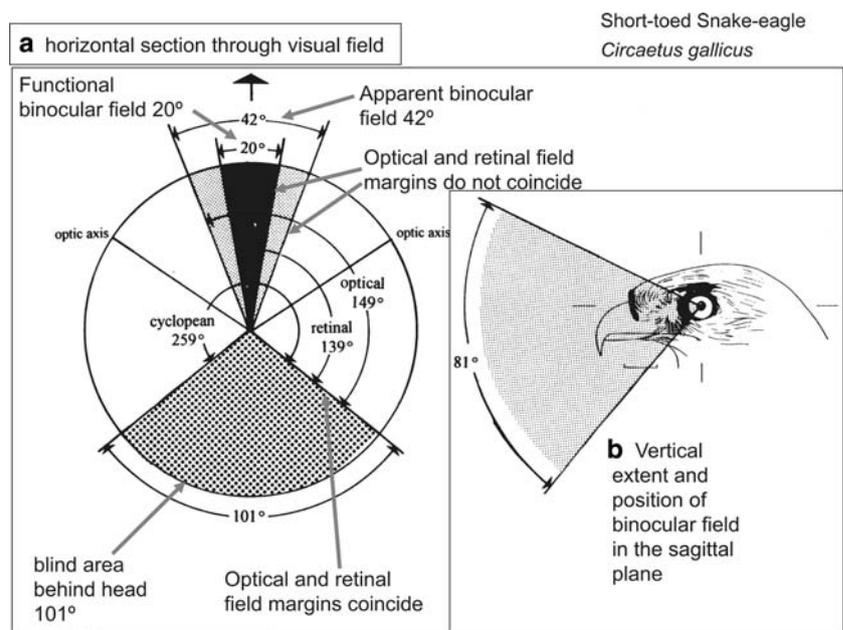
However, it should be noted that to the rear of the head, in all birds examined, the margins of the optical and retinal fields do coincide (for example, Fig. 2) suggesting that visual coverage to the rear of the head is always maximised (within constraints imposed by the width of the optical system of each eye and the degree of frontal binocular overlap).



**Fig. 1** Depiction of visual fields. Example based upon data for Short-toed Snake-eagle. **a** Perspective view of an orthographic project of the visual field showing the binocular sector to the front of the head and the blind area above and behind the margins of the optical fields that are not served by retina. The projections of the optic axes, pectens and of the bill are also shown. It should be imagined that the bird is placed at the centre of a transparent sphere that surrounds the head and the projections of the various features are drawn onto the surface, the orientation of the head is depicted in the *inset drawing*, but the

median sagittal plane of the bird lies in the same plane as the equator of the projection which is vertical and contains the projection of the bill. **b** Photograph of a bird taken at a position in the sagittal plane below the bird that lies outside of the retinal visual field. This gives the impression that the bird has binocular vision at this point since it is possible to see into the eye. However, there is no retina serving vision at this elevation and so the bird could not see the camera

**Fig. 2** Depiction of visual fields. Example based upon data for Short-toed Snake-eagle. **a** Horizontal section through the visual field showing the key features in a single plane. The median sagittal plane of the bird is vertical and perpendicular to the plane of the drawing, the bill points in the direction of the *arrow* at the *top*. Key features of the visual field are indicated. **b** The vertical extent of the visual field in the median sagittal plane (which is in the same plane as the drawing) relative to the bird's head as depicted in the drawing. In this plane, the visual field is always binocular



**Types of visual field in birds**

Interspecific comparison suggests that with respect to the features of the frontal, particularly the binocular field, three main types of visual field topography are found in birds. It is hypothesised that the characteristics of each particular type is determined primarily by feeding ecology, and

secondarily by the requirements of provisioning young, rather than phylogeny or more general aspects of ecology and behaviour (Martin et al. 2005). Of prime importance is the degree to which vision is used for the accurate control of bill position when pecking or lunging at prey, or when feeding chicks, regardless of whether feeding takes place in an aerial or aquatic environment, or is primarily diurnal or

nocturnally active. In species that feed in this way a type 1 visual field is found with characteristics similar to those shown in Fig. 1.

### Type 1 fields

The projection of the bill falls either centrally or just below the centre of the frontal binocular field which is narrow and vertically long. Fields of this type have been found in a wide range of species (“Appendix 2”). In type 1 fields, the maximum width of the binocular field lies between  $20^\circ$  and  $30^\circ$ .

Although the projection of the direction of the bill falls approximately centrally within the binocular field this does not necessarily mean that the bird can see its own bill tip. In species that lung or peck at items (e.g., pigeons, herons, albatrosses, penguins), or take prey in the feet (eagles), the bill tip probably cannot be seen (in a similar way a human cannot see their own nose even though the binocular field encompasses its projection). In species which search for prey between the open mandibles (e.g. European Starling), or manipulate and inspect items held in the bill (e.g. hornbills, skimmers, cormorants), the bill tip, and hence the items held in the bill, can be seen.

In type 1 fields, the vertical extent of the binocular field can vary considerably. For example, it is  $80^\circ$  in the eagle and  $180^\circ$  in herons. In herons, the maximum width of the frontal binocular field is  $20^\circ$  (and, as in the eagle, it is half the width that could be achieved if it were maximised within the constraints of the optical field), but the field extends from directly above to directly below the head when the bill is held horizontal (Fig. 3). It seems likely that this arrangement allows the birds to observe what is at its

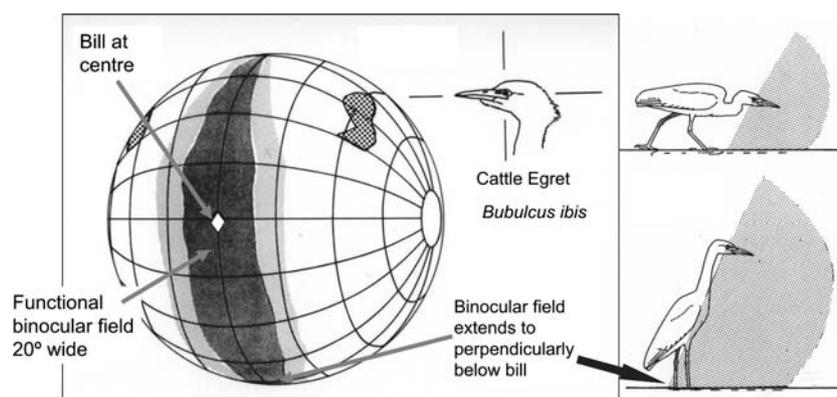
feet while standing with the head horizontal. Thus, the bird can wait motionless while detecting prey beneath it and wait for it to come within striking distance before lunging. This visual field arrangement also gives rise to the often illustrated ability of herons, particularly bitterns (*Botaurus*, *Ixobrychus*) to “look forward” while the bill points skywards. However, this apparently unusual phenomenon among bitterns appears to be a trait common to herons. It is simply seen more readily in bitterns because of their habit of pointing the bill vertically when seeking to conceal their presence.

To the rear of the head all birds with type 1 fields have a blind area. This varies in width from about  $40^\circ$  in herons to  $100^\circ$  in eagles. The presence of this blind area has consequences for vigilance behaviour, and this is discussed below.

Figure 4 shows examples of birds which have type 1 fields that feed using quite different techniques.

### Type 2 fields

These are characterised by a frontal binocular field  $\leq 10^\circ$  wide with the bill falling at the periphery or outside the visual field. There does not appear to be a blind optical margin to the frontal field, i.e. full use is made of the available optical field at both the front and rear of the head. Furthermore, the binocular field extends through approximately  $180^\circ$  in the sagittal plane, approximately from the horizontal in front of the head to the horizontal behind. The consequence of this is that the bird gains panoramic vision above and around the head, i.e. it has complete visual coverage of the celestial hemisphere. There is no blind area



**Fig. 3** Depiction of visual fields. Example based upon data for Cattle Egret. The diagram shows a perspective view of an orthographic project of the visual field showing the binocular sector, which extends from perpendicularly above to perpendicularly below the horizontal plane. The diagrams use a conventional latitude and longitude coordinate system with the equator aligned vertically in the median sagittal plane of the bird (grid at  $20^\circ$  intervals). It should be imagined

that the bird’s head is positioned at the centre of a transparent sphere with the bill tips and field boundaries projected onto the surface of the sphere. The drawings to the right depict postures typical of birds when foraging and the shading indicates the extent of the binocular field in the median sagittal plane. This indicates that the birds can gain extensive visual coverage below the bill allowing binocular viewing of objects at or close to its feet when the bill is held horizontal



**Fig. 4** Examples of bird species whose visual fields are described in the text and in “Appendix 2”. Filter feeding. Flamingos (a) feed with their head upside down and filter microscopic particles from the water surface. This technique would not seem to require accurate bill placement guided by visual cues. However, flamingo visual fields show the characteristics of birds which feed by accurate visually guided pecking in which the bill is placed centrally within the binocular field. It is argued that this visual field configuration is necessary when feeding the chick. This entails accurately dripping “crop-milk” into the juvenile’s open bill (b) and this presumably can only be achieved by guidance from visual cues. Tactile feeding. Skimmers (c–e) are unique in their feeding technique. They forage apparently “blindly” with the lengthened lower mandible trailing in the water as the bird flies a level straight course (d). Birds may feed by both night and day. The bill is snapped shut on a prey item when

triggered by tactile or vestibular cues produced when the mandible strikes prey. Skimmers’ visual fields also show the characteristics of birds which feed by accurate visually guided pecking, but it is argued that this configuration is necessary not for accurate bill placement but for visual inspection of prey items caught during “blind trawling”. Precision-pecking and visually guided manipulation of items. Hornbills (h,i) have massive down-curved bills which are used to locate and excavate for, and manipulate, a wide range of prey and other food items. The birds have type 1 visual fields with binocular vision about the bill and eye movements of relatively large amplitude, which can bring about marked changes in visual field configuration. All hornbills have relatively large eyes and have some of the most elaborate “sun shade” optical adnexa found in birds, including extensive brows and eye lashes (g) (see Fig. 11 and text)

above or to the rear. This has implications for vigilance behaviour and this is discussed below.

Type 2 fields are found in species whose foraging is guided by non-visual cues. These include species that locate prey using tactile cues derived from sensory pits containing Herbst and Grandry corpuscles located around the tips of the maxilla and mandible (Gottschaldt 1985; Nebel et al. 2005; Piersma et al. 1998), as are found in long-billed probing shorebirds, for example Woodcock. The other group of birds in which type 2 fields are found are the filter-feeding ducks (e.g. Mallard, Northern Shoveler, Pink-eared Duck) (Fig. 5) which feed by filtering particles from water surfaces using palatal lamellae. However, not all birds which feed using tactile cues or who filter feed have type 2 visual fields. All of the species in which these field types occur also produce precocial self-feeding chicks. In the filter-feeding flamingos (Fig. 4), chicks are not precocial and their feeding involves the parent dripping liquid directly into the mouth. This requires precision bill placement, which is thought to account for the occurrence of a type 1 field in these birds even though accurate visual guidance of the bill is not required for filter feeding. A similar situation may apply in Antarctic Prions, which filter feed on the wing. These birds have a type 1 field in which the bill is positioned in the lower half of the binocular region and a 50° wide blind area behind the head. In these birds, accurate placement of the bill at the water surface is required. The feeding of skimmers (Fig. 4) is thought to involve tactile cues that trigger bill closure on prey items hit by the lower mandible as it is ploughed through surface waters during flight (Zusi 1996). This tactile feeder also has a type 1, rather than the predicted type 2, visual field and in fact is one of the few species described so far that can see its own bill tip or what lies between the opened mandibles. This arrangement has two possible functions: (1) visual information derived from the binocular field is required for accurate bill placement during foraging (chick feeding does not seem to require accurate bill placement in these birds); and (2), since prey is seized in the bill before it can be visually identified (in most, if not all, other bird species individual items of food are visually inspected before capture), skimmers may also need to visually inspect caught items held in the bill before their ingestion. For example, skimmers are known to often “catch” non-food items when skimming.

### Type 3 fields

These are found in owls (*Strigidae*, *Tytonidae*). In these birds, there is a broad frontal binocular field 50° wide with the bill tip projection just outside the lower periphery of the frontal field. There is an extensive blind area above the head which reaches a maximum width of approximately

160° directly behind. Although the eyes appear to be frontally placed and exhibit superficial similarity to the situation in humans, the eyes in fact diverge by 55° and the binocular field is not maximised within the constraints imposed by the optical system, i.e. as in the case of the eagle illustrated in Fig. 1 the binocular field appears considerably broader than it functionally is. In owls, prey is taken in the feet, which are swung up into the binocular area just prior to prey capture. Prey capture in owls can be mediated exclusively by auditory cues (Payne 1971; Martin 1986b) and accurate auditory localisation is achieved through elaborate external ear structures (Norberg 1968, 1978) that are a unique characteristic of owls. While the visual fields of owls are quite different to those of other species it is not clear with which aspects of their behaviour and ecology they are functionally linked. It has been argued that extensive binocular overlap is associated with the nocturnal habit (Walls 1942; Tansley 1965). However, comparison with other highly nocturnal birds, [Oilbird, nightjars (*Caprimulgidae*), Black-crowned Night Heron, and kiwis, show that more extensive binocularity is not linked simply to nocturnality. The Oilbird, nightjars and Black-crowned Night Heron have type 1 visual fields (Fig. 6), while the kiwis' fields are very small in both binocular and total extent (Fig. 7). Possible links between visual fields and nocturnality are discussed below.

### Visual fields and eye movements

Eye movements can result in significant changes in visual field topography. Most dramatic is the spontaneous abolition of binocularity in some species, and the reduction in the width of the blind area behind the head. This is exemplified in herons and Great Cormorants where in the horizontal plane maximum eye movement amplitude is about 14°–18°. In herons, when the eyes are rotated fully forward binocular overlap is 22° and in Great Cormorants it is 28°, but when the eyes are rotated backwards binocularity is abolished. In herons, there is a blind sector 14° wide (Fig. 8) while in cormorants the visual field margins just meet retaining visual coverage of the frontal field but without binocularity (Figs. 9, 10). However, eye movements do not necessarily result in translational movements in a given plane. For example, in Great Cormorants eye movements involve rotation as well as translation, and this results in the width of the frontal binocular field being significantly altered so that binocularity is abolished (Fig. 9), while the width of the blind area behind the head is only marginally altered (Fig. 10). Furthermore, eye movements in birds are non-conjugate, with the result that while one eye is fully forward the other may be fully back, and between these two extremes a wide range of possible visual field configurations are

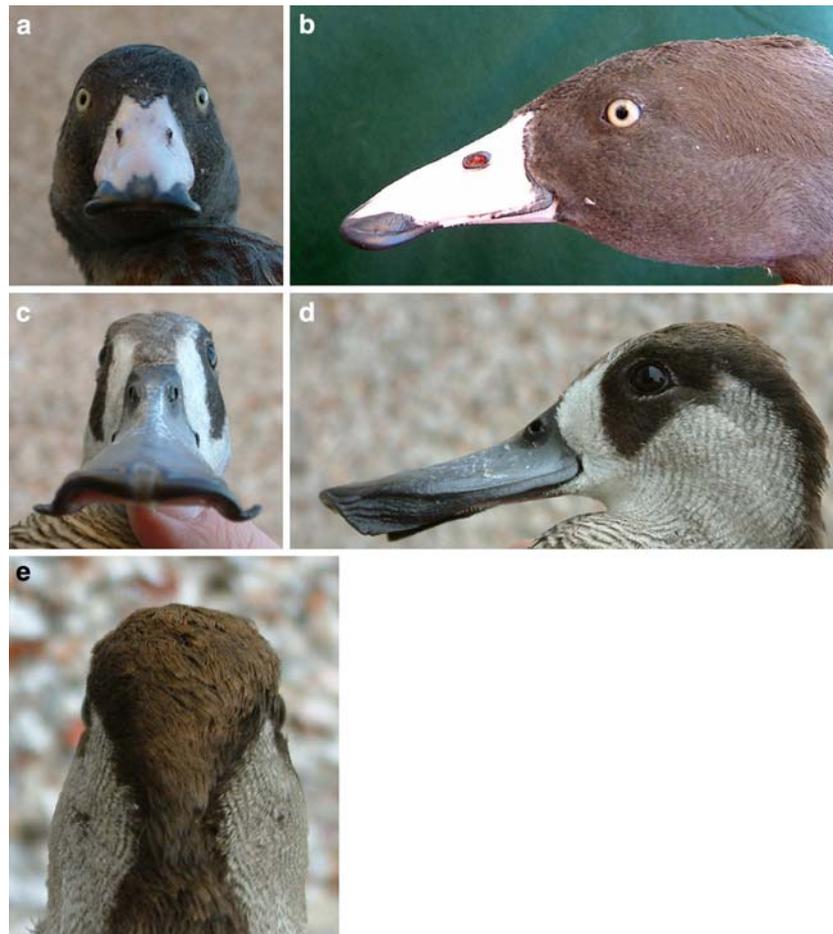
possible; see examples in hornbills (Martin and Coetzee 2004) and cormorants (Martin et al. 2007d). However, translational eye movements that can significantly alter visual field topography do not occur in all birds; in many species eye movements are virtually absent. The functional significance of these visual field changes produced by eye movements is not clear. Increased visual coverage to the rear of the head may be significant in some species, but it is not clear how the loss of binocularity can have a specific

function. It seems more likely that these visual field changes are the result of eye movements that would allow an area of high resolution (probably incorporating a fovea) placed centrally within each eye's visual field, to track or inspect a target using an area of vision in which acuity is highest. Such a function probably underlies the flush-foraging technique of Great Cormorants allowing the birds to detecting an escaping prey item within a wide arc about the head (White et al. 2007; Martin et al. 2007d).



**Fig. 5** Examples of bird species whose visual fields are described in the text and in “Appendix 2. Nocturnally active birds. Although apparently facing similar visual challenges in the nocturnal and crepuscular environment these birds exhibit a wide range of visual field configurations that are probably related to particular foraging techniques. Oilbirds (**a,b**) are arguably the most nocturnal of all birds and rarely, if ever, see daylight since they roost in caves during the day and only emerge to forage at night to feed on fruit in the tropical rain forest canopy. Although their eyes are relatively large and protrude noticeably from the skull, their visual fields show the characteristics of type 1 fields suggesting that accurate bill placement towards items may be guided by visual cues. However, these birds are also thought to employ olfactory cues in determining the general location of ripe fruits. A similar visual field configuration is found in nightjars (**c,d**), which take insect prey on the wing from the open airspace in twilight and at night. Despite being totally nocturnal, kiwis

(**e**) have relatively very small eyes and the smallest binocular and total visual fields yet recorded in a bird (Fig. 7). It is possible that vision in these flightless birds has been subject to regressive evolution and that locomotion and food finding are guided primarily by olfactory and tactile cues gained from the bill tip. In contrast, owls (**f**) have the most frontally placed eyes and the broadest binocular field yet described in birds (type 3 field), and these are thought to be correlated with prey capture using the feet and with the use of auditory cues to locate prey. Owls are unique among birds in having elaborate external ear structures (placed at the edge of the feathers of the facial disc and just behind the eyes) which function to locate sounds accurately, mainly in the region in front of the head. Although owls appear to have forward-facing eyes the optic axes diverge by nearly 50°, also, because the retina does not serve the whole of the available optical field, the degree of binocular overlap appears to be much broader than it functionally is



**Fig. 6** Examples of bird species whose visual fields are described in the text and in “Appendix 2”. Duck species feed using a range of different foraging techniques. In Blue Ducks (a,b), although the eyes are set relatively high in the skull the visual field shows the typical characteristics of a visually guided forager (type 1 field), but these birds also gain near comprehensive vision around the head. Blue Ducks feed on mobile and sessile prey in fast flowing mountain–rivers and are thought to be visually guided towards individual items. On the other hand, Pink-eared Ducks (c,d) filter feed on small items taken from the surface of often highly turbid waters. In these birds, the eyes are set very high on side of the skull and this results in a very narrow

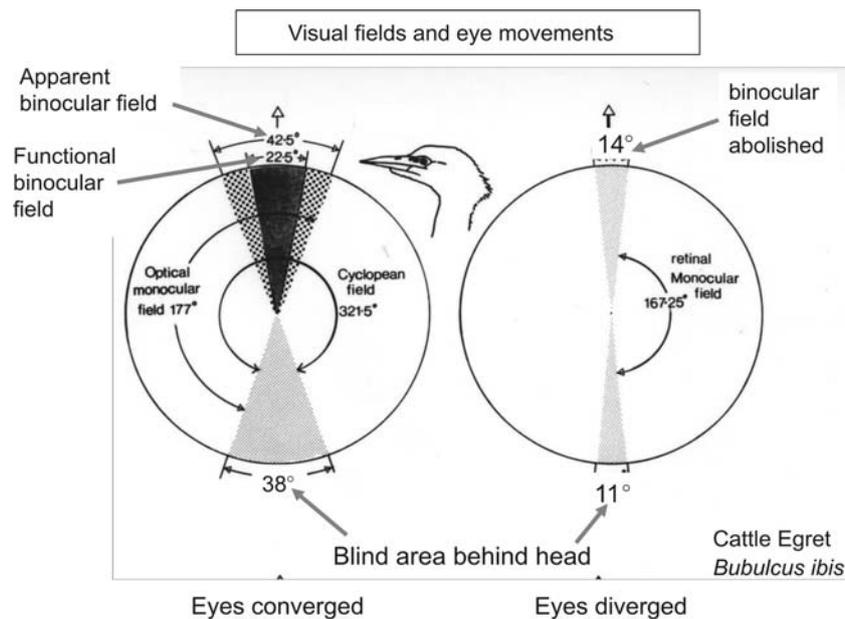
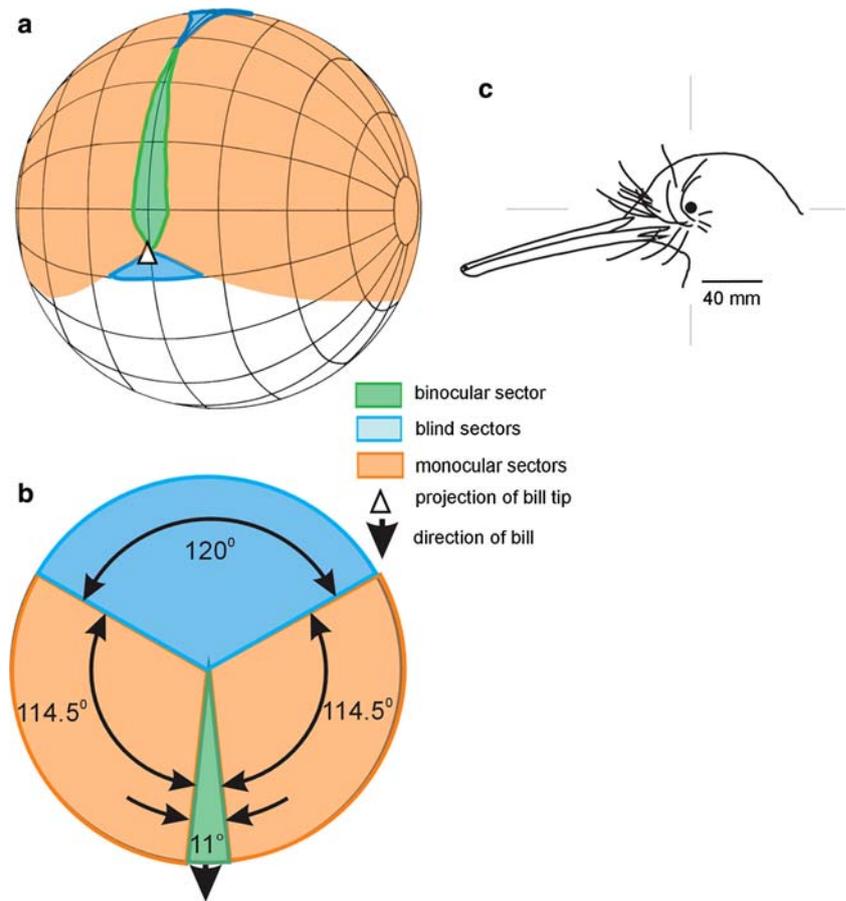
area of binocularity which extends from directly in front of the head to directly behind (e) giving the birds comprehensive visual coverage of the hemisphere about the head. However, the birds cannot see their own bill tip suggesting that bill position does not rely upon accurate visual guidance. It is argued that such comprehensive vision is only possible since these birds can not only feed themselves without reliance upon visual cues to guide the bill, but also the juvenile birds are precocial and self-feeding and do not need provisioning by the parent, unlike the example of the filter-feeding flamingos which need to provision their young

### The function of binocularity in birds

Particular attention has been paid above to the extent and position of binocular overlap and its relationship to the use of vision in foraging. It seems clear that, in species which use vision to guide the taking of food or prey items in the bill or with the feet, a frontal binocular field with a maximum width of 20°–30° occurs irrespective of their phylogeny or specific ecology. This binocular field topography and size looks as though it may be an optimal solution to a common problem. However, narrower binocular fields, with a maximum width of between 5° and 10° in the approximate horizontal plane, are found in some bird species. They occur in species, which have comprehensive

vision of the celestial hemisphere such as Woodcock and Mallard. However, a narrow binocular field (<10° wide) in the direction of travel is also found in Black Skimmers, which do not have comprehensive visual coverage of the celestial hemisphere. In these birds, the eyes are more frontally placed to provide vision between the mandibles for the identification of items caught during “blind trawling”. However, all of these birds despite their narrow binocular fields are capable of fast flight and of manoeuvring within both open and woodland habitats. This shows that such narrow binocular fields are sufficient to control locomotion. Thus, binocular fields that are 20°–30° in width would appear to have a function beyond the control of locomotion.

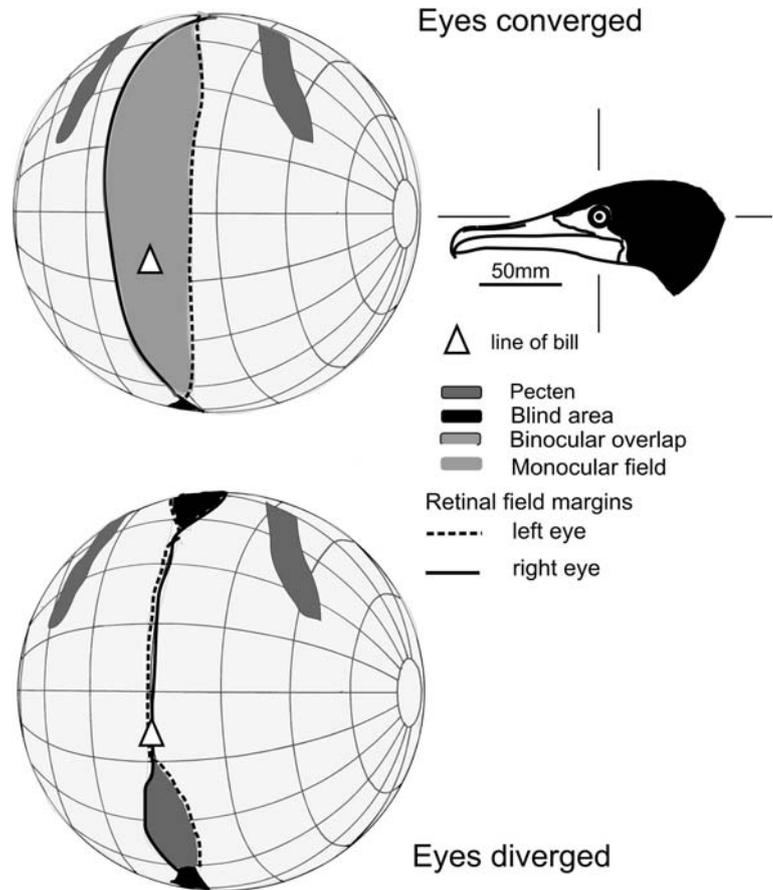
**Fig. 7** Visual fields of kiwis.  
**a** Perspective view of an orthographic projection of the frontal field. The head is in the same posture as depicted in (c).  
**b** Horizontal section through the visual field in the plane of maximum binocular field width which is the horizontal plane in (a) and (c).  
**c** Drawing of a side view of a kiwi head, the bill tip projects 20° below the horizontal as shown in (a)



**Fig. 8** Visual fields and eye movements. Example based upon data for Cattle Egrets. Each diagram depicts a section through the visual fields in the horizontal plane. In this plane, the margins of the field of each eye can move by up to 18° as a result of eye rotation. When the two eyes are fully rotated to the front of the bird’s head (i.e. to the top of the diagram) there is a binocular overlap of 22° (left diagram), but when the eyes are rotated backwards the binocular field is abolished

and there is a blind sector 14° wide (right diagram). The eyes can move independently of each other and, therefore, a wide variety of visual field configurations are possible. For example, if one eye is fully forward and the other rotated fully back then 4° of binocular overlap remains, but this is not symmetrically displaced about the median sagittal plane

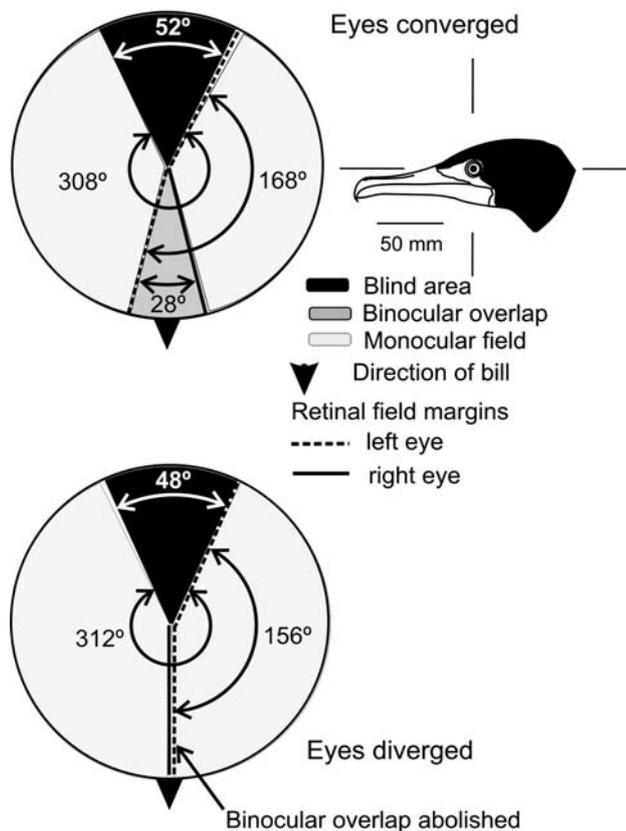
**Fig. 9** Visual fields and eye movements. Perspective views of an orthographic projection of the boundaries of the retinal fields in Great Cormorants when the eyes are fully converged and when fully diverged. The adjacent drawing shows the head in the same orientation as when the measurements were made. Note how eye movements can abolish binocularity in the frontal field



General functional explanations of binocular vision in vertebrates (Hughes 1977) have been influenced by the assumption that *binocular vision* (two eyes viewing the same position in space) results in *stereopsis* (the perception of relative depth achieved through detection of the disparities between the images of the same objects produced in each eye). However, while binocular vision is essential for stereopsis, the assumption that binocularity inevitably results in stereopsis has been questioned in birds (McFadden 1993, 1994; Davies and Green 1994). Davies and Green (1994) have pointed out that stereopsis involves considerable neural processing and is too slow to control the estimation of distance and depth when a bird is landing upon a perch. Pigeons have depth perception, and are sensitive to disparities of about 1 arc min (compared to 4 s in humans), but it is doubtful that this ability is used in foraging (McFadden 1993). Motion-parallax is probably an important source of depth information for birds (Kral 2003). Although there is evidence that owls have stereopsis (Nieder and Wagner 2000, 2001; Willigen et al. 2003), this is unlikely to provide a general function for binocularity in birds. Instead, it is likely that the general function of binocularity is concerned with optic flow-fields (Martin and Katzir 1999).

### Binocularity and optic flow-fields

Binocularity is the result of having part of each eye's monocular field extending across the sagittal plane. This ensures that a section of each eye's visual field looks in the direction of travel and means that each monocular field encompasses a pole in the linear optic flow-field that is generated during forward motion (Gibson 1986). Such flow-fields about a pole are symmetrical and are thought to be important for the control of locomotion in birds, mammals and insects (Gibson 1986). This is because a symmetrical optic flow about a pole gives robust information about the point where the animal is heading, and the time to contact that point (Lee 1980, 1994; Davies and Green 1994). Birds need to determine both heading and time to contact rapidly and accurately since they often move at speed towards objects, e.g. a bird's head may rapidly approach an object or a surface when pecking or lunging. Flow-field variables have been shown to control landing responses in some bird species (Davies and Green 1994), wing closure in plunging gannets (Lee and Reddish 1981), and accurate docking of the bill at a food source in hovering hummingbirds (Lee et al. 1991). Neurons that respond selectively to various types of flow-fields, including symmetrically expanding



**Fig. 10** Visual fields and eye movements. Horizontal sections through the visual fields of Great Cormorants in a horizontal plane when the eyes are fully converged and when fully diverged. This horizontal plane with respect to the bird's head is indicated by the *horizontal line* in the drawing of the bird's head. Note how eye movements can abolish binocularity in the frontal field but, because of the complex rotational movements of the eyes, the width of the blind area to the rear of the head is little altered by eye movements

images, which are produced around a flow-field pole, are found in the nucleus rotundus of pigeon forebrains (Frost et al. 1994).

In normal forward motion of the head, the visual field of an eye must extend contralaterally in order to contain a pole in the optic flow-field, which encompasses the object or surface towards which the animal's head is moving. For movement towards a relatively distant target, the disparity of viewpoint of two eyes with overlapping contralateral fields will be negligible. This will result in the two eyes receiving identical optical flow-field information and this may of itself enhance accuracy through redundancy (as, for example, in humans where two eyes are superior to one eye even when binocular viewing is devoid of stereoscopic cues (Jones and Lee 1981). Furthermore, it has been argued that, for close objects, movement with respect to a target (as in pecking or bill striking) is accurately specified by the fact that the optic image of the target can be symmetrically positioned with respect to the pole of each flow-field (Lee et al. 1991).

Thus, it has been proposed (Martin and Katzir 1999) that the essential function of binocularity in birds may lie in the provision in each eye of an optic flow-field, which expands symmetrically about a target point in front of the head. Two eyes with identical or similar flow-fields may increase, through redundancy, the accuracy of information with respect to that target, but they are unlikely to provide higher order information, which can be extracted exclusively from two eyes imaging the same portion of a scene.

Why does the maximum width of the binocular field in a range of bird species equal only 20°–30°? It can be suggested that this width represents an optimal trade-off that provides sufficient optic flow-field information to ensure accurately controlled rapid approaches towards objects during foraging, while at the same time maximising the width of the peripheral, and hence cyclopean, visual field within constraints imposed by each eye's optical design. The reason why this optimal functional width should be between 20° and 30° is still not resolved, but it is worth noting that in many species (exemplified by eagles, Fig. 1, and herons, Fig. 3) the binocular field could be twice the width found if full use was made of the available optical field. It is, therefore, pertinent to consider why full use is not made of the available optical field in frontal vision to give a wider binocular field.

In any lateral eyed animal, frontal vision is in fact peripheral vision with respect to the optical systems of each eye. In all optical systems, the optical quality of the periphery tends to be of poorer (e.g. increased spherical and chromatic aberrations) than central vision. There is no information on optical quality in the periphery of any bird eyes, but it can be hypothesised that to serve frontal (binocular) vision optical quality must be relatively high. Employing the very periphery of the optical system to look forward may not allow the extraction of sufficient information from the optical flow-field to guide behaviour. Thus, for frontal vision, a portion of each eye's visual field away from the very periphery of their optical systems must be employed. No advantage is gained by having contralateral vision to the very periphery of each eye since the section of space that would be viewed contralaterally, but with poor quality optics, is already covered by more central portions of the optical system of the ipsilateral eye, which will have higher image quality.

### Binocular vision and the nocturnal habit

The visual fields of owls pose an interesting problem. The wide binocular field described above as type 3 has so far been found only in owls (Strigiformes). Such broad binocular fields have long been associated with the nocturnal activity and/or the predatory habit of these birds (Walls

1942; Tansley 1965). However, similar frontal visual fields are not found in other predatory birds (such as the Short-toed Snake-eagle) which like owls take prey in the feet, but during daylight, or in both flying and flightless birds which are highly nocturnal in their activity (kiwis, Oilbird, nightjars, Black-crowned Night Heron). Two factors may account for the particular visual field characteristics of owls: eye size and the use of hearing in the location and capture of prey.

To maximise information gain at lowlight levels, vertebrate eyes must achieve an image of high relative brightness (the pupil must be large compared with the focal length of the optical system, resulting in a low  $f$ -number; Martin 1985) and have an absolutely large entrance aperture to maximise the capture of light photons from the scene (Land and Nilsson 2002). The result of these two requirements is that the eye must be absolutely large. However, eyes are in effect heavy fluid-filled chambers, which are placed at the periphery of the avian body plan. In the evolution of birds, there has been strong selection for adaptations that reduce total body weight and concentrate its distribution towards the body centre (King and King 1980). Owl eyes are absolutely large in terms of axial length (cf. eye axial length in Tawny Owl = 28.5 mm and in human = 24.0 mm) but tubular in shape (which may be considered a weight reducing adaptation (Martin 1982). However, if eyes of this size were placed so as to point more laterally the total width of the skull would have to be greatly increased (in fact, owl eyes protrude considerably from the skull compared to those of all other birds examined to date). Therefore, eye position may, at least in part, be a matter of the geometry of squeezing a very large eye into a small skull, and this has resulted in the more forward placement of the optic axes and the larger binocular overlap.

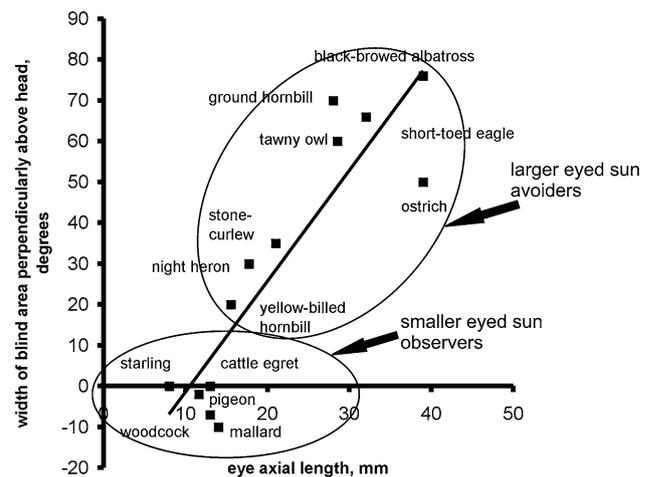
An additional factor may be associated with the elaborate external ear structures of owls which function in the accurate location of sounds (Norberg 1968; Payne 1971; Konishi 1973). Owls are unique in the possession of these elaborate external ear structures and these may of themselves have resulted in the placement of the eyes more forward in the skull. Furthermore, these large external structures prohibit vision to the rear of the head. It can be suggested that the evolution of these ear elaborations has resulted in both the more forward placement of the eyes in the skull, resulting in both the larger frontal binocular overlap, and the larger blind area to the rear of the head, which is also a characteristic of these birds' visual fields.

### Blind area above the head and eye size: sunshades in birds

The discussion above has concentrated upon visual field characteristics to the front of the head, and the case has

been made that there is some degree of convergence upon frontal binocular field characteristics. In these same species, there is, however, considerable variation in the topography of the total visual field, especially in the extent of the cyclopean field in the horizontal plane and in the width of the blind area above the head.

It has been shown that the width of the blind area above the head is a function of eye size (Fig. 11), and the explanation advanced for this is that as eye size increases viewing the sun becomes increasingly a problem for gaining visual information from within the whole of the visual field. In effect, the image of the sun can act as a secondary source of light within the eye, which scatters light around inside the chamber and produces the phenomenon that is described in humans as "disability glare" (Ho and Bilton 1986; Dickinson 1991) which can prevent target detection, particularly when the original object is of low contrast (Le Claire et al. 1982). In support of this hypothesis is the observation that only in larger eyed birds are found external structures (eye lashes and enlarged brows, such as those seen in the eagle depicted in Fig. 1) that can shade the eye. The reason why glare is especially problematic for large eyes is not obvious, but it may be that the effects are felt disproportionately in retinae adapted for high resolution. In smaller eyes which have not evolved to achieve the highest resolution, light scattered from an image of the sun upon the retina may not degrade image contrast sufficiently that the benefits of



**Fig. 11** Eye size and sunshades. The width of the blind area perpendicular to the head as a function of eye axial length in 13 species of terrestrial birds. Positive values indicate the width of a blind area, negative values indicate the width of a binocular field. All measurements employed the same ophthalmoscopic reflex technique and show values when the head is held in its typical posture for the species. The *line* is the linear regression. The Spearman correlation between the two variables is significant ( $r = 0.85$ ,  $P < 0.005$ ,  $n = 13$ ). Species are grouped as *larger eyed sun avoiders* that have a blind area above the head and possess optic adnexa (eye lashes, eye brows) capable of shading the eye, and *smaller eyed sun observers* which have vision above the head and do not have optic adnexa

gaining comprehensive visual coverage are outweighed by a reduction in the ability to gain spatial information across the whole of that visual field.

### Concluding remarks

The primary determinants of visual fields in birds

It is hypothesised above that the frontal visual fields in birds are of only three main types and that these are determined by the extent to which vision is used in the guidance of the bill (pecking or lunging movements) or feet towards objects when foraging, or when provisioning chicks. This has resulted in convergence in the width of the frontal binocular field that is independent of phylogeny and ecology (nocturnal–diurnal, aquatic–terrestrial–aerial). The width of the binocular field in these species is relatively narrow ( $20^{\circ}$ – $30^{\circ}$ ) and possibly represents an optimal width for the extraction of optic flow-field information that specifies directly the direction of travel and time to contact a target with the bill or feet. Although the projection of the direction of the bill falls close to the centre of the frontal binocular field in these species, only in some species can the birds see their own bill tip or see what is held between the mandibles, and this ability is associated with particular foraging techniques involving the inspection of items held within, or positioned between, the open mandibles. In all species, which use vision to guide their foraging in this way there is a blind area above and to the rear of the head. The width of this area is a function of eye size and may result from the avoidance of disability glare, which would be caused by imaging the sun upon the retina.

In species which do not use vision to guide bill or feet position in foraging, but rely upon tactile cues from the bill tip to locate items, or filter feed from surface waters, and do not provision their young, a quite different type of visual field topography is found. In these birds, complete visual coverage of the celestial hemisphere around and above the head is achieved. Maximum binocular field width is only about  $10^{\circ}$ , and the binocular field may be only  $5^{\circ}$  wide at the horizontal, the direction of travel when flying. This suggests that the control of flight in both open and complex woodland habitats does not require extensive frontal binocularity.

In owls, which are nocturnal and can use audition alone to guide prey capture, the eyes are more frontally placed with wide binocular overlap (approx.  $50^{\circ}$ ) and an extensive blind area both above and to the rear of the head. It is hypothesised that this visual field topography results from the combination of large eyes (to maximise information retrieval at low light levels) placed within a relatively small skull, and elaborate external ear structures. Both of these factors have resulted in the eyes being more forward placed

in the skull. The outer ear elaborations prohibit vision above and to the rear of the head. It is hypothesised that nocturnal activity per se is not correlated with this particular visual field topography since it is not found in other highly nocturnal species or in species, which forage at nocturnal light levels, such as the deep diving penguins.

### Appendix 1

The ophthalmoscopic technique for determining retinal visual fields

This technique has been used in a range of birds of different phylogeny, ecology and feeding techniques and readily permits interspecific comparisons (Martin and Coetzee 2004; Martin et al. 2005, 2004b; Martin and Prince 2001). For a detailed description of the apparatus and methods see Martin and Katzir (1994a). Briefly, each bird is held in a foam rubber cradle with its head held in position at the centre of a visual perimeter by a holder specially manufactured to hold the bill of each species. The perimeter's co-ordinate system follows conventional latitude and longitude with the equator aligned vertically in the birds' median sagittal plane and this co-ordinate system is used for the presentation of visual field data (Fig. 2). The bill is closed and the head positioned so that the tip of the lower mandible projects in the approximate direction adopted spontaneously by the bird when at rest. Head position is also recorded in photographs of birds held in the hand in the open or when at rest in the field. The results are corrected to this spontaneously adopted head position.

The eyes are examined using an ophthalmoscope mounted on the perimeter arm. For each eye, the visual projections of the following are usually determined as a function of elevation in the median sagittal plane at  $10^{\circ}$  intervals: (1) the limits of the retinal visual field, and (2) the edges of the pecten. From these data (corrected for viewing from an hypothetical viewing point placed at infinity) a topographical map of the visual field and its principal features is constructed. These features are: (1) the monocular fields, the visual field of a single eye; (2) the binocular field, the area where monocular fields overlap; (3) the cyclopean field, the total visual field produced by the combination of both monocular fields; and (4) projection of the pectens. Each pecten creates a blind area within each eye's visual field. The pecten is a highly vascular and pigmented structure that overlies the exit of the optic nerve and functions as a nutrient organ within the anterior chamber of the eye. Its projection provides a landmark in the field of each eye. Depending upon the species and the time available to hold the birds constrained in this way, it is possible to measure limits of almost the entire frontal

visual field from directly below the head through approximately 270° in the sagittal plane to the horizontal behind the head. Determining the positions of the visual field margins both directly in front and behind the head, i.e. in an approximately horizontal plane, allows determination of monocular field widths and the extent of the cyclopean field in this plane. In some birds, spontaneous eye movements are readily observed and their amplitude as a function of elevation are determined by making light tapping sounds or flashing a small light source in the periphery of the visual field, and then determining the maximum and

minimum limits of the retinal margin at each elevation. These procedures are non-invasive and follow guidelines established by the United Kingdom, Animals (Scientific Procedures) Act, 1986.

## Appendix 2

Bird species in which visual fields have been determined using the ophthalmoscopic reflex method (14 Orders; 20 families; 32 spp.)

- Struthioniformes
  - Struthionidae
    - Ostrich *Struthio camelus* (type 1) (Martin and Katzir 1995)
  - Apterygidae
    - Brown Kiwi *Apteryx mantelli* (Martin et al. 2007)
    - Great Spotted Kiwi *Apteryx haastii* (Martin et al. 2007)
- Sphenisciformes
  - Spheniscidae
    - Humboldt penguin *Spheniscus humboldti* (type 1) (Martin and Young 1984)
    - King Penguin *Aptenodytes patagonicus* (type 1) (Martin 1999)
- Procellariiformes
  - Diomedidae
    - Black-browed albatross *Diomedea melanophris* (type 1) (Martin 1998)
    - Grey headed albatross *Diomedea chrysostoma* (type 1) (Martin 1998)
  - Procellariidae
    - Manx shearwater *Puffinus puffinus* (type 1) (Martin and Brooke 1991)
    - White-chinned petrel *Procellaria aequinoctialis* (type 1) (Martin and Prince 2001)
  - 2001)
    - Antarctic prion *Pachyptila desolata* (Martin and Prince 2001)
- Pelecaniformes
  - Phalacrocoracidae
    - Great Cormorant *Phalacrocorax carbo* (type 1) (Martin et al. in review)
- Ciconiiformes
  - Ardeidae
    - Cattle egret *Bubulcus ibis* (Martin and Katzir 1994a)
    - Reef heron *Egretta gularis* (Martin and Katzir 1994a)
    - Squacco heron *Ardeola ralloides* (Martin and Katzir 1994a)
    - Black-crowned night heron *Nycticorax nycticorax* (Katzir and Martin 1998)
- Phoenicopteriformes
  - Phoenicopteridae
    - Lesser Flamingo *Phoeniconaias minor* (Martin et al. 2005)
- Anseriformes
  - Anatidae
    - Mallard *Anas platyrhynchos* (Type 2) (Martin 1986c)
    - Northern Shoveler *Anas clypeata* (Type 2) (Guillemain et al. 2002)
    - Wigeon *Anas penelope* (Type 1) (Guillemain et al. 2002)
    - Blue Duck *Hymenolaimus malacorhynchos* (Type 1) (Martin et al. 2007)
    - Pink-eared Duck *Malacorhynchus membranaceus* (Type 2) (Martin et al. 2007)
- Falconiformes
  - Accipitridae
    - Short-toed snake eagle *Circaetus gallicus* (Type 1) (Martin and Katzir 1999)
- Charadriiformes
  - Burhinidae
    - Stone-curlew *Burhinus oedipnemus* (Type 1) (Martin and Katzir 1994b)
  - Scolopacidae
    - Woodcock *Scolopax rusticola* (Type 2) (Martin 1994)
  - Laridae
    - Black Skimmer (Type 1) *Rynchops niger* (Martin et al. 2007)
- Columbiformes
  - Columbidae
    - Pigeon *Columba livia* (Type 1) (Martin and Young 1983)

- Strigiformes  
Strigidae  
Tawny owl *Strix aluco* (Type 3) (Martin 1984)
- Caprimulgiformes  
Steatornithidae  
Oilbird *Steatornis caripensis* (Type 1) (Martin et al. 2004b)  
Caprimulgidae  
Paraque *Nyctidromus albicollis* (Type 1) (Martin et al. 2004a)
- Coraciiformes  
Bucerotidae  
Southern Ground Hornbill *Bucorvus leadbeateri* (Type 1) (Martin and Coetzee 2004)  
Southern Yellow-billed Hornbill *Tockus leucomelas* (Type 1) (Martin and Coetzee 2004)
- Passeriformes  
Sturnidae  
European Starling *Sturnus vulgaris* (Type 1) (Martin 1986a)

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