Visual fields in hornbills: precision-grasping and sunshades

GRAHAM R. MARTIN[1]* & HENDRI C. COETZEE[2]
[1]*School of Biosciences, The University of Birmingham, Edgbaston, Birmingham B15 2TT, UK*
[2]*Ground Hornbill Research and Conservation Project, Private Bag X1644, Warmbaths, 0480, Republic of South Africa*

Retinal visual fields were determined in Southern Ground Hornbills *Bucorvus leadbeateri* and Southern Yellow-billed Hornbills *Tockus leucomelas* (Coraciiformes, Bucerotidae) using an ophthalmoscopic reflex technique. In both species the binocular field is relatively long and narrow with a maximum width of 30° occurring 40° above the bill. The bill tip projects into the lower half of the binocular field. This frontal visual field topography exhibits a number of key features that are also found in other terrestrial birds. This supports the hypothesis that avian visual fields are of three principal types that are correlated with the degree to which vision is employed when taking food items, rather than with phylogeny. However, unlike other species studied to date, in both hornbill species the bill intrudes into the binocular field. This intrusion of the bill restricts the width of the binocular field but allows the birds to view their own bill tips. It is suggested that this is associated with the precision-grasping feeding technique of hornbills. This involves forceps-like grasping and manipulation of items in the tips of the large decurved bill. The two hornbill species differ in the extent of the blind area perpendicularly above the head. Interspecific comparison shows that eye size and the width of the blind area above the head are significantly correlated. The limit of the upper visual field in hornbills is viewed through the long lash-like feathers of the upper lids and these appear to be used as a sunshade mechanism. In Ground Hornbills eye movements are non-conjugate and have sufficient amplitude (30–40°) to abolish the frontal binocular field and to produce markedly asymmetric visual field configurations.

Vision is widely regarded as the primary sense employed in the control of many aspects of avian behaviour, including feeding and flight (Zeigler & Bischof 1993, Davies & Green 1994b). However, vision is a multifaceted sense and it is not clear which capacities are most closely correlated with the control of particular behaviours. Interspecific comparisons of the topography of avian visual fields have indicated that the extent and position of the frontal binocular field is related to the degree to which vision is employed to control the position of the bill or feet when they are used to take food items (Martin & Katzir 1999).

Based upon these comparisons, it has been hypothesized that avian frontal visual field topography falls into three principal types that are the result of ecological convergence rather than common ancestry

(Martin & Katzir 1999). It is suggested that this convergence results from an interaction between the function of the frontal field as a source of optic flow-field information for the guidance of locomotion and feeding behaviour, and the function of lateral and posterior portions of the visual field for the detection of predators or conspecifics (Martin & Katzir 1999).

In Type 1 visual fields (see Appendix 1 for lists of species that exhibit the different field types) there appears to be convergence upon a maximum frontal binocular field width of 20–30° at or above the elevation of the bill, with the bill placed either centrally or in the lower half of the binocular field. Species with this type of field topography typically have straight bills that are used to take food items in pecking or lunging movements. However, diurnal raptorial species that take prey in their feet also appear to have the same field topography, with the feet swung into the binocular area just before prey capture.

*Corresponding author.
E-mail: G.R.Martin@bham.ac.uk

Type 2 visual fields have a narrower frontal binocular field (typically ≤ 10°) with the bill falling at the periphery or outside the binocular field. This type of visual field is coupled with comprehensive, or near comprehensive, visual coverage of the hemisphere above the head. Such species do not appear to rely on vision for the detection and procurement of food items but employ tactile cues and/or filter feeding techniques.

A Type 3 visual field consists of a broader frontal binocular field (≈ 50°), coupled with extensive blind areas above and to the rear of the head. This visual field topography has been described in Tawny Owls *Strix aluco* (Martin 1984) and appears to be related to the acoustic location of prey mainly under nocturnal conditions. As in other raptors, prey is taken in the feet, which are swung up into the broad area of binocular vision (which coincides with the area of most acute auditory localization) just prior to prey capture (Martin 1986b).

These interspecific comparisons are not, however, comprehensive with respect to the ways in which food items are procured by birds. Investigations to date have included only either species in which food items are taken without direct visual control of the bill, or species in which vision is employed to control the taking of prey directly with the bill through pecking or lunging at individual items, or with the feet. There are other avian foraging techniques that appear to employ vision and that could be associated with other visual field topographies. Hence data on species that employ other techniques, such as the precision-grasping of hornbills, provide a test of the generality of the three principal types of avian visual field topographies.

Species, principally among the Coraciiformes (Upupidae [hoopoes], Phoeniculidae [woodhoopoes], Bucerotidae [hornbills] and Ramphastidae [toucans]; Sibley & Monroe 1990, Sibley & Ahlquist 1991), have decurved bills that are not used in typical pecking movements. When feeding, hornbills employ 'precision-grasping'. In this the bill is used as a pair of forceps, grasping an item between the tips and then tossing it back into the throat or further back into the mouth where it is transported into the throat by the relatively short tongue (Burton 1984). Items are often manipulated in the bill tips and in some species the bill may also be used to excavate soil or wood (Kemp 1995). The bills of hornbills are typically large and appear to intrude into the frontal visual field, and there is often a casque. This is a large structure formed from the horny layer of keratin on

Figure 1. Lateral views of the heads of Southern Yellow-billed Hornbill and Southern Ground Hornbill.

the upper mandible. Its function is uncertain but it appears to limit the visual field in the upper frontal quadrant (Kemp 1995).

The 54 species of hornbills exploit both savanna and forest habitats in the Old World (Kemp 1995, Kemp 2001). We describe here visual field topography in two sympatric savanna species from southern Africa: Southern Ground Hornbills *Bucorvus leadbeateri* Bucorvinae, and Southern Yellow-billed Hornbills *Tockus leucomelas* Bucerotinae (Fig. 1). Although these birds differ in size by more than ten-fold (weight of Ground Hornbills 2230–4580 g; Yellow-billed Hornbills 138–242 g) their feeding ecology is similar and there is overlap in their diet. In both species, 'most food is simply picked from the ground or low vegetation' (Kemp 1995, pp. 97, 138). Both species feed on a wide variety of small animals with Ground Hornbills taking items of a larger size range. The bulk of the Yellow-billed Hornbill diet is 'termites, beetles and their larvae, grasshoppers and caterpillars' (Kemp 1995, p. 138). A Ground Hornbill 'eats any animals it can overpower, up to the size of hares, squirrels,

large tortoises and snakes'; however, the diet also contains, 'arthropods, especially termites, beetles and grasshoppers, toads, snails, lizards, snakes … chameleons, scorpions and earthworms' (Kemp 1995, p. 97).

In both Ground Hornbills and Yellow-billed Hornbills males (m) tend to be larger than females (f) in most morphological parameters, but there is considerable overlap between the sexes. Bill size in Ground Hornbills shows considerable overlap, with average length of m: 207 mm, f: 192 mm. However, in Yellow-billed Hornbills there is no overlap in bill size between the sexes with average lengths of m: 90 mm, f: 74 mm, and bill length is considered a reliable characteristic for sex determination in the field. Throughout this paper it is assumed that there are no intraspecific sex differences in visual field topography and that data presented here are representative of the species.

METHODS

Subjects

Measurements were conducted of two Southern Ground Hornbills (approximate weight 4000 g) and two Southern Yellow-billed Hornbills (approximate weight 200 g). Birds were obtained from the Mabula Game Reserve, Northern Province, Republic of South Africa (8500 ha of sourish mixed bushveld, centred at approximately 24°46′S, 27°54′E: Acocks 1988, Low & Rebelo 1998, Muller 1998). All measurements were conducted at the premises of the Ground Hornbill Research and Conservation Project situated on the reserve. The Ground Hornbills were females, 2 years old, free-living, semi-tame and part of a group re-established on the reserve. The Yellow-billed Hornbills were wild-caught males of unknown age. After measurement, all birds were released at the places where they were caught. The procedures used were performed under guidelines established by the *United Kingdom, Animals (Scientific Procedures) Act, 1986*.

Measurements

Measurements of retinal visual fields and eye movement amplitude were made in alert birds using an ophthalmoscopic reflex technique and employed procedures similar to those used previously with the species listed in Appendix 1. For a description of the apparatus and methods see Appendix 2.

Calculation of the approximate axial length of the eyes was based on the separation of the corneal vertices,

the estimated divergence of the optic axes (based on scaled photographs taken perpendicularly above the head) and the assumption that the eyes meet in the median sagittal plane of the skull (Martin 1985).

RESULTS

The maximum binocular field

The results for the two birds of each species were similar and are presented as means.

In Ground Hornbills and Yellow-billed Hornbills eye axial lengths were ≈ 28 mm and ≈ 15 mm, respectively. Maximum binocular field width in both species is similar (30° in Yellow-billed Hornbills, 26° in Ground Hornbills) and occurs in the region 20–40° above the bill (Fig. 2). However, the vertical
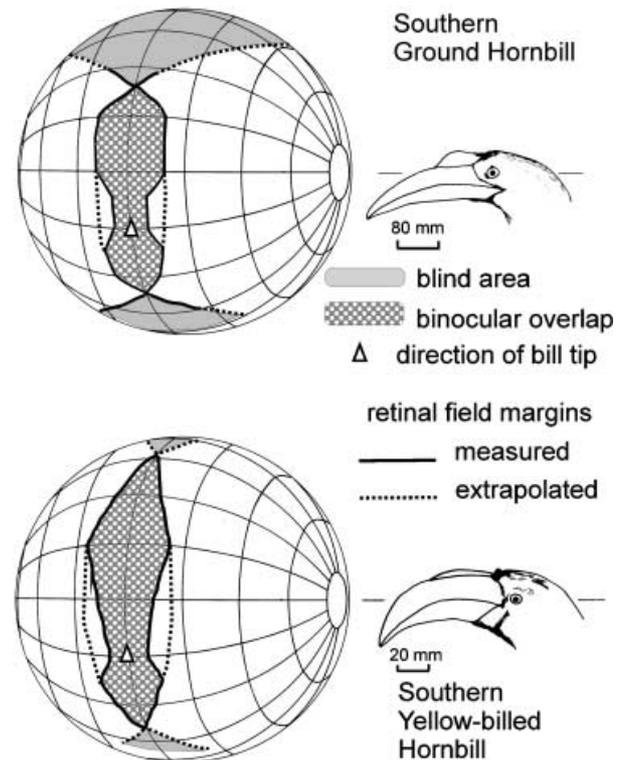
Figure 2. Visual fields of Southern Ground Hornbills and Southern Yellow-billed Hornbills when the eyes are fully converged (maximum binocular overlap). Each diagram shows a perspective view of an orthographic projection of the boundaries of the retinal fields of the two eyes. It should be imagined that the bird's head is positioned at the centre of a transparent sphere with the bill tip projecting towards the point shown and the field projected onto the surface of the sphere (grid at 20° intervals). The drawing adjacent to each diagram shows the head with the bill at the correct orientation.

extent of the area of maximal binocular overlap differs between the two species. In Ground Hornbills binocularity extends through 80°, from approximately 30° below the line of the bill tip to 50° above, whereas in the Yellow-billed Hornbills the vertical extent is 110°: 30° below to 80° above.

Intrusion of the bill and casque into the visual field

At certain elevations we observed that the bill determined the limit of the binocular field in both species. This is clearly evident in Figure 2 where the binocular field narrows to approximately 14° at the elevation of the direction of the bill tip and broadens both above and below this elevation. Thus the bill intrudes into the frontal field sufficiently to limit the extent of maximum binocularity, implying that hornbills can observe their own bill tips. In Figure 2 the extrapolated retinal field margin indicates the probable limit of the retinal projection if the bill had not intruded and hence indicates the extent to which the frontal binocular field is limited by the bill. The extrapolated margin is based on the assumption that the retinal margin follows an approximately circular projection as noted in other species (Martin & Katzir 1994a). The vertical range over which the bill limits the retinal field is greater in the Yellow-billed Hornbill than in the Ground Hornbill (Fig. 3). In neither species did the casque limit the extent of the retinal field.

Eyelashes

In both species, from approximately 30° above the horizontal (Fig. 3) the margin of the retina was observed through the eyelash-like feathers of the upper eyelid (Fig. 4a). However, although these eyelash-like feathers are relatively long and thick (length up to 18 mm in Ground Hornbill, Fig. 4a) they are relatively widely spaced. Birds in bright sunlight were seen to position their heads so that the lashes shaded the cornea from light falling upon the eye, the lashes casting a graduated comb-like shadow (Fig. 4b).

Eye movements

In both species spontaneous non-conjugate eye movements occurred. Through the ophthalmoscope it was possible to observe that on occasion these movements resulted in the spontaneous abolition of
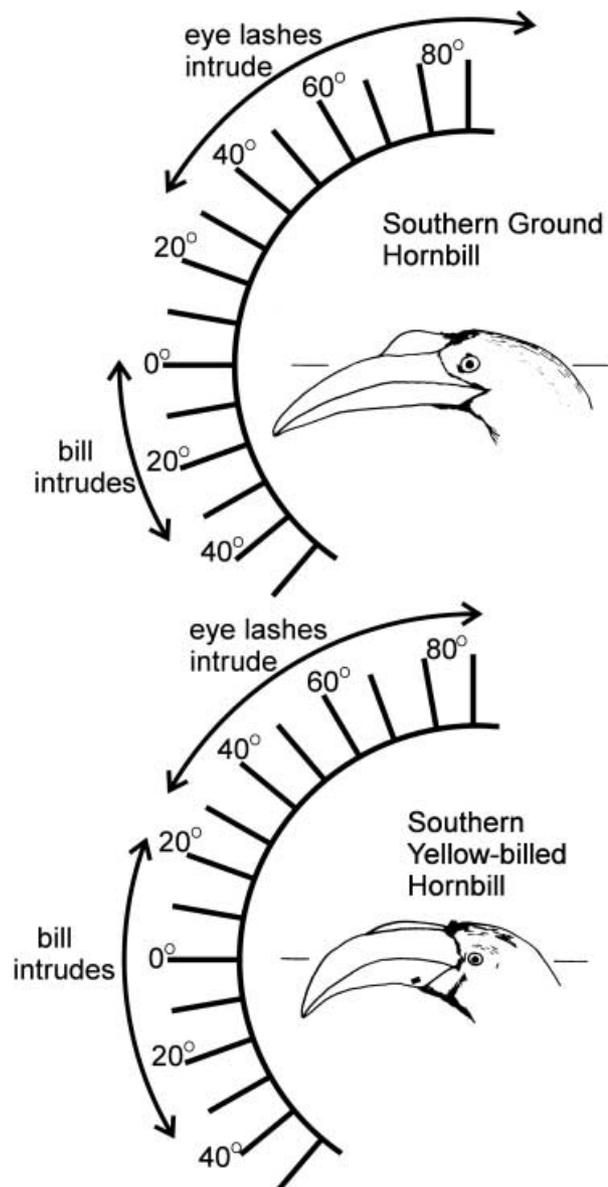
Figure 3. The vertical extent of the region in which the bill limits the width of the binocular field, and the vertical range in which the limit of the retinal field is viewed through the eyelash-like feathers. The drawings show the birds' heads in the correct orientation with the eye-bill tip angle at 20° below the horizontal.

the binocular field. In the Ground Hornbills it was possible to quantify some aspects of this behaviour. Eye movements at elevations throughout that of the binocular field were of large amplitude ($\approx 30–40°$) and Figure 5 compares the visual field topographies that result when both eyes are fully converged (Fig. 5a), fully diverged (Fig. 5b) and when one eye is rotated fully forward and the other fully back
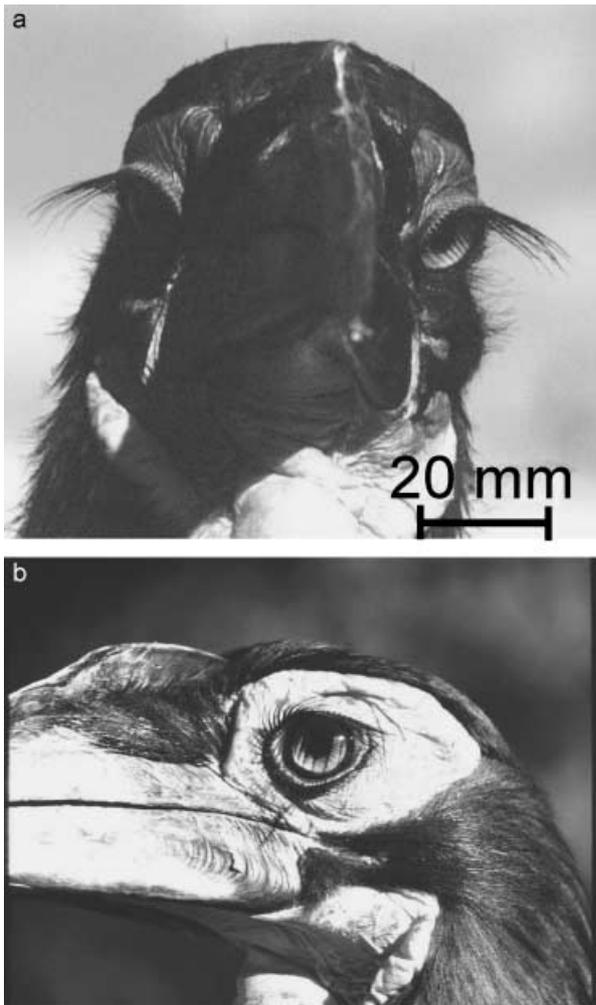
Figure 4. The shading effect (a) and shadows on the cornea (b) of the eyelash-like feathers in Southern Ground Hornbills. Photographs were taken of birds in natural postures when the sun was at high elevation.

(Fig. 5c). At all elevations eye movements are sufficient to abolish the frontal binocular field by a wide margin. For example, in the horizontal plane Ground Hornbills may achieve a binocular overlap of 26° (Fig. 5a) that can be replaced by a blind area 46° wide (Fig. 5b). This results from the amplitude of eye movements equalling 36° at this elevation. When one eye is rotated fully forward and the other rotated fully backward (Fig. 5c) an irregularly shaped narrow blind sector (≈ 10° wide) offset from the median sagittal plane is produced with the bill visible to the bird through one eye. Between these three extreme positions of the eyes a range of visual field topographies involving asymmetric binocular areas can result.
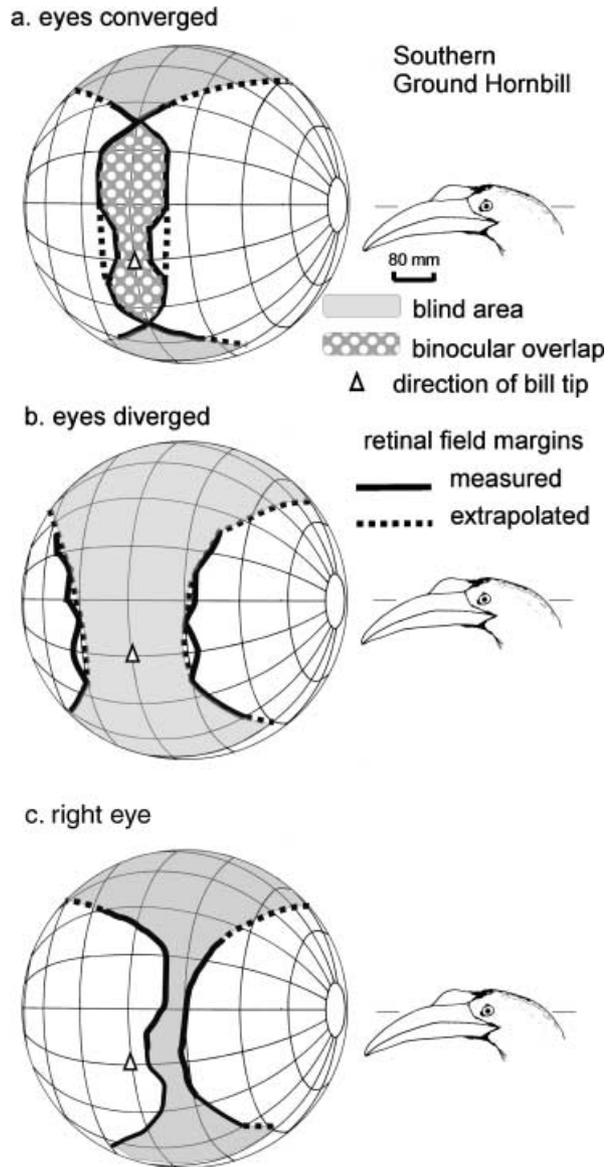
Figure 5. Visual fields of Southern Ground Hornbills when both eyes are (a) fully converged (eyes rotated fully forward), (b) both eyes fully diverged (eyes rotated fully backward) and (c) the right eye is fully forward and the left eye fully backward.

DISCUSSION

Visual field type

The topography of the maximal frontal binocular fields in Ground and Yellow-billed Hornbills (Fig. 2) exhibits three principal features that classify them as Type 1 visual fields: (i) the bill tip projection falls within the lower half of the binocular area, (ii) the

binocular field is relatively long and narrow with maximum binocularity of approximately 30° and (iii) maximum binocularity occurs 20–40° above the projection of the bill tip. Thus, although these hornbills differ markedly in size, and have large decurved bills that are typically used as a pair of forceps to take food items, their visual field topographies are similar to those of unrelated species that use straight bills to take food items in typical pecking or lunging movements. This supports the hypothesis that avian visual field topographies exhibit a narrow range of characteristics that are correlated with behavioural and visual factors rather than with phylogeny.

Visual fields and precision-grasping

Although the hornbill fields are of Type 1 they exhibit a feature not found in other species to date: intrusion of the bill into the margins of the frontal visual fields (Figs 2 & 3). This intrusion implies that a hornbill can see its own bill tip. In other species (e.g. herons, ostriches) the projection of the bill tip just coincides with the projection of the retinal margin and hence does not intrude into the field, whereas in some species (e.g. mallards, woodcocks) the bill falls at the periphery or outside the visual field.

The intrusion of the bill into the visual field in hornbills may be of particular importance when they are using their bills for their characteristic precision-grasping feeding technique. This precise use of the bill tips by the hornbills is likely to require quite different visual guidance from that employed by birds which peck or lunge at items. In species that feed by pecking, the eyes are not used for fine guidance of the bill in the final stages of its approach towards an item. Rather, when pecking, the final stages of approach are ballistic and accompanied by eye closure (Zeigler *et al.* 1993).

It should also be noted that when the mandible are open, hornbills would be able to view with binocular vision an object lying between their tips. This is similar to the situation in Common Starlings *Sturnus vulgaris*. During their characteristic open-billed probing feeding technique starlings are able to converge their eyes further and are thus able binocularly to view objects that lie between the opened mandibles (Feare 1984, Martin 1986a).

Figure 3 indicates that the casque does not intrude into the visual field. In these hornbill species, however, the casque is relatively small and laterally flattened (Figs 1 & 4). Other species of hornbills have a much larger casque (Kemp 1995) and it would clearly be worth investigating whether this is large enough to limit the visual field in the upper frontal sector.

Visual fields and eye size

Although the binocular fields of the two hornbill species show important similarities as regards maximum width and the relative position of the bill with respect to the field, the binocular fields differ in their vertical extents (Fig. 2). Such variation is also found among other species with Type 1 visual fields (Appendix 1). For example, a field of similar vertical dimension and width to that of the Ground Hornbills is found in Ostriches *Struthio camelus*, Stone-curlews *Burhinus oedicnemus* and albatrosses. The longer vertical extent of the binocular field found in Yellow-billed Hornbills is also found in, for example, Rock Doves *Columba livia* and herons.

It seems unlikely that this interspecific difference in the vertical extent of hornbill binocular fields is related to foraging ecology, because the species forage in a similar way and for similar food items. In both species food items are precision-grasped from the ground or low vegetation, and although the maximum size of food items differs between the species, they both take a variety of invertebrates and vertebrates, with overlap in specific items (see Introduction).

These interspecific differences in the vertical extent of the binocular fields may, however, be a function of eye size, and this is reflected in the extent of the blind area above and behind the head (Fig. 2). Figure 6 indicates that the two hornbill species fall within the approximately linear relationship between eye size and the extent of the blind area above the head already identified in birds (Martin & Katzir 2000). The significant correlation between these two variables, and the presence of optical adnexa only in the larger-eyed species (e.g. enlarged brow, hair-like feathers on the eyelids and around the eyes), have been interpreted as indicating that the consequences of sunlight falling directly on the cornea, or of the eye imaging the sun upon the retina, are increasingly deleterious with increased eye size (Martin & Katzir 2000). This arises because the larger eyes in diurnally active species function primarily to mediate high acuity (Land & Nilsson 2002). Imaging the sun produces 'disability glare' that reduces contrast across the retinal image and so negates any increased resolution that a larger eye can achieve compared with a
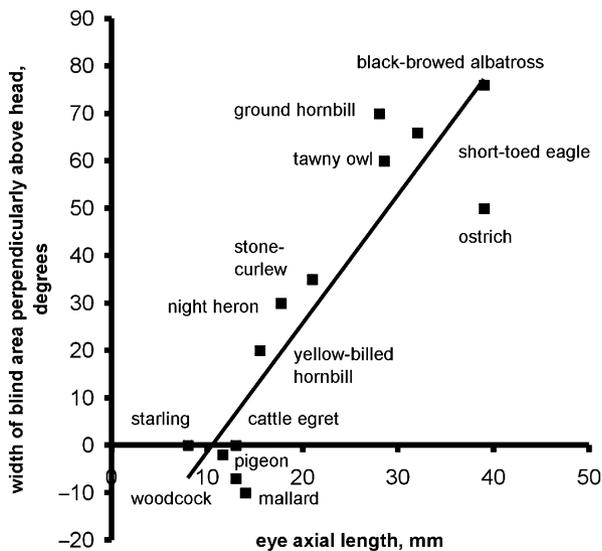
Figure 6. Width of the blind area perpendicularly above the head as a function of eye axial length in 13 species of terrestrial birds (based upon Martin & Katzir 2000). Positive values indicate the width of a blind area, negative values the width of a binocular field. All measurements employed the same technique as described in Appendix 2 and show values when the head is held in its typical posture for the species. The reference to each data point is from those listed in Appendix 1. The straight line is the linear regression. The Spearman correlation between the two variables is significant ($r = 0.85$, $P < 0.005$, $n = 13$).

smaller one when viewing the same scene (Ho & Bilton 1986, Dickinson 1991). Both species of hornbills have eyelash-like feathers that are employed to shade the eye from sunlight. The effect of such shading in Ground Hornbills is illustrated in Figure 4. Given the strength of the relationship between eye size and the size of the blind area above the head (Figure 6), it seems likely that the difference in the vertical extent of the binocular fields in these birds primarily reflects constraints imposed by optical considerations rather than any differences in foraging or other behaviours.

Visual fields and eye movements

Figure 5 illustrates the changes in visual field topography that can be achieved by the independent, large-amplitude eye movements in Ground Hornbills. These clearly produce a wide range of possible configurations that may be both symmetric and asymmetric about the median sagittal plane of the head.

We recorded only the maximum amplitude (30–40°) by which the birds spontaneously moved their

eyes at various elevations. It is noteworthy that these movements are of larger amplitude than recorded to date in other birds; for example, among herons maximum eye movement amplitude $\approx 20°$ (Martin & Katzir 1994a). It is argued (Wallman & Letelier 1993) that the majority of eye movements in vertebrates function to achieve gaze stabilization as the head moves, although scanning or successive sampling of the environment is also important (Land & Nilsson 2002). The movements that we measured when the bird's head was held stationary were clearly functioning to scan the environment rather than stabilize gaze. Our anecdotal observations showed that large-amplitude eye movements suggestive of scanning or successive sampling, rather than gaze stabilization, also occur when Ground Hornbills are foraging.

It seems likely that binocular vision in the majority of birds is primarily concerned with each eye projecting contralaterally and thus gaining in each eye independently an optical flow field that is symmetrical about the point towards which the eye, head or beak is moving (Martin & Katzir 1999). From such symmetrical flow fields, information can be rapidly extracted concerning distance from, and time to contact, objects and surfaces as the animal moves through its environment, or as its beak approaches a target (Davies & Green 1994a, Lee 1994). Such information would seem necessary for the control of pecking, lunging or precision-grasping by birds. This interpretation of binocular vision should be contrasted with that which considers binocularity as providing the foundation for stereoscopic vision (the extraction of relative depth information) as a result of the two eyes receiving near identical images of the same scene on corresponding sections of the retinas in each eye (McFadden 1994). The large and non-conjugate eye movements of the kind recorded in Ground Hornbills would seem to reduce the possibility that such retinal correspondence occurs readily in these birds.

Thus, further investigation is required to determine under what circumstances eye movements occur in freely moving birds and whether hornbills employ optical flow field information to control their precision-pecking.

REFERENCES

Acocks, J.P.H. 1988. Veld types of South Africa. *Memoires Bot., South Africa* **57**: 1–146.

Burton, P.J.K. 1984. Anatomy and evolution of feeding apparatus in the avian orders Coraciiformes and Piciformes. *Bull. Br. Mus. Nat. Hist., Zool.* **47**: 331–443.

Davies, M.N.O. & Green, P.R. 1994a. Multiple sources of depth information: an ecological approach. In Davies, M.N.O. & Green, P.R. (eds) *Perception and Motor Control in Birds: an Ecological Approach*: 339–356. Berlin: Springer-Verlag.

Davies, M.N.O. & Green, P.R. 1994b. *Perception and Motor Control in Birds: an Ecological Approach*. Berlin: Springer-Verlag.

Dickinson, C.M. 1991. Optical aids for low vision. In Charman, W.N. (ed.) *Vision and Visual Dysfunction*: 183–228. London: Macmillan.

Feare, C.J. 1984. *The Starling*. Oxford: Oxford University Press.

Guillemaine, M., Martin, G.R. & Fritz, H. 2002. Feeding methods, visual fields and vigilance in dabbling ducks (Anatidae). *Funct. Ecol.* **16**: 522–529.

Ho, A. & Bilton, S.M. 1986. Low contrast charts effectively differentiate between types of blur. *Am. J. Ophthal. Physiol. Opt.* **63**: 202–208.

Katzir, G. & Martin, G.R. 1998. Visual fields in the Black-crowned Night Heron *Nycticorax nycticorax*: nocturnality does not result in owl-like features. *Ibis* **140**: 157–162.

Kemp, A. 1995. *The Hornbills*. Oxford: Oxford University Press.

Kemp, A.C. 2001. Family Bucerotidae (Hornbills). In del Hoyo, J., Elliott, A. & Sargatal, J. (eds) *Handbook of the Birds of the World*, Vol. 6: 436–523. Barcelona: Lynx Edicions.

Land, M.F. & Nilsson, D.-E. 2002. *Animal Eyes*. Oxford: Oxford University Press.

Lee, D.N. 1994. An eye or ear for flying. In Davies, M.N.O. & Green, P.R. (eds) *Perception and Motor Control in Birds: an Ecological Approach*: 270–291. Berlin: Springer-Verlag.

Low, A.B. & Rebelo, A.G. 1998. *Vegetation of South Africa, Lesotho and Swaziland*. Pretoria: Department of Environmental Affairs.

Martin, G.R. 1984. The visual fields of the Tawny Owl, *Strix aluco* L. *Vision Res.* **24**: 1739–1751.

Martin, G.R. 1985. Eye. In King, A.S. & McLelland, J. (eds) *Form and Function in Birds*: 311–373. London: Academic Press.

Martin, G.R. 1986a. The eye of a passeriform bird, the European Starling (*Sturnus vulgaris*): eye movement amplitude, visual fields and schematic optics. *J. Comp. Physiol. A* **159**: 545–557.

Martin, G.R. 1986b. Sensory capacities and the nocturnal habit of owls (Strigiformes). *Ibis* **128**: 266–277.

Martin, G.R. 1986c. Total panoramic vision in the Mallard duck, *Anas platyrhynchos*. *Vision Res.* **26**: 1303–1306.

Martin, G.R. 1994. Visual fields in Woodcocks *Scolopax rusticola* (Scolopacidae; Charadriiformes). *J. Comp. Physiol. A* **174**: 787–793.

Martin, G.R. 1998. Eye structure and amphibious foraging in albatrosses. *Proc. R. Soc. Lond. B* **265**: 1–7.

Martin, G.R. 1999. Eye structure and foraging in King Penguins *Aptenodytes patagonicus*. *Ibis* **141**: 444–450.

Martin, G.R. & Katzir, G. 1994a. Visual fields and eye movements in herons (Ardeidae). *Brain Behav. Evol.* **44**: 74–85.

Martin, G.R. & Katzir, G. 1994b. Visual fields in the Stone Curlew *Burhinus oedicnemus*. *Ibis* **136**: 448–453.

Martin, G.R. & Katzir, G. 1995. Visual fields in ostriches. *Nature* **374**: 19–20.

Martin, G.R. & Katzir, G. 1999. Visual field in Short-toed Eagles *Circaetus gallicus* and the function of binocularity in birds. *Brain Behav. Evol.* **53**: 55–66.

Martin, G.R. & Katzir, G. 2000. Sun shades and eye size in birds. *Brain Behav. Evol.* **56**: 340–344.

Martin, G.R. & Prince, P.A. 2001. Visual fields and foraging in Procellariiform seabirds: sensory aspects of dietary segregation. *Brain Behav. Evol.* **57**: 33–38.

Martin, G.R. & Young, S.R. 1983. The retinal binocular field of the Pigeon (*Columba livia*): English racing homer. *Vision Res.* **23**: 911–915.

McFadden, S.A. 1994. Binocular depth perception. In Davies, M.N.O. & Green, P.R. (eds) *Perception and Motor Control in Birds: an Ecological Approach*: 54–73. Berlin: Springer-Verlag.

Muller, J.B. 1998. *An Ecological Study of the Plant Communities and Animal Population Dynamics of Mabula Game Reserve, with Management Recommendations*. BSc Dissertation, University of Pretoria.

Sibley, C.G. & Ahlquist, J.E. 1991. *Phylogeny and Classification of Birds: a Study in Molecular Evolution*. New Haven: Yale University Press.

Sibley, C.G. & Monroe, B.L. 1990. *Distribution and Taxonomy of Birds of the World*. New Haven: Yale University Press.

Wallman, J. & Letelier, J.-C. 1993. Eye movements, head movements, and gaze stabilization in birds. In Zeigler, H.P. & Bischof, H.-J. (eds) *Vision, Brain, and Behaviour in Birds*: 245–263. Cambridge, MA: MIT Press.

Zeigler, H.P. & Bischof, H.-J. (eds) 1993. *Vision, Brain, and Behaviour in Birds*. Cambridge, MA: MIT Press.

Zeigler, H.P., Jager, R. & Palacios, A.G. 1993. Sensorimotor mechanisms and pecking in the pigeon. In Zeigler, H.P. & Bischof, H.-J. (eds) *Vision, Brain and Behavior in Birds*: 265–283. Cambridge, MA: MIT Press.

APPENDIX 1

Bird species in which visual field types have been determined using the ophthalmoscopic reflex technique.

Type 1. Ostriches *Struthio camelus* Struthionidae (Martin & Katzir 1995), King Penguins *Aptenodytes patagonicus* Spheniscidae (Martin 1999), albatrosses Diomedeidae (Martin 1998), White-chinned Petrels *Procellaria aequinoctialis* Procellariidae (Martin & Prince 2001), heron species Ardeidae (Martin & Katzir 1994a, Katzir & Martin 1998), Wigeons *Anas penelope* (Guillemaine *et al.* 2002), Short-toed Eagles *Circaetus gallicus* Accipitridae (Martin & Katzir 1999), Stone-curlews *Burhinus oedicnemus* Burhinidae (Martin & Katzir 1994b), Rock Doves *Columba livia* Columbidae (Martin & Young 1983), and Common Starlings *Sturnus vulgaris* Sturnidae (Martin 1986a).

Type 2. Antarctic Prions *Pachyptila desolata* Procellariidae (Martin & Prince 2001), Mallards *Anas platyrhynchos* and Northern Shovelers *A. clypeata* Anatidae (Martin 1986c, Guillemaine *et al.* 2002) and Eurasian Woodcocks *Scolopax rusticola* Scolopacidae (Martin 1994).

Type 3. Tawny Owls *Strix aluco* (Martin 1984).

APPENDIX 2

Procedure. Each bird was restrained with the body immobilized and the head position fixed by holding the bill. In both species the bill was held in a specially built metal holder coated with cured silicone sealant to produce a non-slip surface and the bill held in position by tape (Micropore®). The Yellow-billed Hornbill body was held in a cradle of foam rubber and secured by straps (Velcro®). Because of the large size of Ground Hornbills this type of body restraint was not practicable with the species and these were held physically by one of us, H.C.C., who has extensive experience of handling these birds. The bill holder was mounted on an adjustable mechanism and the head positioned so that the mid-point of a line joining the corneal vertices was at the approximate centre of a visual perimeter apparatus. The perimeter's coordinate system followed conventional latitude and longitude with the equator aligned vertically in the bird's median sagittal plane and this coordinate system is used for the presentation of the visual field data (Figs 2 & 3). Each bird's head was positioned with the plane through the eyes and bill tip pointing at an angle of approximately 20° below the horizontal. This head position approximated that which the birds adopted spontaneously when held in the hand. Similar head positions were also recorded in photographs and video sequences of birds walking and resting on the ground. Heads in this position are depicted in Figure 2. The projection of the bill tip when measurements were made was determined accurately and the visual field data corrected for this.

The eyes were examined using an ophthalmoscope mounted on the perimeter arm. The visual projections of the limits of the frontal retinal visual field at elevations above and below the bill for each eye were determined as a function of elevation (10° intervals) in the median sagittal plane. Procedures that in other bird species, e.g. herons Ardeidae (Martin & Katzir 1994a) have readily elicited eye movements when birds are positioned in similar apparatus (such as light tapping sounds in the periphery of the visual field), were employed to determine the maximum amplitude of eye movements at each elevation. These were defined as the difference between the extreme positions at which the same retinal margin could be detected during a series of successive measurements. In the Ground Hornbills these eye movements were of large amplitude and relatively slow and hence could be readily observed. In the Yellow-billed Hornbills eye movements were more rapid and it was not possible to determine the diverged position with accuracy because this appeared to be adopted only fleetingly and we did not wish to prolong the restraint of the birds in order to make these measurements. Hence in the Yellow-billed Hornbills only the eye positions adopted when the eyes were at rest and apparently converged were recorded. We were not able to quantify eye movement amplitude in these birds. From these data (corrected for viewing from a hypothetical viewing point placed at infinity) topographical maps of the frontal visual fields were constructed for each species.