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Short communication

Visual fields, foraging and collision vulnerability in *Gyps* vultures

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The visual fields of vultures contain a small binocular region and large blind areas above, below and behind the head. Head positions typically adopted by foraging vultures suggest that these visual fields provide comprehensive visual coverage of the ground below, prohibit the eyes from imaging the sun and provide extensive visual coverage laterally. However, vultures will often be blind in the direction of travel. We conclude that by erecting structures such as wind turbines, which extend into open airspace, humans have provided a perceptual challenge that the vision of foraging vultures cannot overcome.

Keywords: binocular vision, blind area, *Gyps africanus*, *Gyps fulvus*, vision, visual fields, wind turbines.

Visual fields define the space around an animal from which information can be retrieved (Martin 2007, 2011a). They differ between bird species, especially in the extent and position of the binocular field relative to the bill, and the extent of blind areas above and behind the head. These differences are primarily correlated with differences in foraging ecology, even among closely related species (Martin & Portugal 2011). In cranes and bustards, even a relatively small-amplitude forward pitch of the head, which may occur when scanning the ground below during flight, renders the birds blind in the direction of travel and unable to detect a hazard ahead of them (Martin & Shaw 2010). This has been suggested as a key cause of their vulnerability to collision with human artefacts such as wind turbines and power lines (Martin 2011b).

The high vulnerability of large raptors, especially eagles and vultures, to collisions with power lines and wind turbines is a cause of current international concern, with recent conferences in Europe and North America focusing on these issues (see http://www.cww2011.nina.no, http://www.energiaeolicayfauna.org and http://www.rmrp.info for examples). Mortality rates due to such collisions are sufficiently high to lead to population declines, and extinctions of local populations are predicted (Drewitt & Langston 2008, de Lucas *et al.* 2008, Carette *et al.* 2009, Jenkins *et al.* 2010). Understanding the cause of these collisions is therefore of increasing concern in light of the rapidly expanding deployment of wind turbines across the globe (Moccia & Arapogianni 2011).

It is puzzling that turbines are a hazard to large raptors because these birds have the highest visual acuity yet determined (Land & Nilsson 2002). Turbines appear highly conspicuous to humans and, as these birds fly by day, collisions occur at high light levels when the obstacles should be easy to see. Furthermore, large raptors can achieve high manoeuvrability in flight through rapid partial wing closure and tumbling, and they can fly slowly (Thiollay 1994). These attributes should allow a bird to take evasive action once a hazard has been detected ahead. Among raptors, vision is the main source of information for control of flight, detection of food and, in the case of many species of vultures, the observation of conspecifics using the same airspace whose behaviour may indicate the detection of food (Houston 1974, Thiollay 1994, Jackson *et al.* 2008). Despite this apparent reliance upon visual information, we assessed whether there might be a perceptual basis to the vulnerability of large raptors to collisions.

A perceptual basis to collisions in birds has theoretical support based upon the general properties of vision and flight in birds (Martin 2011b), and empirical support has come from studies of collision susceptibility in bustards and cranes. We describe here the visual field topography of two species of *Gyps* vultures: Eurasian Griffon Vultures *Gyps fulvus* and African White-backed Vultures *Gyps africanus*. We show how they are related to the foraging ecology and collision vulnerability of these birds.

METHODS

Subjects

Visual fields were measured in two individuals of each species. The birds are held in the collection of The Hawk Conservancy Trust. The birds were in good health and flown regularly. Birds were adults and had been held in captivity for a number of years. Birds were studied in the clinical facilities of The Hawk Conservancy Trust close to their holding aviaries and were returned to their aviaries soon after measurement.

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Determination of visual fields

The ophthalmoscopic reflex technique was used to measure the characteristics of visual fields in alert birds. This is a non-invasive technique that has been used on more than 50 different bird species. It has recently been described in detail by Martin and Portugal (2011), and that paper should be consulted for full details of methods.

In this study each bird was hand-held with the neck resting on a foam rubber cradle with the body and legs supported by one of the authors (C.P.M.). The head was held in position at the centre of a visual perimeter by specially manufactured steel and aluminium bill holders. The bill was held firmly in place by Micropore™ tape. The perimeter's coordinate system followed conventional latitude and longitude with the equator aligned vertically in the median sagittal plane of the head (a vertical plane which divides the head symmetrically into its left and right halves) and this coordinate system is used for the presentation of visual field data (Figs 1 and 2). When the measurements were made, the tips of the bills projected at approximately 20° below the horizontal, as shown in the diagram insert of Figure 1. We observed spontaneous eye movements and their amplitude was determined as described previously (Martin & Portugal 2011). In each individual the measured visual field parameters were very similar (± 2°) for repeated measurements at a number of selected elevations, and differences between individuals for the two species at the same elevation did not differ by more than 5° and typically differed by less than 2°. Therefore, we present mean visual field data for both species combined (Fig. 1). From these data a mean topographical map of the visual field and its principal features was constructed (Fig. 2).

Head position in foraging flight

We examined photographs and video clips of the two vulture species available on the internet including Google Images and Arkive (http://www.arkive.org), and illustrations and photographs in Thiollay (1994). We looked for photographs that showed birds in flight and apparently foraging and gave a view close to side on. Few illustrations met this requirement but all photographs of birds in flight indicated that the bill was held at a steeper angle than that adopted for our measurements. We estimated that the eye-bill tip angle in all flight photographs was always in excess of 40° and in the typical foraging flight the bill was held at an angle ≈60°, as shown in Figure 3 (photograph from Terje Kolaas; http://www.naturspesialisten.no) and sometimes the head was rolled so that one eye looked more directly down towards the ground. C.P.M. also has extensive experience of observing *G. africanus* in flight, often from aircraft flying alongside the birds when foraging, and was able to confirm that the head can frequently be pitched forward to an angle ≈ 60° or greater, particularly when flying below approximately 200 m above ground level (AGL).

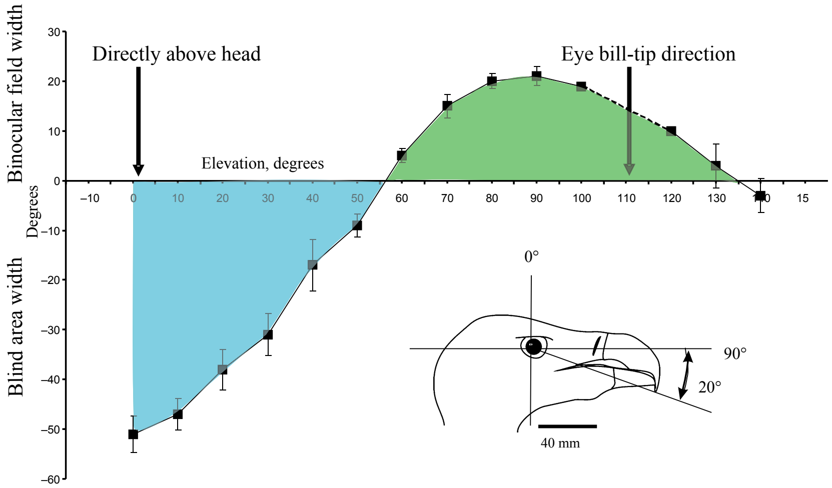

Figure 1. Mean (± se) angular separation of the retinal field margins as a function of elevation in the median sagittal plane in *Gyps* vultures. Positive values indicate overlap of the field margins (binocular vision), and negative values indicate the width of the blind areas. The coordinate system is such that the horizontal plane is defined by the 9° (in front of the head) and 0° lies directly above the head; the same coordinates are used in Figure 2. These directions are indicated in the outline scaled drawing of the head of a Griffon Vulture. The projection of the eye–bill tip axis is also indicated. The value of the binocular field width at elevation 110° could not be determined directly because of the intrusion of the bill-holder into the view of the eye, and this value was interpolated from the mean recorded field width values at 100° and 120° elevations.

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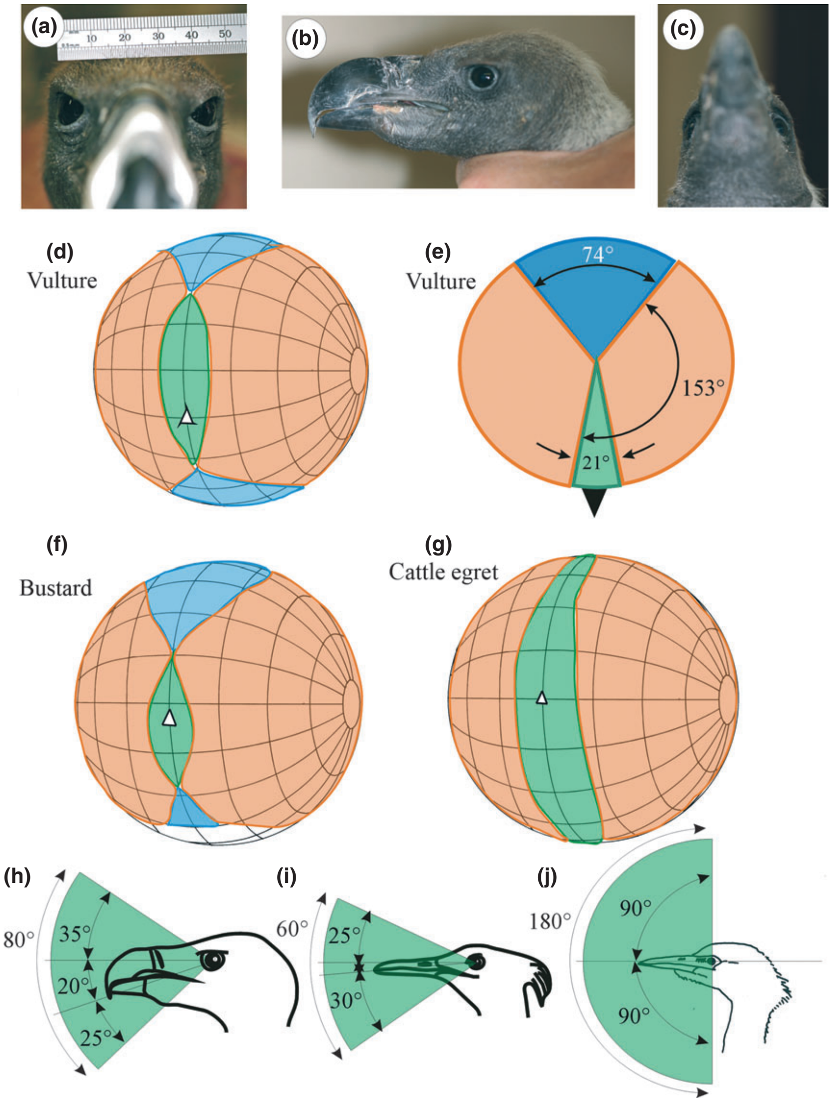

Figure 2. Visual fields of *Gyps* vultures. The figure shows data for the vultures but also allows interspecific comparisons with the visual field of Kori Bustards *Ardeotis kori* and Cattle Egrets *Bulbulcus ibis* (Martin & Katzir 1994, Martin & Shaw 2010). The top row shows photographs of the head of an African White-backed Vulture (a) from along the horizontal (with reference to the head position shown in Fig. 1), (b) laterally and (c) from below at an angle of approximately 140°, which is at the lower limit of the binocular field. Note the prominent ridges above the eyes in all three photographs. (d) Perspective views of orthographic projections of the boundaries of the retinal fields of the two eyes and the line of the eye–bill tip projection (indicated by a white triangle). The diagrams use conventional latitude and longitude coordinate systems with the equator aligned vertically in the median sagittal plane of the bird (grid at 20° intervals) and values in the sagittal plane correspond to those shown in Figure 1. 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 with the heads in the orientations shown in (b). (e) Horizontal section through the visual fields in a horizontal plane. (f,g) Perspective views of orthographic projections of the visual fields in Kori Bustards and Cattle Egrets, respectively. (h–j) Vertical sections through the binocular fields in the median sagittal plane of the head in vulture, bustard and egret, respectively. Green areas, binocular sectors; pink areas, monocular sectors; blue areas, blind sectors; downward pointing black arrowhead in (e) indicates direction of the bill; white triangles indicate the direction of bill projections in (d,f,g).

RESULTS

The mean (± se) angular separations of the retinal field margins as a function of elevation in the median sagittal plane of the head are shown in Figure 1. Photographs of the head of an African White-backed Vulture are shown in Figure 2(a–c). A map of the visual field in the frontal sector is shown in Figure 2(d). Figure 2(e) shows a section

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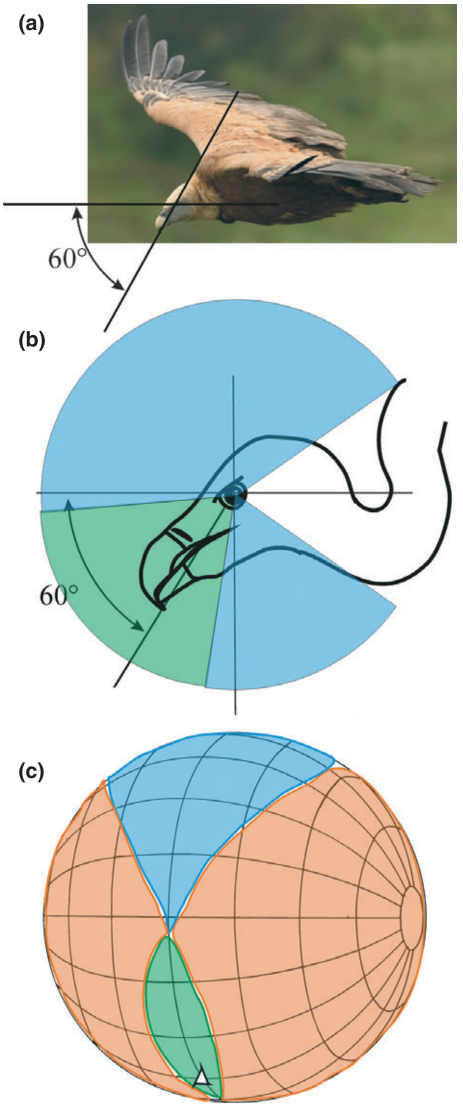

Figure 3. Visual fields and foraging in *Gyps* vultures. (a) Photograph of a bird in foraging flight showing the typical angle of the eye–bill tip projection when foraging (60° with respect to the horizontal). (b) Projection of the binocular and blind areas in the sagittal plane and (c) perspective view of orthographic projections of the visual field, when the head is held at the eye–bill tip angle depicted in (a). Green, binocular sector; blue, blind sector.

through the field at an approximately horizontal plane when the head is held in the position shown in Figures 1 and 2(b). A vertical section through the binocular field in the median sagittal plane is shown in Figure 2(h).

General topography of the visual field

The binocular region of these vultures is small with limited extent in width (max. 22°) and height (80°) with the bill tip projecting below the centre; cf. human binocular field: ≈ 120° width × 120° height (Martin 2011b). In vultures there are large blind areas above (50° wide), below and behind (74° wide) the head.

DISCUSSION

Vulture visual fields

The relatively small frontal binocular field of the vultures may seem surprising given these birds reliance upon visual information. However, frontal binocular fields of these dimensions have also been described in Short-toed Snake Eagles *Circaetus gallicus* (Martin & Katzir 1999) and in cranes and bustards, species which are known to be vulnerable to collisions with power lines. Visual field data for Kori Bustards *Ardeotis kori* are shown alongside that of the vultures (cf. Fig. 2d,f). Also shown is more detailed information on the dimensions of visual fields in vultures: the vertical extent of the binocular field and its position relative to the bill (Fig. 2h), and a horizontal section through the visual field (Fig. 2e).

Binocular vision in birds serves to control the position of bill and feet with respect to relatively close objects rather than locomotion with respect to more distant targets (Martin 2009, 2011a). Narrow binocular fields are common among birds but there is considerable variation in their vertical extent (Martin 2007). The frequent assumption that raptors have wide or generally large binocular fields is not supported by empirical data either from these vultures or from other diurnal raptors including Short-toed Snake Eagle (Martin & Katzir 1999), Red-tailed Hawk *Buteo jamaicensis*, Cooper's Hawk *Accipiter cooperi*, and American Kestrel *Falco sparverius* (O'Rourke *et al.* 2010). However, the visual fields of raptors, cranes and bustards do differ in their vertical extent from those commonly found in many other bird species, including herons (Ardeidae), shorebirds (Scolopacidae), pigeons (Columbidae) and waterfowl (Anatidae) (Martin 2007). These latter groups have a binocular field of greater vertical height than found in these vultures and they have smaller blind areas above and behind the head. In some of these species the binocular field extends vertically through 180°, resulting in comprehensive visual coverage of the frontal hemisphere. An example of this is shown in Figure 2(g) for Cattle Egrets *Bubulcus ibis*, which are typical of herons (Martin & Katzir 1994).

Projection of visual fields in flight

The visual fields described in Figure 2 are shown with respect to the head itself. How these visual fields project into the world around the bird will depend upon the head position adopted when a bird is engaged in various tasks. In flight and when foraging, birds tend to adopt head positions which can be described by the angle between the eye and the bill tip with respect to the horizontal (Martin & Portugal 2011). It is clear that the head positions of vultures shown in Figures 1 and 2 are not those typically adopted in flight, especially when the birds are foraging. Images of flying birds indicate that the head is pitched forward and that when foraging the eye–bill tip angle is typically ≈ 60° (Fig. 3a). In other words, the head will be pitched through approximately 40° compared with the position shown in Figure 2(h). With this head position a vulture will gain binocular and comprehensive visual coverage of the terrain below and extensive monocular visual coverage laterally (Fig. 3b,c), but will be blind in the direction of travel and above the horizontal. The blind area will be 25° wide at an angle of 20° above the horizontal, and neither roll nor yaw movements of the head through 20° will abolish the blind area in the forward direction.

While it may seem maladaptive to be unable to maintain constant surveillance of the way ahead, the extensive blind area above the horizontal may serve an important function in preventing the eyes from imaging the sun. Imaging the sun can seriously degrade image quality across the whole retina and hence reduce the probability of detecting a target on the ground below (Martin & Katzir 2000). Indeed vultures and eagles are among those birds that have prominent brows above the eyes (enlarged supra-orbital ridges) and relatively long (up to 5 mm) eyelashes (Fig. 2a–c). Such features, which are absent in many birds, may function physically to protect the eye but their main function is to reduce the probability that the sun will be imaged in the eye (Martin & Katzir 2000, Martin & Coetzee 2004). The extensive lateral, monocular visual coverage (Figs 2d and 3e) allows vultures to observe the behaviour of conspecifics also foraging in the same airspace. Detecting when other birds move towards a food item is a key aspect of the social foraging behaviour of *Gyps* vultures (Houston 1974, Mundy *et al.* 1992, Jackson *et al.* 2008).

Overall, the visual fields of these *Gyps* vultures and their characteristic in-flight head postures which are known to be adopted in the lower air space (< 200 m AGL) result in a combination of features which can be correlated readily with their foraging behaviour; that is, extensive visual coverage of the world below them, surveillance of the airspace laterally and avoidance of imaging the sun. However, this results in the birds frequently being unable to see directly ahead in the direction of travel, rendering them vulnerable to collisions with objects, such as wind turbines, which intrude into otherwise empty airspace. Bird species which have more comprehensive coverage of the frontal hemisphere such as herons, shorebirds, pigeons and waterfowl (Martin 2007) gain full visual coverage of the airspace ahead of them regardless of the head position adopted in flight (Fig. 2g). This is likely to contribute to lower vulnerability to collisions, at least at high light levels, in these birds (Drewitt & Langston 2006, 2008).

Reducing vulture collisions

Our analysis suggests that by erecting wind turbines and other artefacts, humans have provided a perceptual challenge that the vision of foraging vultures cannot readily overcome. Measures aimed at reducing the collision probability of vultures (and probably other large raptors) with structures that intrude into the open airspace (wind turbines typically extend 40–120 m AGL, and electricity pylons 15–55 m AGL) need to take account of these constraints, and the fact that the visual adaptations of vultures maximize the detection of objects below a bird when in flight. We suggest that increasing the conspicuousness of man-made obstacles will achieve only marginal gains with respect to collision reduction because the obstacles will often simply not be seen by the birds when foraging. Reducing the probability that vultures are attracted to forage in areas containing wind turbines is a high priority. This would mean reducing food availability in such areas, and maintaining or developing attractive foraging habitat away from wind turbine installations. This may be achieved partly by provision of feeding stations, also known as 'vulture restaurants' (Gilbert *et al.* 2007). The wide-ranging behaviour of foraging vultures means that threat reduction should be implemented at the landscape scale, rather than only at specific sites (Bright *et al.* 2008, Murn & Anderson 2008), although landscape-scale modelling of collision vulnerability in *Gyps* vultures is not always supported by empirical studies (Ferrer *et al.* 2012). These considerations aside, we conclude that because of perceptual constraints, foraging vultures and wind turbines need to be kept apart.

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