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White-headed Vultures *Trigonoceps occipitalis* show visual field characteristics of hunting raptors

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ABSTRACT

The visual fields of Aegypiinae vultures have been shown to be adapted primarily to meet two key perceptual challenges of their obligate carrion-feeding behaviour: scanning the ground and preventing the sun's image falling upon the retina. However, field observations have shown that foraging White-headed Vultures (*Trigonoceps occipitalis*) are not exclusively carrion-feeders; they are also facultative predators of live prey. Such feeding is likely to present perceptual challenges that are additional to those posed by carrion-feeding. Binocularity is the key component of all visual fields and in birds it is thought to function primarily in the accurate placement and time of contact of the talons and bill, especially in the location and seizure of food items. We determined visual fields in White-headed Vultures and two species of carrion-eating *Gyps* vultures, and show that the visual field of White-headed Vultures have more similarities with those of predatory raptors (e.g. Accipitrid hawks), compared with the taxonomically more closely related *Gyps* vultures. We found that maximum binocular field width in White-headed vultures (30°) is significantly wider than *Gyps* vultures (20°). The broader binocular fields in White-headed Vultures probably facilitate accurate placement and timing of the talons when capturing evasive live prey.

The visual field topographies of vultures (Accipitridae, Aegypiinae) have been shown to be adapted primarily for scanning the ground below and preventing the eyes from imaging the sun (Martin *et al.* 2011). These visual field characteristics play a vital role in allowing vultures, generally considered to be obligate scavengers (Mundy *et al*. 1992), to locate suitable food sources. However, recent field observations indicate that one species (White-headed Vultures, *Trigonoceps occipitalis*) is a scavenger that also regularly takes evasive prey (Murn 2014); the requirements on the visual system for such hunting behaviour would be expected to be markedly different to that for scavenging alone (Martin 2014, Potier *et al.* 2016).

Visual fields define the space around an animal from which information can be retrieved at any instant (Martin 2007), and subtleties in visual field topography can be attributed to species-specific foraging ecology, as opposed to being only a consequence of shared ancestry (Martin 2009, Martin 2014). Binocularity is an important component of all visual fields. In birds, binocularity is thought to function primarily in the detection of symmetrical optic flow-fields that provide almost instantaneous information on direction of travel and time-to-contact with an object, as opposed to detecting relative depth based upon static stereoscopic cues, which is often considered the prime function of binocularity in mammals (Martin 2009, Martin & Portugal 2011). Small-scale differences in visual fields, including the degree of binocularity, are evident both between and within bird groups, depending on the extent that vision is used for foraging (Guillemain *et al*. 2002).

In general, among active hunting Accipiters, binocular fields are broader and total visual fields narrower compared with those species that rely primarily upon scavenging for static items (Martin *et al*. 2012, Martin 2014, O'Rourke *et al*. 2010, Potier *et al*. 2016). We tested the hypothesis that the visual fields of White-headed Vultures would have binocularity characteristics more typical of predatory raptors, as opposed to the carrion-feeding vultures to which they are related.

METHODS

Visual fields were measured in two individuals from each of the following species; White-headed Vultures, and two species that are exclusively carrion-feeding: African White-backed (*Gyps africanus*) and Griffon (*Gyps fulvus*) Vultures. The birds are held in the collection of the Hawk Conservancy Trust (HCT; Hampshire, UK). Birds were adults and had been held at the HCT for a number of years. Birds were studied in the clinical facilities block of the HCT, close to their holding aviaries and were returned to their aviaries soon after measurement. The Griffon and White-backed Vultures were measured during a previous study, the full details of that can be found in Martin *et al*. (2012), with further detailed methodological information in Martin and Portugal (2011). Briefly, the ophthalmoscopic reflex technique (Martin 2009) was used to measure the characteristics of visual fields in alert birds (Martin & Coetzee 2004). Each bird was hand-held with the head and neck resting on a foam rubber cradle with the body and legs supported by one of the authors (C.P.M.). Aluminium and steel bill holders maintained each bird's head position at the centre of the visual perimeter, with the bill held 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 that 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 & 2). For each individual, the measured visual field parameters were very similar for repeated measurements at a number of selected elevations (± 2°), and differences between individuals for each species at the same elevation did not differ by more than 5° and typically less than 2°.

In all species, eye movements were present and, as in other birds, were non-conjugate (Martin 2007). Due to time constraints on holding the birds in the apparatus, we were only able to quantify eye movement amplitude at a small number of elevations around the horizontal plane where binocular field width was close to the maximum and eye movements typically have their largest amplitude (Martin 2007). We observed spontaneous eye movements away from their forward positions, which defined the maximum degree of binocular overlap that we report here. Amplitudes of eye movements were determined by making a rapid series of observations of the position of the retinal margin as the eye spontaneously moved from the forward resting position. In this way the maximum and minimum position at which the retinal margin could be seen for a given elevation in the frontal hemisphere was determined and the difference between them defined the maximum amplitude of eye movement at that elevation.

Data presented are mean visual field data for the two carrion-feeding vulture species combined, and the White-headed Vultures (N=2).

RESULTS

The mean angular separation of the retinal field margins as a function of elevation in the median sagittal plane of the head are shown in Fig. 1. Maps, based upon these data show the visual fields (Fig. 2) in the frontal sector (2*c*,*d*) and in a horizontal section (2*e*,*f*). The visual fields of individual eyes are of similar width in the *Gyps* (White-backed and Griffon Vultures) and *Trigonoceps* (White-headed Vultures) species, 153° and 155° respectively (2*e*,*f*), but differences in their positions in the skull result in differences in the main parameters of the visual fields. Thus in *Gyps* the binocular field is smaller in both width and vertical height compared with White-headed Vultures. All of the birds have extensive blind areas above and behind the head, and the blind region behind the head in White-headed Vultures is 10° broader than in *Gyps*. This can be correlated with the more forward eye positions that results in greater binocular overlap in White-headed Vultures. Thus, while the fields of individual eyes are similar in White-headed Vultures and *Gyps* and the visual field topographies of all three vulture species show a similar general pattern in shape (Fig. 2 c,d), the dimensions of each key component (binocular width, binocular vertical height, blind sector widths above and behind the head) differ. These differences are shown to be statistically different, the White-headed Vultures having on average 2.3 × greater binocular field width across all elevations in comparison to the *Gyps* species (overall visual field, ANOVA $F = 3.97$, $P < 0.05$).

< Figure 1 about here>

<Figure 2 about here>

DISCUSSION

The visual fields of *Trigonoceps* (White-headed Vultures) are significantly different from those of the obligate carrion-feeding *Gyps* vultures. This can be interpreted as corroborating field observations of White-headed Vultures as hunters of evasive prey (Murn 2014). Compared to carrion-feeding vulture species, the White-headed Vultures have a larger binocular field and it is likely that this increased binocularity increases precision in the placement and timing of the talons and bill when capturing an evasive prey item (Martin 2009). High precision, especially of timing, is not such a vital component when approaching carrion.

The trade-off between frontal vision (and binocularity) and the necessity for vigilance against potential predators (i.e. minimising the blind area behind the head) is a characteristic that shapes all avian visual fields (Martin 2014). However, for vultures, with few natural predators, this compromise between frontal and rear visual balance may be biased towards requirements for frontal and lateral vision, and the need to be vigilant for conspecifics, or other raptors (Kane *et al.* 2014), that may have successfully located a food source. For the White-headed Vultures, that are often solitary foragers (Mundy *et al*. 1982), this requisite for conspecific surveillance is reduced and perhaps outweighed by the necessity for accurate direction of the talons and bill when capturing live prey. This social versus non-social foraging element is likely, therefore, to be an important contributing factor to the development and maintenance of significant differences in visual fields between the obligate carrion-eating birds and the more predatory White-headed Vultures.

White-headed Vultures show visual characteristics that are more similar to some phylogenetically distant diurnal hunting raptors (Griffiths *et al*. 2007, O'Rourke *et al*. 2010) as opposed to closely-related carrion-feeding vultures (Martin *et al*. 2012). Maximum binocular field width in White-headed Vultures (30 °), is very similar to the widths of the binocular fields in Red-tailed Hawks *Buteo jamaicensis*, Cooper's Hawks *Accipiter cooperii* and American Kestrels *Falco sparverius*, (33°, 36° and 33°, respectively) (O'Rourke *et al*. 2010), and is 10° wider than in carrion-feeding vultures

(Martin *et al*. 2012). The fine-tuning of visual fields that we have shown in these vulture species is similar to the kinds of fine-tuning with respect to differences in the foraging modes reported among species of ducks (Martin *et al*. 2007a), ibises (Martin & Portugal 2011), and shorebirds (Martin & Piersma 2009). This lends further support to the hypothesis that vision is as finely tuned to foraging mode as are other morphologies associated with prey capture such as the shape, strength and dimension of talons and bills (Fowler *et al*. 2009, , Martin 2017).

The visual fields of the White-headed Vultures corroborate the observations from the field that this species is predatory. That the vision of White-headed Vultures shows adaptation to a predatory foraging mode suggests that such behaviour must have occurred over an extended time period and the recent observations (Murn 2014) are not simply evidence of opportunistic behaviour or isolated incidences.

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REFERENCES

Fowler, D.W., Freedman, E.A. & Scannella, J.B. 2009. Predatory functional morphology in raptors. Interdigital variation in talon size is related to prey restraint and immobilisation techniques. *PLoS ONE* **4**: e7999.

Griffiths, C.S., Barrowclough, G.F., Groth, J.G. & Mertz, L.A. 2007. Phylogeny, diversity, and classification of the Accipitridae based on DNA sequences of the RAG-1 exon. *J. Avian Biol.* **38**: 587–602.

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

Kane, A, Jackson, A.L., Darcy, L.O., Monadjem, A. & McNally, L. 2014. Vultures acquire information on carcass location from scavenging eagles. *Proc. Roy. Soc. B.* **281**: 1793–20141072.

Martin, G.R. 2007. Visual fields and their functions in birds. *J. Ornithol.* **148**: 547–562.

Martin, G.R. 2009. What is binocular vision for? A birds' eye view *J. Vis.* **9**: 1–19.

Martin, G.R. 2014. The subtlety of simple eyes: the tuning of visual fields to perceptual challenges in birds. *Phil. Trans. Roy. Soc. B.* **369**: 20130040.

Martin, G. R. 2017 *The Sensory Ecology of Birds.* Oxford: Oxford University Press.**Martin, G.R & Coetzee, H.C.** 2004. Visual fields in Hornbills: precision-grasping and sunshades. *Ibis* **146**: 18–26.

Martin, G.R., Jarrett, N. & Williams, M. 2007a. Visual fields in Blue Ducks and Pink-eared Ducks: visual and tactile foraging. *Ibis* **149**: 112–120.

Martin, G.R. & Piersma, T. 2009. Vision and touch in relation to foraging and predator detection: insightful contrasts between a plover and a sandpiper. *Proc. R. Soc. Lond. B.* **276**: 437–445.

Martin, G.R. & Portugal, S.J. 2011. Differences in foraging ecology determine variation in visual field in ibises and spoonbills (Threskiornithidae). *Ibis* **153**: 662–671.

Martin, G.R., Portugal, S.J. & Murn, C.P. 2012. Visual fields, foraging and collision vulnerability in *Gyps* vultures. *Ibis* **154**: 626–631.

Mundy, P.J. 1982. The comparative biology of southern African vultures. Vulture Study Group, Johannesburg, South Africa.

Mundy, P.D., Butchart, J. & Piper, S. 1992. The Vultures of Africa. Academic Press, London.

Murn, C.P. 2014. Observations of predatory behavior by white-headed vultures. *J. Raptor Res*. **48**: 297–299.

O'Rourke, C., Hall, M., Pitlik, T. & Fernandez-Juricic, E. 2010. Hawk Eyes. I: Diurnal raptors differ in visual fields and degree of eye movement. *PLoS ONE* **5**: e12802.

Potier, S., Bonadonna, F., Kelber, A., Martin, G.R., Isard, P-F., Dulaurent, T. & Duriez, O. 2016. Visual abilities in two raptors with different ecology. *J.Exp. Biol.* **219**: 2639-2649.

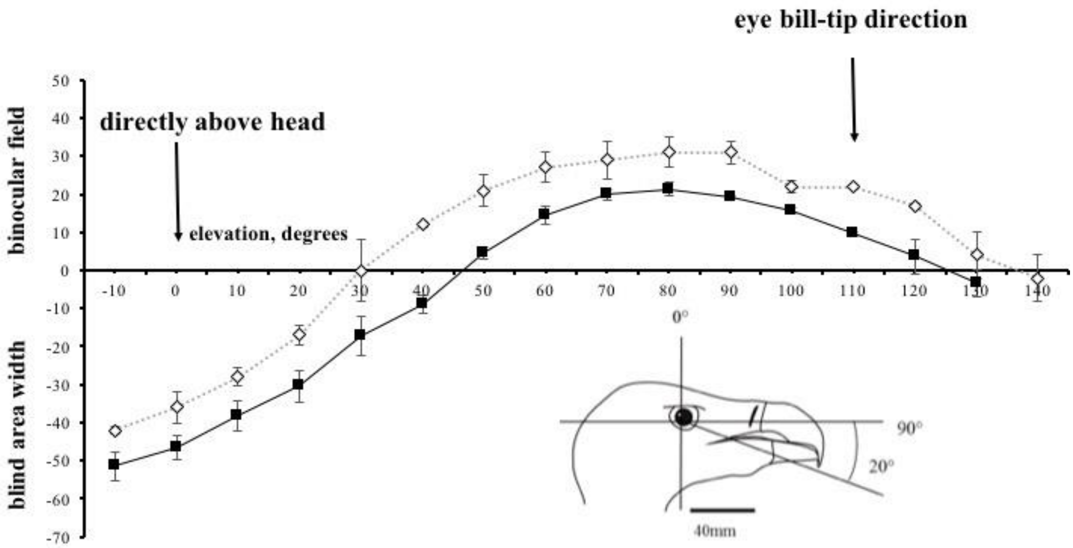

Figure 1. Mean (± se) angular separation of the retinal field margins as a function of elevation in the median sagittal plane in vultures. Positive values indicate overlap of the field margins (binocular vision), and negative values indicate the width of the blind areas. The coordinate system is such that the horizontal plane is defined by the 9° (in front of the head) and 0° lies directly above the head. 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. The upper dashed line represents the mean values for White-headed Vultures, and the black solid line the mean for two carrion feeding vulture species (White-backed and Griffon; N=2 for all species). The visual field topography of White-headed Vultures are significantly different in comparison to the other two vulture species.

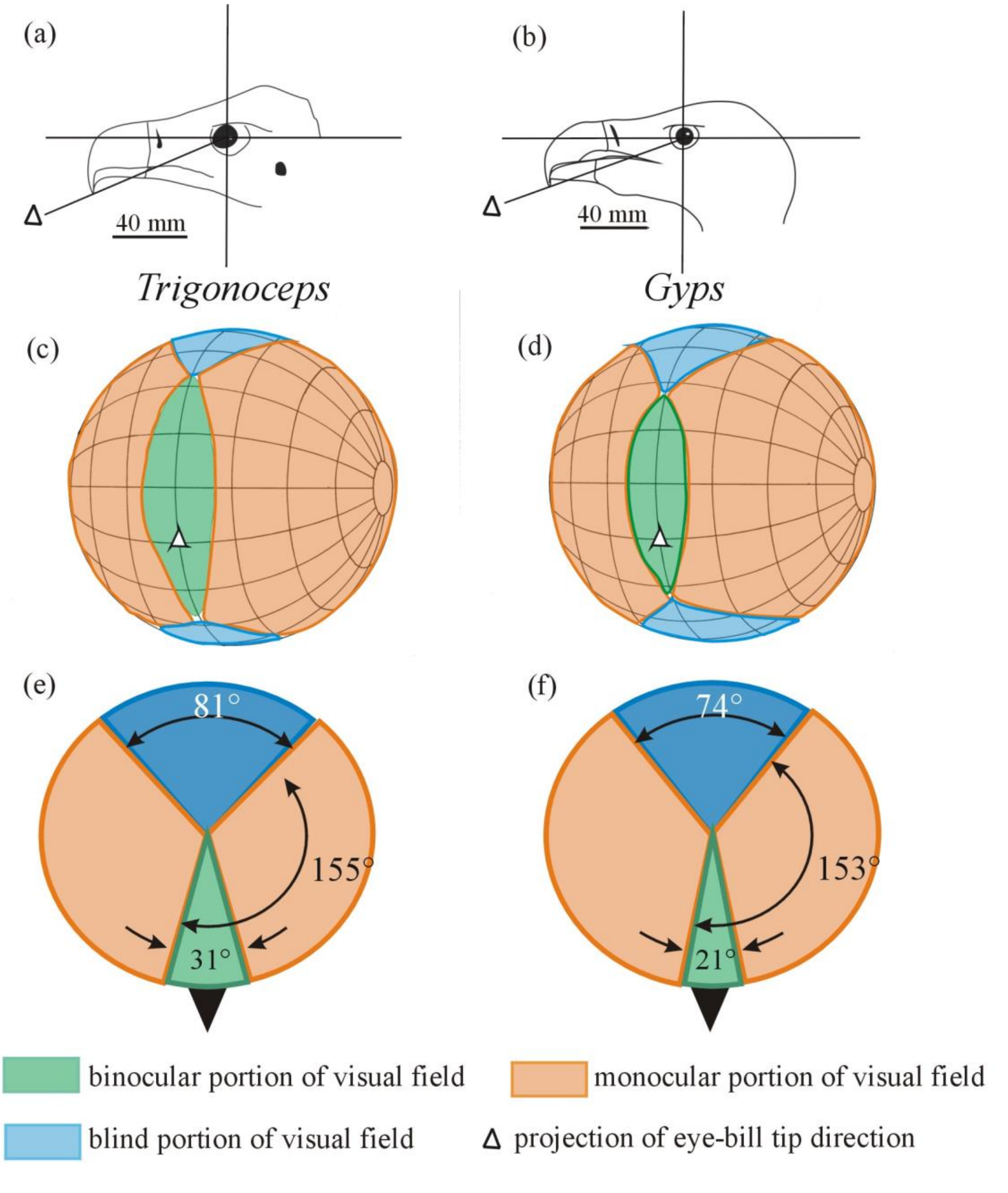

Figure 2. Visual fields of White-headed Vultures (*Trigonoceps*) and Griffon and White-backed Vultures (*Gyps*). (*a*, *b*) Drawings of a lateral view of the heads in the positions at that the visual fields were measured and as shown in the diagrams. The eye-bill tip direction projects 20° below the horizontal. (*c*, *d*) Perspective views of orthographic projections of the boundaries of the retinal fields of the two eyes. 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° intervals). It should be imagined that the bird's head is positioned at the centre of a transparent sphere with the directions of the bill tips and field boundaries projected onto the surface of the sphere. (*e*, *f*) Sections through the visual fields in the horizontal plane.