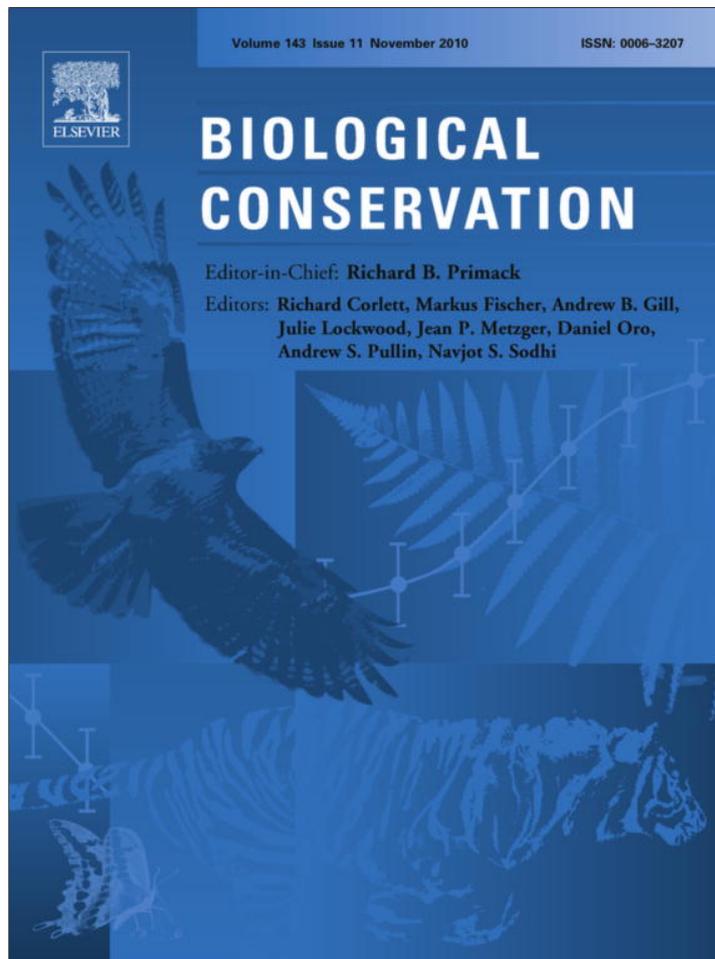


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Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/biocon

Bird collisions with power lines: Failing to see the way ahead?

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ARTICLE INFO

Article history:

Received 22 April 2010

Received in revised form 4 June 2010

Accepted 14 July 2010

Available online 3 August 2010

Keywords:

Vision

Blind areas

Collisions

Mitigations

Bustards

Cranes

Storks

ABSTRACT

Visual fields were determined in three bird species representative of families known to be subject to high levels of mortality associated with power lines; kori bustards *Ardeotis kori*, Otididae, blue cranes *Anthropoides paradisea*, Gruidae and white storks *Ciconia ciconia*, Ciconiidae. In all species the frontal visual fields showed narrow and vertically long binocular fields typical of birds that take food items directly in the bill under visual guidance. However, these species differed markedly in the vertical extent of their binocular fields and in the extent of the blind areas which project above and below the binocular fields in the forward facing hemisphere. The importance of these blind areas is that when in flight, head movements in the vertical plane (pitching the head to look downwards) will render the bird blind in the direction of travel. Such movements may frequently occur when birds are scanning below them (for foraging or roost sites, or for conspecifics). In bustards and cranes pitch movements of only 25° and 35° respectively are sufficient to render the birds blind in the direction of travel; in storks head movements of 55° are necessary. That flying birds can render themselves blind in the direction of travel has not been previously recognised and has important implications for the effective mitigation of collisions with human artefacts including wind turbines and power lines. These findings have applicability to species outside of these families especially raptors (Accipitridae) which are known to have small binocular fields and large blind areas similar to those of bustards and cranes, and are also known to be vulnerable to power line collisions.

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1. Introduction

Many species of birds are prone to collisions with human artefacts such as wind turbines and power lines, especially where these obstacles occur as apparently prominent features in open air space (Drewitt and Langston, 2008). This is surprising since it is widely held that flight in birds is primarily controlled by vision (Gill, 2007) and many of the species most vulnerable to such collisions have relatively large eyes which can potentially provide high visual acuity at daytime light levels (Land and Nilsson, 2002).

While there has been little research into the demographic impacts of power line mortality, preliminary efforts suggest this is likely to be severe for some bird species. For example, in Europe over a 16 year period it was estimated that approximately 25% of juveniles and 6% of adult white storks *Ciconia ciconia* (Ciconiidae, Ciconiiformes) died annually from power line collisions and electrocutions (Schaub and Pradel, 2004). In the Overberg region of South Africa even higher power line mortality rates have recently been estimated, with 12% of blue cranes *Anthropoides paradisea*, Gruidae, Gruiformes; classified as a species of vulnerable conserva-

tion status (BirdLife, 2009), and 30% of Denham's bustards *Neotis denhami* (Otididae, Gruiformes) killed annually by power line collisions (Shaw, 2009). Ludwig's bustards *Neotis ludwigii*, white storks, grey crowned cranes *Balearica regulorum* and kori bustards *Ardeotis kori* are amongst the other most commonly reported collision victims in South Africa (Eskom/EWT Strategic Partnership, 2008). For Ludwig's bustards, it is estimated that the rate of mortality from collisions is probably unsustainable, ultimately threatening the survival of this species (Jenkins et al., 2010).

The particular circumstances that lead to a collision between a bird and power lines are highly variable both temporally and spatially, making widespread predictions of dangerous lines for mitigation difficult; there are estimated to be 65 million km of medium–high voltage power lines presently in use around the world (ABS Energy Research, 2008). Analysis of collated data on collision incidents has focused primarily upon collision susceptibility that results from flight behaviour, especially manoeuvrability with respect to velocity of approach to an obstacle (Bevanger, 1998; Drewitt and Langston, 2008; Janss, 2000). Perceptual aspects of collisions have not received investigation beyond the general observation that some collisions occur when visibility is reduced due to lower light levels or weather conditions, but it is thought that many collisions occur under daytime light levels and when

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visibility is high (Drewitt and Langston, 2008). Measures to reduce the probability of collisions have usually involved marking obstructions with devices designed to increase the probability of detection from a greater distance, the assumption being that the obstruction is below the limit of visual resolution within the flight avoidance distance of many bird species. For example, power lines have been marked with objects such as reflective balls, flapping flags, and wire coils (Bevanger, 1994; Janss and Ferrer, 1998). However, despite more than 30 years of using such devices the probability of mortality caused by power line collisions remains high for certain species (Drewitt and Langston, 2008; Janss and Ferrer, 2000).

It has been generally assumed that birds will perceive a hazard in a comparable way to human observers; indeed, such assumptions underpin the design of most hazard markers (Janss and Ferrer, 1998). However, it is clear that the information that birds extract visually from their environment can be quite different from that extracted by humans in the same circumstance. This is due to fundamental differences between birds and primates at all levels of organisation of their visual systems, including retina, physiological optics, visual fields, and the higher order processing of visual information (Bowmaker et al., 1997; Hunt et al., 2009; Martin and Osorio, 2008; Reiner et al., 2005; Shimizu and Bowers, 1999). A key aspect of these differences which could have a direct impact on collision susceptibility is visual fields. This is because regardless of the ways in which visual information is processed, visual fields determine what part of an animal's environment can influence its behaviour at any one instant (Martin, 2007). Especially important will be the characteristics of that section of a bird's visual field which projects forward and hence normally "looks" in the direction of travel.

The visual field of an animal is a function of the optics of the eyes and of their placement in the head, and among birds a number of visual field arrangements have been described (Martin, 2007). Visual fields need to serve two key functions: (1) the detection of predators, conspecifics, obstacles and potential food sources that are remote from the animal, and (2) the control of accurate behaviours, such as the procurement of food items, at close quarters. Both functions are potent sources of natural selection but they are potentially antagonistic (Fernandez-Juricici et al., 2008; Martin and Piersma, 2009).

In bird species that employ visual information for the guidance of bill position when taking food items, the projection of the bill falls approximately centrally within the binocular section of the visual field and in the majority of birds which feed in this way the binocular field is relatively narrow, between 15° and 30° in maximum width, and vertically long (Martin, 2007). However, the vertical extent of the binocular field varies markedly. For example in herons (Ardeidae), it extends through 180° so that these birds have comprehensive visual coverage of the hemisphere in front of the head (Martin and Katzir, 1994), while in eagles it extends through only 80° giving these birds extensive blind areas both above and below the bill in the frontal hemisphere (Martin and Katzir, 1999). In birds which do not employ visual information to guide bill position (e.g. some duck species (Anatidae) which filter feed, some long-billed shorebirds (Scolopacidae) and kiwi (Apteryx spp.), which feed by probing in soft substrates guided by tactile cues, the bill falls at the very periphery or outside the visual field. In the case of the ducks and shorebirds the eyes are positioned high in the skull giving comprehensive visual coverage of the hemisphere around and above the head, i.e. there are no blind areas in their visual field except that produced by their own body (Martin, 2007).

In birds the function of binocular vision appears to lie primarily in the control of behaviours requiring the accurate positioning and timing of bill-opening towards objects close to the animal (primarily

the control of bill position for food procurement and/or chick provisioning). The control of locomotion with respect to more distant objects is a less important determinant of binocular field characteristics (Martin, 2009). Indeed for birds such as the filter feeding ducks or the tactile probing shorebirds the binocular field can be very narrow ($\approx 5^\circ$) in the direction of travel. Furthermore, it seems likely that in many birds the detection of food items is primarily under the control of lateral vision, with control of item procurement transferred to forward vision just prior to seizure (Land, 1999; Montgomerie and Weatherhead, 1997; Rogers, 2008; Tucker, 2000; Tucker et al., 2000).

We hypothesised that the frontal visual fields of birds may have characteristics that result in them not always being able to see objects directly ahead. We measured visual field topography in white storks, blue cranes and kori bustards. These species live predominantly in open habitats, and are visually guided ground feeders that typically roost between dusk and dawn (Archibald and Meine, 1996; Collar, 1996; Elliot, 1992; Hancock et al., 1992). In southern Africa, storks, cranes and bustards can be found utilising similar habitats (Hockey et al., 2005) and are susceptible to collisions with power lines, but they differ in their susceptibility to such events (Jenkins et al., 2010). They all have large eyes of similar size and thus, assuming similar retinal structure, are likely to have similar and relatively high visual acuity (Martin, 1985).

Based upon previous comparative analyses of visual fields in birds (Martin, 2009) we predicted that all three species would have visual fields in which the bill projects centrally within a relatively narrow binocular field (15–30° wide), which is in conformity to their similar foraging behaviours involving visual guidance of the bill towards individual items (Archibald and Meine, 1996; Collar, 1996; Elliot, 1992). We predicted however, that these birds differ in the vertical extent of their binocular fields. This would result in differences in the extent of the blind areas to the front of the head; the key region for the detection of obstacles in flight.

2. Materials and methods

We used an ophthalmoscopic reflex technique to measure visual field parameters (monocular, binocular and cyclopean fields) and eye movement amplitudes of live blue cranes, kori bustards and white storks obtained from zoological parks in South Africa.

The ophthalmoscopic reflex technique has been used in excess of 20 years on more than 30 different bird species of different phylogeny, ecology and feeding techniques and has the advantage of readily permitting interspecific comparisons (Martin, 2007).

The procedure used is non-invasive. It involves the restraint of birds for between 30 and 45 min, and was reviewed by a UK Home Office Inspector in 2008. It was not considered to fall within the regulations that govern licensed procedures with animals, which apply in the UK. However, the ethical guidelines with respect to handling and restraining birds required for licensed procedures in the UK (UK Animals (Scientific Procedures) Act 1986) were followed.

Birds were adults and had been held in captivity for a number of years. Birds were studied close to their holding aviaries to which they were immediately returned after measurement. Sexes were unknown. Four blue cranes were studied at Tygerberg Zoo (Cape Town), and two white storks and two kori bustards were studied at Johannesburg Zoological Park.

For a detailed description of the apparatus and methods see Martin et al. (2007). Briefly, each bird was hand held with the breast resting in a foam rubber cradle and the legs held out behind the body. The head was fixed in position at the centre of a visual perimeter; a device which permits the eyes to be examined from known positions about the head. Each bird's head was fixed by tap-

ing (Micropore™ tape) the bill in place in a specially manufactured bill holder. The surfaces of the holder were coated in cured silicone sealant to provide a non-slip cushioned surface. Different bill holders were used for each species. Holder characteristics were determined prior to the study by examination and measurement of skulls held in the collection of the United Kingdom Natural History Museum (Bird Group, Tring). Each holder takes account of the size and shape of the bill of the species. In the cranes the bill was held closed; in the storks and bustards the bill was held slightly open. Whether the bill was held open or closed was determined by the need for the birds to ventilate freely and this in turn was determined by the position of the nares which had to be left uncovered by the Micropore™ tape, or the mouth had to remain slightly open. We judged that a slightly opened mouth was preferable in the storks and bustards, but a closed mouth position was suitable for the cranes.

The visual perimeter's co-ordinate system followed 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.

The eyes were examined using an ophthalmoscope mounted against the perimeter arm and its latitudinal position read to $\pm 0.5^\circ$. Eyes were found to be mobile and their movements non-conjugate, i.e. the eyes could move independently. To determine the limits of the visual fields and the magnitude of eye movements the following procedure was used. For each eye, as a function of elevation (longitude) in the median sagittal plane at $10^\circ (\pm 1.0^\circ)$ intervals, the visual projections of the maximum and minimum limits of the retinal visual field were determined. The limit of the visual field is determined by the projection of the limit of the retina, the ora serrata. This is seen as a clear difference between the bright reflection from the retinal surface and the black of the ciliary folds. At each elevation (longitude) the perimeter co-ordinates (latitude) at which the limit of the retina was seen to lie at the centre of the pupil was determined. However, because of eye movements the visual projection of these limits is not fixed. Therefore the maximum and minimum limits of the visual field at each elevation

were determined. These were defined by the positions that the retinal margins spontaneously adopted when the eyes were fully rotated "forwards" (converged) and "backwards" (diverged). To determine these positions, successive measures of the projection of the retinal margin at each elevation were made in quick succession and the maximum and minimum values recorded. The amplitude of eye movements at each elevation was determined by the difference between these maximum and minimum values. Eye movements are complex rotational movements and this procedure enables the translational effect of these movements to be recorded at each elevation and hence determine how the limits of the visual field are altered by these movements. At some elevations eye movements made no discernable difference to the position of the field margins, at other elevations the effects of eye movements on the limits of the visual field were substantial.

Because of small sample size no statistical analysis would be meaningful. However, it should be noted that measure of the projections of retinal field margins using this technique within an individual bird are generally highly repeatable to within $\pm 2^\circ$ and that intraspecific variation is typically within $\pm 4^\circ$ (Martin, 2007), leading to small standard errors, as indicated in Fig. 1.

By combining data on the projections of the retinal margin as a function of elevation (corrected for viewing from a hypothetical viewing point placed at infinity (Martin, 1984); this correction is based upon the distance between the eyes and the viewing distance (320 mm) used in the perimeter apparatus) a topographical map of the visual field and its principal features was constructed for each species. These features are: monocular fields, the visual field of a single eye; binocular field, the area where monocular fields overlap; cyclopean field, the total visual field produced by the combination of both monocular fields. It was possible to measure limits of the visual field at 10° intervals of elevation in an arc from directly behind the head, to above the head and then down to 60° below the horizontal in front of the head. Alignment of the birds' heads in the perimeter was such that the ophthalmoscope viewing aperture was, in effect, moved over the surface of a sphere centred on the mid-point of the line joining the centres of the pu-

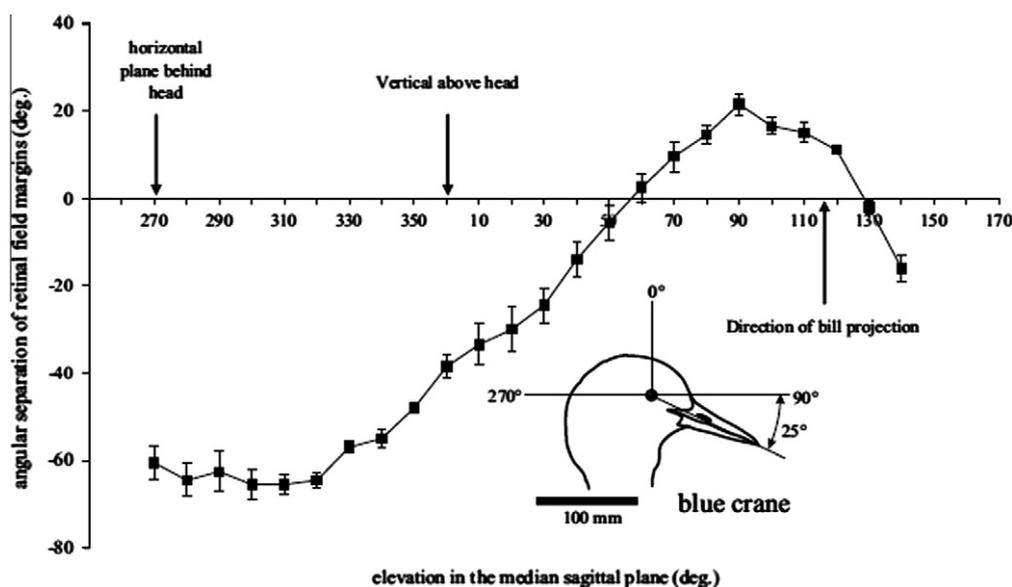


Fig. 1. Mean (\pm SE) angular separation of the retinal field margins as a function of elevation in the median sagittal plane in blue cranes. Positive values indicate overlap of the field margins (binocular vision), negative values indicate the width of the blind areas. The co-ordinate system is such that the horizontal plane is defined by the elevations 270° (behind the head) and 90° (in front of the head), and 0° directly above the head, the same co-ordinates are used in Fig. 2. These directions are indicated in the outline scaled drawing of the head of a blue crane. The projection of the eye–bill tip axis is also indicated. The value of the binocular field width at elevation 120° 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 value at elevations 110° and 130° .

pils. This point was defined as the cyclopean projection centre, and the position of the visual fields are described by reference to it.

Calibrated photographs of the head of each bird when held in the hands and in the apparatus were taken. These were used to determine eye positions within the skull, the relationship between the horizontal and the eye-bill tip angle when the measurements were taken, and to estimate the axial length (the distance from the cornea to the posterior pole of the eyes). The latter estimate was based upon the divergence of the optic axes (see below) and the assumption that the fundus (posterior portion of the eye) is semicircular and that the eyes meet in the sagittal plane of the skull.

In each of the birds the direction of the optic axis (the line along which the cornea and the lens refractive surfaces are centred) of each eye was determined by recording the perimeter co-ordinates at which the 1st and 2nd Purkinje images (reflections from the cornea and from the lens anterior surface) of a discrete source of light held close to the line of sight were most closely aligned.

In common with most other birds when held at various body angles, head position in all three species was relatively stable. This eye-bill tip angle was approximately 5° below the horizontal in the bustards, 40° in the storks and 25° in the cranes. Photographs of the birds when at rest in the holding facilities also confirmed these bill angles in unrestrained but alert birds. Inspection of illustrations in handbooks depicting these species at rest (Archibald and Meine, 1996; Collar, 1996; Elliot, 1992) also show similar bill angles to the horizontal. However, these head positions are not necessarily the same as those adopted by the birds in flight. Our own observations and analysis of photographs and illustrations of birds in flight available through internet searching (Arkive, 2010; <http://www.arkive.org/>, Google Images, 2010 <http://www.google.co.uk/imghp>), and in field guides (Sinclair et al., 1997; Hockey et al., 2005) (we examined 30 of our own photographs of blue cranes entering a roost site, and 10 photographs/illustration from published sources of the bustards and storks), indicate that the in-flight bill angle is approximately 20° below the horizontal in both storks and cranes and 5° below the horizontal in the bustards. When the visual field measurements were made the tips of the mandibles projected at approximately 5° below the horizontal in the bustards, and 20° below the horizontal in the storks and cranes, i.e. the typical in flight head positions.

3. Results

The mean (\pm SE) angular separations of the retinal field margins as a function of elevation in the median sagittal plane in blue cranes are shown in Fig. 1. Photographs of the lateral views of the heads of a kori bustard, blue crane and white stork with the heads held at their typical resting angle are shown in Fig. 2. Maps of the visual fields in the frontal sector are shown in Fig. 2 row a. Vertical sections through the binocular field in the median sagittal plane are shown in Fig. 2 row c. In these figures the birds' heads are depicted at the eye-bill tip angles similar to those typically adopted by the birds in flight. Sections through the visual fields are shown in Fig. 2 row b. These sections are at an approximately horizontal plane when the head is held in the positions shown in Fig. 2 row c.

3.1. General topography of visual fields

Fig. 2 row a indicates that the general topography of the visual fields of these three species is similar and show features associated with the use of vision to guide the procurement of prey by the bill (Martin, 2009). Thus all three species have a narrow but vertically

long binocular field with the projection of the bill either central or below the horizontal (Fig. 2 rows a and c).

3.2. Interspecific differences in visual fields

The horizontal widths of the visual field of each eye are similar; 162°, 160.5° and 158° in bustards, cranes and storks respectively (Fig. 2 row b) suggesting that the eyes of these three species are of similar optical design (Martin, 1983). However, the combination of the monocular fields in each species gives rise to systematic interspecific differences in all visual field parameters. Thus, the maximum widths and vertical extent of the binocular area differ systematically between the species; 17° × 60°, 21.5° × 75°, 28° × 120° in bustard, crane and stork respectively (Fig. 2 rows b and c). The widths of the blind areas behind and above the head also differ systematically; 52°, 60.5° and 72° in bustard, crane and stork respectively (Fig. 2 row b). This results in the proportion of the sphere around the head that is covered by the visual fields differing markedly between these species, with total visual coverage very much reduced in bustards compared with storks (Fig. 2 row a). In particular, the proportion of the hemisphere that projects forward has the least visual coverage in bustards with a large blind area in the dorsal quadrant and a smaller blind area in the ventral quadrant. Storks have almost comprehensive coverage of the frontal hemisphere, while cranes also have substantial portions of the frontal hemisphere that are not covered by the visual field (Fig. 2 row a).

3.3. Eye axial length and eye movement amplitude

Mean eye axial lengths were estimated to be 22 mm, 25 mm and 30 mm in the storks, cranes and bustards respectively. Mean eye movement amplitude in the cranes based upon two birds measured at two elevations in the region where binocular field width was maximal was 14°. In all birds casual observations through the ophthalmoscope showed spontaneous and non-conjugate eye movements to be present and of sufficient amplitude to abolish binocularity in the region about the horizontal.

4. Discussion

4.1. Visual fields and foraging

Based upon the foraging technique of these three species, which involves taking food items directly by the bill under visual guidance (Archibald and Meine, 1996; Collar, 1996; Elliot, 1992), we hypothesized that all three species would have visual fields in which the bill projects centrally or below the horizontal within a relatively narrow binocular field (15–30° wide). Such frontal visual field topography has been described in a wide range of birds species which, although differing in phylogeny, general ecology and prey type, share in common visual guidance of the bill towards prey and food objects, regardless of whether they are taken by pecking or lunging (Martin, 2007, 2009). Data from all three species (Fig. 2 row a) support this hypothesis. This indicates that although these species are assigned to two phylogenetically distinct orders (cranes and bustards, Gruiformes; storks Ciconiiformes, (Hackett et al., 2008; Livezey and Zusi, 2007)) the fundamental configuration of their binocular fields show evidence of convergence associated with the visual challenges of aiming accurately towards an item with the bill, and of determining time to reach that item in order to seize it with the bill (Martin, 2007, 2009).

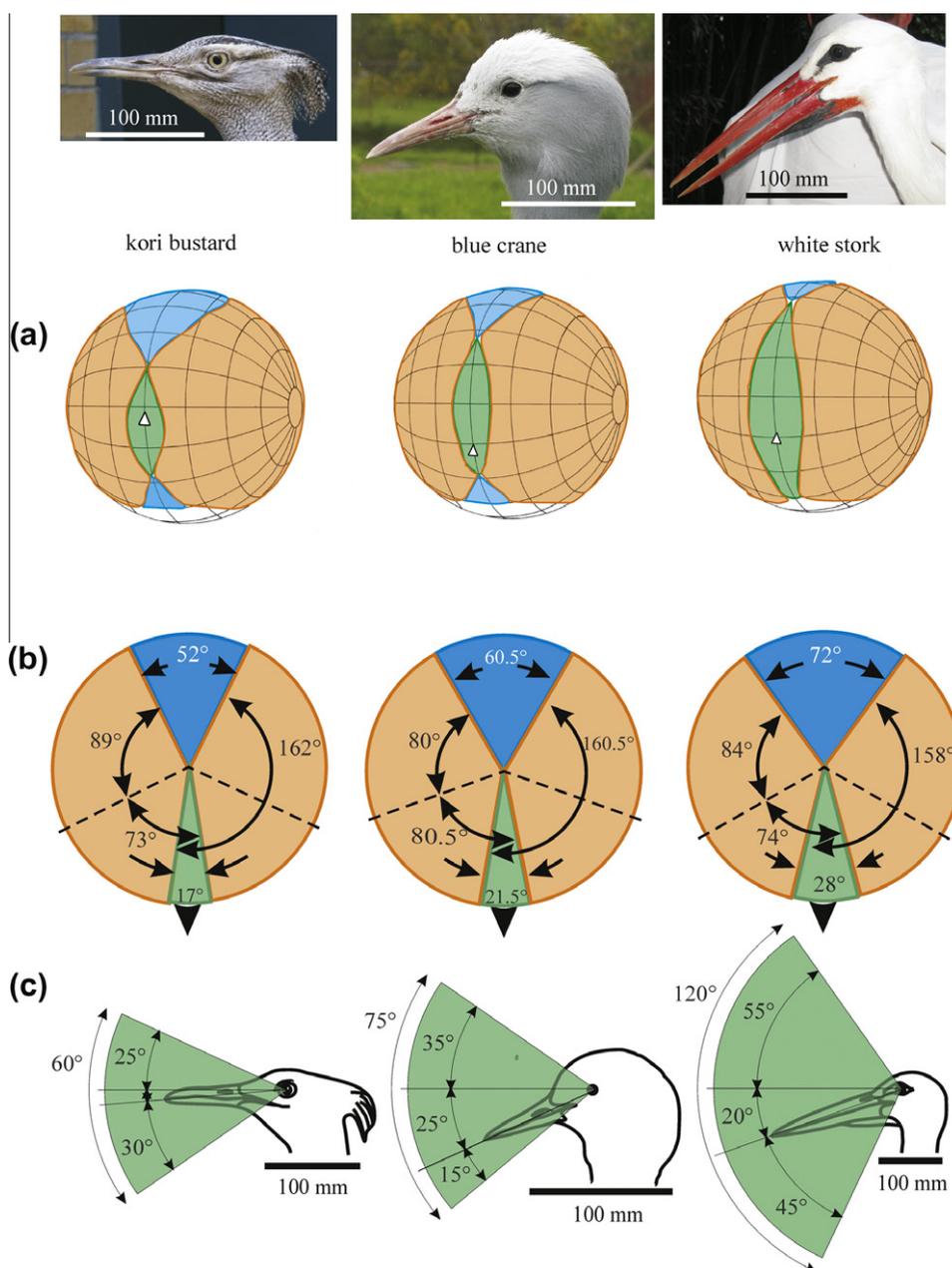


Fig. 2. Visual fields in kori bustards, blue cranes, and white storks. The figure is a matrix that allows interspecific comparison of the same information across rows, while columns show information for each species. Each species is depicted by a photograph showing a lateral view of the head at the head of a column. (row a) 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 co-ordinate 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 with those shown in Fig. 1 for blue cranes. 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 row c. (row b) Horizontal sections through the visual fields in a horizontal plane defined by the elevations 270° and 90° in Fig. 1, dashed lines indicate the directions of the optic axes. (row c) Vertical sections through the binocular fields in the median sagittal plane defined by the vertically oriented equators of the diagrams in row a. The line drawings of the heads of the birds show them in the approximate orientations typically adopted by the species in flight (see discussion in Section 2). Green areas, binocular sectors; pink areas, monocular sectors; blue areas, blind sectors; downward pointing black arrowheads in row b, direction of the bill; white triangle direction of bill projection in row a; white pentagon direction of optic axes in row a. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

4.2. Interspecific differences in visual fields

Despite the similarity in general topography of binocular fields there are some notable interspecific differences in the visual fields of these birds. These include the vertical extent of the binocular fields (Fig. 2 rows a and c), the direction of the projection of the bill within the binocular fields (Fig. 2 rows a and c), the extent of blind areas above and behind the head (Fig. 2 rows a and b), and the extent of visual coverage in the hemisphere to the front of the head

(Fig. 2 row a). These differences must arise primarily due to differences in the positioning of eyes in the skull since the visual field of a single eye in each species is of similar width (Fig. 2 row b), suggesting that they are similar in optical design. The function of these differences in visual field parameters may lie in detailed differences in the foraging ecology of these species and/or in phylogeny.

The near comprehensive visual coverage of the frontal hemisphere in the storks, which is achieved by the vertically long binocular field, is similar to the configuration found in other birds of the

same order, herons (Ardeidae). In herons this frontal field configuration is thought to be associated with stealth-foraging upon evasive prey, such as fish and amphibians, it being argued that the near comprehensive visual coverage of the frontal hemisphere may allow a stationary or slow moving bird to detect prey below it without moving the head, and thus initiating an escape response in the prey item, until a prey strike is initiated (Katzir and Martin, 1994). Storks may face similar visual challenges when foraging on evasive prey such as small mammals, reptiles, amphibian and fish which make up the bulk of their diet, and which are typically detected when walking slowly forward (Hancock et al., 1992).

Although bustards and cranes are also thought to be visually guided in their foraging, they take a broader array of items than storks. These include a wide range of stationary vegetable matter (seeds, berries, bulbs) and animal resources which are not necessarily evasive such as snails, orthoptera, small rodents, lizards, snakes, and bird eggs and nestlings (Ellis et al., 1996; Johnsgard, 1991). Thus these species do not need to employ a stealth-foraging technique, which could account for the smaller vertical extent of the binocular fields found in both the bustards and cranes. However, what might these birds gain by having less extensive coverage of their frontal field? The answer probably lies in comparison of the extent of the blind area behind the head. Fig. 2 row b shows that storks have the widest blind area behind the head and since all three species have eyes with similar visual fields, more extensive frontal vision can only be achieved at the cost of less comprehensive vision behind the head. Thus there is a trade-off between the frontal and hind portions of the visual fields in which a wider blind area, and presumably greater vulnerability to attack by predators from behind, is traded against the requirement for more comprehensive frontal field coverage necessary for visually guided stealth-foraging.

Such a trade-off has been noted previously. It has been argued that the primary driver of visual field configuration is predator detection, within the constraints of sufficient visual coverage about the bill to guide its placement when foraging, or when provisioning chicks. In birds which do not require vision for such tasks, as for example some ducks (Anatidae) and shorebird (Scolopacidae) species which employ either filter feeding or tactile cues for prey detection, and which have precocial self-feeding chicks, totally comprehensive visual coverage of the hemisphere above the head is achieved (Martin, 2007; Martin et al., 2007). However, in all other species there appears to be a trade-off between minimising the width of the blind area behind the head, and the minimum requirements for binocularity for the control of bill position (Martin, 2007).

4.3. Visual fields and susceptibility to collisions

That birds can, and should, maintain visual coverage of the region ahead of them when in flight would seem a reasonable assumption. However, our data provides evidence that this may not always be the case. In bustards and cranes there are extensive blind regions in the frontal hemisphere and movements of the head downwards (forward pitch) by greater than 25° and 35° respectively (Fig. 2 rows a and c) would bring these blind areas to project forwards in the direction of flight. Under these circumstances any object directly ahead of the flying bird could not be detected regardless of the visual capacities of the bird's eyes or the size and contrast of the object. However, the same argument would not seem to apply so readily to the storks. In these birds the vertically longer binocular field and its greater extent above the horizontal means that a downward head movement of 55° or greater (which would result in the bill pointing slight backwards from vertical beneath the bird) is necessary to abolish all vision forward in the direction of travel.

Little appears to be known about where birds are looking during flight, especially when they are flying in open airspace above the height of local natural vegetation. There are however, anecdotal observations (photographs and video of birds in flight) which show that at least larger species frequently turn their heads sideways or orientate their head downwards when in flight. There is evidence that gull-billed terns *Gelochelidon nilotica* turn their heads systematically to look both laterally and downwards (forward pitch of the head by 60°) when searching for prey over mud flats in order to bring central (probably foveal) vision to guide the task of detection (Land, 1999). Peregrine falcons are also thought to use lateral (possibly foveal) vision to detect and approach prey in aerial pursuit, and do not bring forward vision to bear upon the prey object until very close to contact (Tucker, 2000; Tucker et al., 2000).

We also observed the spontaneous abolition of binocularity in all three species, and in the cranes we were able to quantify eye movement amplitudes in the horizontal plane and show that they are sufficient to abolish the binocular field. Thus in flight, cranes could move their eyes sufficiently to temporarily abolish vision directly in front of them. What triggers these spontaneous and non-conjugate eye movements of birds is unknown but their function may be primarily concerned with scanning a scene with central and/or foveal vision since this is likely to have highest spatial resolution within the entire visual field. The abolition of binocularity may be viewed as a consequence rather than a function of such eye movements. However, such temporary abolition of vision forwards in the direction of flight could also have important consequences with respect to the probability of collision with objects that intrude into the open airspace.

A further aspect of these visual field characteristics that can render cranes and bustards especially vulnerable to collisions relates to power line configuration. In most high tension transmission systems, the power lines are protected from lightning strike by relatively small diameter earth wires suspended above the array of heavier conductor lines used to transmit power. It is well known that collisions with earth wires are more frequent than collisions with conductors and this is often explained by lower visibility of these wires with the result that they are seen too late to be avoided by birds trying to fly over the more obvious conductors (Bevanger, 1994; Drewitt and Langston, 2008). However, because of the configuration of the forward visual field, earth wires may often fall within the blind area that projects forwards and upwards. Thus birds flying upwards to avoid colliding with conductors may not be able to see earth wires. Again, this argument would not apply so readily to the storks where the greater vertical extent of the binocular field means that the earth wire is likely to always fall within the visual field.

4.4. Power line mortality: failing to see the way ahead?

Data presented here shows clearly that in a group of birds known to be vulnerable to collisions with power lines, aspects of their visual fields, especially the extent of blind areas that project in the frontal hemisphere above the binocular field, mean that the birds may frequently be unable to see what lies ahead of them. This will occur if the birds are searching the area below them (for conspecifics, foraging and roosting sites) and pitching their head downwards. Inability to see power lines may also occur as these birds fly upwards, either from the ground close to a power line array or in trying to avoid collision with conductors which lie directly ahead. In these situations lines may fall within the upward and forward projecting blind portion of the visual field above the binocular area. These considerations are likely to apply in other birds with similarly small binocular fields and extensive blind areas above them. For example, short-toed snake-eagles *Circaetus gallicus*, which fly slowly forwards foraging for reptiles on the ground, have

a binocular field (max. width 20°, height 81°) which is of very similar dimensions to those of cranes (21.5° × 75°) with an extensive blind area above (Martin and Katzir, 1999). In these eagles a downward head movement of only 25° would render the birds blind directly ahead. Raptors are regularly recorded as collision victims, with this source of mortality implicated in the decline of the Bonelli's eagle *Hieraetus fasciatus* population in Europe (Bevanger, 1998; Mañosa and Real, 2001).

Vulnerability to collision depends on many factors, including bird behaviour and manoeuvrability, topography, weather and power line design and placement (Bevanger, 1994). Our data show that vision is probably a key aspect of this problem. While there are no good comparative data on the collision mortality rates of the species studied here, where systematic surveys for collision victims have been conducted within their ranges, bustards and cranes are usually among the most numerous victims found (Brown and Drewien, 1995; Janss, 2000; Shaw, 2009). In a study conducted in Spain, great bustards *Otis tarda* and little bustards *Tetrax tetrax* were clearly shown to have the highest chance of collision of all species considered relative to the number of line crossings made (Janss and Ferrer, 2000).

White storks are known to suffer high mortality associated with power lines (Schaub and Pradel, 2004), but these birds have almost comprehensive visual coverage of the frontal hemisphere and head movements of even large amplitude will not render these birds blind in the direction of flight. Therefore these birds are more likely than bustards and cranes to detect power lines and other obstacles ahead of them in flight. However, unlike cranes and bustards, storks commonly nest on power infrastructure (Elliot, 1992). As well as putting them at risk of electrocution, this could escalate the probability of collision by increasing the amount of time spent flying close to power lines. However, further information is needed to fully understand the interactions of white storks with power wires that lead to high mortality. For example, information on such topics as the stage of the breeding season when mortality is highest, the age of birds and the number of years that a bird has used a particular nest site before collision mortality occurs, could all throw light on the role of vision or other factors in the power wire collision mortality of these species.

Thus visual field topographies which have evolved primarily to meet visual challenges associated with foraging may render certain bird species particularly vulnerable to collisions with human artefacts, such as power lines and wind turbines, that extend into the otherwise open airspace above their preferred habitats. For these species placing devices upon power lines to render them more visible may have limited success since no matter what the device the birds may not see them. This may help to explain why line marking appears to be ineffective for bustards (Janss, 2000; Jenkins et al., 2010). We suggest that in certain situations it may be necessary to distract birds away from the obstacles, or encourage them to land nearby (for example by the use of decoy models of conspecifics, or the provision of sites attractive for roosting) since increased marking of the obstacle cannot be guaranteed to render it visible if the visual field configuration prevents it being detected. Perhaps most importantly, our results indicate that collision mitigation may need to vary substantially for different collision prone species, taking account of species specific behaviours, habitat and foraging preferences, since an effective all-purpose marking device is probably not realistic if some birds do not see the obstacle at all.

Acknowledgements

We dedicate this paper to the late John Spence proprietor of Tygerberg Zoo who provided us with access to blue cranes and facilities in which to conduct measurements. John died before we were able to tell him of our findings. Viviane Barquete provided ex-

pert assistance in holding the blue cranes while we conducted the measurements. Jeanne Marie Pittman and Michelle Barrows of Johannesburg Zoological Park provided us with access to white storks and kori bustards and Jeanne Marie Pittman also provided expert help in holding the bustards and storks while measurements were conducted. Work was made possible through financial support from the South African national utility Eskom to the Wildlife and Energy Interaction Group of the Endangered Wildlife Trust. We thank two people from the Endangered Wildlife Trust; Andrew Jenkins for help in instigating this work and Jon Smallie for facilitating its completion.

References

- ABS Energy Research, 2008. The T&D Report, seventh ed. ABS Energy Research, London.
- Archibald, G.W., Meine, C.D., 1996. Family Gruidae (Cranes). In: del Hoyo, J., Elliot, A., Sargatal, J. (Eds.), *Handbook of the Birds of the World*, vol. 3. Lynx Edicions, Barcelona, pp. 60–89.
- Arkive, 2010. <<http://www.arkive.org/>> (consulted January 2010).
- Bevanger, K., 1994. Bird interactions with utility structures – collision and electrocution, causes and mitigating measures. *Ibis* 136, 412–425.
- Bevanger, K., 1998. Biological and conservation aspects of bird mortality caused by electricity power lines: a review. *Biological Conservation* 86, 67–76.
- BirdLife, 2009. Species Factsheet: *Grus paradisea*. <<http://www.birdlife.org/>> (consulted January 2010).
- Bowmaker, J.K., Heath, L.A., Wilkie, S.E., Hunt, D.M., 1997. Visual pigments and oil droplets from six classes of photoreceptors in the retinas of birds. *Vision Research* 37, 2183–2194.
- Brown, W.M., Drewien, R.C., 1995. Evaluation of two power-line markers to reduce crane and waterfowl collision mortality. *Wildlife Society Bulletin* 23, 217–227.
- Collar, N.J., 1996. Family Otidae (Bustards). In: del Hoyo, J., Elliot, A., Sargatal, J. (Eds.), *Handbook of the Birds of the World*, vol. 3. Lynx Edicions, Barcelona, pp. 240–273.
- Drewitt, A.L., Langston, R.H.W., 2008. Collision effects of wind-power generators and other obstacles on birds. *Year in Ecology and Conservation Biology* 1134, 233–266.
- Elliot, A., 1992. Family Ciconiidae (Storks). In: del Hoyo, J., Elliot, A., Sargatal, J. (Eds.), *Handbook of the Birds of the World*, vol. 1. Lynx Edicions, Barcelona, pp. 436–465.
- Ellis, D.H., Gee, G.F., Mirande, C.M., 1996. *Cranes: Their Biology, Husbandry and Conservation*. National Biological Service/International Crane Foundation, Washington, DC.
- Eskom/EWT Strategic Partnership, 2008. Central Incident Register. Held and Curated by the Wildlife and Energy Interaction Group. Endangered Wildlife Trust, Johannesburg.
- Fernandez-Juricci, E., Gall, M., Dolan, T., Tisdale, V., Martin, G.R., 2008. The visual fields of two ground foraging birds, House Finches and House Sparrows, allow for simultaneous foraging and antipredator vigilance. *Ibis* 150, 779–787.
- Gill, F.B., 2007. *Ornithology*, third ed. W.H. Freeman, New York.
- Google Images, 2010. <<http://www.google.co.uk/imghp>> (consulted January 2010).
- Hackett, S.J., Kimball, R.T., Reddy, S., Bowie, R.C., Braun, E.L., Braun, M.J., Chojnowski, J.L., Cox, A., Han, K.-L., Harshman, J., Huddleston, C.J., Marks, B.D., Miglia, K.J., Moore, W.S., Sheldon, F.H., Steadman, D.W., Witt, C.C., Yuri, T., 2008. A phylogenomic study of birds reveals their evolutionary history. *Science* 1763, 1768.
- Hancock, J.A., Kushlan, J.A., Kahl, M.P., 1992. *Storks, Ibises and Spoonbills of the World*. Academic Press, London.
- Hockey, P.A.R., Dean, W.R.J., Ryan, P.G., 2005. *Roberts Birds of southern Africa*, seventh ed. The Trustees of the John Voelcker Bird Book Fund, Cape Town.
- Hunt, D.M., Carvalho, L.S., Cowing, J.A., Davies, W.L., 2009. Evolution and spectral tuning of visual pigments in birds and mammals. *Philosophical Transactions of the Royal Society B – Biological Sciences* 364, 2941–2955.
- Janss, G.F.E., 2000. Avian mortality from power lines: a morphological approach of a species-specific mortality. *Biological Conservation* 95, 353–359.
- Janss, G.F.E., Ferrer, M., 1998. Rate of bird collision with power lines: effects of conductor-marking and static wire-marking. *Journal of Field Ornithology* 69, 8–17.
- Janss, G.F.E., Ferrer, M., 2000. Common crane and great bustard collision with power lines: collision rate and risk exposure. *Wildlife Society Bulletin* 28, 675–680.
- Jenkins, A.R., Smallie, J.J., Diamond, M., 2010. South African Perspectives on a Global Search for Ways to Prevent Avian Collisions with Overhead Lines, in press, doi:10.1017/S0959270910000122.
- Johnsgard, P.A., 1991. *Bustards, Hemipodes and Sandgrouse*. Oxford University Press, Oxford.
- Katzir, G., Martin, G.R., 1994. Visual fields in herons (Ardeidae) – panoramic vision beneath the bill. *Naturwissenschaften* 81, 182–184.
- Land, M.F., 1999. The roles of head movements in the search and capture strategy of a tern (Aves, Laridae). *Journal of Comparative Physiology A – Neuroethology Sensory Neural and Behavioral Physiology* 184, 265–272.
- Land, M.F., Nilsson, D.-E., 2002. *Animal Eyes*. Oxford University Press, Oxford.

- Livezey, B.C., Zusi, R.L., 2007. Higher-order phylogeny of modern birds (Theropoda, Aves: Neornithes) based on comparative anatomy. II. Analysis and discussion. *Zoological Journal of the Linnean Society* 149, 1–95.
- Mañosa, S., Real, J., 2001. Potential negative effects of collisions with transmission lines on a Bonelli's Eagle population. *Journal of Raptor Research* 35, 247–252.
- Martin, G.R., 1983. Schematic eye models in vertebrates. In: Ottoson, D. (Ed.), *Progress in Sensory Physiology*, vol. 4. Springer-Verlag, Berlin, pp. 43–81.
- Martin, G.R., 1984. The visual fields of the tawny owl, *Strix aluco* L. *Vision Research* 24, 1739–1751.
- Martin, G.R., 1985. Eye. In: King, A.S., McLelland, J. (Eds.), *Form and Function in Birds*, vol. 3. Academic Press, London, pp. 311–373.
- Martin, G.R., 2007. Visual fields and their functions in birds. *Journal of Ornithology* 148 (Suppl. 2), 547–562.
- Martin, G.R., 2009. What is binocular vision for? A birds' eye view. *Journal of Vision* 9, 1–19.
- Martin, G.R., Jarrett, N., Williams, M., 2007. Visual fields in Blue Ducks and Pink-eared Ducks: visual and tactile foraging. *Ibis* 149, 112–120.
- Martin, G.R., Katzir, G., 1994. Visual fields and eye movements in herons (Ardeidae). *Brain, Behavior and Evolution* 44, 74–85.
- Martin, G.R., Katzir, G., 1999. Visual field in short-toed eagles *Circetus gallicus* and the function of binocularly in birds. *Brain, Behavior and Evolution* 53, 55–66.
- Martin, G.R., Osorio, D., 2008. Vision in birds. In: Basbaum, A.I., Kaneko, A., Shepherd, G.M., Westheimer, G. (Eds.), *The Senses: A Comprehensive Reference*, *Vision* 1, vol. 1. Academic press, San Diego, pp. 25–52.
- Martin, G.R., Piersma, T., 2009. Vision and touch in relation to foraging and predator detection: insightful contrasts between a plover and a sandpiper. *Proceedings of the Royal Society of London. Series B: Biological Sciences* 276, 437–445.
- Montgomerie, R., Weatherhead, P.J., 1997. How do robins find worms? *Animal Behaviour* 54, 143–151.
- Reiner, A., Yamamoto, K., Karten, H.J., 2005. Organization and evolution of the avian forebrain. *Anatomical Record Part A – Discoveries in Molecular Cellular and Evolutionary Biology* 287A, 1080–1102.
- Rogers, L.J., 2008. Development and function of lateralization in the avian brain. *Brain Research Bulletin* 76, 235–244.
- Schaub, M., Pradel, R., 2004. Assessing the relative importance of different sources of mortality from recoveries of marked animals. *Ecology* 85, 930–938.
- Shaw, J.M., 2009. The End of the Line for South Africa's National Bird? Modelling Power Line Collision Risk for the Blue Crane. Masters Thesis Percy Fitzpatrick Institute of African Ornithology, University of Cape Town.
- Shimizu, T., Bowers, A.N., 1999. Visual circuits of the avian telencephalon: evolutionary implications. *Behavioural Brain Research* 98, 183–191.
- Sinclair, I., Hockey, P., Tarboton, W., 1997. *Sasol Birds of Southern Africa*, second ed. Struik New Holland, Cape Town.
- Tucker, V.A., 2000. The deep fovea, sideways vision and spiral flight paths in raptors. *Journal of Experimental Biology* 203, 3745–3754.
- Tucker, V.A., Tucker, A.E., Akers, K., Enderson, J.H., 2000. Curved flight paths and sideways vision in peregrine falcons (*Falco peregrinus*). *Journal of Experimental Biology* 203, 3755–3763.