

Review article

**Understanding bird collisions with man-made objects:
a sensory ecology approach**

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Sensory ecology investigates the information that underlies an animal's interactions with its environment. A sensory ecology framework is used here to seek to assess why flying birds collide with prominent structures, such as power lines, fences, communication masts, wind turbines and buildings, which intrude into the open airspace. Such collisions occur under conditions of both high and low visibility. It is argued that a human perspective of the problems posed by these obstacles is unhelpful. Birds live in different visual worlds and key aspects of these differences are summarized. When in flight, birds may turn their heads in both pitch and yaw to look down, either with the binocular field or with the lateral part of an eye's visual field. Such behaviour may be usual and results in certain species being at least temporarily blind in the direction of travel. Furthermore, even if birds are looking ahead, frontal vision may not be in high resolution. In general, high resolution occurs in the lateral fields of view and frontal vision in birds may be tuned for the detection of movement concerned with the extraction of information from the optical flow field, rather than the detection of high spatial detail. Birds probably employ lateral vision for the detection of conspecifics, foraging opportunities and predators. The detection of these may be more important than simply looking ahead during flight in the open airspace. Birds in flight may predict that the environment ahead is not cluttered. Even if they are facing forward, they may fail to see an obstacle as they may not predict obstructions; perceptually they have no 'prior' for human artefacts such as buildings, power wires or wind turbines. Birds have only a restricted range of flight speeds that can be used to adjust their rate of gain of visual information as the sensory challenges of the environment change. It is argued that to reduce collisions with known hazards, something placed upon the ground may be more important than something placed on the obstacle itself. Foraging patches, conspecific models or alerting sounds placed a suitable distance from the hazard may be an effective way of reducing collisions in certain locations. However, there is unlikely to be a single effective way to reduce collisions for multiple species at any one site. Warning or diversion and distraction solutions may need to be tailored for particular target species.

Keywords: acuity, binocular vision, colour, lateralization, optic flow, power lines, sensory ecology, vision, visual information, visual perception, wind turbines.

Sensory ecology investigates the information that underlies an animal's interactions with its environment. Relationships between the sensory chal-

lenges posed by particular environments and the information that organisms extract from them have been described in general terms (Lythgoe 1979, Archer *et al.* 1999) and some interesting examples of how sensory capacities are linked to particular behaviours have been described in birds,

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including olfactory-guided foraging in seabirds (Nevitt 2010), visually guided foraging in amphibious predatory birds (White *et al.* 2007) and tactile cues in probing shorebirds (Piersma *et al.* 1998). However, to gain a more complete understanding of the interactions of an animal with its environment, account must be taken of cognitive or perceptual components that determine how the sensory information available under particular environmental circumstances is interpreted for the control of particular behaviours.

We have no difficulty in accepting that in our own species perception plays a significant role in the control of behaviour by mediating the interpretation of information that is made available through our sensory systems (Gibson 1986, Bruce *et al.* 2003). There is no reason to suppose that humans are special in this regard; interactions between sensory information that is extracted from the environment, its interpretation by the brain and the behaviour of an animal must underlie key aspects of most animals' behavioural repertoires. However, identifying the role of sensory and perceptual components in non-human animals is problematic because there is no recourse to subjective information to investigate cognitive components. Nevertheless, the role of sensory and cognitive components may be revealed by the investigation of behaviours that occur in environ-

ments that limit sensory inputs, or in the analysis of particular behaviours. For example, it has been argued that both general and specific knowledge of particular environments allows nocturnal owls (Strigidae) successfully to interpret the limited visual and auditory information that is available to them under a woodland canopy at night (Martin 1986a, 1990).

This review takes a similar approach to explain why flying birds collide with human artefacts. I argue that a subtle set of interrelationships exists between visual capacities and perceptual aspects of the interpretation of that information and the behaviour of the birds when flying in open airspace. Together these factors may explain why some birds are more vulnerable to collisions with obstacles than others, and help to inform the development of guidelines for reducing collisions.

BIRDS AND COLLISIONS

Many bird species are prone to collisions with static artefacts that to humans appear conspicuous, especially when they extend into the open airspace above vegetation. Structures such as power lines, fences, communication masts and buildings have long been recognized as posing major problems for certain bird species both in locations where the object may be partially obscured by vegetation, as



Figure 1. Artefacts that appear conspicuous in the environment to human observers but present high collision risks to birds. (a) Wind turbines on the island of Smøla, Norway (photo: NINA, Trondheim). The wind farm covers 18 km² and contains 68 turbines. Each wind turbine is 70 m high and has a rotor blade diameter of 83 m. They are the only large obstacles in an otherwise open landscape (vehicles near the bases of the turbines provide scale). Between 2003 and 2009, 24 species of birds were recorded to have collided fatally with these turbines. Willow Ptarmigan *Lagopus lagopus* and White-tailed Eagle *Haliaeetus albicilla* were the most frequent casualties (May *et al.* 2010). Observations of the behaviour of birds at this site led to the conclusion, 'Preliminary data suggests White-tailed Sea Eagles show no tendency to avoid turbine blades, treating them as if they are not there' (Halley *et al.* 2010). (b) Power lines in the Karoo region of South Africa (photo Jessica Shaw). Although these power lines appear very conspicuous to human observers in these open habitats, bustards and Blue Cranes *Anthropoides paradiseus* are particularly vulnerable to collisions with these artefacts (Shaw 2009, Jenkins *et al.* 2010).

in the case of fences in woodlands (Catt *et al.* 1994, Summers & Dugan 2001), but also when artefacts extend prominently into the open airspace above surrounding vegetation and appear very conspicuous to the human eye (Fig. 1) (Avery *et al.* 1980, Bevanger 1998, Manville 2005, Drewitt & Langston 2008).

Many birds also die as a result of being hit by fast-moving objects such as road vehicles, aircraft and trains (Kelly *et al.* 2000, Sodhi 2002, Thorpe 2003) and some die as a result of collisions with the fast rotating blades of wind turbines (Hodos 2003, Drewitt & Langston 2008, Rothery *et al.* 2009), although collisions with wind turbines can involve the pylon and stationary blades as well as blades in motion.

There have been claims that mortality caused by collisions with human artefacts is the largest unintended human cause of avian fatalities worldwide (Banks 1979, Klem *et al.* 2004), although this also includes collisions with windows, which probably involves a different set of sensory and perceptual problems compared with collisions with artefacts in open airspace. Certainly, there is evidence that collisions with large and prominent obstacles may threaten the survival of specific populations or even the survival of certain endangered species (Shaw *et al.* 2010). For example, in Europe over a 16-year period it was estimated that approximately 25% of juvenile and 6% of adult White Storks *Ciconia ciconia* died annually from power line collisions and electrocutions (Schaub & Pradel 2004). In the Overberg region of South Africa, still higher power line mortality rates have recently been estimated, with 12% of Blue Cranes *Anthropoides paradiseus* classified as globally Vulnerable (BirdLife International 2009), and 30% of Denham's Bustards *Neotis denhami* killed annually by power line collisions (Shaw 2009). Ludwig's Bustard *Neotis ludwigii*, White Stork, Grey Crowned-crane *Balearica regulorum* and Kori Bustard *Ardeotis kori* are amongst the other most commonly reported power line collision victims in southern Africa (Eskom 2008). For Ludwig's Bustard, it is estimated that the rate of mortality from collisions is probably unsustainable, ultimately threatening the survival of this species (Jenkins *et al.* 2010).

That birds are prone to collisions with large static objects is surprising as it is widely held that flight in birds is primarily controlled by vision, an idea captured by the phrase 'a bird is a wing guided

by an eye' (Rochon-Duvigneaud 1943) and that vision is the prime sense used by birds to gain information from their environment (Gill 2007, Perrins 2009, Sibley 2009). Furthermore, collisions frequently occur when birds are apparently in control of their flight and under conditions of good visibility (Drewitt & Langston 2008).

WHY DO BIRDS COLLIDE WITH STATIC OBJECTS?

Analysis of 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, Janss 2000, Drewitt & Langston 2008). Visual and perceptual aspects of collisions have received little investigation beyond the general observation that some collisions may occur when visibility is reduced due to lower light levels or weather conditions such as rain or mist, which reduce the amount of visual information available for the control of flight. Measures to reduce the probability of collisions have usually involved marking obstructions with devices designed to increase the probability of their 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 & Ferrer 1998), fences have been marked with flags (Summers & Dugan 2001) and there have been laboratory simulations of the effectiveness of marking turbine blades with patterns designed to reduce 'motion smear' (also known as 'motion transparency' and 'motion blur') (McIsaac 2001, Hodos 2003). However, despite more than 30 years of using static markers on power wires, the probability of mortality caused by power line collisions remains high for certain species (Janss & Ferrer 2000, Drewitt & Langston 2008). Also, at the time of writing, Hodos (pers. comm.) confirms that there have been no field trials of his recommendations (Hodos 2003) for the reduction of motion smear and increased conspicuousness of rotating turbine blades that were commissioned by the US National Renewable Energy Laboratory (http://www.nrel.gov/wind/avian_reports.html).

It is clear from this work that little insight has yet been gained into why birds actually collide

with obstacles under conditions of clear visibility. Beyond the untested proposals for 'motion smear' reduction of turbine blades, there is no clear analysis of the problems of bird collisions that brings together knowledge of vision and behaviour in susceptible bird species. An analysis of how these birds might actually perceive the hazard of a static object in open airspace is required. It also seems that most of the solutions proposed to date are based upon a human perspective of the problem. Put simply, it has been a matter of finding a solution to bird collision problems based upon making the perceived hazard more conspicuous to human observers. Furthermore, work on the development of hazard markers has had to find solutions working within the constraints of initial cost, ease of application and ease of maintenance. The nub of the argument presented here is that the human view provides just one way of appreciating the world and that the differences between human and birds' eye views are sufficient to render a human view of the problem of bird collisions inaccurate and possibly misleading.

BIRDS' EYE VIEWS

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 (Martin & Osorio 2008). This is due to fundamental differences between birds and primates at all levels of organization of their visual systems, including retina, physiological optics, visual fields and the processing of visual information by the brain (Bowmaker *et al.* 1997, Shimizu & Bowers 1999, Reiner *et al.* 2005, Martin & Osorio 2008, Hunt *et al.* 2009). Furthermore, there are also interspecific variations of each of these levels of organization of the visual system. During their evolution, vertebrate eyes have been subject to many selective pressures, some of which are antagonistic and dictated by the physical constraints that underlie the sampling of information from the array of photoreceptors that make up any retina. Prominent among such constraints is the trade-off between resolution and sensitivity, such that in general an eye, or region of retina, primarily adapted for spatial or spectral resolution cannot achieve high sensitivity and vice versa (Land & Nilsson 2002). Thus, each eye can provide only certain information about the environment; no eye is all-seeing and even if the eyes of two species

have similar capacities, the two eyes operating together may provide different world views with respect to both the information that is extracted and how much of the world is sampled at any one instant by their combined visual fields. Furthermore, while the eyes extract basic information about the environment, the way that this information is interpreted by the brain (i.e. what the animal perceives) differs depending upon the information available at any one time. In other words, perceptions fluctuate for all species (Gibson 1986, Bruce *et al.* 2003).

It should be noted that important parallels have been described between the ways in which the brains of birds and primates interpret the visual information provided by their eyes. This suggests that bird and primate brains use similar mechanisms to segregate their visual worlds into meaningful entities (objects). Examples that support this idea are to be found in the mechanisms employed by birds and humans for object completion and object unity when only partial information is available (Regolin & Vallortigara 1995, Lea *et al.* 1996). Thus, birds and humans experience similar perceptual illusions (Clara *et al.* 2006) and there is evidence that birds and humans determine relative depth from two-dimensional and ambiguous images in a similar way (Forkman 1998, Forkman & Vallortigara 1999). We are primarily concerned here with what information is available for processing by a bird's visual system and how this may influence its ability to detect obstacles in unfamiliar circumstances. That there are parallels between primate and avian brains in aspects of the higher order processing of visual information does, however, legitimize comparisons between flying birds and the perceptual problems that face humans under particular visual challenges (see below).

FOUR FUNDAMENTAL WAYS IN WHICH HUMAN AND AVIAN VIEWS DIFFER

Vision is both complex and multidimensional, so considerable ingenuity, involving a range of anatomical, physiological and behavioural techniques, has been used to isolate particular capacities and their underlying mechanisms in birds and other animals. Not all aspects of visual capacity are equally well understood but there are four key areas that are important to consider when attempting to understand the vulnerability of birds to collisions.

Colour

The function of colour vision is to enhance the detection of objects by extracting information about their differential reflection in the spectrum. It is sobering to realise that colour, which appears such an important part of our world view, is not a property of the physical world but a construct of the visual system that analyses it (Wright 1963). It has long been recognized that the colour vision mechanism of avian retinas differs in quite fundamental ways from that of mammals, and its mechanisms have been summarized a number of times as knowledge has grown (Walls 1942, Jacobs 1981, Bowmaker *et al.* 1997, Land & Nilsson 2002, Martin & Osorio 2008, Hunt *et al.* 2009). Although there are differences among bird species, the fundamental property of avian colour vision compared with mammals, and particularly primates, lies in the extent of the visible spectrum and the subtlety of colour discrimination that can be made within that spectrum. It was first recognized that birds have colour vision which extends into the ultraviolet, thus broadening (compared with humans) the range of stimuli to which the avian eye can respond, through behavioural studies of Rock Pigeons *Columba livia* (Wright 1972, Emmer-ton & Delius 1980) and later of hummingbirds (Trochilidae) (Goldsmith 1980). Subsequently, behavioural and physiological work has shown that vision in the UV or near-UV part of the spectrum is widespread among avian families (Cuthill *et al.* 2000, Hunt *et al.* 2009). In view of the wide taxonomic distribution of vision in the UV region among birds, it would now seem safe to assume that the visible spectrum of most birds extends into the UV and that vision in this part of the spectrum should no longer be viewed as exceptional.

The few detailed psychophysical studies of colour discrimination in birds suggest that birds are capable of subtle discriminations throughout their visible spectrum, including the UV and near-UV (Wright 1979). This has been supported by general models of how the different types of retinal cone photoreceptors in birds mediate colour discrimination (Vorobyev & Osorio 1998, Vorobyev 2003, Endler & Mielke 2005).

Acuity

Resolution (the precision with which an eye splits up light according to its direction of origin) is

usually referred to as acuity. It is tempting to characterize this with a single value of best performance for a particular species. This value describes the smallest spatial detail that can be resolved under high light levels using stimuli of high contrast, giving a basis for interspecific comparisons and allowing estimates to be made of the finest details or smallest object that can be detected at a certain distance under ideal viewing conditions. However, natural stimuli are often of lower contrast and a full characterization of spatial resolution requires the determination of a spatial contrast function which characterizes visual thresholds across a range of contrasts and spatial frequencies (Ghim & Hodos 2006). As with colour vision, there are few behavioural studies of contrast sensitivity or even acuity in birds, but it has been possible to estimate acuity from knowledge of the structure of the retina in a number of species. Two key findings come from these studies. First, acuity in birds is high compared with those in other vertebrates with eyes of similar size, suggesting that the eyes of the majority of diurnally active birds can be characterized as adapted to maximize resolution rather than sensitivity (Land & Nilsson 2002). However, despite earlier claims based upon anecdotal observations, the highest known acuity in birds is not exceptionally superior to that of humans. For example, earlier claims of exceptional acuity in falcons and eagles have been more recently revised downwards to suggest that the highest acuity of falcons (0.4–0.75 min of arc) is approximately equal to that of the eye of a young human (0.4–1.0 min of arc: Fox *et al.* 1976, Hirsch 1982, Reymond 1987, Land & Nilsson 2002, Gaffney & Hodos 2003), while that of the largest eagles (0.2 min of arc) is perhaps 2.5 times higher than that of human eyes (Reymond 1985). For many bird species, acuity is below that of the human fovea at similar light levels, for example Rock Pigeon, 1.7 min of arc; Rook *Corvus frugilegus*, 1.0 min of arc; domestic fowl *Gallus domesticus*, 3.4 min of arc (Hodos 1993).

Secondly, acuity varies markedly within the visual field of an eye. In humans, there is a single region of high acuity vision which projects directly forwards, typically in the direction of travel. This region is of small angular size ($\approx 2^\circ$ diameter) compared with the total visual field ($\approx 160^\circ$) and is mediated by the foveal region of the retina (Westheimer 1972). Acuity decreases rapidly towards the periphery of the eye's visual field. In

birds there may be two areas of high acuity in each eye (Meyer 1977). One typically projects laterally with respect to the axis of the head, approximately along the optical axis of the eye, but there may be other frontal or ventrally projecting areas of higher acuity, or even an area of higher acuity that extends in a band across the field of view. There have been a number of attempts to explain the occurrence and visual projection of these areas of high acuity by reference to the visual challenges that life in different habitat types present (Meyer 1977, Martin 1985). Typically, the regions of highest acuity occur laterally, not frontally, with respect to the head and when behavioural techniques are used in assessments of a bird's acuity, a bird usually chooses to use its lateral field of view. Anatomical evidence also corroborates the use of these laterally projecting regions for tasks involving the determination of the highest visual acuity by freely moving birds (Reymond 1985, 1987).

Relative depth, distance and time to contact

Determination of the position of an object in relative depth from an animal, as well as its absolute distance, is a complex perceptual process for any visual system (Goldstein 1984, Bruce *et al.* 2003). However, it is clearly a process that is central to understanding collisions.

Estimation of depth and distance are not a property of the eye alone, but a perception based upon higher order processing by the brain. In humans, relative depth close to the observer is usually analysed by reference to the process of stereopsis (Bruce *et al.* 2003). Perception of the distance of objects further away depends upon cues that are available in each eye alone but which also require a high degree of cognitive processing. Stereopsis is based upon the small differences in the images of the same object produced on the retinas of the two eyes, which occur because of the lateral displacement of the eyes in the skull. Human eyes are relatively far apart compared with birds and even in humans the process of stereopsis provides relative depth information for only a few metres ahead and is typically employed for tasks conducted closer to the eyes (e.g. manipulation of objects by the hands). Whether birds whose eyes are relatively close together (typically, avian eyes almost touch in the median sagittal plane of the skull) are able to employ stereopsis to gain relative depth infor-

mation is uncertain. An early behavioural demonstration of stereopsis in a falcon (Fox *et al.* 1977) has not been replicated or extended more generally among bird species, although McFadden (1994) found some behavioural evidence of stereopsis for close objects in pigeons. More recently, Martin (2009) has argued that birds, with perhaps the exception of some owl species (Strigidae, Tytonidae), do not have stereopsis and that the function of binocular vision lies primarily in the control of the bill (and/or feet in some species) towards objects at close range, and not for the control of locomotion towards more remote targets. Martin (2009) also argues that for any bird, the most vital visual information beyond recognition of an object is the object's position and, if there is relative speed between the object and the observer, information on time to contact. The actual distance of an object from a bird may be of little importance compared with its direction and the time it may take to make contact with it.

Such information is available from optic flow-fields (Lee & Lishman 1977, Lee 1980, Warren 2008) and it has been shown that Northern Gannets *Morus bassanus* and hummingbirds, when carrying out manoeuvres that require accurate visual information regarding time to contact a target, appear to employ optic flow-field information (Lee & Reddish 1981, Lee *et al.* 1991). The informational properties of optic flow-fields were first analysed in detail by Gibson (1966) and derive directly from the way images of objects flow across the retina as they move relative to the observer (Warren 2008). They can specify very accurately both the direction of travel and the time to contact with an object that is being approached and they may underpin many tasks undertaken by humans, such as driving, cycling, running, jumping and ball-catching: tasks in which the observer has to adjust speed of approach to achieve accurate timing of arrival at a given point (Lee 1980). However, the information extracted from the optic flow-field across the retina is contained not in highly detailed spatial information but in information extracted from moving images at relatively low resolution.

Fields of view

Visual fields and the variation of visual capacities within them are likely to have a direct impact on collision susceptibility. 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, 2009) and because visual capacities can vary markedly within the visual field (Martin & Osorio 2008). This is true of humans, where there are marked changes in visual capacity from central to peripheral vision within an eye, but such differences appear to be more extreme within avian eyes. Especially important are the characteristics of that section of a bird's visual field that are used to detect and analyse objects of interest, and the characteristics and general functions of the section of the visual field that projects forward and hence 'looks' in the direction of travel.

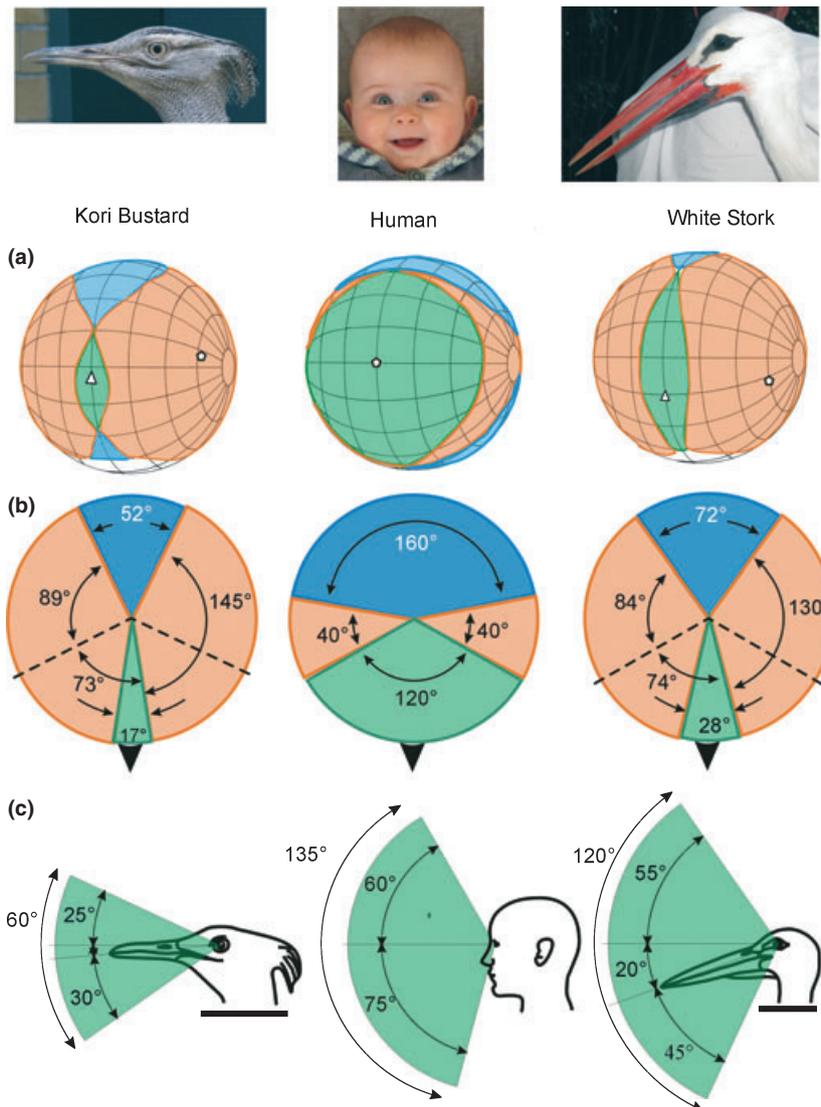
In humans, that section of the visual field that is used for detailed analysis of objects looks directly forward, and there is a very extensive region of forward binocular vision that constitutes the major portion of the total visual field (Fig. 2). However, this is not the case in most, perhaps all, birds. For humans, the detailed world lies ahead, whereas for the majority of birds the detailed world lies laterally. Furthermore for birds (indeed any animals with eyes placed laterally in the skull), forward/binocular vision is achieved through the peripheral vision of the each eye; in other words vision at the edge of the visual field of an individual eye, away from the optical axis (Fig. 2). In contrast, in most manufactured optical systems, such as binoculars, the quality of optics in the periphery is always inferior to the quality of optics along the optical axis of the system. As little is known about the quality of peripheral optics in bird eyes, it is not possible to be sure that when birds look forward with their binocular field, which is typically a very small portion of the total visual field (Fig. 2), they are employing the best quality optics.

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) (Fig. 2). 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-Juricic *et al.* 2008, Martin & Piersma 2009). While there is evidence that some birds have optical systems that

keep both distant and close objects in focus without the need to change the refractive state of the eye, this occurs in the laterally projecting visual field, not the frontal projection of the field (Martin 1986b, Hodos & Erichsen 1990). The human eye, with its frontal orientation, has continuously to accommodate for objects that lie ahead at different distances.

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 (frontal) section of the visual field, and in the majority of birds that feed in this way, the binocular field is relatively narrow, between 15° and 30° in maximum width, and vertically long (Martin 2007) (Fig. 2). However, the vertical extent of the binocular field varies markedly. For example, in herons (Ardeidae) and storks (Ciconiidae), it extends through 180°, so that these birds have comprehensive visual coverage of the hemisphere in front of the head (Martin & Katzir 1994), while in eagles, bustards and cranes it extends through only 80°, vertically giving these birds extensive blind areas both above and below the head in the frontal hemisphere (Martin & Katzir 1999, Martin & Shaw 2010) (Fig. 2). In birds that do not employ visual information to guide bill position (e.g. some duck species which filter-feed, and some long-billed shorebirds which feed by probing in soft substrates guided by tactile cues), the bill falls at the very periphery or outside the visual field. In these cases the eyes are positioned high in the skull, giving comprehensive visual coverage of the hemisphere around and above the head such that there are no blind areas in their visual field except that produced by their own body (Martin 2007, Martin *et al.* 2007).

Eye movements are present in many bird species and these are typically independent complex rotations of the eyes that can have markedly different effects on visual coverage around the head. In a number of species (e.g. herons, hornbills and cormorants; Martin & Katzir 1994, Martin & Coetzee 2004, Martin *et al.* 2008), it has been shown that binocular vision to the front of the head can be abolished by eye movements. Such abolition of binocular vision occurs frequently when birds are held in the hand, suggesting that they switch spontaneously between binocular coverage of frontal field and its abolition. The function of such abolition of frontal binocular vision is unclear but it may be an incidental consequence of using the region of an eye's



best optical quality, which projects along the optic axis laterally, to examine an object or track its movement (Martin *et al.* 2008).

In birds, the function of binocular vision appears primarily to be the control of behaviours requiring the accurate positioning and timing of bill-opening towards objects close to the animal (particularly 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 probing shorebirds, the binocular field can be very narrow ($\approx 5^\circ$) in the direction of travel when flying. Fur-

thermore, 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 (Montgomerie & Weatherhead 1997, Land 1999, Tucker 2000, Tucker *et al.* 2000, Rogers 2008).

A COMPARISON OF AVIAN AND HUMAN VIEWS

A summary comparison of human and bird's views which are likely to be relevant to collision susceptibility should recognize the following elements.

Figure 2. Visual fields in Kori Bustards, humans and White Storks. The differences between a 'human eye view' and a 'birds' eye view' are readily apparent from these diagrams. Bustards are particularly prone to collisions with power lines of the kind depicted in Figure 1. Storks, although vulnerable to collisions with such power lines, are more likely to be electrocuted by low-tension power wires (because their wide wing span is sufficient to earth between two current-carrying wires in low-tension power transmission systems). The figure is a matrix that allows interspecific comparison of the same information across rows, while columns show information for each species. Row (a): perspective views of orthographic projections of the boundaries of the retinal fields of the two eyes and in the birds the line of the eye–bill tip projections (indicated by a white triangle). The direction of the optic axes of the eyes is indicated by a white pentagon. The diagrams use conventional latitude and longitude coordinate systems with the equator aligned vertically in the median sagittal plane of the head. The grid is at 20° intervals. It should be imagined that in each diagram the head is positioned at the centre of a transparent sphere with the field boundaries and optic axes projected onto the surface of the sphere with the heads in the orientations shown in row (c). Green areas, binocular sectors; pink areas, monocular sectors; blue areas, blind sectors. Row (b): horizontal sections through the visual fields in a horizontal plane defined by the straight line running through the middle of each of the visual field projections shown in row (a). Dashed lines indicate the directions of the optic axes. In the birds, the axis of each eye projects laterally, in humans, the optic axes of each eye project forward and coincide (colour coding of each sector of the visual fields as in row (a)). Row (c): vertical sections through the binocular fields (green) 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. In humans, the head is in a typical upright posture. The visual fields are presented with respect to these typical head positions. Key features of visual fields in birds that forage using visual guidance are shown in the case of the bustards and storks. These are features typical of the majority of bird species (Martin 2007). The eyes project laterally and the best optical quality and the direction of best resolution projects laterally. The binocular field is narrow and vertically long with the bill projecting approximately centrally; there is extensive visual coverage by each eye to the side and behind the head, resulting in a small blind sector above and to the rear of the head. In humans the visual field is arranged very differently from those of the two birds. The eyes project forwards and almost the whole of the visual field is binocular, there is a large blind area behind the head and the best optical quality and highest resolution lie directly ahead. One crucial difference between the two bird species depicted here lies in the vertical extent of their binocular fields and the effect of moving the head on visual coverage of the frontal hemisphere. In bustards, a relatively small forward head pitch of 25° (rows a and c) is sufficient to bring the extensive blind area above the head to project forwards in the direction of forward travel. However, in storks, visual coverage of the frontal field is not abolished until the head has pitched forward by 55°, which would mean that the bill is pointing vertically downwards. This amplitude of head movement that is necessary to abolish forward vision is similar to that required for the same effect in humans. The visual field of bustards is similar to those found in cranes and eagles, which are also highly vulnerable to collisions with artefacts. The visual field of storks is similar to those found in other members of the Ciconiformes and in duck species (Martin 2007). The figure is based upon Martin and Shaw (2010).

Human eye view

In humans, two eyes at the front of the head provide extensive binocular overlap in the direction of travel (Fig. 2). Highest spatial acuity and most acute colour discriminations lie directly ahead and there are extensive blind regions above and behind the head. The best appreciation of relative depth also lies directly ahead. In essence, humans see the world as being 'in front', and we move 'into' it.

Birds' eye views

Two eyes placed laterally in the skull provide some visual coverage of the world ahead, but there is also typically extensive coverage above and behind the head (Fig. 2). Binocular and blind areas differ in extent and position depending upon the ecology of the species. In general, the region of binocular vision is small and even in fast-flying species, such as some ducks with high wing loadings, binocular vision in the forward direction can be very narrow in the direction of travel (< 10° in Mallards *Anas platyrhynchos*). In some species, binocular vision

can at times be spontaneously abolished. There are marked differences in visual capacities within a field of view but typically, retinal regions that provide the highest resolution and colour discrimination capacities project laterally, not forwards. These regions typically lie close to the optical axes of each eye (Fig. 2). Binocular/frontal vision is primarily concerned with near tasks such as the control of bill position in foraging (pecking/lunging), chick provisioning and nest building, not the control of locomotion. Control of locomotion is achieved through the use of information extracted from optic flow-fields and this requires the detection of movement, not necessarily of high resolution. Optic flow-fields are the primary source of information on the direction of travel and time to contact. In essence, birds probably see the world as 'around them' and they move 'through' it.

THE FUNCTIONS OF LATERAL VISION IN BIRDS

Birds use their lateral visual fields rather than binocular/frontal fields for many key tasks. Typically,

lateral vision has been seen as serving for the detection of predators or conspecifics (Fernandez-Juricic *et al.* 2004). However, it is now clear that lateral vision in birds has a prime role in sophisticated aspects of foraging and predator detection tasks, including the response to novel stimuli and the reliable separation of pertinent from distracting stimuli (Rogers 2008). Moreover, it is also clear that the avian brain is functionally lateralized in the conduct of such tasks and that these are revealed by birds preferentially using their left and right eyes for different tasks (Rogers 2008). This use of lateral vision is seen clearly in tasks in which birds choose to examine different types of objects and scenes preferentially with the left or right eye, rather than binocularly (Mench & Andrew 1986, Rogers 1991, Dharmaretnam & Andrew 1994, Vallortigara *et al.* 2001, Koboroff *et al.* 2008, Franklin & Lima 2010). Furthermore, use of the left and right eye is secondary to selective activation of the contralateral hemisphere of the brain, and this can change during free viewing depending on the task (Vallortigara 2000). This refers not only to eye use but more generally to allocation of attention in the left and right visual hemispaces (Diekamp *et al.* 2005). Therefore birds seem to be highly lateralized with respect to both eye and brain function.

Preferential use of lateral vision has been described both in tasks involving close objects, which require approach or a pecking response towards the object, and in tasks that involve flight towards distant objects. Thus a Peregrine Falcon *Falco peregrinus* stooping upon its prey seems to be under the control of lateral rather than frontal/binocular vision, in that the bird approaches along a curving path that allows the prey object to be kept in the vision of the laterally projecting fovea of one eye until the final closure upon the prey object, when transfer is passed to frontal vision at close range (Tucker 2000, Tucker *et al.* 2000). This use of lateral vision to detect an object, and the control of behaviour passing to the frontal field only when the object is in close proximity, is similar to that described in thrushes (Montgomerie & Weatherhead 1997), Zebra Finches *Taeniopygia guttata* (Bischof 1988), Rock Pigeons (Bloch *et al.* 1988) and domestic fowl (Dharmaretnam & Andrew 1994), all of which take items by detecting them when standing and pecking at them from a surface. All these examples suggest that both lateral

and binocular vision are used for specific tasks and are not interchangeable in their function. Therefore for tasks requiring high spatial resolution, and perhaps separation of pertinent from distracting stimuli, birds seem to fixate initially upon a target with one of their lateral fields of view, and behavioural control typically passes to frontal (binocular) vision for final seizure of object/food only at close range: this may apply to a very wide range of species and tasks.

WHEN BIRDS ARE FLYING IN OPEN AIRSPACE, WHAT ARE THEY DOING?

When flying in open airspace, are birds looking ahead for obstacles? The complexity of visual fields and the topographical distribution of visual capacities within them suggest that it is wrong to assume that birds are looking forward into the open airspace and attending to what might lie ahead of them. What birds might actually be attending to in flight presents a more complex set of possibilities than the situation in humans. Humans have two eyes whose visual fields project forwards and the key visual capacities of high spectral and spatial resolution also project forwards in the direction of travel. This is clearly not the case in the majority of birds.

Looking but failing to see

Humans also exemplify an additional problem for the analysis of collisions – the need to differentiate between vision and visual perception. Even when looking ahead in the direction of travel it has been established that car drivers may ‘look but fail to see’ and that people may frequently drive beyond their ‘perceptual limit’. In other words, they drive in a manner that relies on information which is not in fact immediately available via their visual system (Hills 1980); such a framework has been used in the analysis of collisions (Clarke *et al.* 1995, 1998). Collisions are generally avoided, however, because the available visual information is supplemented by experience of the nature of roads and traffic and specific knowledge of road layout. The driver simply interprets a meagre set of information in a useful way, assuming that the road will continue much as before, unless specific signals suggest otherwise. Indeed, much road engineering is concerned with making roads as predictable as

possible within a region or country, so that only minimal cues are needed to drive safely (Hills 1980). That drivers are often beyond their perceptual limit is indicated by what happens when there is an unpredictable obstruction in the road. At such times, it is more likely that a collision will happen. This is because the rate at which a driver is gaining information about the environment ahead is not sufficient to match the challenge posed. This is one of the main reasons why known hazards have to be so well indicated, to warn or prime the driver that the world ahead will be less predictable and that they should reduce speed to adjust their rate of gain of information to match the requirements of the changing or changed circumstances.

Car driving may not seem particularly relevant to birds in flight. However, it does seem likely that the same principles concerning the role of cognition in the correct interpretation of cues and the adjustment of the rate of gain of information to match the challenges of the environment are of wide application (Gibson 1986).

Two key questions

Are there similar perceptual and attentional problems posed by obstacles that intrude into the open airspace for flying birds? Two key questions arise. First, when in flight can birds adjust their rate of gain of information to meet the perceptual challenge of the environment? For example, under conditions of reduced visibility (which will result in a reduced rate of information gain), can birds slow down and adjust their rate of gain of information to meet the perceptual challenge? Secondly, in open habitats, are flying birds always looking ahead?

Can flying birds adjust their rate of gain of visual information?

It is well established that the aerobic range of flight speeds for any bird is restricted. The well-established U-shaped function of aerodynamic power requirement as a function of flight speed has wide applicability. It shows that for most birds, slow flight, even for short periods, is not possible and this becomes more acute for birds with high wing loading and consequently higher average flight speeds (Norberg 1990, Biewener 2003). In essence, birds cannot readily slow down; sustained slow flight is costly or aerodynamically impossible

and hence reducing speed to match the rate of gain of information to increasing perceptual challenges is unlikely to occur. In other words, when the environment restricts the information available (e.g. because of rain, mist, low light levels), birds cannot fly more slowly to meet the increased perceptual challenge. Thus if birds are to fly under non-ideal perceptual conditions, or visibility conditions change during a flight, they cannot act in the way that a careful car driver should and reduce their speed to gain information at a rate sufficient to match the new perceptual challenge.

Are flying birds always looking ahead?

The second question, relating to whether birds in open airspace fail to see the way ahead, is more challenging to address. Vision in the direction of travel that is mediated by the forward-projecting binocular region may provide far less spatial information (derived either from spectral or luminance contrasts) than vision laterally. Furthermore, binocular (frontal) vision may have quite restricted functions that are concerned primarily with nearby objects rather than more distant ones. That is not to say that birds may not 'see' objects that lie ahead at a distance, but it is likely that frontal binocular vision does not match the best visual performance derived from the laterally projecting sections of the visual fields. Furthermore, open airspace above vegetation is a highly predictable environment, usually clear of hazards, and birds may not be perceptually primed either through learning or evolutionary selection to detect hazards that extend into this airspace from below. Much in the same way that a car driver requires perceptual priming when a predictable road becomes less predictable, birds may also fail to detect objects because they too 'look but fail to see' what lies ahead when flying in open airspace. This is not to imply that birds are unaware of their surroundings when in flight above vegetation, as it is likely that they are perceptually primed to detect aerial predators, but that these are specific targets that are likely to appear above or behind the flying bird, not in the frontal visual hemifield. That birds appear to be primed for the detection of predators is supported by the rapid response shown when predator silhouettes are presented, for example in studies of escape or avoidance behaviours (Devereux *et al.* 2006).

Do birds sometimes actually fail to see the way ahead? Certainly the evidence that some birds can

spontaneously abolish their binocular (frontal) field suggests that, at least momentarily, birds of some species could simply not look ahead during flight. In addition, birds can turn their heads sideways (yaw) to bring the laterally projecting visual field more forwards with respect to the direction of travel. More important, however, are examples where birds have frontal binocular fields that are of restricted vertical extent (Fig. 2), and with extensive blind areas above and below them. In these cases, only relatively small amplitude (25–35°) downward pitch movements of the head from those typically adopted in level flight will bring these blind areas to project forward in the direction of travel (Fig. 2). Anecdotal sources, including field observations, video clips and still photographs of birds in flight, show that birds of a wide range of species are often seen with their head pitched downwards during flight. It is worth noting that the well worn cliché of a ‘bird’s eye view’, which usually refers to looking straight down at the world below (as in aerial photographs and satellite imagery), can in fact only be achieved in birds if the head is pitched forward, and would probably also involve yaw and roll movements of the head (Fig. 2). Such pitching and yawing movements have been studied in Gull-billed Terns *Gelochelidon nilotica*, which turn their heads systematically to look both laterally and downwards (forward pitch of the head by 60°) when searching for prey so as to bring central vision to guide the task of detection (Land 1999). But why should birds in flight pitch their head down in this manner? In the case of terns and eagles this may be directly linked with foraging behaviour, as prey and carrion are principally detected on the ground or in water below. In the case of bustards and cranes, birds may not be looking for individual prey items but for foraging patches, conspecifics or roost sites. However, in both cases the birds are more interested in what is below them than what lies ahead in the (presumed) open airspace. Clearly, further studies of the circumstances, amplitude and frequency of forward pitch and yaw head movements during flight in collision-prone birds will help to establish whether these birds are ‘looking but failing to see’ or simply just not looking ahead when flying in open airspace. Recent developments in miniaturized digital imaging, image storing and telemetry might enable such work to be carried out (Carruthers *et al.* 2010).

CONCLUSIONS

General observations

The evidence and arguments reviewed here suggest that bird collisions may be the result of both visual and perceptual constraints. Analyses of the reasons why any particular species may find particular situations hazardous should acknowledge the following:

1. Birds live in quite different visual worlds from that occupied by humans. Birds’ eye views are not the same as the human eye views with respect to many parameters and it is not possible simply to extrapolate from knowledge of human perception of a hazard to understand the problem faced by a bird.
2. In flight, some birds may be blind to what is ahead of them; turning the head in both pitch and yaw to look downwards either with the binocular field or with the central part of an eye’s visual field may not be unusual, and this may leave birds blind in the direction of travel.
3. Frontal vision in birds is not high-resolution vision; high resolution occurs in the lateral fields of view.
4. Frontal vision in birds may be tuned for the detection of movement concerned with the extraction of information from the optical flow-field, rather than high spatial detail.
5. Birds probably employ lateral vision for the detection of conspecifics, foraging opportunities and predators. Attention to these may be more important for a bird than simply looking ahead during flight in the open airspace.
6. Birds in flight may predict that the environment ahead is not cluttered. Even if they are ‘looking ahead’ they may fail to see an obstacle as they may not predict obstructions. Perceptually they have no ‘prior’ for human artefacts such as buildings, power wires or wind turbines.
7. Birds have only a restricted range of flight speeds that can be used to adjust their rate of information gain as the sensory challenges of the environment change due to reduced visibility caused, for example, by rain, mist or lower light levels.

Solutions to collisions?

Armed with this information, are there solutions to the problem of collisions? Some general principles can be suggested:

1. Although birds cannot be guaranteed to be looking at or attending to an obstacle that extends into open airspace, it is still valuable to employ markers to increase their conspicuousness in key situations where collisions rates are high. Stimuli used to draw attention to the obstacle should be of high contrast, incorporate movement and be large, well in excess of the size calculated to be detectable at a given distance based upon acuity measures. This recommendation takes account of the idea that forward vision may be tuned primarily for extracting information from optic flow rather than static stimuli, and that estimates of acuity typically refer to the highest performance of spatial resolution which occurs in the lateral, not the frontal, fields of view. Although birds have an extended visible spectrum compared with humans, it seems unlikely that stimuli specifically employing reflectance in the short wavelength (UV) end of the spectrum will have particular salience. In fact, the target that is likely to remain conspicuous under all possible viewing conditions should simply be of high black-and-white contrast so that it reflects highly or absorbs strongly across the full spectrum of ambient light. This is because the degree to which a coloured target is conspicuous depends upon the spectral characteristics of ambient and background illumination as well as the distribution of spectral information within the target itself (Endler & Mielke 2005) and these can vary markedly with situation, time of day and cloud cover.
2. Collisions with obstacles in the open airspace are as much a perceptual or attentional problem as a visual one. Therefore, if possible, solutions should be found that alert birds well in advance: their attention may need to be primed just as much as the car driver's when approaching a hazard. However, what constitutes a warning or alerting stimulus may be difficult to determine and may vary with species.
3. In locations where collision incidents are high it may be more efficient to divert or distract birds from their flight path with respect to a known hazard rather than attempt to make the hazard more conspicuous. This is because to be effective, a warning on the obstacle itself may have to be very large and probably moving, and that for some collision-vulnerable species it may be best to assume that birds are more likely to be

looking down and laterally rather than forwards. Therefore, any warnings or additional marker may not in any case be seen. To reduce collisions with known hazards, a signal on the ground may be more important than a signal on the obstacle. Foraging patches, conspecific models or alerting sounds placed a suitable distance from the hazard may be necessary.

4. There is unlikely to be a single effective way to reduce collisions for multiple species at any one site. Warning or diversion and distraction solutions may need to be tailored for particular target species. Solutions may need to take account of the foraging ecology and social behaviour of the species as well as its visual capacities in order to understand why it flies in the open airspace at particular locations.

SENSORY ECOLOGY ANALYSES OF ENVIRONMENTAL HAZARDS

Sensory ecology provides a valuable framework for understanding important aspects of animals' interactions with their environment. This review shows that combining a sensory and a perceptual approach may provide valuable insights into how an animal's behaviour may be controlled and constrained by the information they extract from their natural environment. The ways in which humans have altered those environments, particularly through the construction of obstacles, have posed many additional sensory and perceptual challenges for animals that in some circumstances can constitute hazards which threaten the lives of individual birds and even the survival of particular populations. A sensory ecology approach could well be of value for understanding, and suggesting solutions to, other sensory challenges that human activity poses for birds in different environments.

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REFERENCES

- Archer, S.N., Djamgoz, M.B.A., Loew, E., Partridge, J.C. & Vallerga, S. 1999. *Adaptive Mechanisms in the Ecology of Vision*. Dordrecht: Kluwer.

- Avery, M.L., Springer, P.F. & Dailey, N.S. 1980. *Avian Mortality at Man-made Structures: An Annotated Bibliography*. Washington, DC: US Fish and Wildlife Service.
- Banks, R.C. 1979. *Human-related Mortality of Birds in the United States*. Washington, DC: US Fish and Wildlife Service Special Scientific Report.
- 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. *Biol. Conserv.* **86**: 67–76.
- Biewener, A.A. 2003. *Animal Locomotion*. Oxford: Oxford University Press.
- BirdLife International 2009. Species factsheet: *Grus paradisea*. <http://www.birdlife.org>.
- Bischof, H.-J. 1988. The visual field and visually guided behavior in the Zebra Finch (*Taeniopygia guttata*). *J. Comp. Physiol. A* **163**: 329–337.
- Bloch, S., Jäger, R., Lemeignant, M. & Martinoya, C. 1988. Correlations between ocular saccades and head movements in walking pigeons. *J. Physiol.* **406**: 173.
- 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 Res.* **37**: 2183–2194.
- Bruce, V., Green, P.R. & Georgeson, M.A. 2003. *Visual Perception: Physiology, Psychology and Ecology*, 4th edn. Hove: Psychology Press.
- Carruthers, A.C., Thomas, A.L. & Taylor, G.K. 2010. Automatic aeroelastic devices in the wings of a Steppe Eagle *Aquila nipalensis*. *J. Exp. Biol.* **210**: 4136–4149.
- Catt, DC, Dugan, D., Green, R.E., Moncrieff, R., Moss, R., Picozzi, N., Summers, R.W. & Tyler, G.A. 1994. Collisions against fences by woodland grouse in Scotland. *Forestry* **67**: 105–118.
- Clara, E., Regolin, L., Zanforlin, M. & Vallortigara, G. 2006. Domestic chicks perceive stereokinetic illusions. *Perception* **35**: 983–992.
- Clarke, D.D., Forsyth, R.S. & Wright, R.L. 1995. *The Analysis of Pre-accident Sequences*. Crowthorne: Transport Research Laboratory.
- Clarke, D.D., Ward, P.J. & Jones, J. 1998. Overtaking road-accidents: differences in manoeuvre as a function of driver age. *Accid. Anal. Prev.* **30**: 455–467.
- Cuthill, I.C., Partridge, J.C., Bennett, A.T.D., Church, S.C., Hart, N.S. & Hunt, S. 2000. Ultraviolet vision in birds. *Adv. Stud. Behav.* **29**: 159–214.
- Devereux, C.L., Whittingham, M.J., Fernandez-Juricic, E., Vickery, J.A. & Krebs, J.R. 2006. Predator detection and avoidance by Starlings under differing scenarios of predation risk. *Behav. Ecol.* **17**: 303–309.
- Dharmaretnam, M. & Andrew, R.J. 1994. Age- and stimulus-specific use of right and left eyes by domestic chick. *Anim. Behav.* **48**: 1395–1406.
- Diekamp, B., Regolin, L., Gunturkun, O. & Vallortigara, G. 2005. A left-sided visuospatial bias in birds. *Curr. Biol.* **15**: R372–R373.
- Drewitt, A.L. & Langston, R.H.W. 2008. Collision effects of wind-power generators and other obstacles on birds. *Ann. NY Acad. Sci.* **1134**: 233–266.
- Emmerton, J. & Delius, J. 1980. Wavelength discrimination in the 'visible' and ultraviolet spectrum by pigeons. *J. Comp. Physiol. A* **141**: 47–52.
- Endler, J.A. & Mielke, P.W. 2005. Comparing entire colour patterns as birds see them. *Biol. J. Linn. Soc.* **86**: 405–431.
- Eskom, E.W.T. 2008. *Eskom Endangered Wildlife Trust Strategic Partnership Central Incident Register. Held and Curated by the Wildlife & Energy Interaction Group*. Johannesburg: Endangered Wildlife Trust.
- Fernandez-Juricic, E., Erichsen, J.T. & Kacelnik, A. 2004. Visual perception and social foraging in birds. *Trends Ecol. Evol.* **19**: 25–31.
- Fernandez-Juricic, 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.
- Forkman, B. 1998. Hens use occlusion to judge depth in a two-dimensional picture. *Perception* **27**: 861–867.
- Forkman, B. & Vallortigara, G. 1999. Minimization of modal contours: an essential cross species strategy in disambiguating relative depth. *Anim. Cogn.* **4**: 181–185.
- Fox, R., Lehmkuhle, S.W. & Westendorf, D.H. 1976. Falcon visual acuity. *Science* **192**: 263–265.
- Fox, R., Lehmkuhle, S.W. & Bush, R.C. 1977. Stereopsis in the falcon. *Science* **197**: 79–81.
- Franklin, W.E. & Lima, S.L. 2010. Laterality in avian vigilance: do sparrows have a favourite eye? *Anim. Behav.* **62**: 879–885.
- Gaffney, M.F. & Hodos, W. 2003. The visual acuity and refractive state of the American Kestrel (*Falco sparverius*). *Vision Res.* **43**: 2053–2059.
- Ghim, M.M. & Hodos, W. 2006. Spatial contrast sensitivity of birds. *J. Comp. Physiol. A* **192**: 523–534.
- Gibson, J.J. 1966. *The Senses Considered as Perceptual Systems*. Boston: Lawrence Erlbaum Associates.
- Gibson, J.J. 1986. *The Ecological Approach to Visual Perception*. Hove: Erlbaum.
- Gill, F.B. 2007. *Ornithology*, 3rd edn. New York: W.H. Freeman.
- Goldsmith, T.H. 1980. Hummingbirds see near ultraviolet light. *Science* **207**: 786–788.
- Goldstein, B. 1984. *Sensation and Perception*. Belmont, CA: Wadsworth.
- Halley, D.J., Bevanger, K., Berntsen, F.E.H., Clausen, S.M., Dahl, E.L., Flagstad, Ø., Follestad, A., Hanssen, F.O., Hoel, P.L., Johnsen, L., Kvaløy, P., May, R.F., Nygård, T., Pedersen, H.C., Reitan, O., Steinheim, Y. & Vang, R. 2010. *The Effect of Wind Turbines on Birds at the Smøla Wind Power Plant, Norway: Collisions, Displacement, and Avoidance*. Poster presented at the conference Renewable energy 2010, Yokohama, Japan, 27 June–2 July 2010. Trondheim: Norsk Institutt for Naturforskning (NINA).
- Hills, B.L. 1980. Vision, visibility and perception in driving. *Perception* **9**: 183–216.
- Hirsch, J. 1982. Falcon visual sensitivity to grating contrast. *Nature* **300**: 57–58.
- Hodos, W. 1993. The visual capabilities of birds. In Ziegler, H.P. & Bischof, H.J. (eds) *Avian Vision, Brain and Behavior*. 63–76. Cambridge, MA: MIT Press.

- Hodos, W.** 2003. *Minimization of Motion Smear: Reducing Avian Collisions with Wind Turbines. Report NREL/SR-500-33249*. Washington, DC: National Renewable Energy Laboratory.
- Hodos, W. & Erichsen, J.T.** 1990. Lower-field myopia in birds is predicted by the bird's height: an adaptation to keep the ground in focus. *Vision Res.* **30**: 653–657.
- Hunt, D.M., Carvalho, L.S., Cowing, J.A. & Davies, W.L.** 2009. Evolution and spectral tuning of visual pigments in birds and mammals. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **364**: 2941–2955.
- Jacobs, G.H.** 1981. *Comparative Color Vision*. New York: Academic Press.
- Janss, G.F.E.** 2000. Avian mortality from power lines: a morphologic approach of a species-specific mortality. *Biol. Conserv.* **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. *J. Field Ornithol.* **69**: 8–17.
- Janss, G.F.E. & Ferrer, M.** 2000. Common Crane and Great Bustard collision with power lines: collision rate and risk exposure. *Wildl. Soc. Bull.* **28**: 675–680.
- Jenkins, A.R., Smallie, J.J. & Diamond, M.** 2010. Avian collisions with power lines: a global review of causes and mitigation with a South African perspective. *Bird Conserv. Int.* **20**: 263–278.
- Kelly, T.C., Buurma, L., O'Callaghan, M.J.A. & Bolger, R.** 2000. Why do birds collide with aircraft? A behavioural approach. *Int. Bird Strike Committee IBSC25/WP-054*: 47–48.
- Klem, D., Keck, D.C., Marty, K.L., Ball, A.J.M., Niciu, E.E. & Platt, C.T.** 2004. Effects of window angling, feeder placement and scavengers on avian mortality at plate glass. *Wilson Bull.* **116**: 69–73.
- Koboroff, A., Kaplan, G. & Rogers, L.J.** 2008. Lateralization and antipredator behaviour in Australian Magpies (*Gymnorhina tibicen*). *Brain Res. Bull.* **76**: 304–306.
- Land, M.F.** 1999. The roles of head movements in the search and capture strategy of a tern (Aves, Laridae). *J. Comp. Physiol. A.* **184**: 265–272.
- Land, M.F. & Nilsson, D.-E.** 2002. *Animal Eyes*. Oxford: Oxford University Press.
- Lea, S.E.G., Slater, A.M. & Ryan, C.M.E.** 1996. Perception of object unity in chicks: a comparison with the human infant. *Infant Behav. Dev.* **19**: 501–504.
- Lee, D.N.** 1980. The optic flow field: the foundation of vision. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **290**: 169–179.
- Lee, D.N. & Lishman, R.** 1977. Visual control of locomotion. *Scand. J. Psychol.* **18**: 224–230.
- Lee, D.N. & Reddish, P.E.** 1981. Plummeting Gannets: a paradigm of ecological optics. *Nature* **293**: 293–294.
- Lee, D.N., Reddish, P.E. & Rand, D.T.** 1991. Aerial docking by hummingbirds. *Naturwissenschaften* **78**: 526–527.
- Lythgoe, J.N.** 1979. *The Ecology of Vision*. Oxford: Clarendon Press.
- Manville, A.M.** 2005. *Bird Strikes and Electrocutions at Power Lines, Communication Towers, and Wind Turbines: State of the Art and State of the Science – Next Steps Toward Mitigation*: USDA Forest Service General Technical Report PSW-GTR-191.
- Martin, G.R.** 1985. Eye. In King, A.S. & McLelland, J. (eds) *Form and Function in Birds*, Vol. 3: 311–373. London: Academic Press.
- Martin, G.R.** 1986a. Sensory capacities and the nocturnal habit of owls (Strigiformes). *Ibis* **128**: 266–277.
- Martin, G.R.** 1986b. 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.** 1990. *Birds by Night*. London: T. & A.D. Poyser.
- Martin, G.R.** 2007. Visual fields and their functions in birds. *J. Ornithol.* **148**(Suppl. 2): 547–562.
- Martin, G.R.** 2009. What is binocular vision for? A birds' eye view. *J. Vision* **9**: 1–19.
- Martin, G.R. & Coetzee, H.C.** 2004. Visual fields in hornbills: precision-grasping and sunshades. *Ibis* **146**: 18–26.
- Martin, G.R. & Katzir, G.** 1994. Visual fields and eye movements in herons (Ardeidae). *Brain Behav. Evol.* **44**: 74–85.
- 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. & Osorio, D.** 2008. Vision in birds. In Basbaum, A.I., Kaneko, A., Shepherd, G.M. & Westheimer, G. (eds) *The Senses: A Comprehensive Reference, Vol. 1 Vision I*: 25–52. Amsterdam: Elsevier.
- 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. Biol. Sci.* **276**: 437–445.
- Martin, G.R. & Shaw, J.M.** 2010. Bird collisions with power lines: failing to see the way ahead? *Biol. Conserv.* **143**: 2695–2702.
- 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., White, C.R. & Butler, P.J.** 2008. Vision and the foraging technique of Great Cormorants *Phalacrocorax carbo*: pursuit or flush-foraging? *Ibis* **150**: 39–48.
- May, R.F., Hoel, P.L., Langston, R., Dahl, E.L., Bevanger, K., Reitan, O., Nygård, T., Pedersen, H.C., Røskaft, E. & Stokke, B.G.** 2010. *Collision Risk in White-tailed Eagles. Modelling Collision Risk Using Vantage Point Observations in Smøla Wind-power Plant*. Report 639. Trondheim: Norsk Institutt for Naturforskning (NINA).
- 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.
- Mclsaac, H.P.** 2001. Raptor acuity and wind turbine blade conspicuity. In Schwartz, S.S. (ed.) *Proceedings of the National Avian-Wind Power Planning Meeting IV, Carmel, CA, May 2000*: 59–87. Washington, DC: RESOLVE, Inc.
- Mench, J.A. & Andrew, R.J.** 1986. Lateralization of a food search task in the domestic chick. *Behav. Neural Biol.* **46**: 107–114.
- Meyer, D.B.** 1977. The avian eye and its adaptations. In Crescitelli, F. (ed.) *Handbook of Sensory Physiology*, Vol. VII/5: 549–611. Berlin: Springer-Verlag.
- Montgomerie, R. & Weatherhead, P.J.** 1997. How do robins find worms? *Anim. Behav.* **54**: 143–151.
- Nevelt, G.A.** 2010. Sensory ecology on the high seas: the odor world of the procellariiform seabirds. *J. Exp. Biol.* **211**: 1706–1713.

- Norberg, U.M.** 1990. *Vertebrate Flight: Mechanics, Physiology, Morphology, Ecology and Evolution. Zoophysiology Series*, Vol. 27. Berlin: Springer Verlag.
- Perrins, C.M.** 2009. *The Encyclopedia of Birds*. Oxford: Oxford University Press.
- Piersma, T., van Aelst, R., Kurk, K., Berkhoudt, H. & Maas, L.R.M.** 1998. A new pressure sensory mechanisms for prey detection in birds: the use of principles of seabed dynamics? *Proc. Biol. Sci.* **265**: 1377–1383.
- Regolin, L. & Vallortigara, G.** 1995. Perception of partly occluded objects by young chicks. *Percept. Psychophys.* **57**: 971–976.
- Reiner, A., Yamamoto, K. & Karten, H.J.** 2005. Organization and evolution of the avian forebrain. *Anat. Rec. A Discov. Mol. Cell. Evol. Biol.* **287A**: 1080–1102.
- Reymond, L.** 1985. Spatial visual acuity of the Eagle *Aquila audax*: a behavioural, optical and anatomical investigation. *Vision Res.* **25**: 1477–1491.
- Reymond, L.** 1987. Spatial visual acuity of the Falcon, *Falco berigora*: a behavioural, optical and anatomical investigation. *Vision Res.* **27**: 1859–1974.
- Rochon-Duvigneaud, A.** 1943. *Les yeux et la vision des vertébrés*. Paris: Masson.
- Rogers, L.J.** 1991. Development of lateralization. In Andrew, R.J. (ed.) *Neural and Behavioural Plasticity: The Use of the Domestic Chicken and a Model*. 503–535. Oxford: Oxford University Press.
- Rogers, L.J.** 2008. Development and function of lateralization in the avian brain. *Brain Res. Bull.* **76**: 235–244.
- Rothery, P., Newton, I. & Little, B.** 2009. Observations of seabirds at offshore wind turbines near Blyth in northeast England. *Bird Study* **56**: 1–14.
- 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.
- Shaw, J.M., Jenkins, A.R., Smallie, J.J. & Ryan, P.G.** 2010. Modelling power-line collision risk for the Blue Crane *Anthropoides paradiseus* in South Africa. *Ibis* **152**: 590–599.
- Shimizu, T. & Bowers, A.N.** 1999. Visual circuits of the avian telencephalon: evolutionary implications. *Behav. Brain Res.* **98**: 183–191.
- Sibley, D.** 2009. *The Sibley Guide to Bird Life and Behaviour*. London: Croom Helm.
- Sodhi, N.S.** 2002. Competition in the air: birds versus aircraft. *Auk* **119**: 587–595.
- Summers, R.W. & Dugan, D.** 2001. An assessment of methods used to mark fences to reduce bird collisions in pine-woods. *Scott. For.* **55**: 23–29.
- Thorpe, J.** 2003. Fatalities and destroyed civil aircraft due to bird strikes, 1912–2002. IBSC26 WPSA1.
- Tucker, V.A.** 2000. The deep fovea, sideways vision and spiral flight paths in raptors. *J. Exp. Biol.* **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*). *J. Exp. Biol.* **203**: 3755–3763.
- Vallortigara, G.** 2000. Comparative neuropsychology of the dual brain: a stroll through left and right animals' perceptual worlds. *Brain Lang.* **73**: 189–219.
- Vallortigara, G., Cozzutti, C., Tommasi, L. & Rogers, L.** 2001. How birds use their eyes: opposite left-right specialisation for the lateral and frontal visual hemifield in the domestic chick. *Curr. Biol.* **11**: 29–33.
- Vorobyev, M.** 2003. Coloured oil droplets enhance colour discrimination. *Proc. Biol. Sci.* **270**: 1255–1261.
- Vorobyev, M. & Osorio, D.** 1998. Receptor noise as a determinant of colour thresholds. *Proc. Biol. Sci.* **265**: 351–358.
- Walls, G.L.** 1942. *The Vertebrate Eye and its Adaptive Radiation*. Bloomfield Hills, MI: Cranbrook Institute of Science.
- Warren, W.H.** 2008. Optic flow. In Basbaum, A.I., Kaneko, A., Shepherd, G.M. & Westheimer, G. (eds) *The Senses: A Comprehensive Reference Vol.2 Part II*: 219–230. Amsterdam: Elsevier.
- Westheimer, G.** 1972. Visual acuity and spatial modulation thresholds. In Jameson, D. & Hurvich, L.M. (eds) *Handbook of Sensory Physiology*: 170–187. Berlin: Springer-Verlag.
- White, C.R., Day, N., Butler, P.J. & Martin, G.R.** 2007. Vision and foraging in cormorants: more like herons than hawks? *PLoS One* **2**: e639. doi: 10.1371/journal.pone.0000639.
- Wright, W.D.** 1963. The rays are not coloured. *Nature* **198**: 1239–1244.
- Wright, A.A.** 1972. The influence of ultraviolet radiation on the pigeon's color discrimination. *J. Exp. Anal. Behav.* **17**: 325–337.
- Wright, A.A.** 1979. Color-vision psychophysics. In Granda, A.M. & Maxwell, J.H. (eds) *Neural Mechanisms of Behavior in the Pigeon*: 89–127. New York: Plenum Press.

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