

Through birds' eyes: insights into avian sensory ecology

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Abstract Sensory ecology investigates the information that underlies an animal's interactions with its environment. A sensory ecology approach provides a framework in which to investigate a wide range of topics in ornithology. This review provides a range of examples of this approach. Discussed are some of the more general principles which apply with respect to the ways in which information from different sensory systems may complement each other, or information is traded-off within a sensory modality in the achievement of particular tasks. The emphasis is upon the task of foraging, but other behaviours, such as locomotion and predator detection, are also addressed. Examples discussed consider: (1) the perceptual challenges of nocturnal activity and how they are differently solved by information from different sensory system in owls, kiwi, oilbirds and penguins; (2) the use of tactile information in foraging and how this interacts with visual information in probing birds, and in skimmers; and (3) the visual information used to guide stealth foraging in herons, and how vision is influenced by the filter feeding techniques of ducks and flamingos. In addition, two case studies are discussed. These explore: (a) the restrictions on the information available to guide foraging in turbid waters by cormorants, and (b) the application of a sensory ecology approach to understanding why birds collide with artefacts, such as power lines and wind turbines, which intrude into the open airspace. Among the general conclusions discussed are: (1) the idea that all sensory systems are *selective* within their own

modality and that the range of information that is available to a particular species have been tuned to particular perceptual challenges through natural selection; it is also argued that this tuning can take place at the individual species level such that there may be key differences in sensory information even among birds in the same genus; (2) sensory systems detect only a small part of the total information that is available in the environment; no species has available to it all the information that is potentially available in its environment; in essence, all species share the same planet but live in different worlds that are dictated by the information that their sensory systems extract from the environment; (3) there may be complex and subtle trade-offs between different types of sensory information; and (4) the overall conclusion is that the world through birds' eyes is quite different from the world as seen through human eyes but there are many different "bird eye views".

Keywords Sensory ecology · Birds · Vision · Audition · Olfaction · Mechanoreception · Foraging · Visual fields · Binocular vision

Introduction: what is sensory ecology?

Sensory ecology can be summarised as the investigation of the information that underlies an animal's interactions with its environment (Dusenbery 1992). As such, sensory ecology is central to understanding most aspects of an animal's behaviour and ecology. Without knowing, even in general terms, the kinds of information that an animal has at its disposal, it is easy to be misled when trying to understand both the functions and mechanisms of behaviour.

Sensory ecology is not a well-defined endeavour. Ideas and data are gathered from a wide range of sources, and

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hypotheses vary widely in their focus (Cronin 2008; Endler et al. 2005). Data on the information that animals have available to them can range between knowledge of the characteristics of individual sensory receptors to the sensory capacities of whole organisms, and frequent use is made of ideas and concepts from physics and chemistry, at least in defining the limits of the information that it is possible to extract from a given environment. Sometimes, ideas in sensory ecology can be framed as testable hypotheses, but often there is reliance upon comparative data from which general principles can be extracted. Sometimes, intriguing ideas and insights into specific species and their behaviour must rely at least initially upon plausible ad hoc and post hoc analyses of sensory capacity and the perceptual challenges posed by particular environments or tasks. In essence, there are few key ideas which underpin the enterprise of sensory ecology but there are key themes and explanatory frameworks which have served to focus research and its applications.

One almost obvious observation, but nevertheless worth making at the outset, is that the human perspective on what information is available, and necessary, for underpinning the behaviour of other organisms can be seriously misleading. To assume, for example, that a bird “sees” its environment in the same way that we do is quite erroneous. However, it seems to be a widely held assumption. Cognizance is rarely taken, for example, of the fact that humans have two eyes positioned at the front of the skull while birds have eyes on the side of the skull, and these quite different arrangements have important implications for how much of the world about the head can influence behaviour from moment to moment. It is for reasons such as this that I have used the title “Through birds’ eyes”. This emphasises that even when it comes to understanding even the simplest behaviour of birds we must try to appreciate the information from the perspective of the bird, and I am not just referring to visual information. “Through birds’ eyes” is a metaphor for all the ways in which birds gather information about the environment. Of course, appreciating the world through birds’ eyes is in fact an impossible task. We cannot “know” how the world appears to a bird in the same sense that we think we know what information we have available to us. We can only “know about” the information that is available to a bird. The experience of “knowing” is not the same as “knowing about”. The other point in my title is that we must always think in the plural. There is no one “bird’s eye view”, but many “birds’ eye views”. The differences between bird species in the information that they can potentially have at their disposal can be both striking and subtle. For example, while it is clear that birds can have available to them information which humans cannot appreciate at all, it is dangerous to generalise to “all birds”

in any aspect of sensory ecology. There are some clear examples which suggest that sensory capacities, and the information that they provide, have been fine tuned to particular perceptual challenges that are faced by species as they differentiated from recent ancestors. Even within genera, and certainly within avian families, differences in sensory ecology occur.

This paper, and the plenary lecture on which it was based, is but a brief survey of a substantial intellectual enterprise. By illustrating certain key ideas with examples drawn from a rich comparative database, I hope to both intrigue and inspire readers to, at the very least, consider a sensory ecology perspective when considering how to understand the natural history and behaviours of the birds which they are studying. Simply to think about birds from within a sensory ecology perspective should provide both interest and insight.

What follows is a general introduction to the sensory world of birds and an attempt to show how that differs from our own sensory world mainly through examples drawn from vision. The paper then ranges through some examples of what a sensory ecology perspective can bring to understanding how different the visual worlds of birds can be both with respect to comparisons with other animal groups (humans are used as a key reference point) and also in comparisons between bird species. Hypothesis testing has driven many of the individual studies described, but the approach here is mainly comparative, designed to bring out some general themes or intriguing examples. This brief survey does not, by any means, describe all that we know about the sensory ecology of birds; the interested reader will have to read wider than this to get a real flavour of this field of endeavour. Furthermore, there are huge holes in our knowledge. I am often asked quite specific questions about the sensory ecology of certain species and often the answer is “we don’t know”. It may be possible to extrapolate from known examples or to conjecture about possible limits of sensory capacity and sensory information, but the answers to many questions will be found only by gathering new data.

Sensory ecology has a pedigree

This is the first time that the IOC has invited a plenary speaker to explore the theme of sensory ecology. However, sensory ecology is not a new enterprise. The seminal book which took a broad comparative approach to sensory capacities across the animal kingdom and started to interpret those capacities in the context of the perceptual challenges posed by different environments was *The Vertebrate Eye and its Adaptive Radiation* (Walls 1942), an encyclopaedic book which raised many interesting issues and presented

many fascinating examples about the function and diversity of vertebrate visual systems that can still intrigue today. André Rochon-Duvigneaud's (1943) *Les yeux et la vision des Vertébrés* also took an encyclopaedic approach but its influence was less, presumably because of its publication in the French language. Tinbergen's *The Herring Gull's World* (1953), although not a sensory ecology text as such, nevertheless focused ideas on the need to analyse an animal's behaviour from the perspective of its own world, not just the world as seen from a human perspective.

Sensory ecology got its first clear focus with the publication of Lythgoe's *The Ecology of Vision* (1979). Although focused primarily on fish and the marine environment, this book explored what needed to be known to describe the perceptual challenges of different environments. Importantly, it also showed how natural selection could result in sensory capacities that are finely tuned to maximise the information that animals can extract from their environment. The volume edited by Archer et al. (1999) in honour of Lythgoe showed how much progress had been made both conceptually and in terms of data in the general area of sensory ecology in the 20 years following the publication of Lythgoe's book.

It was Rochon-Duvigneaud (1943) who coined the phrase "A bird is a wing guided by an eye" ("L'Oiseau c'est une aile guidée par un oeil, ce qui exige la précision et la vitesse des fonctions rétinienne") which attempted to capture the essence of what a bird is from a sensory ecology perspective. Of course, as I explain below, we now see birds as being much more than an animal with flight that is guided by vision, but as a focus for thinking about birds and their sensory worlds the phrase has probably not been bettered.

The key sensory challenges

What are the key sensory challenges that are likely to have shaped avian sensory capacities? It is reasonable to assume that the most potent environmental challenges which have shaped sensory capacities, and the information that they provide, are those which operate more or less continually throughout an animal's life. Other challenges may be important at certain times of the annual cycle or even at certain stages of development, for example challenges associated with reproduction. However, the following list would seem to present the prime candidates for sensory challenges which are faced more or less continually throughout a bird's life, and have therefore been subject to, and are still subject to, the processes of natural selection. These themes are discussed briefly here and will be returned to later in the discussions of particular examples of investigations of sensory ecology.

Locomotion

Rochon-Duvigneaud considered locomotion (flight) to be the prime sensory challenge that shaped the evolution of vision in birds. This is not surprising since birds typically appear both fast moving and highly manoeuvrable on the wing, and some birds can apparently achieve both fast flight and high manoeuvrability in complex spatial habitats. Such behaviour would seem to pose challenging sensory problems for the visual system that can best be solved by gaining a high degree of spatial detail and also gaining it at a high rate. However, not all birds fly fast, some do not fly at all, and many birds fly in open simple habitats. An albatross flying over the open ocean would seem to face a different suite of sensory challenges compared with those faced by a small passerine that flies habitually within a woodland canopy.

Foraging

Finding and ingesting food would seem to pose a constant information challenge for birds. Furthermore, birds as an Order, exploit a very wide array of food types; algae and diatoms, green vegetation, many different types of fruits and seeds, animals of all the main macro faunal types, etc. Each dietary type and its associated method of acquisition (pecking, lunging, probing, excavation, aerial pursuit, grazing, filtering, etc.) would seem to pose a rich range of sensory challenges which must be dealt with frequently by a bird in its lifetime.

Predator detection

Avoiding being detected and consumed by a predator is a challenge which probably faces most birds almost constantly, only species which live in rare predator-free habitats may be freed of this constant source of selection.

The sensory challenges posed by locomotion, foraging and predator detection would seem to apply almost constantly in the lives of most birds, but the solutions to these challenges may not be mutually reinforcing. Trade-offs in the acquisition of the information that underlies an animal's interactions with its environment with respect to these three sets of challenges may have evolved.

Restricted environments

Additional to the above sensory challenges, there may be further ones posed by life in particular environments in which sensory information may be restricted. Prime among these are nocturnal habitats in which light levels restrict the availability of spectral and spatial information (Martin 1990). Within aquatic habitats, light levels may

also be restricted compared to the surface, and the selective spectral filtering of light by water or dissolved and suspended matter may also restrict both spectral and spatial information (Lythgoe 1979; Lythgoe and Partridge 1989; Jerlov 1976). Turbidity will also restrict the availability of spatial information in the environment. Possible antagonisms and trade-offs may influence the evolution of sensory capacities that meet these perceptual challenges and, in the case of diving birds, these can be further compromised or traded against the information necessary for behaviour above the water surface (Sivak 1978).

Different senses contribute different information

Humans are familiar with the way sensory information can be segmented according to the sensory modality in which environmental information is encoded, and the distance over which information can be retrieved.

Information from a distance

The three main telereceptive senses retrieve information about objects which are remote from an animal's body. *Vision* exploits information encoded in a particular band of wavelengths within the electromagnetic spectrum (light). *Audition* exploits information encoded in a band of frequencies in the propagation of pressure differences through air or water (sound). *Olfaction* exploits information encoded in particular molecules transmitted through air or water (chemical senses). All three modalities can provide information simultaneously about the same object or about different objects at different distances. The efficiency of these different sensory modalities differs with respect to speed of transmission of information, distance over which information retains its integrity, and persistence of the information in the environment (Dusenbery 1992). Clearly, in understanding any one behaviour from a sensory ecology perspective any one, or multiple, modalities can be at play simultaneously or sequentially and there may be trade-offs between these different types of information which may also fluctuate over time and in different environments. For example, information retrieved through audition or olfaction may become more important as ambient light levels decrease.

Information from close proximity- Mechanoreception

This provides information about objects either in physical contact with the body or at a very short distance from it. In birds, a prime source of information obtained through mechanoreception that guides foraging behaviour is retrieved via “bill-tip” organs (Gottschaldt 1985; Cunningham et al. 2010). These are clusters of mechanoreceptors

embedded in pits contained within the bone (in kiwi Apterygidae, ibises and spoonbills Threskiornithidae, ducks and geese Anatidae, shorebirds Scolopacidae) or keratin (parrots Psittacidae) of the distal portions of the mandibles, especially around the bill tip. These receptors are employed for unsighted prey detection (Cunningham 2010; Cunningham et al. 2010) or the manipulation of objects held in the bill (Demery et al. 2011). Prey detection may include the use of “remote touch” in which prey is detected without the bill making direct contact with the item (Piersma et al. 1998) by exploiting the differential back pressure generated by a buried object when the bill is thrust into a fluid-filled substrate.

Magnetoreception

Information about the Earth's magnetic field, and how its variation with position on or near the Earth's surface can be exploited in orientation and navigation, is well established as a key source of information in birds, amphibians and reptiles and possibly fish. The mechanisms by which this information is retrieved has been the subject of much debate and these have been reviewed a number of times, most recently in the plenary lecture given by Wolf Wiltschko at the 25th IOC in 2006 and in reviews (Wiltschko and Wiltschko 2006). In birds, there now seem to be three candidate mechanisms for magnetoreception. These are situated in the eye, the brain close to the olfactory bulb, and the inner ear (Wiltschko and Wiltschko 2006; Wu and Dickman 2011). Clearly, magnetoreception plays an important role in providing key information for the control of some very important behaviours of many, if not most, bird species. However, since it has been reviewed recently elsewhere, it will not be discussed further here. In essence, there is yet to emerge a true sensory ecology perspective in which to view magnetoreception. It is not yet known how magnetoreception might have been modified through natural selection in response to different environmental challenges, and/or how it may be used differentially within a species or between species in response to particular environmental challenges. There are, however, some suggestions of how magnetic field information might sit within a hierarchy of information (for example alongside olfactory, star or sun compass information) to control orientation and navigation under different environmental conditions (Wiltschko and Wiltschko 1999).

Echolocation

This is a refinement of audition which extracts information about objects in the environment. This information is

retrieved from the ways that sounds which have a particular frequency spectrum and intensity that are emitted by the animal are distorted when they are differentially reflected from surfaces (change of intensity as a function of frequency and reflecting surface type) (Busnel and Fish 1980). As a well-defined sensory capacity that is used in orientation by birds, echolocation is known only from Oilbirds *Steatornis caripensis* Caprimulgidae (Konishi and Knudsen 1979) and Cave Swiftlets *Collocalia* spp. Apodidae (Griffin and Thompson 1982; Pye 1985). However, it should be noted that echolocation may not involve any specialised sensory capacities in these birds, instead it may result (as is the case in humans who can echolocate) in learnt or specialised perceptual analysis in the brain rather than being a refinement of audition per se.

Some important general properties of sensory systems

Perhaps the most important general point to make about sensory systems is that they are all selective within their own modality. This selectivity, which restricts the information available to an animal about its environment, arises through both physical and anatomical constraints on the structure and functioning of sense organs in general, and also through natural selection refining the structure and functioning of particular sense organs. Sensory systems detect only a small part of the total information that is available in the environment in which an animal lives. Furthermore, it is clear that gaining one type of information may compromise the ability to gain another type of information, both within the same sensory modality and between sensory modalities. The result is that there may be complex and subtle trade-offs of information both within and between sensory modalities which can influence an animal's behaviour. Many of the examples listed below explore these trade-offs in sensory information, but to emphasise this point it is worth noting that the vertebrate eye embodies many subtle trade-offs in its two main functional parts: the image-producing (optical) system and the initial information extracting/image analysing system, the retina (Martin 1985, 1993).

The optical system of the eye (the image-producing system) determines how much of the world is available for analysis at any one time, and provides a fundamental constraint upon the size of the image (and hence a limit on resolution) and its brightness (and hence a limit on sensitivity) (Land and Nilsson 2002). Although the image-producing system is referred to as a “simple” optical system (compared to the multiple optical systems found in the compound eyes of invertebrates) and indeed contains just two main optical components (the curved cornea through which light enters the eye and the lens), many subtle

variations in the dimensions and properties of these two components are possible (Martin 1993). These affect the performance of an eye with respect to both resolution and sensitivity (Land and Nilsson 2002), and there is evidence in birds that eye optical systems have been subject to natural selection driven especially by the overall sensory challenges presented by the range of light levels which occur naturally over the daily cycle (Martin and Brooke 1991; Martin 1986a, b, c).

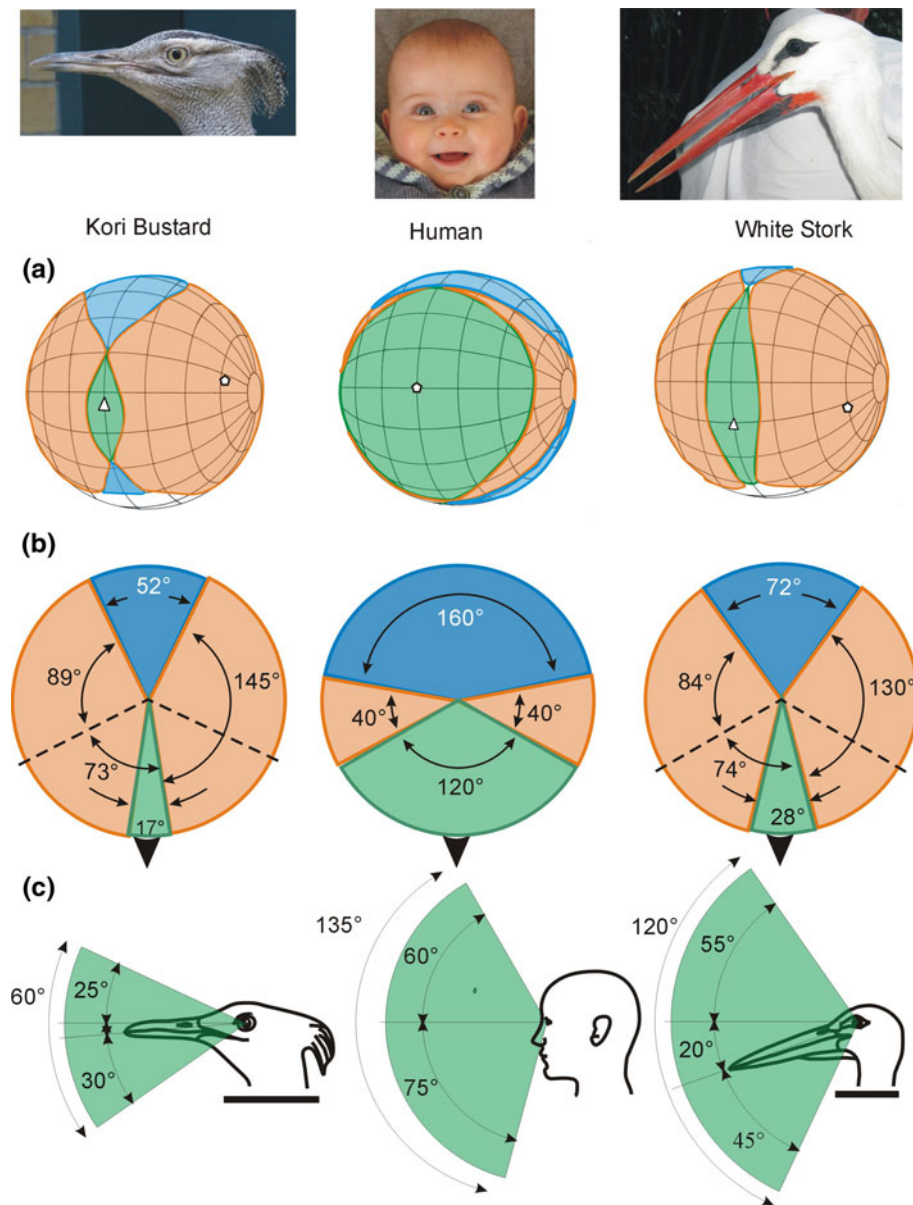
The retina (the start of the image analysis and information extraction system) can also show high degrees of differentiation in the distribution of photoreceptor types (rods and cone types with different sensitivities in the spectrum) and their densities within the retina (Martin 1985; Meyer 1977). This means that the information extracted from the image is not spatially uniform; there may be areas within the retinal image in which the extraction of spectral and spatial information is maximised, and other areas where the detection of movement or sensitivity is maximised. For example, there may be one or two localised areas of high resolution, or areas which stretch linearly across the retina and presumably maximise resolution in a band across the visual field of each eye (Martin 1985).

The ways in which eyes are placed in the skull and how they can be moved will determine the total extent of the world around a bird that can control the extraction of information from moment-to-moment (Martin 2007).

Taken together, these differences between species in the optical and image analysing systems of each eye, and how the two eyes are placed in the skull, can be very striking. So much so that although birds from different species may live within the same environment, the visual information that they extract from that environment supports the contention that these species may actually “live in different worlds”. Furthermore, it now seems to be clear that these different worlds can occur between closely related species within the same family (Martin and Portugal 2011) or even within the same genus (Guillemain et al. 2002), suggesting that natural selection can operate upon sensory systems such that they can be finely tuned to particular perceptual challenges that are faced by species as they differentiate from recent ancestors. Much of the rest of this paper will flesh out, through examples, evidence which supports these general statements.

What is a bird's visual world compared to ours?

The problem with a comparative approach is deciding which interspecific comparisons are appropriate; what should be the point of reference? The only experiential



reference points as regards sensory information are provided by ourselves but rarely are we able to quantify or even explain the information that we have available about the worlds which we inhabit. However, in order to provide some general context for what follows, it is worth describing briefly the general ways in which a bird's visual world differs from that of humans.

Colour vision

Most avian retinas contain more diverse types of photoreceptors than are found in primates (Martin and Osorio 2008; Vorobyev et al. 2001). Human colour vision is described as trichromatic because there are three types of cone photoreceptor types. These types are described by

reference to the peak sensitivity of their visual pigments (in the red, green and blue parts of the visible spectrum). It now seem to be clear that many birds are pentachromatic with at least four photoreceptor pigments in the cones (with peak sensitivities in the red, green, blue and near-ultraviolet or ultraviolet) which, with the filtering of highly pigmented oil droplets positioned within the photoreceptors, results in at least 5 different functional cone types (Martin and Osorio 2008; Hunt et al. 2009; Bowmaker et al. 1997). The consensus seems to be that this richer array of photoreceptors is used to analyse the spectral content of the retinal image to render more subtle colour discriminations than are possible with the human trichromatic system (Martin and Osorio 2008). The general result is that, when viewing the same scene, birds' eyes can extract different,

◀ **Fig. 1** Visual fields in Kori Bustards *Ardeotis kori*, humans and White Storks *Ciconia ciconia*. The differences between a “human eye view” and a “bird eye view” are readily apparent from these diagrams. 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 projections of the boundaries of the visual 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 which are likely to coincide with the direction of best optical quality and highest acuity are indicated by a *white pentagon*. 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 which forage using visual guidance are shown in the case of the bustards and storks. These are features typical of the majority of bird species. 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 to 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 lies 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 and hence render these birds vulnerable to collisions with human artefacts such as power lines and wind turbines which intrude into open airspace (see “[The visual ecology of avian collisions](#)”). 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 in storks 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 such as power lines and wind turbines. (Based upon figures in Martin (2011) and Martin and Shaw (2010)

and possibly more subtle, information based upon the spectral reflectance of objects than can humans.

Furthermore, the visible spectrum of birds, and the spectral region in which birds can distinguish colours, embraces a wider portion of the electromagnetic spectrum that extends beyond what humans can see into the

ultraviolet (UV) portion of the spectrum (Cuthill et al. 2000). That the vision of birds is influenced by light in the UV was first shown using behavioural experiments in pigeons (Wright 1972; Emmerton and Delius 1980) and later in hummingbirds (Goldsmith 1980). Further investigations of the spectral properties of retinal photoreceptor cells using microspectrophotometry, and genetic analysis, have now shown that visual sensitivity within the UV portion of the spectrum is widespread among birds, and is possibly widespread in the animal kingdom (Hunt et al. 2009).

It may be that humans are more the exception in not being able to extract environmental information using light in the UV region. It is misleading to suggest that birds have a secret channel of communication because their visible spectrum extends into the UV. It is more appropriate to consider UV sensitivity as simply resulting in a broader spectrum of light which can provide information about the environment. That vision within the UV and near UV portion of the spectrum is important among birds has been shown through such evidence as the presence of plumage with differential reflectance in the UV in species such as Blue Tits *Cyanistes caeruleus* and Common Starlings *Sturnus vulgaris* (Cuthill et al. 2000), evidence that Common Kestrels *Falco tinnunculus* may preferentially hunt in areas where UV reflective urine trails left by small rodents are prevalent (Viitala et al. 1995), and evidence that certain fruit and foliage combinations provide highly contrasting signals in the UV portion of the spectrum (Burkhardt 1982; Schaefer et al. 2007).

Spatial resolution

The ability to resolve spatial detail within the image projected on to the retina is a function of both image size and the spatial packing of the photoreceptors cells which begin the analysis of the image (Land and Nilsson 2002). There have been a number of studies which show how behaviourally measured acuity (highest resolving power of the visual system using stimuli of high contrast) in birds can be directly related to image size and the highest density of receptor cells within the retina (Reymond 1985, 1987). These studies show that acuity in some birds is superior to that of the human fovea (the area of the human retinas which provides the highest resolving power) but not exceptionally so. In Wedge-tailed eagles *Aquila audax* the difference is about 2.5-fold while the acuity of falcons (Brown Falcon *Falco berigora*, Reymond 1987; American Kestrels *Falco sparverius*, Hirsch 1982; Gaffney and Hodos 2003) is very similar to the highest acuity of humans. In many bird species, acuity is below that of humans (Hodos 1993; Ghim and Hodos 2006). In humans, the retinal areas of highest acuity (highest density of

photoreceptors) is a single region, more or less centrally placed within the field of view of each eye, but in birds there may be more than one area of high receptor density, and in some species there are areas which stretch across the retina in an approximately horizontal orientation relative to typical head posture (Meyer 1977). This suggest that birds' retinas can show high acuity in more than one region, that this region can be extensive, and that in some species it may function to extract most detailed information from the direction of the natural horizon (Martin and Osorio 2008).

One particularly important difference between humans and birds is that in humans the direction of highest acuity (and also the area where spectral discrimination is most acute) projects directly forwards and this is also the direction in which we travel. This direction coincides with the region in the eye of best optical quality; the optical axis about which the cornea and lens are centred. In birds, however, because of the lateral placement of the eyes in the skull, the directions of best optical quality and the directions of highest acuity and spectral discrimination project laterally, not forwards in the direction of travel.

Visual fields

The visual field of an eye describes the volume of space which can be imaged upon the retina and hence from which information can be extracted (Martin 2007). Because all vertebrates have two eyes, the visual fields of each eye are combined to provide a visual field for the whole animal (the cyclopean visual field). This field defines the area about the head from which information can be retrieved at any one moment. Visual fields are complex and can vary considerable between species depending upon the nature of the visual field of each eye and how they are combined. Examples of visual fields in birds and how they differ from those of humans are shown in Fig. 1.

Table 1 compares in general terms the visual field characteristics of humans and birds. In essence, humans (primates) are exceptional in the animal kingdom in having

two eyes placed at the front of the skull with their axes parallel (Hughes 1977). This gives humans extensive binocular overlap in the direction of travel but extensive blind areas above and behind the head, and the region of both highest acuity and colour discrimination coincide and projects forwards. Table 1 summarises this arrangement and contrasts it with the arrangement found in birds in which laterally placed eyes typically result in a narrow region of binocular overlap, extensive monocular visual coverage above and behind the head, and with the regions of highest spatial acuity and most acute colour discrimination projecting laterally (Fig. 1). Within this general arrangement, there are both marked and subtle interspecific differences in visual fields between bird species and some of these are described below along with interpretations of their functional differences.

Two other general functional differences which result from these different visual field arrangements are also summarised in Table 1. In humans, the best appreciation of relative depth lies ahead within the binocular field to the front of the head, and is derived from stereopsis (a computational process in which the brain extracts information from the subtly different views which each eye has of the same scene; Julesz 1978). In birds, however, binocular/frontal vision is primarily concerned with near tasks such as pecking and lunging at objects with the bill (Martin 2009). Stereopsis is absent in most birds, and both the position of the bill and general locomotion are controlled by optic flow-fields (Martin 2009). Optic flow-fields can specify directly both the direction of travel and time to contact an object, and do not require high visual resolution (Lee 1980; Lee and Lishman 1977). Flow-fields are also important in humans for many skilled behaviours (Lee and Young 1985), but stereopsis can play an important additional role in estimating the relative depths of objects that lie relative close to and directly in front of the head.

In essence, humans experience their visual world as “in front” of them and they move “into” that world guided by information derived from the stereoscopic cues and optic

Table 1 Summary of general properties of visual fields in humans and birds

Humans	Birds
Eyes at front of the head	Eyes placed laterally in the head
Extensive binocular overlap in direction of travel	Small binocular overlap in the direction of travel
Extensive blind areas above and behind head	Extensive visual coverage above and behind head
Region of highest spatial acuity and most acute colour discrimination projects forwards	Regions of highest spatial acuity and most acute colour discrimination project laterally
Best appreciation of relative depth lies ahead in the binocular field and can be derived from stereopsis when the head is stationary	Binocular/frontal vision is primarily concerned with near tasks, stereopsis is absent in most birds, locomotion is controlled by optic flow-fields which are derived from relative movement between animal and objects
The human visual world is “in front” and humans move “into” it	The avian world is “around” and birds move “through” it

flow-fields. By contrast, in birds, the world is “around” them and they can be envisaged as moving “through” it guided only by optic flow-fields.

A consequence of these general visual field properties is that for tasks requiring high spatial resolution birds tend to fixate upon a target with one of their lateral fields of view, and that behavioural control typically passes to frontal (binocular) vision for final seizure of object/food in the bill or feet, only at close range. This is compatible with general ideas about the function of binocular vision in birds (Martin 2009) and with the evidence that the processing of information extracted from the fovea (the region of highest acuity which projects laterally) is possible only for one eye at one time (Voss and Bischoff 2009). Examples of this switching of visual control from lateral to frontal visual fields can be seen in, for example, thrushes Turdidae foraging on the ground (Montgomerie and Weatherhead 1997), or in evidence that Peregrine Falcons *Falco peregrinus* fix prey with one of their lateral visual fields and stoop towards it along a curved path holding the item in the lateral field until just before capture, when control passes to frontal vision (Tucker 2000; Tucker et al. 2000).

There are two further correlates of this lateralisation of eye placement in birds. First, if eye movements are present in a species then the eyes can be moved independently and in many species (for example, herons Ardeidae; Martin and Katzir 1994), eye movements are of sufficient amplitude to abolish binocularity. Voss and Bischoff (2009) suggest that eye movements may not be entirely independent. In Zebra Finches *Taeniopygia guttata*, they showed that when one eye moves the other eye often counter rotates, but these movements combined can still lead to the spontaneous abolition of binocularity. Secondly, it has been demonstrated that in some birds one eye may be used preferentially for particular tasks while the other eye is preferred for other types of task, and that this behaviour provides clear evidence of lateralisation of brain function in birds (Rogers 2008) (see Rogers, this volume).

Perhaps the most important insight from all that has been discussed above is the conclusion that for most birds frontal vision is far less important than vision to the side. Because we have eyes at the front of our heads, and as a consequence everything of importance seems to occur in front of us, it is very difficult to imagine what another world view is like; a world in which behaviour can be controlled by objects that lie all around and above the head.

Case studies in avian sensory ecology

Having outlined a general context in which to consider sensory ecology in birds, attention now turns to some specific examples in which a sensory ecology approach has

provided insights into certain behaviours. This is not meant to be a comprehensive survey of all that is known about avian sensory ecology, but rather a means of providing insights into the questions that can be posed and the information that can be brought to throw light on their investigation. The perspective changes with each example, some may seem like “just-so” stories but in most cases arguments are more substantial and are best revealed by reading the original accounts. The context is always a comparative one and testable hypotheses may also require a comparative rather than a directly experimental approach for their resolution.

Sensory ecology of foraging

In the introduction were listed three principal behaviours of birds which would seem to pose different sensory challenges and which are faced more or less continually throughout a bird’s life: locomotion, foraging, predator detection. Because daily life for most birds would seem to require gathering information continually in order to accomplish these behaviours, they are clear candidates for natural selection to have shaped both behaviour and the gathering of information which guides it. Hence, we are likely to find intriguing insights into sensory ecology by investigating any one of these behaviours and their sensory bases and we might also find general principles at work. We might also find trade-offs within particular sensory capacities, and between different sensory systems, by looking at particular examples of apparently exacting tasks which must be accomplished regularly and efficiently. Solutions to the perceptual challenges of foraging in nocturnal (low light level) environments are considered in three examples below.

The Tawny Owl’s world: nocturnal predation beneath a woodland canopy

Tawny Owls *Strix aluco* present a rare example of a bird species which completes all aspects of their life cycle after dusk and before dawn (Martin 1986a, b, c, 1990). They prefer to do this beneath a closed woodland canopy rather than in open habitat. Nocturnal woodland habitats provide many perceptual challenges simply because light levels are so low. It is theoretically well understood that an eye which has evolved to achieve high sensitivity cannot also achieve high spatial resolution at the same time, a problem which has its origins in the problem of capturing sufficient photons at low light levels to provide unambiguous information on their spatial origins (Snyder et al. 1977; Land and Nilsson 2002). It is a problem which will be familiar to photographers and in fact applies to any kind of vision

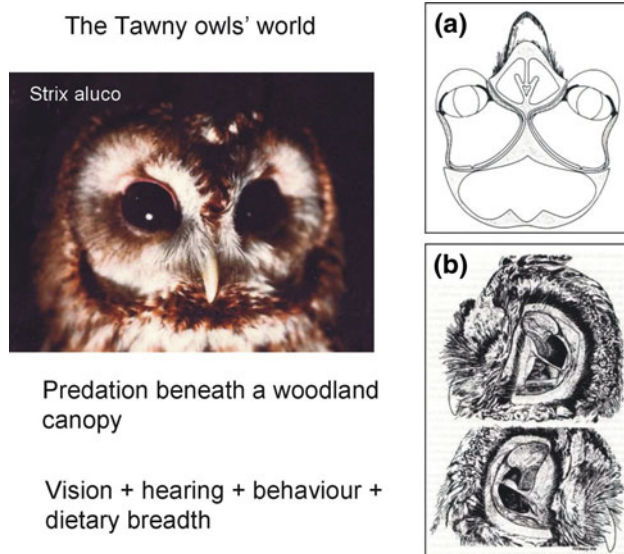


Fig. 2 Nocturnal predation beneath a woodland canopy poses specific sensory challenges for a flying bird. In Tawny Owls *Strix aluco*, these challenges seem to have been met by the evolution of a suite of four particular adaptations. (1) Absolutely large eyes (a) which maximise light gathering capacity of the optical system. The eyes are very large relative to the skull and extend beyond the eye sockets. They are immobile and despite the appearance of frontality they diverge by approximately 50°. (2) Elaborate and asymmetric outer ear structures (b) placed around the opening of the ear canals at the edge of the facial disc feathers. These structures provide accurate sound localisation. (3) Behavioural adaptations which include a perch-and-pounce hunting technique and a high degree of territoriality which enhances familiarity with the spatial structure of a hunting area. Together, these allow Tawny Owls to take prey from the ground using familiar perches combined with knowledge of the structure of a bird's habitat. Such knowledge can enhance the interpretation of minimal visual and acoustic information that can occur under nocturnal conditions. (4) A broad dietary spectrum that allows birds to exploit a wide diversity of prey that can be located, but not necessarily identified, within the familiar territory. Based upon figures in Martin (1990), Norberg (1978) and Wood (1917)

system. Manoeuvrability within woodland would seem to require high spatial resolution to avoid obstacles while the low light levels of night time, especially those which occur under a woodland canopy when there is cloud cover but no moon, would seem to require high sensitivity, i.e. an eye whose optical system gathers as much light as possible. Owls are noted for their large and tubular-shaped eyes which literally bulge outside the skull and because of this they are virtually immobile (Fig. 2a). Owl eyes appear to be more frontally placed than in many other birds; however, they still diverge by about 50° and the area of binocular overlap (47°) is only one-third that of humans (note that appearances are deceptive when casually estimating binocular fields; to the casual observer binocular fields always appear larger than they actually are) (Martin 1984).

The picture which emerges of the sensory ecology of Tawny Owls has been described in some detail (Martin

1986a, b, c, 1990). First, there is evidence that acuity at low light levels is relatively poor and that absolute visual sensitivity (the lowest light level that can be detected), although higher than that of the human eye by a factor of about $\times 2.5$ (Martin 1977), is insufficient to provide detailed visual information within a wide range of light levels which occur naturally beneath a woodland canopy. As a consequence, under relatively frequently occurring conditions, a Tawny Owl cannot extract any visual information when looking downwards at the woodland floor, which is where prey is usually taken from. Some nights, e.g. bright moonlight without cloud cover, do provide enough light for the owls to see smaller branches and some detail on the woodland floor and even on very dark nights large branches should be detectable in silhouette against the sky.

Thus, vision on its own cannot provide sufficient information for these owls to be able to hunt successfully throughout the full range of natural light levels experienced in these birds' natural habitats. However, owls differ from all other birds in their possession of large outer ear structures (Fig. 2b) which occur at the edge of the facial disc of feathers (Norberg 1978). These ear openings are so large that it is possible to see the side of the tubular eyes through them. These ear structures function not to enhance auditory sensitivity, but to provide accurate sound localisation in both the vertical and horizontal planes. The accuracy (at some locations to within $\pm 1^\circ$) is in fact very similar to that achieved by humans for sounds presented to the front of the head (Knudsen 1980). Furthermore, it has been shown that owls are capable of learning to hunt in total darkness. This capture of prey on the ground below a hunting perch is based solely upon the auditory cues produced as prey moves through leaf litter (Payne 1971). In most birds, sound localisation is very much less accurate than that achieved by owls, for example small passerines can locate sounds to an accuracy of only 18° (Klump et al. 1986).

The picture which emerges is that under some natural night time light conditions owls could locate and capture prey using visual cues alone. However, such conditions probably occur rarely within their chosen habitats. At lower light levels, the birds must employ auditory localisation to detect and locate prey and to capture it unseen. Vision may play a role in getting the birds back through branches to a perch since at least the larger branches may be seen in silhouette against the sky. Thus, information from vision and audition play complementary roles in the mediation of prey capture. However, a third component is necessary in order to exploit this sensory information: knowledge of the particular habitat. Without this, the meagre information available from the senses cannot be successfully interpreted. Hunting perches and the distance from them to the ground must be known so that the distance of a pounce can

be judged accurately. Sound localisation gives information on the direction of a sound. However, its distance must be learnt from experience with the complex ways in which familiar sounds degrade in particular circumstances. Thus, the final component of how these birds live within their preferred habitat at night throughout the years is that they are highly sedentary. Tawny Owls are relatively long lived and simply do not stray out of their territory once it has become established. A final piece of this story is that Tawny Owls have a relatively broad dietary spectrum, often taking prey items, such as earthworms and beetles, that would seem to be below optimal size. But if these birds are obliged to stay in one place all of their lives they cannot be dietary specialists, they must take whatever prey that can be detected using vision and hearing, or hearing alone, as it moves about a forest floor (Martin 1986a, b, c).

What this case study shows is that natural selection will drive sensory capacities close to the limit of what is physically possible; owl eyes are very sensitive and the difference in their absolute sensitivity with those of humans and cats can be principally attributed to their optical systems (not to the sensitivity of their retinas), but such sensitivity is inevitably achieved at the price of low acuity. However, even this high sensitivity cannot match the perceptual challenges posed by the very low light levels that occur naturally at night inside a woodland habitat. There will be occasions when very little or no visual information can be retrieved from the woodland floor on which the birds' prey are found. Similarly, natural selection has driven the evolution of elaborate mechanisms that enable sounds to be located with high accuracy, but this alone cannot help a bird to locate prey, catch it and return to a perch. To achieve that requires specific knowledge (familiarity) with the ways in which sounds degrade and so provides information on the distance from the bird to a sound source. Specific knowledge is also required concerning the spatial relationships between the ground, perches, and landmarks within the territory.

The next case study considers another example of bird activity under extreme low light levels. However, this has been solved through the evolution of different sensory capacities to those of Tawny Owls. These capacities provide a different suite of information which can be combined to guide flight and foraging at low light levels.

The Oilbird's world: cave dwelling and nocturnal foraging in a woodland canopy

Oilbirds *Steatornis caripensis* can rightfully be considered the most nocturnal of all birds (Martin et al. 2004). They are cave dwelling and rarely leave the cave until after dusk and return before dawn, perhaps never experiencing

daylight throughout the whole of their lives. The diet is mainly fruit (Snow 1961).

Optically, the eyes of Oilbirds are highly efficient having a very low f-number (a measure of light gathering capacity or retinal image brightness) of 1.07 compared with that of Tawny Owl eye's f-number of 1.30 and 2.13 in human eyes. This low f-number indicates that on the basis of light gathering alone Oilbirds' eyes are 4 times more efficient than human eyes and 1.5 more efficient than the eyes of Tawny Owls. Furthermore, the retinas of Oilbird eyes contain a structure which to date is unique among terrestrial vertebrates. The rod photoreceptors are banked or tiered above each other up to three layers (Rojas et al. 2004; Martin et al. 2004). Such banked retinas have previously been described only in the eyes of some deep sea fish (Lockett 1977) whose eyes are adapted for the detection of very low ambient light levels and/or the small light sources produced by the photophores of other fish.

A tiered retina increases the probability that light photons within the retinal image will be trapped and thus converted to a neural signal. However, the disadvantage of such an arrangement is that it further reduces the resolution of the eye. This is because it is not possible to determine the source of a photon with an accuracy equal to that possible when the rod receptors are arranged across the retina in a single layer, which is the arrangement in most vertebrate eyes. This is another manifestation of the trade-off between sensitivity and resolution. However, the optical and retinal structures of Oilbird eyes suggest that natural selection has pushed them close to the limit of sensitivity (Martin et al. 2004). While this high visual sensitivity can be interpreted in a straight forward manner as an adaptation to the perceptual challenges of nocturnal activity, it cannot provide the full explanation of how these birds' sensory systems meet all the perceptual challenges of their life.

Oilbirds live in caves, to which they usually return at dawn (Holland et al. 2009), and build their nests and raise their young on cave ledges. These caves can be absolutely dark (no light penetrates) yet the birds fly within the cave interior and locate their nests, young and mates. This is achieved by the use of echolocation (Konishi and Knudsen 1979) coupled with the ability to fly at low speed. However, Oilbird echolocation employs sound signals of low frequency, well within the typical avian and human audible range, and this means that spatial resolution is low (Konishi and Knudsen 1979). Thus, activity within the complete darkness of a cave can be accounted for by information obtained through the use of auditory signals with echolocation being used alongside these birds' repertoire of vocalisations which presumably allow the identification of individual mates and chicks.

Outside the cave, Oilbirds forage at night on fruits taken within the forest canopy (Snow 1961), and it seems likely that these food sources are initially detected using olfactory information provided by the ripe fruits (Bang and Wenzel 1985). Olfaction of itself cannot guide flight, it only tells the birds where to find a source of food, and it is presumably in the task of actually reaching the food source that the high visual sensitivity of Oilbird eyes are employed to extract spatial information with respect to obstacles in the canopy and perhaps for the location of individual fruits. However, it should be noted that this task may not be as exacting as that faced by the owls which are attempting to find prey on a woodland floor. Light levels and the contrast of objects against the sky are always likely to be higher than when attempting to detect cryptically coloured prey against a woodland floor.

As in the case of Tawny Owls, there is no simple solution to gaining sufficient information for nocturnal activity. In Oilbirds, natural selection seems to have driven the evolution of eyes close to the theoretical limit of sensitivity, but this sensitivity cannot provide spatial information within the total darkness of a cave, and this lack of visual information is complemented by the evolution of echolocatory abilities which, although of low resolution, clearly provide sufficient information to guide slow flight in the relative spatial simplicity of a cave's interior. In foraging, there is complementarity between the high visual sensitivity but low spatial resolution provided by vision and the low spatial resolution (but effectiveness over a longer distance) of olfaction, which allow sources of ripe fruits to be located.

The Kiwi's world: nocturnal activity without predators and without flight

The case studies of Tawny Owls and Oilbirds provide examples of species which are able to complete all aspects of their life cycle under low light (nocturnal) conditions and are able to use flight. Kiwi are also habitually active under the low light levels that occur beneath a woodland canopy but they have become flightless, presumably because they have evolved in an environment virtually free of ground or aerial predators, so making rapid escape unnecessary (Marchant and Higgins 1990; Wilson 2004). However, Kiwi show a suite of sensory abilities, different from those of both Oilbirds or owls, that provide the information which underpins their nocturnal activity (Cunningham et al. 2007, 2009; Wenzel 1968). Kiwi provide evidence for the idea that any sensory system can be metabolically expensive to maintain (Laughlin 2001) with the result that, unless that sensory system provides information which can be used to reliably

guide behaviour, natural selection will favour its regression and loss. There are clear examples of this in other taxa (Jeffery 2005; Leys et al. 2005), but Kiwi suggest that the forgoing of visual information can also occur in birds.

Compared with owls and Oilbirds, Kiwi have very small eyes which are out of proportion with the mass of their brains or body (Garamszegi et al. 2002; Brooke et al. 1999), presumably resulting in relatively low spatial resolution even at high light levels (Martin et al. 2007a, b, c). The frontal binocular field is very much reduced compared with that of owls (Fig. 3a) and there are very extensive blind areas about the head from which no visual information can be retrieved (Fig. 3b) (Martin et al. 2007a, b, c).

Foraging in Kiwi is mainly mediated by sensory information unavailable to either owls or Oilbirds. Kiwi are one group of birds which have a bill-tip organ (Cunningham et al. 2007). Bill-tip organs are clusters of mechanoreceptors embedded in pits contained within the bone of the distal portions of the mandibles, especially around the bill tip. Kiwi are able to use these bill-tip organs to detect invertebrate prey buried in leaf litter and soft substrates. In addition, Kiwi are the only bird taxon that have nostrils which open at the bill tip such that the gathering of both tactile and olfactory information are centred upon the bill tip. That olfactory information is much more important than any visual information that might be obtained is indicated by the brain structure of Kiwi (Fig. 3d). In these brains, the area that in most birds is associated with the analysis of visual information, the visual wulst, is absent. However, the olfactory bulbs are relatively huge when compared with species which mainly exploit visual information (Martin et al. 2007a, b, c) (Fig. 3d). It has been argued that Kiwi show clear evidence of regressive evolution of one sensory system and the enhancement of other systems to extract a different set of information about the environment compared with most birds (Martin et al. 2007a, b, c). This particular range of evolutionary processes may only have been possible in a predator-free environment. However, they do reinforce the idea that the metabolic costs of vision are relatively high (Laughlin 2001) and that if vision is unable to provide information about objects of interest in the environment, then visual information can be almost dispensed with in favour of the enhancement of information provided through another sensory modality.

The Woodcock's world: tactile guided nocturnal foraging but with predators and with flight

Like Kiwi, Eurasian Woodcocks *Scolopax rusticola* forage at night and employ a bill tip organ to detect prey buried in

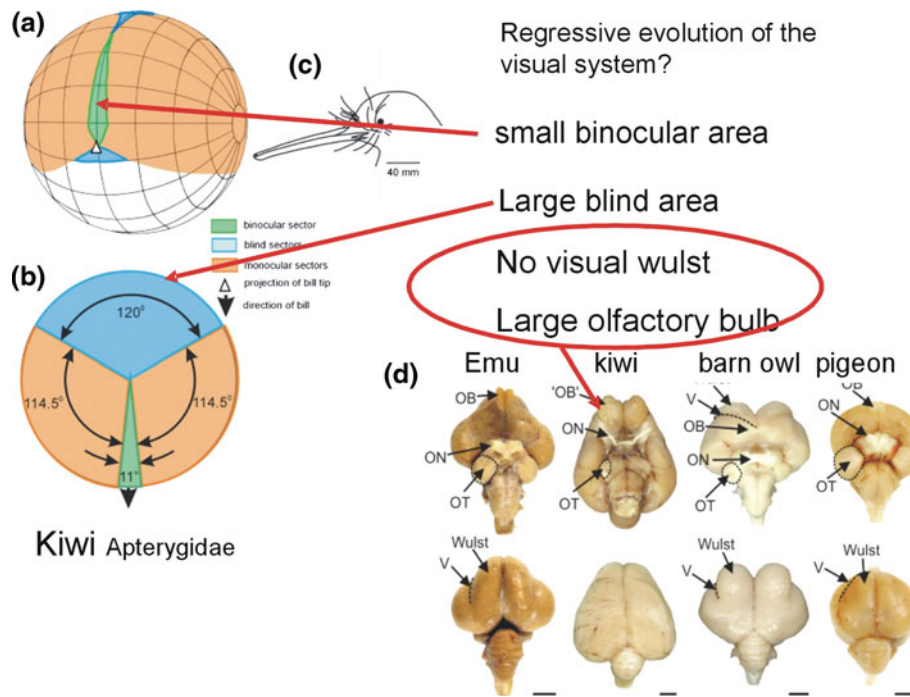


Fig. 3 Nocturnal foraging for buried invertebrates poses specific sensory challenges even for flightless birds which have evolved in a predator-free environment. In Kiwi *Apteryx* spp., these challenges seem to have been met by the evolution of a suite of four particular adaptations. (1) A bill-tip organ which provides tactile information when the bill makes contact with buried prey. (2) The placement of the nostrils at the tip of the bill aiding the location at short range of potential prey and its identification when located through tactile cues. (3) Possibly tactile cues derived from long whisker-like feathers which grow from locations on the head especially around the mouth opening. However, natural selection seems to have favoured the

regression of vision. The eyes are absolutely small and the frontal binocular field is also very small with the projection of the bill tip lying at its lower peripheral edge (a). A section through the visual field in the horizontal plane (b) indicates that there is an extensive blind area behind the head and the very small proportion of the field that is devoted to frontal binocular vision. A comparison of brain structure (c) shows that the area of the brain associated with the analysis of visual information (visual wulst), which is usually large in birds, does not exist in Kiwi, but that the olfactory bulb (OB) is comparatively large. Based upon figures in Martin et al. (2007a, b, c)

soft substrates (Cramp and Simmons 1983; Piersma et al. 1996). However, unlike Kiwi, Woodcocks live in a predator-rich environment and are able to fly.

In Woodcocks, the eyes are relatively large and situated high in the skull (Fig. 4a, b). Woodcocks exemplify an important principle concerning the evolution of visual fields in birds. Put simply: if there is no need to use vision to guide the placement of the bill then natural selection favours eyes that are placed high in the skull providing wide visual coverage of the space around the head (Martin 2007). In Woodcocks, this visual coverage is comprehensive, as there is no blind area above or behind the head, i.e. there is total panoramic vision (Martin 1994) (Fig. 4e).

This is achieved because the visual fields of the two eyes overlap throughout the 180° that extends from in front of the head to behind it. However, the extent of this binocular overlap has a maximum width of only 10° and at the horizontal when the head is held in its typical in-flight orientation it is only 5°. This indicates that a wide binocular field projecting in the direction of forward travel is not

necessary for the control of flight. Thus, when freed of the constraint to see its own bill, natural selection seems to have favoured the evolution of comprehensive vision of the celestial hemisphere, presumably to increase the probability that an approaching predator will be detected.

This finding provides an interesting perspective on the relative importance of binocular vision in birds. Thus, it may be hypothesised that among birds there is “universal urge” towards comprehensive vision and that when this is not achieved it is because binocular vision is required for gaining information to guide the accurate placement of bill position (Martin 2007, 2009). This is contrary to earlier assertions that there was a “universal urge” towards binocularity (e.g. Walls 1942).

The use of tactile information in foraging is, however, not sufficient to lead to the evolution of comprehensive visual coverage of the celestial hemisphere. In essence, Woodcocks use their bills more or less exclusively for foraging, and they do not use their bill for nest construction (nests are on the ground and are a simple scrape) or for

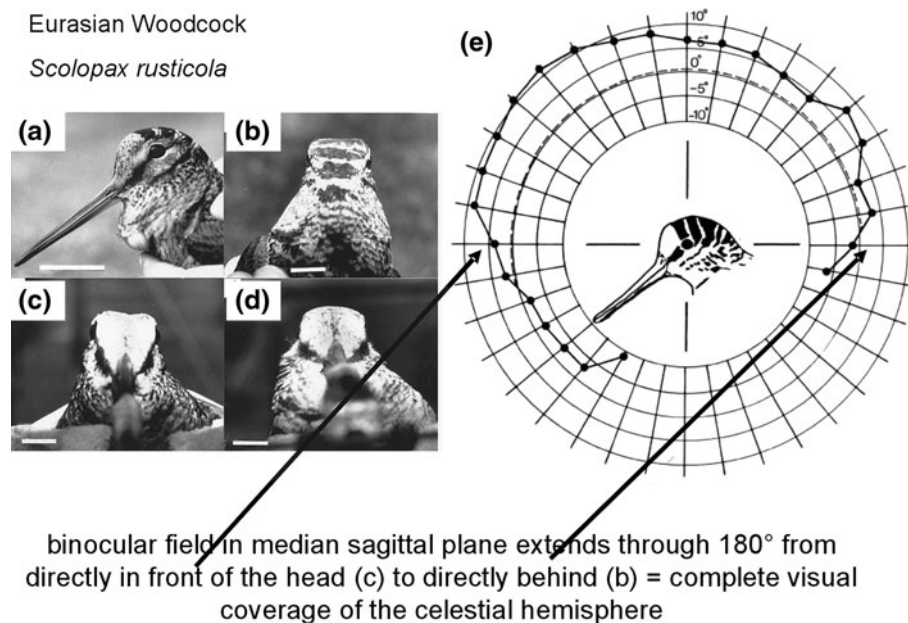


Fig. 4 Nocturnal foraging for buried invertebrates poses specific sensory challenges especially for volant birds inhabiting a predator rich environment. In Eurasian Woodcocks *Scolopax rusticola*, these sensory challenges seem to have been met by the evolution of two particular adaptations. (1) A bill-tip organ provides tactile information with which the birds are able to locate and identify buried prey. (2) The eyes are relatively large and placed high in the skull (a) such that the visual fields of the two eyes overlap (binocular vision) throughout

the 180° which stretches from directly in front to directly behind the head (e). The result is that these birds can retrieve visual information from the whole of the celestial hemisphere without the need to move the head and when they are probing into substrates. However, Woodcocks cannot see their own bill tip. d Shows that the eyes cannot be seen when viewed from the direction of the bill while they are clearly visible when viewed along the horizontal plane from the back (b) and front (c) of the head. Based upon figures in Martin (1994)

chick provisioning (young are precocial self-feeders, which require only brooding and protection) (Cramp and Simmons 1983; Piersma et al. 1996).

Other birds in the same family as Woodcocks, the Scolopacidae, which also employ tactile information from bill-tip organs, and can forage for buried prey using tactile cues alone (Piersma et al. 1998), do not show comprehensive visual coverage of the celestial hemisphere despite them being vulnerable to avian predators when foraging in open habitats (van den Hout et al. 2008; van den Hout 2010). Red Knots *Calidris canutus* are an example of such a species. It is in these birds that the mechanism of “remote touch”, in which buried prey not in direct contact with the bill can be detected (Piersma et al. 1998), was first described. However, Red Knots have a frontal binocular field which is narrow and vertically long which encompasses the bill, resulting in a blind area above and behind the head (Martin and Piersma 2009).

The explanation for the occurrence in a “tactile forager” of a visual field with characteristics that are closely similar to those of bird species which use vision to guide the bill in pecking or lunging at prey is that, for part of the annual cycle (on their breeding grounds in tundra habitats), Red Knots switch their foraging behaviour away from tactile probing to taking surface and aerial insects (Piersma et al. 1996). Such prey is abundant but taking it requires both

visual detection and guidance of the bill. This again indicates that prey detection is the primary driver of visual field topography in birds (Martin 2007). It also indicates that it is only when birds are freed of the need to see their own bill tip, or rather freed of the requirement for the bill’s projection to fall more or less centrally within the binocular portion of the visual field, that comprehensive visual coverage is selected for, even though this would presumably have great selective advantage for the detection of predators.

The worlds of filter feeders: ducks and flamingos

Another foraging strategy which does not require visual information for the guidance of bill position is that of filter feeding. In a similar fashion to tactile guided foraging, vision cannot be used by filter feeders to detect individual food items or to guide their capture in the bill. Water is pumped into the mouth through the area around the bill tip and out through lamellae at the sides of the bill (Gottschaldt 1985).

Freed from the constraint of extracting information to guide accurate bill placement, natural selection has led in these birds (as in Woodcocks) to eyes placed high in the skull giving total panoramic vision with binocular overlap

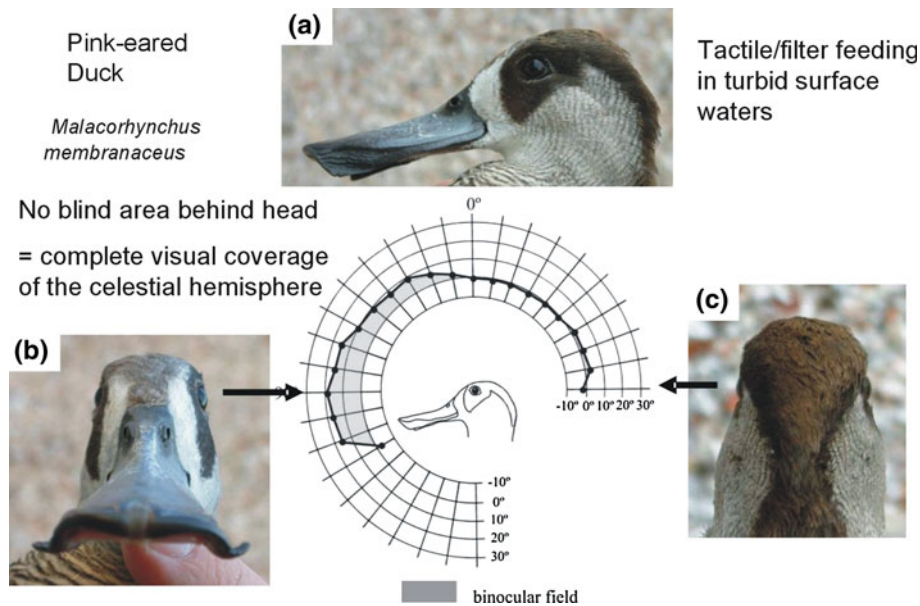


Fig. 5 Extracting food items from beneath the surface of turbid waters prohibits the use of visual information. To meet the sensory challenges posed by such foraging some birds, especially ducks Anatidae, employ tactile cues from the bill coupled with a mechanism for filter feeding. An exemplar of such species are Pink-eared Ducks *Malacorhynchus membranaceus* (a). In them, the eyes are placed high in the skull, the projection of the bill lies at the very edge of the visual

field and, as in Woodcocks (Fig. 4), the visual fields of the two eyes overlap (binocular vision) throughout the 180° which stretches from directly in front (b) to directly behind the head (c). The result is that these birds can retrieve visual information from the whole of the celestial hemisphere whilst the bill is held at the water surface when filter feeding. Based upon figures in Martin et al. (2007a, b, c)

that extends through 180° from directly in front to directly behind the head. This visual field configuration has been described in a number of duck species, Mallards *Anas platyrhynchos* (Martin 1986a, b, c), Northern Shovelers, *A. clypeata* (Guillemain et al. 2002) and Pink-eared Ducks *Malacorhynchus membranaceus* (Martin et al. 2007a, b, c), all of which are filter feeders (Fig. 5). However, in ducks which employ visual information for selective grazing of plant material (Eurasian Wigeon *Anas Penelope*), or for taking individual prey items from within the water column (Blue Ducks *Hymenolaimus malacorhynchos*), the eyes are more frontally placed and the binocular field surrounds the projection of the bill (Martin et al. 2007a, b, c; Guillemain et al. 2002).

That there are these differences in visual fields within this single avian family Anatidae, and even within the same genus, *Anas*, indicates that visual field topography and the information that is retrieved from the environment is driven primarily by the perceptual challenges of the species' foraging ecology, rather than shared ancestry. It also demonstrates that sensory capacities can be fine tuned to the perceptual challenges that are faced by species as their foraging ecology differentiates from that of recent ancestors, a finding recently supported by evidence from spoonbills and Ibises (Threskiornithidae) (Martin and Portugal 2011).

Furthermore, it is clear that these differences in visual fields among ducks can have effects on aspects of behaviour beyond the control of foraging. Thus, a comparison of vigilance behaviour during foraging between Shovelers and Wigeons showed significant differences in the pattern and total amount of time spent foraging, and in vigilance. Wigeons, which have more frontal eyes and a blind area behind the head, spend more time in vigilance and they forage in shorter bouts than Shovelers which have comprehensive visual coverage of the celestial hemisphere (Guillemain et al. 2002).

Although filter feeding does not require visual information for the accurate placement of bill position, flamingos show that this requirement can be overridden by other informational demands. The highly specialised filter feeding technique of flamingos involves the head being inverted and placed close to the level of the feet (del Hoyo et al. 1992; Kear and Duplaix-Hall 1975) (Fig. 6b). It would seem reasonable to have predicted therefore that flamingos should indeed gain comprehensive vision about the head, not only because they do not need to see their bill tip for the control of filter feeding but also because with the head inverted they may require visual coverage of the sector behind the head, which in fact projects forward when the bird is moving with the head inverted. However, this is not the case (Martin et al. 2005). The visual field of Lesser

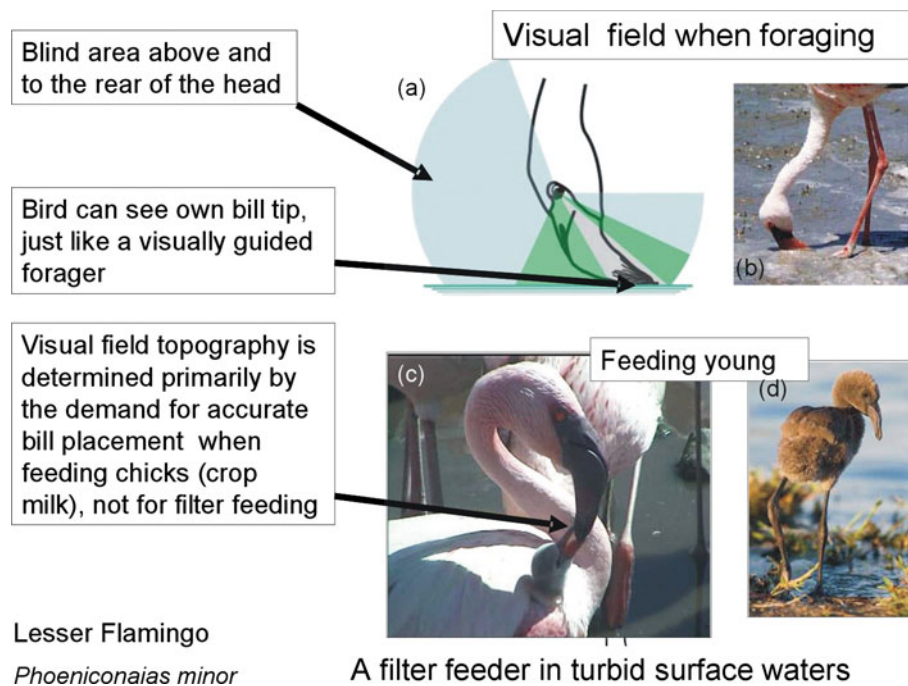


Fig. 6 Flamingos *Phoenicopteridae* are another group of filter-feeding bird species. They filter items from surface or very shallow waters with the head inverted, typically held close to the feet (b). Although it would be reasonable to suppose that these birds would benefit from being able to see directly behind the head, this is not the case. These birds have a frontal binocular field with similar characteristics to those of birds which use visual information to

guide pecking or lunging movements of the bill. This results in a broad blind area behind the head (a). This visual field configuration can be interpreted as a function of the requirement to guide the bill accurately when feeding young birds with “crop-milk” (c) during the first 12 weeks of life. In those species which gain comprehensive visual coverage about the head (Figs. 4 and 5), the young are precocial self-feeders. Based upon figures in Martin et al. (2005)

Flamingos *Phoeniconaias minor* is in fact very similar to those of birds which use vision to control bill position during peck or lunging at individual prey items, with the eyes placed more forward in the skull, and a relatively large blind sector behind the head (Fig. 6a).

The hypothesis advanced to explain this apparent paradox refers to the requirement of chick provisioning. Flamingo chicks (Fig. 6d) have a long period of dependence upon their parents during which time they are fed with “crop milk”, a liquid secretion from cells which line the oesophagus (del Hoyo et al. 1992), and this has to be accurately dripped from the tip of the adult’s bill into the open bill of the chick below (Fig. 6c). This would seem to be an exacting task and requires visual information to position both of the bills accurately. The filter feeding ducks, however, have precocial chicks which are self-feeding and do not require provisioning (Carboneras 1992).

These examples of filter feeding again emphasise that subtle interactions of different and specific perceptual challenges can determine visual field configurations in birds. More importantly, it underlines the hypothesis that sensory capacities, and the information that they provide, can be finely tuned to the perceptual challenges even among closely related species.

Vision and tactile foraging in skimmers

It has been seen that a number of bird species exploit information gathered via mechanoreceptors placed in clusters within a bill-tip organ. The use of such tactile information complements and interacts with visual information gathering, such that some birds may gain comprehensive visual coverage of the hemisphere above the head (Martin and Piersma 2009). However, there are further examples which reveal different solutions to the sensory challenges associated with reliance upon mechanical information in foraging.

Skimmers *Rhynchopidae* are three species whose specialised foraging technique has been well described (Zusi 1962, 1996) (Fig. 7b). It is known that prey is detected when it strikes the mandible as it ploughs through water during flight over slack water areas, such as lagoons and inlets. Foraging can occur during the night as well as during the day and at dusk. That this is a form of tactile foraging rather than visually guided foraging towards individual prey items seems to be well established from observations of feeding behaviour (Zusi 1996). However, the actual mechanism through which the impact of the mandible with a prey item (which is then snatched from the

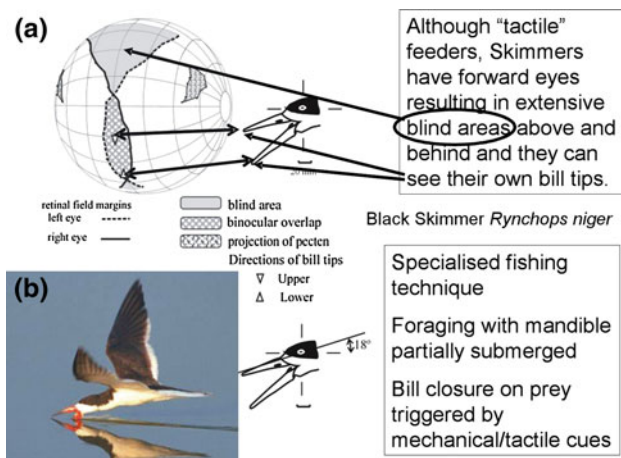


Fig. 7 Skimmers Rhychopidae are a taxon of three species which seem to employ tactile rather than visual cues to guide the capture of fish from surface waters during flight, sometimes at night (b). The basis of this tactile information is not known. The eyes are placed forwards in the skull such that the frontal binocular field encompasses the projections of both the mandible and maxilla when the mouth is open (a) and there is a large blind area above and behind the head. It is likely that this visual field configuration functions primarily to provide information for the identification of prey once it has been caught. Based upon figures in Martin et al. (2007a, b, c)

surface in flight) is registered has not been determined. Cluster of mechanoreceptors within either the bone of the mandible (as in Kiwi and long-bill shorebird bill-tip organs; Cunningham et al. 2007, p. 449; Piersma et al. 1998) or embedded within the keratin of the rhamphotheca (as in parrots; Goujon 1896; Gottschaldt 1985; Demery et al. 2011) have not been found in these birds. It is possible that contact with a potential prey object could be signalled through receptors based in the musculature which controls jaw opening, or even through the vestibular system if the head is forced to pitch forward upon impact with a potential prey item (Martin et al. 2007a, b, c). Whatever the mechanism, the technique is clearly efficient, but it can lead to the registration of impact with non-prey items, and so indigestible materials, such as plant material and floating debris, may be seized in the bill (Zusi 1996).

The visual field of skimmers do not show the characteristics of a species which can rely upon tactile cues alone for prey capture (Fig. 7a). They do not have panoramic vision and the eyes are placed sufficiently far forward in the skull so that when the bill is open in a typical “skimming” posture, both bill tips fall within the frontal binocular field. By analogy with visually guided foragers, this would suggest that vision may play a role in the foraging of these birds. Skimmers like most other Charadriiform birds have precocial or semi-precocial young and do not make elaborate nests, and therefore would not seem to require accurate visual control of bill position for either nest building or chick provisioning (Zusi 1996).

This configuration of visual fields in skimmers would seem to be necessary to provide information not for prey detection and capture but rather for its identification and perhaps to aid its ingestion. A skimming bird that catches an item using tactile cues cannot be certain that the item is indeed prey. Being able to see between and around the mandibles should ensure that information is available to determine whether the caught item should be discarded or swallowed.

Such visual verification of a caught item, and possibly its preparation for swallowing, is found in other bird species which perhaps catch potential prey items whose identity needs verification before ingestion. It has been hypothesised that this may be the case in birds which forage in turbid waters such as Great Cormorants *Phalacrocorax carbo*, whose foraging may often involve lunging at an unidentified “escaping blur” (see discussion below) (Martin et al. 2008). Similarly, ibises and spoonbills Threskiornithidae which also employ tactile cues and can forage in turbid waters may also require visual verification that caught items are in fact ingestible prey (Martin and Portugal 2011).

The herons’ world: the sensory ecology of stealth foraging

The foraging technique of herons Ardeidae involves the catching of prey which are typically highly evasive; prey which have escape responses that remove them rapidly from the immediate area of danger (Hancock and Kushlan 1984; Voisin 1991). Such prey includes fish, amphibians, insects (especially Orthoptera), small birds and some mammals. The perceptual challenge posed by the task of catching such prey requires its identification and judgement of its position, and possibly also its escape trajectory, such that it can be captured while still within range of a single strike of the bill. To achieve such prey capture, many herons employ a tactic of stealth foraging in which they may remain motionless or move very slowly, at a suitable foraging location and wait for prey to come within striking range (Hancock and Kushlan 1984).

Clearly, these birds need to employ visual guidance of bill position with respect to the prey and be able to use visual information to determine the direction of bill travel and the time to contact the target so that the bill may be opened just as it intercepts the prey. Both time to contact, and direction of travel, are information provided directly from optic-flow fields (Lee 1980; Gibson 1986). Optic-flow fields are descriptions of the ways in which the image of the world moves across the retina, and the extraction of this information from flow-fields does not require high visual resolution. It has been argued that the prime function of binocular vision in birds lies in the extraction of such

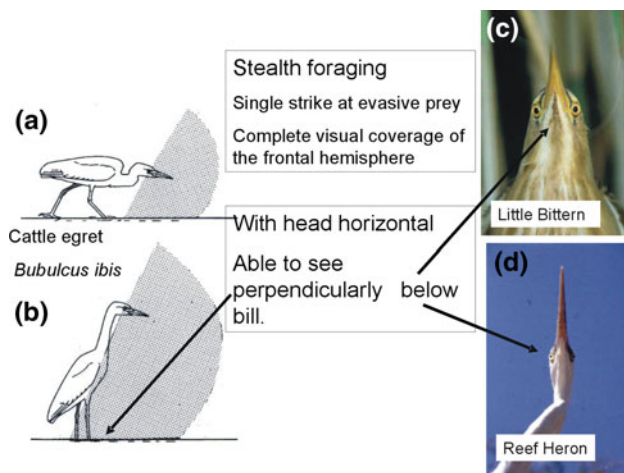


Fig. 8 The capture of highly mobile evasive prey poses particular sensory challenges. Prey has to be visually identified and located accurately before a rapid lunge towards a prey item with the bill is initiated. In herons Ardeidae, the eyes are placed forwards within the skull such that the visual fields of the two eyes overlap (binocular vision) throughout the 180° which stretches from directly above to directly below the head (a, b), such that the birds gain complete visual coverage of the frontal hemisphere. A result of this is that the position of a prey item below the bird can be monitored while it stands motionless and prey capture does not have to be initiated until the prey is within striking distance. Furthermore, when a heron adopts the characteristic “bittern sky pointing posture” in which the bill is pointed vertically up (c, d), a bird can not only see horizontally forwards but also gains comprehensive visual coverage of the whole of the celestial hemisphere. Based upon figures in Martin and Katzir (1994)

information rather than in the determination of relative depth based upon stereoscopic cues (Martin 2009).

The visual fields of herons would seem to be particularly well adapted for the extraction of such information (Katzir and Intrator 1987; Katzir and Martin 1994). The binocular field is relatively narrow (max width 20° – 30°) but vertically long (180°) with the bill placed more or less centrally (Fig. 8a, b). This arrangement would seem to be relevant to the herons’ task of stealth foraging in two ways. First, when a bird is standing with its bill horizontal, it can in fact see what is at its feet. Which allows it to detect potential prey without having to move, which would probably alert the prey animal. Secondly, the position of the bill projects approximately centrally in the frontal field. This will maximise information gain from the optic flow-field once bill movement has been initiated towards the target, since the whole of the frontal field will make up the flow-field with the direction of travel specified close to its centre as the field expands symmetrically about the bill when it travel towards its target. This should increase the accuracy with which direction of travel of the bill, and the time of its contact with the target, can be determined.

It is interesting to note that the visual fields of herons are in one respect similar to that of the tactile feeding

Woodcocks and filter-feeding ducks. Both cover an entire hemisphere about the head, but while in the ducks and Woodcocks this faces upwards to gain coverage of the celestial hemisphere, in herons it is rotated forward through 90° to gain comprehensive coverage of the frontal hemisphere. It is also worth noting that seeing binocularly perpendicularly beneath the bill, a feature often depicted in photographs of bitterns *Botaurus* and *Ixobrychus* spp. which have adopted the “bittern stance” (in which the bird remains immobile with the bill pointed skywards) (Fig. 8c, d), is not unique to this genus of herons but may be a feature of all Ardeidae and derives from the perceptual challenges of stealth foraging.

The King Penguin’s world: diurnal predation under nocturnal conditions

The problems of foraging and general activity under natural night time conditions and even within caves were discussed in some detail above, and it was argued that to achieve this no single source of information could suffice. Depending upon the species, there is complementarity between the use of highly sensitive vision, and environmental information extracted from audition, olfaction, and/or mechanoreception, and specific behavioural adaptations. In the case of Kiwi, evidence was presented that vision has been subject to regressive evolution and that behaviour at low light levels is primarily guided by environmental information obtained through olfaction, mechanoreception, and possibly hearing.

Diving to depth in the ocean also presents problems of low light levels, low enough in fact to be comparable to those commonly experienced on the surface at night. Light levels at depth can be variable depending upon the water body type and the way it attenuates light, and the amount of light incident upon the ocean surface; bright sunlight, moonlight, starlight, etc. (Jerlov 1976; Lythgoe 1979; Land and Nilsson 2002).

King Penguins *Aptenodytes patagonicus* are an example of a bird which forages for fish at depths which are sufficient to render the actual foraging task equivalent to nocturnal foraging (Kooyman et al. 1992; Olsson and North 1997; Pütz and Bost 1994; Martin 1999). They may forage by both night and day and when doing so they go to depths where their main prey is found. By day, this entails travelling to between 200–300 m when light levels equivalent to those experienced at the surface at night occur; at night, prey is nearer the surface. The result is that King Penguins are usually foraging at nocturnal light levels regardless of whether they dive by night or by day.

The eyes of King Penguins are large (the axial length of the eye = 35 mm, cf axial length in Tawny Owls = 28 mm,

humans = 24 mm) and the maximum entrance pupil is also relatively large compared with other eyes. These are structural features which can be interpreted as adaptations to vision at low light levels (Land and Nilsson 2002). However, foraging King Penguins face a particularly difficult problem.

To achieve the highest sensitivity, the retina of any vertebrate eye needs to be dark adapted. Typically full dark adaptation is not achieved until between 30 and 40 min after entering darkness. King Penguins when foraging by day can often be diving from the surface in bright sunlight, but they achieve the foraging depth of 200–300 m in just a few minutes where they will face nocturnal light levels. This clearly does not allow sufficient time for the retina to dark adapt. Similarly, after the end of a dive, which may last 15 min, the birds come from nocturnal to daylight levels in just a few minutes. Overall, the visual challenge of this foraging behaviour is that the birds are in effect switching between daytime and night time conditions and back again approximately every 15 min during a bout of daytime foraging. Clearly, this poses a particular set of perceptual challenges that are perhaps not faced by any other birds.

The solution to this challenge seems to have been the evolution of an extremely dynamic pupil. In pigeons and in humans, the dynamic range of the pupil is sufficient to alter the brightness of the retinal image by about 16-fold. This is sufficient to track small changes in ambient light level that occur, for example, when moving in out of vegetation cover during the day. A 16-fold range cannot compensate for the light level changes that occur as a King Penguin makes its rapid dive from the surface to foraging depths during the day. The pupil of the King Penguin eye has in fact a dynamic range of 300-fold (Martin 1999). This is achieved by having a pupil which changes from a pinhole to a large circular aperture, and this change in pupil size can be achieved very rapidly. Thus, when at the surface, the pupil can be stopped down and this pre-adapts (i.e. dark adapt) the retina to light levels that will be experienced when the birds dives to depth. At depth, the pupil can be opened up to maximise light capture. The prey that King Penguins take are primarily myctophid fish which possess photophores on their body surfaces (Olsson and North 1997). In effect, King Penguins may be foraging for points of light, which indicate the presence of fish, rather than for the fish themselves.

This example is another which indicates that under conditions that restrict the amount of visual information potentially available in the environment, natural selection can lead to the evolution of adaptations which maximise the probability that light can be detected (maximising light gathering), and adaptations which maximise the probability that light that is imaged upon the retina can be correctly interpreted (ensuring an optimal level of dark adaptation of the retina). Unlike the examples of owls, Oilbirds, Kiwi

and Woodcocks, penguins do not seem to have available to them the development of other senses which can provide information that complements the minimal information available through vision. However, King Penguins forage in relatively predator- and obstacle-free conditions. It is only when they return to surface waters that they are faced with increased predation risk.

Two applications of visual ecology

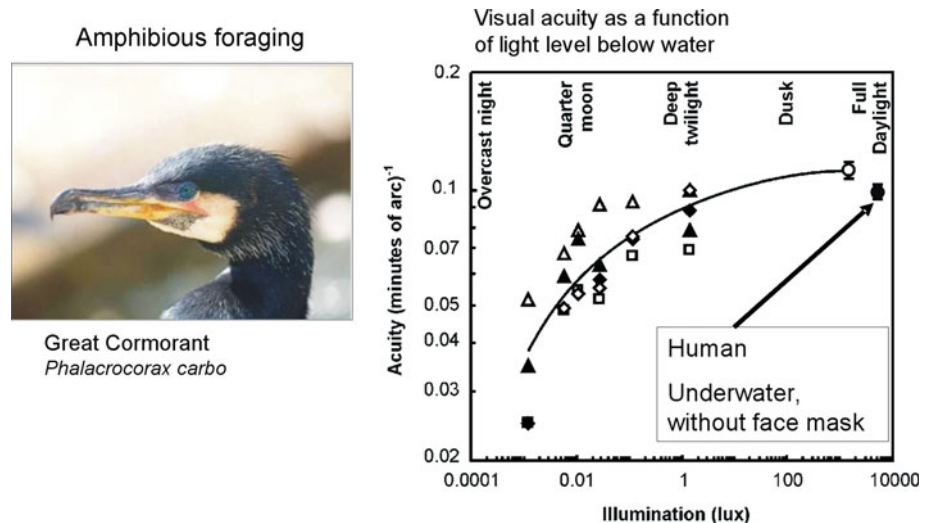
The visual ecology of amphibious foraging:
the challenge of low visual contrast

Great Cormorants present something of a conundrum with respect to their foraging ecology. They are a diving predator of fish and are capable of diving up to 30 m deep (Johnsgard 1993; Orta 1992; Lilliendahl and Solmundsson 2006). They forage in lakes, rivers, estuaries and coastal waters. The water quality in which they forage ranges from clear to highly turbid and they take a wide range of fish, including many cryptic species such as sculpins. They are regarded as highly efficient foragers (Grémillet et al. 2004) and this brings cormorants into conflict with human economic interests resulting in control or eradication programmes in many parts of their range (Carss et al. 2003). This efficiency is also exploited by humans in “cormorant fishing”, in which tame birds are trained to catch and return fish to their handler. Such fishing was once of economic importance for food but its economic importance is now based primarily around presenting this fishing as a tourist attraction.

The visual challenges faced by foraging cormorants can be summarised as the taking of prey which is cryptic and evasive, often at low light levels, and often in highly turbid conditions. What information are cormorants using to achieve prey capture under this range of conditions? There is no evidence that cormorants have at their disposal tactile cues from the bill, i.e. there is no evidence for clusters of mechanoreceptors embedded in the bones or keratin of the bill. The task of foraging would therefore seem to be based upon visual information, but in what way does the vision of cormorants match these challenges?

The first question therefore is what can cormorants see under water? This can be investigated by measuring their visual acuity. Acuity is a measure of the highest spatial resolution possible for the eye as a function of ambient light level (Land and Nilsson 2002). It is based upon the ability to detect (demonstrated by a behavioural response) a simple target made up of equally spaced black and white stripes of varying contrast. The surprising result for Great Cormorants is that the acuity under water is poor (White et al. 2007; Strod et al. 2004). At high light levels

Fig. 9 Visual acuity below water as a function of light level in an amphibious foraging species, Great Cormorant *Phalacrocorax carbo*. Acuity is measured in minutes of arc with respect to the minimum detectable separation of high contrast stripes in a grating pattern. Light levels are shown in Lux and in their equivalent of natural illumination conditions at the earth's surface. The acuity of humans below water without a face mask is indicated. Based upon a figure in White et al. (2007)



(equivalent to full sunlight), the acuity of cormorants is very similar to that of a young human underwater without a face mask (Fig. 9).

To us, vision underwater appears blurred compared with vision in air. However, by presenting striped patterns in a systematic way, this blurred vision can be quantified to give a measure of the smallest object which can be detected at a given viewing distance. It is upon this measure that the underwater vision of cormorants and humans are similar at high light levels. As found in all other visual systems, acuity in cormorants also decreases with light level (Fig. 9). The general conclusion to be drawn from this is that, underwater, the “best resolution” (high light levels and high contrast stimuli) of cormorants is in fact “poor resolution”, approximately 60 times worse than the acuity of an eagle (in air) at comparable light levels (White et al. 2007).

Does this apparently poor resolution match up to the perceptual challenges posed by the cormorants’ foraging tasks? What is a cormorant’s eye view of the task of detecting a prey item in the water column? To examine these questions, models of prey detectability can be constructed which take account of how acuity changes with both target contrast and light level, and Fig. 10b, c shows simulated “cormorant eye views” of a 10-cm fish which has a contrast of 60% with its background and viewed from 1 m (see White et al. 2007 for simulations of other cormorant eye views in which size of fish, contrast and light levels are manipulated).

Do these simulations of visual performance match up with the perceptual tasks which an underwater predator is assumed to face? In other words, does the vision of Great Cormorants meet the visual challenges of their underwater environment? The conclusion appears to be no. What a cormorant would appear to see when faced with a target that contrasts quite markedly with the background, and at a

range of light levels at which they are known to forage, is an ill-defined shape (Fig. 10b, c). At greater distances, lower light levels, or lower contrasts between prey and background, the target object would become less distinct than the simulations shown in Fig. 10b, c. So are these underwater predators acting like aerial predators? Identifying prey from a distance through the water column and pursuing them? This might be possible in very clear waters and at high light levels, but in conditions of higher turbidity and with cryptic prey this seems unlikely. An alternative proposal is that the foraging of cormorants mainly involves lunging at an “escaping blur” (much like some of the modelled images at lower light levels in Fig. 10b, c) which has been disturbed from the substrate or from a hiding place among rocks, roots, or vegetation (White et al. 2007; Martin et al. 2008).

Do Cormorants disturb prey and force an escape response? This could be an appropriate strategy for many conditions in which cormorants are apparently able to catch prey, for example in very turbid conditions or when exploiting highly cryptic prey. Certainly, it seems that the resolution of cormorant vision is unlikely to be able to break the crypsis of sculpins and that the only way that such prey can be caught is by their direct disturbance, perhaps with the bill, that forces an escape response (Martin et al. 2008). While cormorants can move rapidly underwater, they are also highly manoeuvrable. Furthermore, the long neck is typically held in a shallow “S” shape when diving and the head could be shot forward to take the escaping prey, in a similar way to the use of the neck in the lunging prey capture technique of herons.

A particular problem is that if cormorants are often catching an “escaping blur” they may not necessarily know what has been caught. This problem could be overcome by bringing the prey to the surface and examining it when held in the bill before deciding whether to ingest it

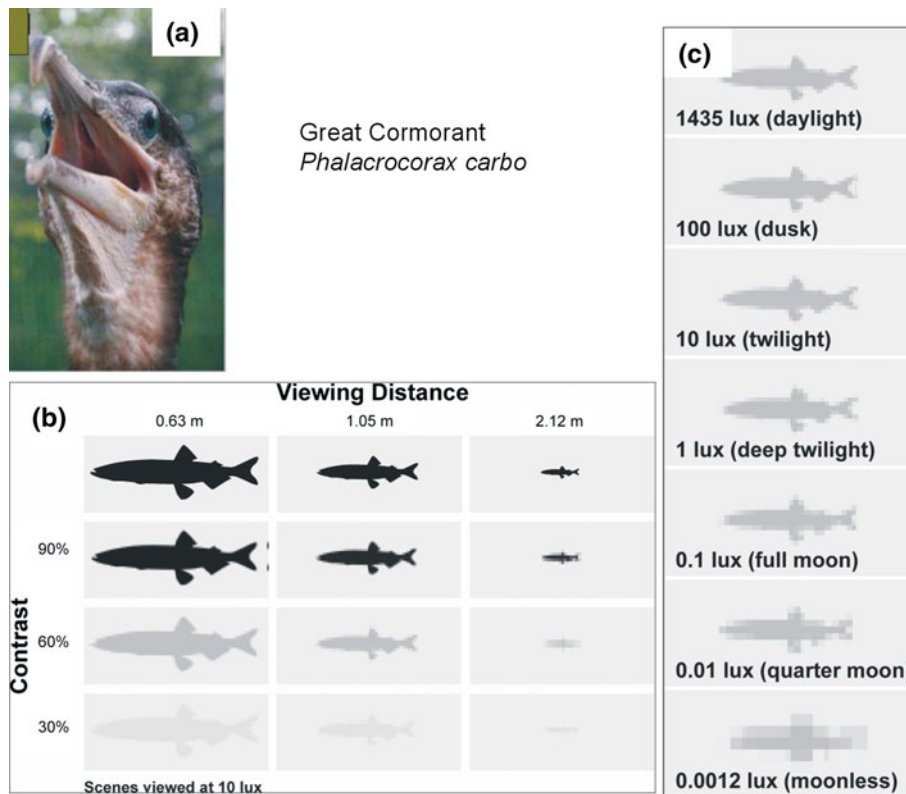


Fig. 10 Simulations of a cormorant’s eye view of a typical underwater target. The target is a 10-cm-long fish and the simulation is based upon data on the acuity of cormorants underwater as a function of target contrast. **(b)** Modelled cormorant eye views at four different levels of contrast of the fish with the background (100, 90, 60, 30%) at a light level of 10 Lux. **(c)** Modelled cormorant eye view of a fish at a distance of 1 m and which contrasts 60% with the background, as a function of light levels. These simulated cormorant eye views suggest

that under many circumstances individual prey items cannot be clearly seen and identified. Under these circumstances, cormorants may in effect lunge at an “escaping blur”. Prey may be brought to the surface for visual identification before ingestion, at which time the caught item can be viewed with the binocular field which encompasses the open mouth **(a)**. Based upon figures in White et al. (2007) and Martin et al. (2008)

and/or to reposition it for ease of swallowing. Cormorants typically do bring prey to the surface, and this is in part exploited in the technique of “cormorant fishing” mentioned above. The visual field of Great Cormorants show the typical arrangement of a relatively narrow but vertically long binocular field surrounding the bill projection (Martin et al. 2008). Crucially, this means that the birds can inspect what is held in the bill (Fig. 10a), much in the same way described above in skimmers which also catch prey that requires visual verification after capture.

A sensory ecology analysis of prey capture in cormorants leads to the following conclusions. Vision does not allow detection and identification of prey items at a distance. This is overcome by the employment of a “close-quarter/flush-foraging technique”. Prey are forced to make an escape and the bird lunges (perhaps using rapid neck extension like herons) at an “escaping blur”. Binocular vision may mediate accurate lunging at escaping prey at short range using flow-field information, and binocular vision may also be important in the identification of caught

prey when brought to the surface and held in the bill. Thus, again there seems to be a close relationship between a limited sensory capacity, the information that it can provide to an animal about its environment, and a behavioural strategy that is employed to overcome the limitations of that information.

One final problem remains. Why is acuity in cormorants apparently so poor underwater? It might have been predicted that as a pursuit predator natural selection would have favoured higher acuity, similar to that of an aerial predator such as a hawk or falcon. However, the high acuity of an eagle perhaps functions principally not to give the birds the ability to detect fine detail at close range but to detect smaller objects (prey-sized objects) at greater distances. A $\times 2$ difference in acuity between two species can be interpreted to indicate the ability to either detect something half as large at a close distance, or to see the same object at twice the distance. However, even highly transparent water degrades spatial information with distance, and natural waters with suspended particles and

dissolved pigments degrade information much more rapidly (Jerlov 1976). Put simply, in most natural waters high spatial information is simply not present in the environment and so its detection cannot be favoured by natural selection. Even if cormorant eyes could detect finer spatial detail underwater, this would not readily translate into the selective advantage of catching smaller prey or larger prey from a greater distance. This is because natural turbidity will result in the absence of spatial information that is necessary to support such prey detection.

The visual ecology of avian collisions: a human-made perceptual challenge

Why do wind turbines and power wires pose problems for birds? Large objects intruding into the open airspace above surrounding vegetation or sea surface are clearly visible to the human eye under most circumstances, at least during daylight. Yet collisions of flying birds with such obstacles can occur under conditions of high visibility and not only when visibility is compromised (low light levels, rain, mist), and consequently the information that can be gained is low (Avery et al. 1980; Bevanger 1998; Manville 2005; Drewitt and Langston 2008). When birds are flying in open airspace, what are they doing?

A human perspective exemplifies a general problem of the use of visual information in the control of locomotion and this has recently been summarised (Martin 2011). Even when “looking ahead”, humans may “look but fail to see”. This is a well-known phenomenon in the causes of car driving accidents, which often occur in what can be described as a familiar habitat and a predictable environment (Hills 1980; Clarke et al. 1995). When humans travel, our behaviour should ideally involve strategies which ensure that the rate of gain of information is matched to the perceptual challenge that lies ahead. Therefore, we are expected to slow down as visibility decreases, which may be the result of lower light levels, rain, mist, etc. However, this is often not the case because we are not directly aware of how information about objects actually change with environmental conditions. Generally as they travel, humans predict that an environment will remain as predictable as it has been in the recent past, so much so that “unpredictable” hazards are frequently undetected; hence the overload of advanced warning signs on fast roads, which are simply providing information that the world ahead is changing, becoming less predictable.

Do human artefacts such as power wires and wind turbines pose similar informational and perceptual problems for birds? Are these in effect “unpredictable hazards” in the predictable environment of the open air space? Two key questions arise: (1) can flying birds adjust their rate of gain of information to meet the perceptual challenge of the

environment, i.e. can flying birds reduce their average velocity to adjust information gain, when faced by reduced visibility, and (2) when flying in open habitats, are birds always looking ahead?

The answer to the first question may be no. The relationships between aerodynamic power requirement and flight speed are well understood (Norberg 1990; Biewener 2003), and these show that the aerobic range of flight speed for most birds is quite restricted. In effect, it seems unlikely that flying birds can readily slow down to match their rate of gain of information to an increased perceptual challenge; they cannot simply put on the brakes or pull back on the throttle and fly slower for a sustained period just because the perceptual challenges of the environment increase. Thus, it seems unlikely that flight speed can be continually tuned to the perceptual challenge of the environment ahead. This may mean that if environmental conditions change during a flight, and the perceptual challenges increase, birds may in effect be flying beyond the perceptual limit necessary for successful detection and avoidance of obstacles.

The answer to the second question is also probably no. Collision-prone species may not always be looking ahead or at least may not be looking ahead with the sector of their visual field which provides the highest resolution (Martin 2011). This may arise because of two factors. First, specialisation of visual capacity within the visual field of a single eye (which was described in general terms in the introductory sections of this paper) typically means that in many, if not most, species highest resolution occurs laterally, not frontally, and that frontal binocular vision is primarily concerned with the perceptual task of foraging and the extraction of information from the near environment (Martin 2009). Lateral vision may also show specialisation of visual function depending upon the task (Rogers 2008). There is evidence that Gull-billed Terns *Gelochelidon nilotica* and Peregrine Falcons employ lateral vision for key tasks when foraging. The Terns rotate their head to look downwards with the fovea as they search for crabs over mud flats (Land 1999), and, as mentioned above, Peregrines approach prey on a curved path to ensure that the prey is viewed with a laterally projecting fovea (Tucker et al. 2000).

A second strand of evidence suggests that some birds which are known to be particularly vulnerable to collisions, may be blind in the direction of travel when in the open air space. This is found from studies of visual fields in Kori Bustards *Ardeotis kori*, Blue Cranes *Grus paradisea* and Short-toed Snake-Eagles *Circaetus gallicus* (Martin and Katzir 1999; Martin and Shaw 2010), and White-backed Vultures *Gyps africanus* (Martin, in preparation). In all these birds, the frontal binocular field is such that a small forward pitch head movement (25°–35°) will render birds

blind directly ahead (Fig. 1). That these birds regularly or habitually make such head movements has not been definitely demonstrated, but there are many anecdotal observations, video clips, and photographs which suggest that this is the case. Under such circumstances, these birds when flying in open airspace will have no visual coverage of what lies directly ahead which renders these birds particularly vulnerable to collisions with obstacles which intrude into the open airspace (Martin 2011).

Thus, a sensory ecology perspective on bird collisions leads to recognition of the following general points. (1) In flight, some birds may be blind ahead of them; turning the head to look downwards may not be unusual. (2) Frontal vision, vision in the direction of travel, is not high resolution vision. Frontal vision may be tuned for the detection of movement rather than spatial detail. (3) Birds employ lateral vision for the detection of conspecifics, foraging opportunities, and predators, and this may be why they turn their heads to look downwards during flight in the open airspace. (4) Birds in flight may predict that the environment ahead is not cluttered. Together, these four factors increase the probability that some species may frequently have no visual coverage in the direction of their travel and that even if flying birds are “looking ahead” they may fail to see an obstacle. Finally, birds have only a restricted range of flight speeds that can be used to tune their rate of information gain to changing perceptual challenges (Martin 2011).

Does this approach suggest particular solutions to collisions? Certainly, it provides an alternative to simply approaching this problem from the perspective of the way in which humans may perceive the problem of detecting unpredictable obstacles in open airspace. Based upon this approach, the following would seem worth further investigation. (1) Stimuli used to draw attention to the actual obstacle (power wire, wind turbine, etc.) should incorporate movement and be large, well in excess of the size calculated to be detectable based upon acuity measures. This is because acuity in the frontal field is likely to be lower than that of the lateral field in which estimates of best or highest acuity are based. (2) If possible, find ways to “warn” birds well in advance that an obstacle may lie ahead, if possible priming their attention. (3) The best solution is likely to lie in “diverting” or “distracting” birds from their flight path: assume that birds are more likely to be looking down and laterally rather than forwards: use foraging patches, conspecific models on the ground, etc. (4) Consider whether something on the ground may be more important than something on the obstacle.

This approach of trying to appreciate the problems of collisions from the perspective of the information that may be available to a bird indicates that there is no single cause

to bird collisions with human artefacts, and equally there is unlikely to be a single solution.

Conclusions: sensory ecology, some key points

The above discussion has ranged widely in an attempt to show the breadth of topics that can be approached from a sensory ecology perspective and the kind of insights that can be achieved. This is certainly not an exhaustive coverage of the field. There are many other examples of work on avian sensory systems which give insights into the information that guides the interactions of birds with their environment. By way of summary, I offer the following general observations:

1. All sensory systems are *selective* within their own modality, no eye can see all, no ear can hear everything, no olfactory system can detect all volatile molecules. However, the particular ranges of information that are available to a particular species have been tuned to particular perceptual challenges through natural selection and that this tuning can take place at the individual species level such that there may be key differences in sensory information even among birds in the same genus. Therefore, generalisations based upon phylogeny may not be a good indication of the information that a particular species has available to guide its interactions with the environment.
2. Sensory systems detect only a small part of the total information that is available in the environment. No species has available to it all the information that is potentially available in its environment. In essence, all species share the same planet but live in different worlds that are dictated by the information that their sensory systems extract from the environment.
3. There may be complex and subtle trade-offs within and between different types of sensory information. Among birds, there are many examples in which visual information is complemented by tactile information, or by olfactory information, and it is these relatively complex interactions of information from different sensory modalities which may underlie key behaviours, such as foraging.
4. The world through birds’ eyes is quite different from the world as seen through human eyes. Having read through this paper, this observation may seem a rather trivial and obvious one. However, it is often tempting to assume that, because birds and humans generally share a reliance upon visual information for many of their interactions with the world, it is only in areas which we do not have direct access to, such as vision

in the ultraviolet or magnetoreception, that important differences are to be found. Important as these differences are, many more subtle differences in visual capacity should be sought when attempting to explain the behaviour of birds. In short, there are many different “bird eye views”; generalise with caution and always bear in mind that there is more to a bird’s world than meets your eyes.

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