



## Review

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# The subtlety of simple eyes: the tuning of visual fields to perceptual challenges in birds

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Birds show interspecific variation both in the size of the fields of individual eyes and in the ways that these fields are brought together to produce the total visual field. Variation is found in the dimensions of all main parameters: binocular region, cyclopean field and blind areas. There is a phylogenetic signal with respect to maximum width of the binocular field in that passerine species have significantly broader field widths than non-passerines; broadest fields are found among crows (Corvidae). Among non-passerines, visual fields show considerable variation within families and even within some genera. It is argued that (i) the main drivers of differences in visual fields are associated with perceptual challenges that arise through different modes of foraging, and (ii) the primary function of binocularity in birds lies in the control of bill position rather than in the control of locomotion. The informational function of binocular vision does not lie in binocularity *per se* (two eyes receiving slightly different information simultaneously about the same objects from which higher-order depth information is extracted), but in the contralateral projection of the visual field of each eye. Contralateral projection ensures that each eye receives information from a symmetrically expanding optic flow-field from which direction of travel and time to contact targets can be extracted, particularly with respect to the control of bill position.

## 1. Introduction

It is 70 years since the publication of the two major surveys on the diversity of vertebrate eyes. Walls' *The vertebrate eye and its adaptive radiation* [1] and Rochon-Duvigneaud's *Les yeux et la vision de vertébré* [2] were encyclopaedic works which jointly brought together all that was then known about vertebrate eyes: their structure, physiology and evolution. Such has been the importance of these books that they are still cited, not only because they provided clear enunciation of some key hypotheses linking the form and function of vertebrate eyes, but also because they contain the only information available on the eyes of many species.

Both books provide descriptions and functional interpretations of the fundamental functional structures that make up the 'simple' eyes of vertebrates. Compared with the diversity found among the 10 types of eyes that have been described in invertebrates [3], the simple eye of vertebrates appears rather straightforward. They contain just two functional components. An optical unit, which itself is made up of just two components (lens and cornea), for producing an image of the world, and a single structure (retina) which initiates analysis of that image. It is probable that vertebrate eyes have a single evolutionary origin and that almost all of the features that characterize modern vertebrate eyes were present at least 500 Ma [4]. All of the diversity that Walls and Rochon-Duvigneaud described, and which many others have described subsequently, are relatively subtle variations within these two main functional components.

The fact that the two main functional components of vertebrate eyes have been able to evolve independently of each other over such a long evolutionary period has contributed to the array of variation now found in both components. Variation within the optical system has been interpreted as being both the result of allometric scaling and of natural selection, i.e. responding to perceptual

challenges presented by the natural world. For example, diversity in eye size has been interpreted both as a function of body size and of naturally occurring ambient light levels [5]. Discussions of variation in retinal structures have considered, for example, the spectral distributions of light reflected from surfaces within different environments [6,7], or the position of key geometrical features within the visual field, such as the position of the horizon, or the projection of the direction of the highest-quality optics [8].

Interpretations of form and function based upon these relatively objective measures of the environment also require knowledge of key behaviours in an animal's repertoire that are guided by visual information. The differing informational demands of such key behaviours need to be understood as much as the overall parameters of the environment in which an animal exists. Behaviours which are subjected to strong natural selection on a daily basis are likely to include locomotion, foraging and the detection of predators [9–12], whereas, less frequent, but highly selected behaviours which are likely to have important informational demands can involve reproduction and the care of young [13].

Behaviours, however, are less easily described and quantified than the objective parameters of environments, and behaviours may differ in subtle but significant ways, even between closely related species. Therefore, determining a causal relationship between eye structure and behavioural function may be problematic. Nevertheless, subtle behavioural differences may provide a crucial underpinning to the partitioning of resources between species within the same or similar environments, and are thus likely to be reflected in aspects of sensory capacity and information processing [14,15].

A 'visual ecology' explanatory framework for eye diversity, i.e. a framework, which combines objective measures of an animal's natural environment and the identification of its key behaviours that are guided by visual information, is often implicit in the works of Walls and Rochon-Duvigneaud. However, it was not until 1979 that these ideas were discussed explicitly by Lythgoe [16] and subsequently expanded upon [17]. Lythgoe also showed that in addition to the need to determine the key perceptual challenges presented by light environments for different animals, it is also necessary to attempt to understand whether evolved structures and physiological mechanisms are optimal solutions for the extraction of information from a particular environment, or trade-offs between competing optimal solutions. This theme has been explored in some detail [18] particularly with respect to the trade-off between visual sensitivity and visual resolution. It is also possible that trade-offs and complementarities exist with respect to the gaining of information across different sensory modes, for example, between visual and acoustic information in foraging under nocturnal conditions [19] or visual and tactile information with respect to the exploitation of food resources buried within substrates [10,20].

Because of the complexity and often imperfect knowledge of both behavioural and environmental parameters that are brought to bear upon evolutionary and functional interpretations of eye structure, it is sometimes possible to regard or dismiss an explanation as an example of a *just-so story*, i.e. 'a speculative style of argument that records anatomy and ecology and then tries to construct historical or adaptive explanations' [21], rather than testable hypotheses. With respect to a specific explanation regarding a single species, or perhaps two species chosen as a contrasting pair, this is a frequently made and

widely discussed criticism [22,23]. One solution to such difficulties is to use a broad comparative approach rather than to rely only upon a detailed analysis of single species [24,25] but this requires a large dataset of readily quantifiable characteristics.

Comparative studies of eye structures have been based mainly around two principal elements: (i) those that combine data from eyes that appear to have similar structures and use these data to determine whether animals which possess those similar structures all face similar perceptual challenges, or (ii) whether the eyes of animals with similar evolutionary histories share features, even though they face different perceptual challenges. A simple example of this might be the influence of activity under low light levels (nocturnality). Do the eyes of all nocturnally active vertebrates share similar features which can be interpreted as adaptations to the perceptual challenges posed by the extraction of information at low light levels? Or do the nocturnally active forms within a taxon differ from those of related species which are not nocturnal?

For any comparative studies of eye structure and function, there is a need to draw study species from a well-established phylogeny, a range of species which occupy different habitats, and species which present a variety of behavioural repertoires. A sample that draws on these criteria is likely to include animals whose visual systems have been shaped by a range of different perceptual challenges and hence common features that have evolved in response to different challenges may become evident. The 10 000 or so species of extant birds [26] provide a good taxon for such studies because, in large part, their ecology and behaviours tend to be well known at least in broad terms, and for many of these species, detailed behavioural and ecological studies have been performed [27]. The taxonomy of birds is reasonably well established at the level of the family, and the behaviours and ecology of many species have been well studied and described. However, at higher taxonomic levels, there is considerable debate [28–30], and there are frequent revisions at the species level [26].

## 2. Perceptual challenges faced by birds

### (a) Flight

Rochon-Duvigneaud (1943) coined the phrase 'A bird is a wing guided by an eye'. He suggested that the essential visual capacities for guiding a wing were that spatial information should be of high accuracy and processed rapidly. His complete phrase is *L'Oiseau c'est une aile guidée par un oeil, ce qui exige la précision et la vitesse des fonctions rétiniennes* (A bird is a wing guided by an eye, which requires precision and speed in retinal function). These phrases attempt to capture the essence of what a bird is. The definition is certainly powerful because it combines a summary of what birds essentially do, with an explanation of how this is controlled. Thus, it is a definition of a bird from a sensory ecology perspective.

Irrespective of the evolutionary origins of birds [31], it does seem to be clear that flight, whether it arose on two or four wings [32], was an early attribute, and so it has been assumed that even among the earliest birds flight may have required a great degree of specialization of the visual system to provide information that is both spatially accurate and processed at high speed [33]. Both attributes are thought necessary in order to cope with the demands of travelling at relatively high speeds. Flightless birds almost certainly had ancestors that flew [34,35], so it would not seem unreasonable to suppose

that the gathering of information necessary for the control of flight is likely to have been important throughout the evolution of the sensory systems of birds. However, birds perform a wide array of tasks that do not involve flight. These may be guided by information from different sensory system as well as from the visual system, and the visual information required for their conduct may be different from that required for the control of flight. Some of these tasks may be performed intermittently but are nevertheless crucial for the daily survival of the animal; others are conducted almost continuously, and the gaining of information for the control of these tasks will have been the subject of constant and exacting natural selection.

### (b) Foraging

Finding and ingesting food would seem to pose a constant perceptual challenge for most birds. Constrained by the requirements for a combination of high-power output and low body weight [36], most birds forage almost continuously, or at frequent intervals, through their waking period each day and usually for a relatively specific range of food items [27]. Extant birds exploit a very wide array of food types, and the efficient detection and ingestion of each type would seem to pose particular perceptual challenges. Food types exploited by birds range from the minute to the relatively large, and from immobile objects to prey that are highly mobile and evasive. Algae and diatoms, plant leaves, many different types of fruits and seeds, animals of all main faunal types, including flying and buried invertebrates, to medium-sized mammals and birds, and carrion; these are all exploited by different species of birds [27].

Each dietary type is associated with a particular method of food acquisition, e.g. pecking, lunging, probing, excavation, aerial pursuit, pursuit under water, grazing, filtering mud and water, etc., these pose a rich array of perceptual challenges which must be dealt with frequently, almost continuously, by a bird throughout its life. Retrieving sufficient information from the environment to allow a bird to do these tasks must be the subject of exacting natural selection. Such selection is likely to be equal in its effects to the selection pressures which can lead to rapid changes in the structures used to actually procure food items, especially bill shape and size, whose study has been the focus of seminal work describing the mechanism and speed of evolutionary change [37,38]. After all, while food items need to be seized and processed by the bill, bill position also needs to be accurately controlled so that items can be procured.

### (c) Predator detection

Avoiding being detected and consumed by a predator is a challenge which is probably faced by the majority of bird species almost constantly [39–41]. Only species which evolved in habitats almost free of predators may have been free of this constant source of selection. Such a situation which may have existed only on islands such as those of New Zealand, where birds were free of mammalian predators for 80 myr before the arrival of man 1000 years ago [42,43], and on other smaller more recently formed oceanic islands, such as the Galápagos and Hawaiian Archipelagos.

### (d) Reproduction

Behaviours associated with reproduction can be subjected to exacting selective pressures and have long been the focus of

research at the heart of understanding evolutionary processes, especially in the field of behavioural ecology [44]. Reproduction can occupy a large proportion of a bird's lifetime, and many of the more intriguing aspects of its behaviour can involve display postures and plumage characteristics which are used as signals associated with reproduction. The specific investigation of these in the context of sensory ecology has been the subject of detailed and insightful analyses, for example [7,45].

Although the sensory information which supports these behaviours has been studied in detail they are not perhaps subjected to such strong and continuous selective forces that are likely to have applied to the more ubiquitous informational demands of locomotion, foraging and predator detection. Indeed, reproduction, and the informational demands that it brings, has to be conducted within the daily context of these more ubiquitous behaviours. It might be predicted, therefore, that the informational demands of locomotion, foraging and predator detection will have been the prime drivers in avian sensory ecology.

### (e) Compromises, trade-offs and the fine-tuning of visual fields

The perceptual challenges posed by locomotion, foraging and predator detection are likely to apply almost constantly in the daily lives of most birds and will have applied throughout their evolution. During every day of a mature bird's life, it is likely to move frequently around a familiar patch, and at less frequent times move over greater distances. Most birds almost certainly forage, and are likely to be exposed to predators, throughout most or all of their waking hours. Frequently, the perceptual challenges associated with moving, foraging and exposure to predation will occur simultaneously, or there may be rapid switching between them. For example, a foraging bird may require information to guide the detection of a food object while at the same time needing information on predatory dangers [46,47]. It may also instantaneously require information to control flight once a predator has been detected. The information required to meet these general challenges may be quite different from each other, and they may not be mutually reinforcing. For example, in a particular species, the gaining of specific information to optimize the detection of food may not optimize the way information is gained for the detection of predators. Indeed, it has often been assumed that because these informational demands are so dissimilar, the tasks of foraging and of predator detection cannot be conducted simultaneously and require a bird to switch between discrete behaviours in order to carry them out [46,48,49].

As well as different tasks providing conflicting demands for different information, it is also possible that the optimal solutions for gaining information for the conduct of a particular task may pose apparently insurmountable problems when birds are faced with a new set of tasks. This may be seen, for example, when the gathering of information for the control of locomotion appears not to be adequate to meet new perceptual challenges posed by human artefacts, such as fences, power lines or wind turbines. The result of such new informational demands is that birds may collide fatally with such objects, even though these objects appear to humans as very obvious features in the environment [50]. Another set of examples involves large illuminated objects such as

gas platforms, radio masts and tall buildings. Birds migrating at night appear to be attracted to such objects and may fatally collide with them, sometimes in large numbers at a single event [51–53]. Such problems may have their roots in sensory ecology, because information which is used to control flight behaviour under natural circumstances is insufficient or misleading in the face of new perceptual challenges created by human artefacts [54].

Trade-offs and compromises can apply within a single sensory modality, particularly so in vision. Vision is a multifaceted sense, described as embodying many capacities which are measured independently of one another [55]. However, different facets of visual performance cannot all be maximized simultaneously within a single visual system as has been elegantly described with respect to the trade-off between sensitivity and resolution [18]. Conflicts in the information required for different tasks may result in compromises and trade-offs between different types or qualities of information and this was first systematically explored by Lythgoe [16] with respect to whether the spectral sensitivity of photoreceptors in fish retinae should match or be offset from the spectral distribution of the light from different sectors of the water column [56].

It is argued below that differences in visual fields can indicate fine-tuning to the perceptual challenges faced by individual species such that there can be functionally significant differences in visual ecology even between congeneric species. This indicates that sensory capacities can be fine-tuned to the demands of particular tasks and that it is necessary to be cautious in making generalizations about sensory ecology between species and even within families.

While these arguments are made here by reference to just one aspect of the properties of the eyes of birds, i.e. how the visual fields of the two eyes are combined, it is possible that the same fine-tuning may apply to many aspects of vertebrate eye characteristics, for example the distribution of retinal photopigments [57]. Data are drawn here from studies of the visual fields in 59 bird species (from 31 families and 20 avian orders) which differ markedly in their general ecology. The list of species, key parameters of their visual fields and references to individual studies are given in the electronic supplementary material, table S1. Electronic supplementary material, S2 gives details of the methods used to measure visual fields, the ways in which they are presented diagrammatically, and definitions of the key parameters that form the basis of the comparisons discussed here. Also shown in the electronic supplementary material, S2 are diagrams of a sample of visual fields of three species. The discussion below draws out general themes concerning the visual ecology and functional interpretations of the visual fields of birds but it will be necessary to consult references to studies of particular species (given in the electronic supplementary material, table S1 and supplementary material, S3), to follow the detailed arguments. It is to be hoped that others will attempt to develop this comparative database of visual field parameters in birds and also extend this visual field data to other vertebrate taxa.

### 3. General characteristics of the visual fields of birds

Although we know that the world surrounds us, at any one moment we do not experience it like that. We, as humans,

experience the visual world as ‘in front’ and we ‘move forward into it’. This perception of the world is a result of the particular configuration of our visual field. The visual field defines the space around the head of an animal from which information can be extracted at any one instant. Human eyes are placed in the front of the skull; the eyes look horizontally, neither up nor down, not sideways or back, just forwards. Effectively, what the left eye sees is very similar to what the right eye sees, i.e. we have a large area of binocular overlap, with our two eyes looking at the same scene from slightly different viewpoints. The whole of the human visual field lies within the hemisphere in front of the face. However, compared with most vertebrates, including nearly all birds, human eye placement and the resultant visual field is unusual. In effect, birds are surrounded by their visual world and they ‘flow through’ their visual world, rather than move into it [49].

In birds, the eyes are positioned on the side of the skull, each eye looks outwards at a different scene with the region of overlap of the two visual fields relatively small, typically between 20° and 30° but as narrow as 5–10° in some birds, although the field of an individual eye may be wider than 180° (see electronic supplementary material, table S1). For many birds, the eyes not only look sideways, but they are also positioned more towards the top of the skull, and the axes of the eyes project upwards rather than project horizontally. The result is that for the large majority of birds the visual world is all around; there is little or no blind area above or to the rear of the head. Some bird species, e.g. some ducks (Anatidae) and some wading (shore) birds (Scolopacidae), can achieve complete visual coverage of the hemisphere above the head, and also extensive coverage below, such that at any one instant they can extract information from anywhere within their surroundings, other than the space occupied by their own body. For some birds, the eyes may point slightly downwards with the result that when the head is held horizontal they are able to attend to objects at their feet (e.g. herons Ardeidae) or comprehensively scan below them when foraging on the wing (e.g. eagles and vultures Accipitridae).

Despite these very marked departures from the human world view, it has been widely held that frontal eyes are the optimal or preferred position of eyes in the vertebrate skull. Thus, Walls [1, p. 326] concluded that, *Vertebrates have had a powerful incentive to develop binocularity wherever their snouts and their beaks and their requirements for periscopy would permit, and, two eyes are better than one, and that vertebrates in general have seemingly striven to enlarge binocular fields at the expense of unioocular ones. Animals which have clung to strong laterality have done so in obedience to powerful factors, such as defencelessness or total absence of cover in the environment which makes the retention of periscopy vitally important. The various degree of partial frontality are compromises between the urge for binocularity and the need for periscopy* (p. 291). These kinds of conclusions, which are based very much upon an anthropocentric perspective, have achieved wide currency in popular natural history and also in the investigation of binocularity.

### 4. Functional interpretations of the visual fields of birds

A framework for explaining both the general and detailed features of the visual field topographies found among birds



has eschewed the more anthropocentric perspective taken by Walls, and has also suggested that the *wing guided by an eye* model of birds is not fundamental, if anything the general sensory ecology model of birds is primarily that of a *bill guided by an eye*. It is argued here that both the general and detailed features of bird visual fields, down to the level of individual species, have been driven primarily by the key perceptual challenges of foraging, i.e. the accurate positioning of the bill or feet when taking food or prey, which have been traded-off against the perceptual demands of predator detection, and in large-eyed birds, the need to avoid imaging the sun on the retina. It is argued that the perceptual requirements for the control of locomotion are met within the requirements of selection for efficient foraging and predator detection. Evidence in support of this general argument has been built up from a series of detailed studies of visual ecology and visual fields in the species listed in the electronic supplementary material, table S1. Some of these arguments have been described in detail in a series of papers [58–62].

## (a) Evidence in support of the general argument

### (i) Control of bill position in foraging

The foraging of most birds requires exact positioning of the bill (or in some species the feet) with respect to a target, regardless of whether the items are taken by pecking or lunging. Control of bill position (both the direction of travel towards a target and time to contact the target) can be achieved from the optic flow-field produced as the head moves towards the target. The target is usually detected visually in the lateral field of view of a single eye, probably using a region with the highest-quality optics and the highest retinal resolution [62]. After detection, visual control of the approach towards the target is passed to the frontal binocular field, within which the direction of the bill projects, but this switch may occur at only a relatively close distance from the target, and hence at a short time before making contact with the target. This allows accurate direction of the bill towards the target and accurate timing of arrival, so that bill opening can be coordinated with arrival at the target object. In some birds, pecking has a ballistic phase, wherein the eyes are closed during the final approach towards the target. In other bird species, prey may be taken in the feet which are brought up into the central projection of the binocular field just prior to prey capture.

### (ii) Visual coverage of the celestial hemisphere

Comprehensive visual coverage of the celestial hemisphere is found in a number of bird species (see electronic supplementary material, table S1). It is coupled with a small degree of binocular overlap (less than  $10^\circ$ ) which extends through  $180^\circ$  from directly in front to directly behind the head. This visual field topography appears to have evolved independently in two quite different avian orders: ducks Anseriformes and shorebirds Charadriiformes. Only a few species in each order show this particular visual field topography but all share a common feature in that their foraging does not require visual control of bill position; foraging in these species relies upon tactile cues from the bill to detect food items. It appears that when freed from the constraint for the accurate visually guided control of bill position, natural selection has favoured the evolution of comprehensive visual coverage about the head to aid predator

detection. Crucially, however, the width of binocular overlap in these species is minimal, between  $5^\circ$  and  $10^\circ$ . Furthermore, these birds are capable of fast flight often in complex habitats which suggests that a frontal binocular field of this minimal width is sufficient for the control of flight.

### (iii) Congeneric and intra-family differences in visual fields

There is evidence from these taxa that the development of all-encompassing visual fields and the ability to use a binocular field of minimal width for the control of flight can evolve relatively rapidly at the level of individual species. Thus, significant differences in vigilance behaviour, that are coupled to differences in visual fields, occur between two species of congeneric ducks, the non-visual (tactile) feeding northern shovellers *Anas clypeata* and Eurasian wigeons *Anas penelope* (whose foraging involves selective grazing guided by visual cues) [12]. Shovellers have comprehensive visual coverage of the celestial hemisphere, whereas wigeons have a narrow blind sector to the rear of the head, but a wider binocular field that encompasses the projection of the bill tip. Thus, two congeneric species, which can be observed exploiting different resources in the same locality, differ in their visual field configurations, foraging technique and vigilance behaviour.

Similar differences in visual fields have also been found between more distantly related species of ducks (blue ducks *Hymenolaimus malacorhynchos* and pink-eared ducks *Malacorhynchus membranaceus*), two species which also differ in their use of visual and tactile cues when foraging [9]. Among shorebirds differences exist in visual fields that are correlated with differences in the use of tactile or visual cues in prey detection and capture among species (red knots *Calidris canutus* and Eurasian woodcocks *Scolopax rusticola*) within the same family, Scolopacidae [10].

Although not involving comprehensive vision and tactile foraging, there are examples among the Ciconiiformes, of significant differences in visual fields between species in the same family which have been correlated with differences in foraging technique. Thus, among the ibises (Threskiornithidae), significant differences in visual fields are found between species whose foraging ecology involves surface pecking in dry terrestrial habitats (northern bald ibis *Geronticus eremita*) and species which probe in the soft substrates of marsh habitats (puna ibis *Plegadis ridgwayi*) [15]. However, among the herons (family Ardeidae) within the Ciconiiformes, there is a marked similarity in visual field configurations even among species from different genera. This suggests that all of these species face a similar perceptual challenge when trying to detect and capture highly evasive prey [63].

### (iv) Visual fields and the perceptual demands of foraging

The above examples indicate that closely related species, even within the same genus (which use different perceptual cues for foraging) can differ in their visual field characteristics in subtle, but functionally distinct ways, suggesting that visual fields (and the optical and anatomical structures which underpin them) are subjected to strong selective forces driven by the perceptual demands of foraging. These evolutionary outcomes can be considered comparable in their functional importance to the much more widely studied subtle differences in bill structures that are driven by the mechanical demands of procuring different food types [38]. These examples reinforce the hypothesis that the configuration of visual fields is driven

primarily by the perceptual challenges of foraging which are traded-off against the requirement for predator detection. Only in those species which do not need to use vision to guide their bill position during foraging is comprehensive visual coverage of the world about the bird attained.

## 5. The functions of binocular vision in birds

The functions of binocularity in birds have been discussed in detail [62]. In summary, it has been proposed that with the possible exception of owls, binocularity in birds does not have a higher-order visual function that results in the perception of solidity and relative depth through a mechanism of stereopsis. Rather, it is argued that binocularity is a consequence of the requirement of having a portion of the visual field that looks in the direction of travel; hence, each eye must have a contralateral projection and it is this requirement that gives rise to binocularity. This contralateral projection is necessary to gain a symmetrically expanding optic flow-field about the bill. This specifies the direction of travel of the bill and its time to contact a target during feeding or when provisioning chicks. In birds which do not need such control of their bill, binocular field widths are very small suggesting that binocular vision plays only a minor role in the control of locomotion. In the majority of birds, the function of binocularity would seem to lie in what each eye does independently rather than in what the two eyes might be able to do together.

### (a) Evidence in support of the general argument

#### (i) Horizontal width of binocular fields

In birds which use vision to control bill position when taking food items, the visual fields show a narrow and vertically elongated frontal binocular field in which the bill is placed either centrally or slightly below the centre. Such an arrangement is found in a remarkably wide range of species (see electronic supplementary material, table S1) that differ both in their ecology and in their evolutionary origins. In all of these birds, there is a blind area behind the head. The width of this blind area differs between species, and it may extend to above the head and even into the frontal hemisphere (e.g. vultures [64] and bustards [50]). However, the topographies of the frontal binocular fields are very similar in all species which use vision to guide bill (or feet) position, reaching a maximum width in the horizontal plane in non-passerines species of between 20° and 30° (see electronic supplementary material, table S1). Such visual field arrangements are found in birds that feed in many different ways. For example, in species which peck at small mainly immobile items (e.g. ostriches *Struthio camelus*, Eurasian stone-curlew *Burhinus oedicnemus*, rock doves *Columba livia*, Eurasian wigeons *A. penelope*, southern ground hornbills *Bucorvus leadbeateri*); those which take prey by lunging at or pursuing evasive prey that are taken directly in the bill (e.g. heron Ardeidae and penguin Spheniscidae species); those which take prey in the feet (e.g. eagles, vultures Accipitridae), and those which snatch prey from a water surface while swimming or flying (e.g. petrels Procellariidae and albatrosses Diomedidae).

This similarity in binocular field configuration across such diverse groups of birds, and across such diverse feeding techniques, suggests a degree of ecological convergence upon an optimal binocular field width. That is, a 20–30° binocular

field is as broad as it need be to fulfil a particular function that is common to all of these species. Beyond such a width, there is little advantage to be gained, and in the majority of birds, it is the extent of the peripheral fields that are maximized to reduce vulnerability to attack by predators. There would seem to be a trade-off between the demands for accurately controlling bill or head position when approaching a target (which requires some degree of binocular vision), and the requirement to gain as comprehensive a view of the world as is possible.

In all of the birds mentioned above, although the bill is placed approximately at or just below the centre of the binocular field, there are some subtle variations that reveal further fine-tuning of the visual field in the frontal (binocular) region to particular visual tasks and ecological conditions. For example, in the majority of birds studied so far, the bill does not actually intrude into the visual field. The result is that ostriches and herons, for example, cannot actually see their own bill nor can they see what is held in the bill, much in the same way that humans cannot see their nose or mouth. This may explain why true pecking behaviour typically involves a ballistic final phase in which objects are approached with eyes closed usually from a characteristic distance for the species [65]. However, in birds that use precision-grasping as opposed to ballistic pecking, it appears that the bill does intrude into the visual field and this means that these birds can also see what lies between their mandibles when an object is grasped. Thus, hornbills, which pick up small items with forceps-like action in the tips of their large decurved bills, can visually inspect objects that lie between their bill tips before ingesting them [66]. This is also found in common starlings *Sturnus vulgaris* which use a specialized technique of ‘open-billed probing’ to uncover prey in the surface layers of a substrate [67]. Another example of where the visual fields allow the inspection of an item held between the mandibles is found in great cormorants *Phalacrocorax carbo*. The poor underwater visual acuity of these birds, and their flush foraging technique in which prey is disturbed and grabbed only at short range rather than pursued through the water, may not allow the identification of prey items before they are captured [11]. Items are brought above the water surface to be inspected and positioned accurately before they can be swallowed and this is facilitated by their ability to see between their opened mandibles [68]. New Caledonian crows *Corvus moneduloides* are among the small group of birds which forage using stick tools that are used for the extractive foraging of grubs from cavities [69]. Their visual field allows the birds to see along the line of their stick tools which are held in the tips of the bill and usually propped against the cheek below the eye. Their broad binocular field (which is the widest so far recorded in any bird species) allows these crows to see what is held between the mandibles and also to see along the line of the tool even though the tool typically projects laterally away from the direct line of the bill’s projection [70].

#### (ii) Vertical extent of binocular fields

The vertical extent of frontal binocular fields differs between species (see electronic supplementary material, table S1). Thus, while species with diverse evolutionary origins have a common maximum binocular field width of between 20° and 30° degrees the vertical extent of these binocular regions

may vary between  $60^\circ$  (e.g. bustards Otididae),  $80^\circ$  (e.g. ostriches, stone-curlews, hornbills, vultures),  $120^\circ$  (e.g. storks Ciconiidae) to  $180^\circ$  (herons Ardeidae). This has consequences for the extent to which the birds can see above and below them. Thus, a heron standing with its bill horizontal and the head slightly forward can see what is at its feet. (It is worth noting that the visual field of herons is very similar to those of the tactile feeding ducks, such as mallards, but with the crucial difference that the whole field is rotated forward through  $90^\circ$  in herons.) Seeing what lies perpendicularly beneath the bill clearly has the advantage that a foraging heron can remain motionless, monitoring what is going on all around, while it waits for a prey item, such as a frog or fish, to come within striking range beneath it. Because these prey have evolved rapid escape responses herons may get only a one-strike chance to catch each item. Therefore, monitoring what is going on below, without having to move the head or body, and waiting for a prey item, is clearly a significant advantage for a heron. On the other hand, such comprehensive coverage of the frontal hemisphere would appear not to have an advantage for the majority of bird species which pursue either immobile food items, or mobile prey which is usually taken when the bird is already in motion and the element of surprise seizure, perfected by herons, is not possible.

### (iii) Binocular field widths, nocturnality and predation

The widest binocular fields in birds are not found in owls Strigidae or diurnal raptors Accipitridae as is commonly supposed and was asserted by both Walls [1] and Rochon-Duvigneaud [2]. It is not clear at what date the idea that a link between nocturnality and broad binocularity arose, and it seems to be based upon casual observations of owls with the assumption that the eyes of owls are frontally placed and have a binocular field of similar width to that of humans ( $160^\circ$ ). The eyes of owls are in fact laterally placed in the skull although they are more frontal than in other birds. However, in tawny owls *Strix aluco* (which are highly nocturnal), the optic axes diverge by  $55^\circ$ , and the binocular field has a maximum width of  $48^\circ$ . It has been argued that the advantage of binocularity with respect to sensitivity is probably marginal, especially in the context of the extreme range of light levels (up to one million fold) which can occur at night [19]. In humans, using two eyes instead of one to view a scene provides an increase in sensitivity of only  $0.15 \log_{10}$  units [71]. This suggests that increased sensitivity is unlikely to be a strong driver for the selection of increased binocular overlap.

The maximum binocular field width of tawny owls is similar to that reported in a number of bird species (see electronic supplementary material, table S1) including the majority of passerines investigated to date. As noted above, the largest degree of binocular overlap yet recorded in a bird ( $61^\circ$ ) occurs in a crow (New Caledonian crows) and it is likely that this degree of binocular overlap is associated with tool use [70]. However, the binocular fields of owls are broader than those found in all other non-passerine bird species examined to date (see electronic supplementary material, table S1), but this width of binocular field may not in fact be associated with the visual challenges of nocturnal activity. Thus, it has been argued [62] that the width of the owls' binocular fields may in fact be the product of an interaction between enlarged eyes (probably associated

with maximized light gathering and/or maximizing resolution at low light levels [72]), and the elaborate outer ear structures which are unique to owls and are part of the mechanism underlying their enhanced sound localization abilities [73,74]. These large outer ear structures may prevent more lateral placement of the eyes. Put simply, more extensive visual coverage laterally would not be possible because these ear structures would get in the way.

The wider binocular field of owls may also have an adaptive explanation that is associated with prey capture rather than with nocturnal habit and enhanced visual sensitivity. In owls, the bill lies below the binocular field and when catching prey the feet are swung up before the bird's face, directly into the binocular field, and directly into the flight path of the bird. It seems likely that the binocular field is used in conjunction with accurate sound localization to guide the feet in the final stages of prey capture. In the final approach towards a prey item, the feet are raised, and the talons spread wide to fill the visual field in front of the head, which is also the region where sound localization is most accurate.

True nocturnality (completing all waking activities throughout the annual cycle between sunset and sunrise) in birds is uncommon and restricted mainly to owls (Strigiformes), nightjars and their allies (Caprimulgiformes) and kiwi (Apterygiformes). However, many birds conduct at least some of their activities at night [19]. For example, many species migrate at night, some enter and leave nest sites only at night, some may forage at night when following a tidal cycle, some may feed at night on a more seasonal cycle, and some penguin species may forage at such depths that they regularly search for prey at the equivalent of night-time light levels [75]. Furthermore, not all owls are nocturnal hunters. The nocturnal owls are mainly perch and pounce hunters, who can use accurate sound location as well as vision in prey capture [76]. On the other hand, nightjars feed mainly by trawling for insects in the open air space, although the frogmouths (Podargidae) and potoos (Nyctibiidae) also perch and pounce, but without the apparent use of hearing [77]. It is clear (see electronic supplementary material, table S1) that the visual fields of bird species which forage at nocturnal light levels, or are nocturnally active during key parts of their annual cycle (e.g. black-crowned night herons *Nycticorax nycticorax*, paraques *Nyctidromus albigollis*, oilbirds *Steatornis caripensis*, Manx shearwaters *Puffinus puffinus*, woodcocks, golden plovers *Pluvialis apricaria*, red knot *C. canutus*, stone-curlews, king penguins *Aptenodytes patagonicus*, kiwi *Apteryx mantelli*, black skimmers *Rynchops niger*) show no evidence that nocturnality is associated with wide binocularity. In all of these species, binocular field widths are considerably less than those of passerines species which do not forage at night.

Oilbirds are instructive because they are among the most nocturnal of birds. They roost and breed colonially in caves, only emerging after dusk and flying within the forest canopy, and returning before dawn. Their eyes appear to show a great deal of adaptation in both their optics and their retina, aimed towards increased photic sensitivity, yet their binocular field width is similar to those of other non-passerine species which are typically active only during day light [78,79].

Another, perhaps unusual, example of a bird that feeds at nocturnal light levels is provided by king penguins *Aptenodytes patagonicus* [75]. These birds feed at shallow depths at



night and also forage during the day when they dive to depths (more than 200 m) where light levels are in the night-time range. In effect, king penguins are nocturnal foragers and their eyes have a low  $f$ -number and a wide cornea which correlates with the maximization of light gathering. Yet, their visual fields show the same narrow and vertically long binocular field characteristic of other birds whose bill position is guided by visual cues and that forage at day-time light levels.

## 6. Visual fields, eye size and imaging the sun

Systematic data on eye size (eye axial length) in all of the species listed in the electronic supplementary material, table S1 are not available. However, eye size data are available for some species and it seems clear that a relationship does exist between eye size and the width of the blind region above the head. However, in the same species, there is no simple relationship between eye size and the width of the frontal binocular field. It may be concluded therefore that these two key parameters of visual fields have been selected independently of each other.

It seems that the sun poses a particular set of perceptual problems that have shaped the visual fields of birds. It has been argued [49] that the principal selection pressure driving visual field configuration in birds, and which has led to subtle variations even within genera, is a trade-off between the perceptual demands for control of bill positioning in the execution of different types of foraging tasks and the detection of predators. With the latter driving the total extent of the visual field (the width of the cyclopean field; electronic supplementary material, table S1) in the majority of species. However, extensive visual fields that allow birds to see all, or nearly all, of the world around them at any one instant, may not be without cost. Comprehensive visual coverage of the world about the head must mean that when the sun is in the sky its image will always fall upon the retina. In humans, the problems of imaging the sun are generally recognized to be threefold: there can be temporary or permanent damage to the retina from even brief direct exposure to the sun, the lens and cornea can be damaged due to exposure over a long period, and there can be direct disruptive effects to vision caused by glare and afterimages which leave temporary 'holes' in the field of view [80,81].

That most birds must be imaging the sun on their retinas for much of their waking time seems inevitable [82]. However, it could be that birds can position themselves such that the sun is always imaged at the periphery of the visual field, so that the effective aperture of the eye for the sun's image is a slit with effectively a high  $f$ -number and hence low image brightness [83]. So, the problem may not be as great as it first appears, although lifetime exposure of the cornea and lens is potentially a major problem, but perhaps most birds do not live long enough for the damaging effects to accumulate. However, that some have sunshade devices which help reduce the possibility that the sun is imaged on the retina is clear [82]. In fact, a significant linear relationship has been found between the size of the blind area above the head and eye size (axial length of the eye) [66]. At one extreme are large-eyed species, including eagles, vultures, ostriches, hornbills and albatrosses, which have a broad blind area (up to 80° wide) above the head, whereas

smaller-eyed species, including herons, pigeons, ducks and starlings, have no blind area above the head. Furthermore, the large-eyed birds that have a blind area above the head also have various optical adnexa which can function as 'sunshade' devices. These include brow ridges and thick and elongated eye lashes. Such structures are absent in other birds. In fact, it has been suggested that birds can be divided into two groups: 'large-eyed sun avoiders', which have sunshades and a blind area above the head, and 'smaller-eyed sun viewers', which have no sunshade devices and no blind area above the head [60].

The reasons for this dichotomy may lie in the reasons for having a large eye in the first place. Large eyes have probably evolved primarily to give high visual acuity, and, in general, the resolution of the retina matches the level of detail that can be produced by the larger image [18]. However, a large eye also has a large entrance aperture and will produce a relatively bright retinal image. In humans, the image of the sun on the retina is, in fact, sufficiently bright that it acts as a secondary light source within the eye, scattering light and degrading the rest of the retinal image [84]. Clearly, if selective pressure has been to evolve a large eye to maximize acuity, then it would have been maladaptive to compromise that acuity by degrading the image with light scattered from an image of the sun. Smaller eyes, on the other hand, can only ever have lower acuity and, so veiling glare produced by light scattered from a retinal image of the sun may do relatively little to degrade the image generally and lower acuity across the visual field.

It is important to note that there is no relationship between eye axial length and the maximum width of the frontal binocular field in the same species. This provides good evidence that the dimensions of the field above the head are not simply traded-off with the width of the binocular field as a result of geometrical constraints arising from the intersection of the visual fields of the two eyes. Rather, it reinforces the idea that within a species, the characteristics of the frontal binocular field and the width of blind area above the head have evolved independently in response to different perceptual challenges.

Thus, the general hypothesis that the configuration of visual fields in birds is driven primarily by the perceptual challenges of foraging, rather than the perceptual challenges posed by locomotion, and that these are traded-off against the requirement for predator detection, requires an additional hypothesis. In larger-eyed species, the requirement for the detection of predators, which drives the extent of the cyclopean field, is subjected to a constraint imposed by the need to avoid imaging the sun upon the retina.

## 7. The informational function of binocular vision in birds

That some bird species, such as woodcocks and mallards have frontal binocular fields as narrow as 10° and are still capable of taking off, flying and landing safely, in structurally complex habitats, supports the argument that extensive binocular vision is not a prerequisite for the control of flight. Furthermore, it has been argued that the binocular field is primarily used in the control of bill (or sometimes feet) position towards objects that are close to the bird, with the lateral field of view used to detect and initiate movements



towards more distant objects. It has further been argued that the function of binocular vision in birds does not lie in stereopsis but rather in the abstraction of information from optic flow-fields which may function independently in each eye. This latter argument has been presented in some detail [62], and it is not appropriate to rehearse all of the arguments here. However, it is worth noting the following points:

- in birds (and any other vertebrates with eyes placed laterally in the skull) binocular vision is, in fact, served by peripheral vision in each eye. (This is quite unlike the situation in animals with frontal eyes, such as humans where the central optics of each eye project forward and serve the binocular region.) There is an important consequence of this use of the peripheral field of each eye to provide forward binocular vision; the question of corresponding points. Neural pathways that could potentially link points of correspondence in the binocular portions of the two eyes must be more complex than in species with parallel optic axes. This is because an image point in the far retinal periphery of one eye will correspond with one that is more centrally placed in the retina of the other eye [62]. Furthermore, in bird species in which eye movements are present they are non-conjugate with each eye able to make different rotations independently of the other, and it has also been shown that some bird species spontaneously abolished their binocular field, e.g. great cormorants *P. carbo* [68]. Therefore, in birds, what constitutes a 'binocular portion' of the retina, and hence its projection through the optic nerve to higher centres, is not fixed;
- the behaviours with which binocularity seems most closely associated in birds (e.g. pecking or lunging at prey items) would seem to require information that identifies an object as a target, information about the location of that target with respect to the animal, and especially how its location changes over time owing to relative movement between target and animal; and
- the visual identification of a target is likely to have a significant cognitive component especially with respect to food objects, chick feeding and nest materials. There is evidence that such targets are identified primarily through lateral rather than through frontal vision [85]. Target location, however, requires more generic information. This could be derived from a 'percept of solidity' based upon binocular fusion and stereopsis. However, apart from the evidence of binocular neurons and stereopsis in owls [86], there is little evidence to support the idea that birds, in general, have either binocular fusion or stereopsis [62]. Much of the evidence argues against the assertion that birds have either global or local stereopsis. In particular, the finding that birds with eye movements frequently and spontaneously abolish their binocular fields [68], and that unocular vision can control pecking as accurately as binocular vision [87], suggests that birds' eyes may function independently (and indeed the left and right eyes may process information differently [85]), and that higher-order information is not extracted from the simultaneous view of the same object by the two eyes. Thus, rather than trying to find evidence of binocular fusion and stereopsis, it might be more parsimonious to consider what the function of binocularity could be if birds viewed objects diplopically within their binocular fields.

## 8. Binocular vision, optic flow-fields and contralateral vision

For any bird, the vital information beyond recognition of an object is the accurate identification of its position and, if there is relative speed between the object and the observer, to gain information on time to contact. The actual distance of an object from a bird may be of little importance compared with knowing its direction and the time it may take to make contact with it. Such information is available from optic flow-fields [88,89]. Furthermore, it has been shown that northern gannets *Morus bassanus* and hummingbirds (Trochilidae) when carrying out manoeuvres that require accurate visual information regarding speed of approach to a target, appear to use flow-field information [90,91]. In mammals, optic flow-field information is analysed in the accessory optic system [92] and pretectum [93], and a similar accessory system has been identified in birds [94,95].

Flow-field information is potentially available from any pattern of optical flow across the retina; it is not necessarily associated with binocular portions of a visual field. However, information on direction of travel towards a target and time to contact a target can be derived most efficiently when travel is directly towards a target. This will result in an optical flow-field which expands symmetrically about the image of the target. This would seem to be the situation in the key tasks described above. For example, when pecking or lunging at an object, both position and time to contact need to be accurately specified. The essential consideration, however, is that a flow-field which symmetrically expands about an object directly ahead of the bird can only be achieved if the visual field of each eye extends contralaterally, i.e. across the median sagittal plane of the bird. Thus, the important consideration is contralateral vision, not binocular vision. Binocular vision can be seen simply as a by-product of the need to have eyes that look forward across the median sagittal plane, not as an adaptation that has evolved specifically to achieve simultaneous views of the same object from slightly different positions. Binocular vision is perhaps irrelevant in birds; what is important is contralateral vision.

It can be concluded that binocularity in birds functions to provide information on the direction of travel and time to contact a target. However, this information can be provided by each eye independently and for this reason it might be more appropriate to refer to 'contralateral vision' rather than to 'binocular vision', because the latter brings with it assumptions concerning the percept of solidity and stereopsis with which binocular vision in birds does not appear to be associated. Thus, in the majority of birds, the function of binocularity would seem to lie in what each eye does independently (i.e. diplopically) rather than in what the two eyes might be able to do together.

## 9. Conclusion: the subtlety of visual fields in birds

- The above discussions have shown that there is much subtle variation in the parameters of visual fields in birds. These variations seem to be functional and it has been argued that they are driven primarily by the perceptual challenges associated with foraging, and the simultaneous perceptual demands for predator detection, rather than the control of

locomotion. The overall driver of frontal visual field characteristics is the demand for the accurate positioning of the bill. Visual field characteristics above the head are driven by the need to avoid imaging the sun on the retina in larger-eyed, but not small-eyed, species. The fine characteristics of the frontal binocular field may also be driven by the requirement to visually inspect items held between the mandibles. Small differences in foraging techniques can give rise to different perceptual challenges and these have resulted in subtle differences in visual fields between some closely related species, even within the same genus and certainly within the same family. Therefore, it is advisable to be cautious when making interspecific generalizations about visual fields in birds, each species may show subtle adaptations to quite specific perceptual demands.

- It should be noted that visual fields are complex three-dimensional constructs. Reducing these to the single values of key parameters (as in the electronic supplementary material, table S1) is probably ignoring other subtle but significant differences between visual fields (see example diagrams of visual fields in the electronic supplementary material, S2). The functions and evolutionary drivers of these variations are likely to be worth investigating.

- Among birds, there is a strong phylogenetic signal with respect to the maximum width of the binocular field, with passerine species showing broader widths than non-passerines, and within the passerines the broadest fields are found among the Corvidae. However, sample size with respect to the total number of passerines is small and more comprehensive species sampling of passerines, as well as non-passerines, is required.
- The informational function of binocular vision in birds seems to lie not in binocularity *per se* (i.e. two eyes receiving slightly different information simultaneously about the same objects from which higher-order depth information is extracted) but in the contralateral projection of the visual field of each eye. This ensures that each eye receives information from a symmetrically expanding optic flow-field from which direction of travel and time to contact can be extracted. In birds, and in many other vertebrate taxa, the eyes are placed laterally in the skull. This means that forward facing contralateral vision is served by the peripheral vision of each eye and the concept of ‘corresponding points’ as applied to human vision may be inapplicable. The neurophysiology of contralateral vision in birds would seem worthy of further investigation.

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