

Marine birds: vision-based wind turbine collision mitigation

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Prof Graham R. Martin



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Natural England Project managers

Dr Alex Banks (Principal Specialist) and Matthew Stone (Specialist)

alex.banks@naturalengland.org.uk

Author

Prof Graham R. Martin

Professor Emeritus of Avian Sensory Science, The University of Birmingham, UK

g.r.martin@bham.ac.uk

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Further information

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Foreword

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Executive summary

Throughout their evolution seabirds have not had to contend with obstacles which extend into their flight space above the water surface. However, the recent introduction and expansion of the Offshore Wind sector has significantly increased the potential for collisions with turbines. Bird collision risk with Offshore Wind Farm (OWF) turbines is now a major consenting consideration for OWF projects. Therefore, the possibility of reducing those risks through a simple vision-based mitigation is highly desirable. It has the potential to help both governments and developers accelerate the growth of OWF to achieve renewable energy targets.

The report's Appendix presents a review of the vision of birds. This is used to determine key elements for the design of vision based mitigation measures aimed at reducing the collision of marine birds with Offshore Wind Farms.

The review was prompted by the findings of May *et al* (2020) which tested a vision-based wind turbine mitigation measure. They reported a modelled 70% reduction in annual turbine-blade collision mortality rate in a suite of 19 bird species at a terrestrial location. The aim of the report is to extend this mitigation approach and increase its general applicability to a broader suite of bird species at sea, and to a wider range of viewing conditions.

The review explores key aspects of the vision, behaviour and ecology of marine birds which contribute to their collision risk under a range of natural viewing conditions. The same information is then employed to give insights into the requirements of mitigation measures.

The review concludes that there is a justifiable ecological basis to believe that the principle of increasing the internal visual contrast of turbines through blade marking should benefit seabirds. Although white-tailed eagle and seabird vision is comparable, it is important to consider differences in environments that influence relative collision risk. These include familiarity with areas where turbines are encountered, and factors which affect visibility at sea, especially light levels and weather conditions. As such, simple blade marking may not yield seabird collision reductions at rates recorded for white-tailed eagles at coastal wind farms. It is recommended that more complex markings of turbines should also be considered.

A mitigation measure is proposed which is neither site or species specific and can be employed generally in marine situations. The principle aim of the mitigation measure is to increase the conspicuousness of wind turbines across a wide range of natural viewing conditions such that a turbine can be detected by an approaching bird sufficiently early to allow change in their flight path and avoid collision.

The proposed mitigation requires modest changes to the appearance of wind turbines that can be implemented at the time of manufacture. These changes will increase the internal achromatic contrast of turbines and increase their contrast against a wide range of sky and

sea conditions. The measures will allow birds with different flight speeds and visual acuities to detect turbines sufficiently early to allow alteration of flight direction and avoid collision.

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1. Summary

Marine birds (38 species from 7 avian Orders) have been ranked according to two possible outcomes of their interactions with wind turbines: 1, A direct effect on individual birds through collisions and, 2, The indirect effects of disturbance and/or displacement from key habitats caused by the presence of wind turbines.

The ultimate cause of collision vulnerability is the propensity of species to fly at the height swept by turbine blades. The proximate cause of collision vulnerability in these birds is the result of limitations of their vision. This reduces their ability to detect a turbine and to determine the time at which they will contact it.

Collision vulnerability due to reduced visual information is increased under poor viewing conditions (low light levels, low visibility).

Birds are known to conduct complex tasks, especially associated with foraging, using only partial information based upon gross spatial information. Some bird species are known to effectively fly blind, or only acquire information on the way ahead intermittently. This occurs particularly when species use flight to forage for prey on the surface below them. Under these circumstances birds are predicting that when they fly in the open airspace the way ahead is clear.

It is not possible to “warn” wild birds of hazards since this requires birds to learn a link between the hazard and a specific stimulus. However, it is possible to increase the conspicuousness of a hazard by employing knowledge of the sensory performance, especially vision, of species.

Vision is a multifaceted sense and bird species differ markedly in their spatial resolution, sensitivity to visual contrast, speed of vision (detection of flicker), and the topography of vision. All four aspects of vision are likely to contribute to the collision vulnerability of a species.

The direction of highest spatial resolution does not project directly ahead of a bird; it projects forwards and laterally on both sides of the head.

The design of collision mitigation needs to take account of: 1. Birds may be traveling under non-optimal viewing conditions and are thus able to extract visual information based upon only low spatial resolution, 2. Some species may fly while gaining information from the surface below and only intermittently acquiring information about what lies ahead, 3. Under all visibility conditions birds are likely to fly only at their optimal flight speed, 4. Forward vision used in the control of flight (direction of travel and time to contact a target), primarily extracts information from the optical flow patterns that are based upon relatively gross spatial details.

The ideal requirements of a collision mitigation measure based upon vision are: 1. The mitigation needs to be as conspicuous as possible, 2. The mitigation must be effective under a wide range of light levels (bright sunlight to night-time, a million-fold range), 3. The

target must be detected at least 10 seconds (150 – 200 m distance) before potential impact and ideally should be detected 30 seconds (450 – 600 m) before impact, 4. The mitigation needs to have high internal contrast and not rely upon contrasting with the background (sea or sky scape). 5. The mitigation should embody a degree of movement or flicker.

Mitigations that take account of these requirements can be achieved by the application of high contrast achromatic (black and white) patterns to the blades and pylons of wind turbines. To maximise contrast, surfaces should reflect (white) or absorb (black) light equally across the range 300 – 700 nm. This maximises contrast for all species, including those whose daytime sensitivity extends into the UV portion of the spectrum.

To maximally enhance the conspicuousness of a turbine, each blade (both front and rear surfaces) should be divided into thirds with two of the blades showing black tips, a white middle section and a black section close to the nacelle (Figure 1). The other blade should be the reverse of this pattern. The pylon supporting the turbines should be in alternating bands of black and white with the length of each section equal to half that of the blade pattern sections. All turbines in a wind farm should have these patterns.

Dividing a blade into thirds lengthways and making it alternately black and white, should serve to increase the probability that there is always a flickering contrast pattern set up between the sections of adjacent blades as they rotate, and between the rotating blades and the pylon.

On large turbines, dividing a blade into thirds lengthways and making it alternately black and white, will make the dimensions of the individual elements in the contrast patterns detectable at sufficient distance for a bird to change its flight path early enough to avoid collision under a wide range of viewing conditions.

The recommended pattern is not designed to be particularly visible to any one species or taxon of marine birds. The pattern is a general solution which should increase the detectability of turbines to all bird species considered to be collision vulnerable. It would apply equally well to other cohorts of marine birds and to terrestrial species.

The recommended collision mitigation patterns can be implemented at the production stage of turbines. The use of suitable surface coatings should be maintenance free and unlikely to reduce the generation efficiency of wind turbines.

2. Introduction

A literature survey of behaviour and ecology was used to assess the population vulnerabilities of birds to wind farms worldwide (Thaxter et al. 2017). This work built upon the approach used by Furness et al (2013) to assess the vulnerabilities of marine bird species populations to wind farms around the coast of Scotland. That study identified 38 species as vulnerable to wind farms and ranked them according to two possible effects of

their interactions with wind turbines: direct effects through collisions and, indirect effects of displacement from key habitats (Table 1).

3. Turbine collision-vulnerable and displacement-vulnerable bird species

Gulls, terns and skuas (Charadriiformes; Laridae and Stercorariidae) were found to be most vulnerable to collisions with turbines (Table 1). Divers (Gaviiformes; Gaviidae) and some species of ducks (Anseriformes; Anatidae) were found to be more prone to disturbance from key habitats, but less vulnerable to collision impacts (Table 1). While there is a degree of nuance in these rankings, with many species showing similar risk factor scores, they give a valuable overall summary of the relative vulnerability of marine birds to the presence of wind turbines in Scottish waters.

Neither of the rankings directly assessed impacts. There is limited data on collision rates of marine birds based upon radar monitoring (Skov et al. 2018) but it has not been possible to robustly assess collision rates as has been the case in land-based studies of the collision impacts of human artefacts (Shaw et al. 2021; Shaw et al. 2010). This is because of the difficulty of collecting collision damaged birds (cadavers or injured) from marine locations. The ranking of collision impacts by Furness et al (2013) are based upon three factors: observations of how frequently species fly over the sea surface within the height range of rotating turbine blades, an assessment of flight manoeuvrability, and the likelihood that birds fly at night over the sea.

Table 1: Marine bird species identified as vulnerable to collision or displacement from wind turbines in Scottish waters, ranked from most to least vulnerable.

Species vulnerable to collision	Species vulnerable to displacement
Herring gull	Black-throated diver
Great black-backed gull	Red-throated diver
Lesser black-backed gull	Great northern diver
White-tailed eagle	Common scoter
Northern gannet	Common goldeneye
Common gull	Greater scaup
Black-legged kittiwake	Velvet scoter
Arctic skua	Common eider
Great skua	Black guillemot
Black-headed gull	Slavonian grebe
Sandwich tern	Common guillemot
Black-throated diver	Razorbill
Great northern diver	Shag
Common tern	Great cormorant
Red-throated diver	Little tern
Little tern	Arctic tern
Arctic tern	Atlantic puffin
Roseate tern	Long-tailed duck
Shag	Roseate tern
Slavonian grebe	Sandwich tern

Greater scaup	Common tern
Common eider	Great-crested grebe
Great cormorant	Great black-backed gull
Common goldeneye	Black-legged kittiwake
Common scoter	Common gull
European storm-petrel	Black-headed gull
Velvet scoter	Little auk
Leach's storm-petrel	Northern gannet
Great-crested grebe	Herring gull
Long-tailed duck	Great skua
Northern fulmar	Lesser black-backed gull
Common guillemot	Arctic skua
Razorbill	White-tailed eagle
Black guillemot	Manx shearwater
Atlantic puffin	European storm-petrel
Little auk	Leach's storm-petrel
Manx shearwater	Northern fulmar
Sooty shearwater	Sooty shearwater

4. Sensory bases of collisions

In the Furness et al (2013) review there is an implicit suggestion that sensory factors play a role in collision vulnerability in that it was suggested that propensity to fly at night increases collision risk. This assumes that lower levels of visual spatial information available to birds when flying at night (Appendix section 8), increases collision risk.

There is a growing body of evidence that sensory and perceptual factors play the key role in determining the general vulnerability of birds to collisions with human artefacts including power lines, glass panes, fences, moving vehicles, and wind turbines (Martin 2011). A sensory ecology approach to understanding bird collisions (Martin 2017a), suggests that interspecific differences in vulnerability can arise because some species are less likely to detect human artefacts, and that marked differences in detectability can occur due to changes in viewing conditions, especially light level and visibility. In essence, sensory and perceptual factors are likely to play a key role in both vulnerability to collisions and in vulnerability to displacement from the vicinity of turbines.

The analysis of Furness et al (2013) is based primarily upon the premise that the ultimate cause of collisions in the more vulnerable species is that they are more likely to be “in the wrong place at the wrong time” (flying at the height of turbine blades), and that they have lower flight manoeuvrability. However, it is valid to consider the proximate cause of collisions in these species. If a bird is flying in the vicinity of turbines, why does it not detect the hazard posed by a turbine and make evasive manoeuvres in sufficient time to avoid collisions? This is important because if failures of detection and perception contribute to vulnerability then it should be possible to employ mitigations which increase the probability that turbines will be detected. This report recommends what can be done to increase the detection of wind turbines sufficiently early to allow birds to alter their flight paths and avoid collisions.

5. Perceptual bases of collisions

The key driver of bird senses is regarded as primarily stemming from the informational demands of foraging: the detection, acquisition, and screening of food items (Martin, 2017). Vision is driven primarily by the demands of detection and acquisition. The second key driver that has shaped bird vision is the detection of predators. However, the visual tasks of foraging and predator detection make antagonist demands for information, and these can be seen played out in the vision of most birds. The informational demands for controlling flight are best considered to be met within the requirements set by the primary sensory challenges of foraging and predator detection.

These different demands and their relative weighting have led to the argument that the essence of birds is encapsulated in the phrase “a bird is a bill guided by an eye”. This is to be juxtaposed with the older phrase, coined by the French anatomist André Rochon-Duvigneaud in 1948, which depicted a bird as “a wing guided by an eye”. The change of emphasis from “wing” to “bill” as the prime focus of adaptations of avian vision reflects the idea that bird vision is primarily adapted to the control of the bill as the key tool with which a bird interacts intimately with its environment. In most species, survival depends upon bringing the bill to “the right place at the right time”. This change in the short-hand way of describing birds is important because it changes how we might think about birds in an everyday sense. It indicates that the main task of a bird, day-in-day-out is getting its bill (or feet if they are used in prey capture) to the right-place at the right-time, over-and-over again. There is no value in having a tool (bill or feet) that cannot be effectively controlled. Making a sensory based error when flying may be important, but it is not as important as being unable to explore the environment at close range and use the bill to acquire food.

This emphasis upon vision as primarily driven by the task of foraging provides an explanation of why birds are vulnerable to collisions with a wide range of human artefacts, especially those that intrude into the open-air space, and which have proliferated only very recently in the evolutionary history of birds (Martin 2011).

Humans, like birds, are also susceptible to collisions due to recently developed artefacts that take us beyond the evolved limits of our vision. Thus, humans are particularly vulnerable to collisions involving fast moving vehicles and most such collisions have their roots in two phenomenon that stem from sensory or perceptual considerations. Collisions can be considered as due to “looked but failed to see” or “saw but failed to avoid” (Clarke et al. 1995; Hills 1980). The first type is primarily a failure of sensory information, while the second is primarily a failure of perception i.e., the incorrect interpretation of sensory information.

At root, both “looked but failed to see” and “saw but failed to avoid” types of collision arise because insufficient information is retrieved from the environment and employed for the control of behaviour. When moving through an environment the rate of gain of information about what lies ahead, and estimation of the time to reach it, must match the challenges set by the detection of a target and the velocity of approach towards it.

5.1 Collisions and partial information

Both types of collision occur in human car driving when the vehicle travels too fast for the gain of information about the road ahead to match the task of controlling the vehicle. This can occur frequently at low light levels or when there is impaired visibility due to rain or mist, but it can occur also under favourable viewing conditions when the target/hazard is incorrectly interpreted due to excessive speed of travel. Under poor viewing conditions (low light level, low visibility) the information that can be extracted from the scene ahead is only partial, compared to that usually employed to avoid a collision. However, much car driving is based on predictions that the environment will continue much as it has done in the immediate past. This is adequate for most circumstances since roads are on the whole highly predictable environments due to standard engineering and signage whose learnt meaning provides more information than simply seeing the sign itself.

The idea that complex tasks, such as car driving at night, are achieved by humans when using incomplete or partial information is also applicable to complex behaviours in birds. For example, there is good evidence that nocturnal birds, especially owls, may forage successfully at night in complex environments using partial sensory information (Martin 2017a), or that cormorants may frequently forage successfully in dark and turbid water using only sparse or partial visual cues (White et al. 2007).

5.2 Failing to see the way ahead

There is good evidence that some birds regularly fly without keeping a look out ahead. Collisions may occur not because they look but fail to see, or because they saw but failed to avoid the hazard, they may simply have not been looking ahead. This has been shown in larger birds of prey (eagles and vultures), which can be highly vulnerable to collisions with turbines (Dahl et al. 2013; Martin et al. 2012; Thaxter et al. 2017), despite them having the highest spatial resolution of any animal (Appendix section 8). A key cause of their vulnerability is the configuration of their visual fields (Appendix section 7). The result is that when searching the ground below for prey an eagle may gain no, or only intermittent, information about the flight path ahead (Martin et al. 2012). This has also been found in other collision prone bird species, especially cranes and bustards (Martin and Shaw 2010) and may be common in birds which regularly make use of the open airspace to search the surface below.

5.3 Predicting the way ahead

The above examples suggest that apparently complex and essential tasks are habitually carried out by birds (and by car-driving humans) with only incomplete information about what lies ahead, and sometimes when no, or only intermittent information, is gained. However, successful conduct of these tasks is achieved when they are executed regularly in familiar environments. This means that safe control of these tasks may not be achieved when circumstances are changed in unpredictable ways. Such changes include the introduction of human artefacts (power lines, wind turbines) into flight space or the introduction of nets in underwater environments (Field et al. 2019; Martin and Crawford 2015). In the case of human car driving a cow or deer wandering into the roadway is a sufficiently rare event that it can cause a collision. At such times it is evident that the

vehicle is being driven beyond the driver's perceptual limit for the detection of that hazard, suggesting that drivers frequently rely on predictions about the road ahead based on information that is only partial with respect to the task.

5.4 Collision mitigation measures

The above considerations suggest that it may be possible to mitigate turbine collision vulnerability in birds by increasing the probability of turbine detection, especially in conditions (low light level, poor visibility) when information about what lies ahead is either non-existent or only partial. This approach is, in effect, attempting to mimic some of the collision mitigation measures that have been effective in reducing human road vehicle collisions.

In the case of human collision mitigation, however, techniques have been tried, tested, and honed over many years. It has also been possible to teach drivers about the meaning of a set of stimuli so that they become “warning signs” which predict changed circumstances ahead. It has also been possible to restrict the speed of approach towards a hazard to increase the probability that they are detected. Unfortunately, neither speed restrictions nor “warnings” are possible with wild birds.

When using level powered flight under calm conditions each bird species flies within a relatively narrow range of speeds and cannot fly either faster or slower (Biewener 2003). Also, it is not possible to train free-living wild birds the salience of stimuli so that they may become “warnings”. There are few options with wild birds other than to increase the probability that a flight hazard will be detected (Martin 2011; Martin 2021). Furthermore, detection must be achieved early enough to allow an approaching bird to change its flight trajectory before time-to-contact. Birds are not going to slow down to obtain more information, as a prudent driver would. In designing collision mitigations that enhance the probability of detecting a hazard, it is also necessary to take account of the visual capacities of birds, and not to simply design something that would be conspicuous to a human observer.

6. Vision in bird species that are vulnerable to collisions with marine wind turbines

The Appendix describes fundamental properties of vision, and its interspecific diversity, among bird species. Table 1 lists bird species ranked according to their population vulnerability to collisions with wind turbines. It is legitimate to ask whether knowledge of their vision can inform the design of mitigations that will increase their ability to detect turbines early enough to reduce the probability of a collision.

6.1 Diversity in the vision of birds

Vision is a multifaceted sense and bird species differ markedly in their spatial resolution (Appendix section 8), their sensitivity to visual contrast (Appendix section 9), their speed of vision (Appendix section 10), and the topography of their vision (Appendix sections 6 and 7). The latter describes the directions about the head in which a bird is best equipped to

extract particular information from the world about them. These four aspects of vision are all likely to contribute to the collision vulnerability of a species (Martin 2021).

The 38 marine bird species ranked by their vulnerability to wind turbine collisions (Table 1) are taxonomically diverse and includes species from seven avian orders: Anseriformes (ducks and geese), Podicipediformes (grebes), Charadriiformes (gulls and auks), Suliformes (gannets and cormorants), Gaviiformes (divers/loons), Procellariiformes (shearwaters, petrels, and storm petrels), and Accipitriformes (eagles). Half of these collision vulnerable species are from the order Charadriiformes (18 species), and they are also considered to be the most vulnerable, being placed in the top half of the rankings of vulnerability. The top three most vulnerable species are from the same charadriiform family, the Laridae (gulls). Two notable non-Charadriiform species that are placed high in the vulnerability ranking are white-tailed eagle (Accipitriformes) and northern gannet (Suliformes). Unfortunately, few details about the vision of any of the species listed in Table 1 are available. It is possible, however, to describe general features of bird vision which contribute to collision vulnerability, and these can inform the design features of a mitigation that should have wide applicability.

6.2 Limitations on the gain of visual information in flight

In all bird species the direction of highest spatial resolution does not project directly ahead, in the direction of flight. The direction of highest resolution within the visual field projects forwards but laterally either side of the head (Appendix sections 7 and 8, Appendix Figure 6). Spatial resolution forwards is likely to be lower, perhaps up to an order of magnitude lower in the forward direction, compared with lateral vision. This correlates with the general rule that birds use their lateral vision to detect objects of interest, especially when foraging, and that visual control of approach to an object is passed to forward (binocular) vision relatively late when the object is close (Martin 2009; Martin 2017b). Forward vision is used for the control of flight towards a target to which the bird is heading, especially the determination of time-to-contact, the target. This is achieved using relatively low spatial resolution vision which is more sensitive to detecting the optic flow pattern of images across the retina within the forward field of view (Appendix section 8). The important implication of this is that in birds' frontal vision is not concerned primarily with the detection of detail, but with the detection of movement.

This will be true even in white-tailed eagles (Table 1) whose spatial resolution is among the highest in the animal kingdom (Appendix section 8). Eagles are also particularly vulnerable to collisions because when in foraging flight they pitch their head forwards to survey the surface below. When they do so the configuration of their visual field renders them blind in the direction of travel (Appendix section 7). There is evidence that terns when foraging in flight turn their heads "sideways" in order to examine the surface below with one eye using the area of highest resolution (Land 1999). This may be a common strategy employed in the foraging in all the gull and tern species listed in Table 1. It is also likely to apply in northern gannets when searching for prey on or just below the water surface. Whether this head turning abolishes forward vision in these birds, as it does in eagles, is not clear. Certainly, gulls have more extensive visual fields than eagles (Cantlay, personal communication) and they may retain some forward vision regardless of

head position. However, the forward projection of the binocular field, used to determine direction towards and time-to-contact a target, will be much reduced.

Other visual factors are also likely to increase collision vulnerability in all the marine species. Most significant are: 1. The comparatively lower spatial resolution of these species (except for the eagle) (Appendix section 8, Appendix Table 1), 2. The decrease in spatial resolution with ambient light level (Appendix section 8), 3. The comparatively low flicker fusion frequency that is likely to be found in these species (Appendix section 10), and 4. The comparatively low contrast sensitivity of bird vision (Appendix section 9).

All these factors are likely to be especially important in species which choose to fly at lower light levels, especially at light levels that occur at twilight and into night-time. Combined, these factors are likely to result in only low-level spatial information being available to many marine birds when flying above the sea surface under a range of natural environmental conditions. Hence, compared with what might be supposed to be available to guide flight in terrestrial environments at high light levels, these marine birds may be considered to have only partial information (gross spatial cues) to guide their flight under many conditions. However, as described in section 4.1, there is good evidence that birds do conduct complex tasks guided only by incomplete information, responding to relatively gross spatial cues.

7. General vision factors to be considered in the design of collision mitigation measures

Considering the above discussion, a vision-based intervention that can mitigate the general collision vulnerability of flying birds must take account of the following considerations.

- Birds may be traveling under non-optimal conditions for the acquisition of visual information.
- Some species may fly while primarily gaining information from the surface below (searching for food items and conspecifics) and acquiring only intermittent information about what lies ahead.
- Birds flying at low light levels, and in reduced visibility conditions (which decrease the contrast in the scene), will be able to extract information based upon only low spatial resolution of the scene.
- Under all visibility conditions, birds using powered flight are likely to fly at their characteristic optimal flight cruising speed, and are unlikely to reduce speed, even in the presence of a hazard.
- Even under conditions of high light levels and high visibility, the detection of high spatial detail is likely to be available only in a bird's lateral fields of vision.

- Forward vision used in the control of flight (direction of travel and time to contact a target), primarily extracts information from the optical flow patterns that are based upon relatively gross spatial details (Bhagavatula et al. 2011; Lee 1980; Lee and Reddish 1981).

8. Requirements of vision-based collision mitigation measures

The ideal requirements of a collision mitigation measure based upon vision are:

- The mitigation needs to be made as conspicuous as possible to an approaching bird.
- The mitigation must be effective under a wide range of light levels from bright sunlight to night-time (a change in ambient illumination over a range of 1 million-fold).
- The mitigation needs to embody gross spatial information that can be detected at sufficient distance to allow course change by approaching birds. The typical range of flight air speeds of collision vulnerable marine birds (Table 1) lies between 13 and 20 m/sec [for example: herring gulls, 13.4; lesser black-backed gulls, 14.4; common eider, 19.0; great cormorant, 17.4; red-throated diver, 20.6, (Pennycuik et al. 2013) and to avoid collision the target should ideally be detected at no later than 10 seconds (130 - 200 m distance) before potential impact. This should allow a bird to change course and fly across the span of the rotating blades (≥ 100 m) to avoid collision. Perhaps, at a minimum, the turbine should be detectable at least 30 seconds (450 – 600 m) before potential impact. Allowing this amount of time before possible collision should increase the probability of turbine detection by a bird that is approaching while scanning the surface below, and which only intermittently checks the way ahead.
- As is the case of warning signage on roads aimed at human observers, it is best to underestimate the spatial resolution of an observer rather than base it upon what can be detected under high visibility viewing conditions. A concise figure cannot be put on this, but it would be advisable to employ an assumed spatial resolution at least 10 times lower than the measured visual acuity value for a species.
- The mitigation needs to have high internal contrast. The range of background conditions against which a flight obstacle appears under natural conditions, is highly variable. This variation arises because of changes in the brightness and colour of clouds and skylight. Even at high ambient light levels clouds may vary from white to extreme black, and red colours can occur in twilight. It is important therefore to render an obstacle detectable through its own internal contrast pattern which will be present regardless of the ambient conditions, rather than trying to make the obstacle contrast with the background. This principle is embodied in the design of warning and indicating patterns used in human collision-vulnerable situations,

especially where warning is to be effective throughout the full range of natural light conditions and where they cannot be illuminated. Under these requirements a simple high contrast pattern of black and white is commonly employed. This ensures that regardless of the background the warning pattern is likely to be conspicuous.

- The mitigation should embody a degree of movement or flicker. The salience of high contrast flickering patterns is readily appreciated in everyday term in humans when a waving flag is more readily detected than a static one. There is good evidence from physiological investigations of vertebrate vision that flickering single lights, high contrast oscillating patterns of gratings or chequerboards, and high contrast patterns with rotating elements, produce high amplitude physiological responses, measured directly from the eye (Electroretinograms, ERG) (Ghim and Hodos 2006; Hodos et al. 2002). This has been demonstrated in the eyes of different bird species, most notably rock doves *Columba livia* and American kestrels *Falco sparverius*, using rotating high contrast (black and white) patterns (Hodos 2003).

9. Application of vision-based mitigation to wind-turbines

The application of the above ideal requirements for collision mitigation measures to wind turbines is relatively straightforward. A particular advantage of making wind turbines conspicuous under a range of light levels and ambient conditions is that they are intrinsically large and can therefore embody large, repeated elements of a high contrast pattern. However, turbines do not present a continuous surface, they are structurally complex, and blades can move at high speed. These two features, however, have the advantage that a high contrast pattern on a moving surface is likely to increase its conspicuousness since it will be rendered as a flickering stimulus.

This approach has already been trialled under field conditions (May et al. 2020). That work built upon the laboratory based physiological investigations using electroretinograms of Hodos (2003). The May et al (2020) field trial involved a single wind turbine with one black and two white rotor blades and a white pylon, at a land based wind farm site in Norway. At this site bird-turbine collisions had been monitored over an extended period. Introducing contrast into the turbine by painting a single blade black, was shown to be effective in significantly reducing bird-turbine collisions, with white-tailed eagles the main beneficiaries at this site. These eagles are vulnerable to collisions because of their visual field configuration which reduces their ability to see ahead while foraging (Appendix section 7 and section 4.2 above), but it is also important to note that they have high spatial resolution (Appendix section 8).

9.1 Blade and pylon contrast patterns

Clearly, there would seem to be a case for employing the approach trialled by May et al (2020). However, white-tailed eagles are long-lived and establish home ranges and are

thus able to build knowledge of turbine distributions in their local area. Furthermore, they are diurnally active and rarely fly under poor visibility conditions. This contrasts with the more collision-vulnerable marine species (Table 1). They have lower spatial resolution than eagles (Appendix section 8, Table 1). They are not likely to be resident with the area of a wind farm, usually passing through on migration or travelling to foraging areas. These birds also regularly fly at low light levels, including night-time, and under conditions of poor visibility (Furness et al 2013) which further reduces the spatial information that they have available to them. This means that the May et al (2020) findings may not generalise well to the majority of vulnerable marine species. Therefore, the simple intervention of painting a single blade black (as used in the May et al trial) should be improved upon to maximise the conspicuousness of turbines to all marine birds under a wide range of visibility conditions. This can be achieved by introducing more elaborate contrast patterns and taking advantage of blade movement.

9.2 Contrast and Colour

It is not advisable to use colour to generate the contrast pattern. While colour may appear attractive or salient to human observers, colour is detectable only at higher (daytime) light levels (Appendix section 6.1). In addition, spatial resolution to chromatic patterns is always lower than to achromatic patterns (Appendix section 8). This means that even under high light levels a chromatic pattern will become detectable at a closer distance than the same pattern rendered achromatically. At low light levels (twilight and lower) a chromatic pattern is perceived in shades of grey. Therefore, although a chromatic pattern may have high detectability at daytime light levels, detectability is much reduced as light levels fall. An achromatic pattern will have higher detectability throughout the full range of naturally occurring light levels. This applies to the vision of all vertebrates and so it is always advisable to use achromatic patterns to enhance detectability if there is concern that collision prone animals are active at lower light levels. This will be especially important to many of the collision susceptible marine bird species listed in Table 1.

9.3 Spectral reflection and spectral absorption of surfaces

The contrast of achromatic (black and white) patterns can be enhanced by careful choice of surfaces with respect to their reflection and absorption within the spectrum. Gulls and terns are one of the few taxa of non-passerine birds which have vision that extends into the UV portion of the electromagnetic spectrum; their spectral sensitivity extends from about 300 – 700 nm (Appendix section 6.1). All other species listed in Table 1 have a spectral range of approximately 400 – 700 nm (similar to the human visible spectrum). To gain maximum contrast in achromatic patterns, black sections should be highly absorbing, and white should be highly reflective, across the full spectrum of incident light. Given that nearly half of the collision vulnerable species of Table 1, have spectral sensitivity that extends from 300 – 700 nm, it is advisable to ensure that an achromatic pattern absorbs and reflects across this full spectral range. This will ensure that contrast is always maximised regardless of the spectral distribution of the ambient light. It is worth noting that sun and moonlight (reflected sunlight) have an almost flat spectrum from below 300 nm to above 750 nm.

9.4 The contrast pattern for use on wind turbines

To enhance contrast across each blade and across the full area swept by the blades, each blade (both surfaces) should be divided into thirds with two of the blades showing black tips, a white middle section and a black section close to the nacelle. The other blade should be the reverse of this pattern (Figure 1). The pylon supporting the turbines should be in alternating bands of black and white with the length of each section equal to half that of the blade pattern sections. Bands on the pylon should be vertically aligned with the lengths of the contrasting bands on the blades (Figure 1). The black and white bands on the pylon should extend down to at least the level of the blade sweep. All turbines within an array should have these patterns. This is to increase the probability that a bird which deflected from its flight path when it detects the pattern on one turbine, will detect adjacent turbines, rather than collide with them.



Figure 1: Illustration of high contrast blade markings. Left: diagrammatic indication of high contrast blade and pylon markings. Right: impression of markings applied to a turbine. Blades are divided into equal length black or white sections each one third the length of blade. The pylon is divided into equal length black or white sections each one half the length of the blade sections. N.B. Any final design or prototype would need to be compliant with regulations applying to marine structures, e.g., potentially painting the tips of individual blades red in accordance with Civil Aviation Authority, CAA guidance. Source: G R Martin, 2022. © 2022, G R Martin.

9.5 Rationale of contrast patterns

The recommended patterns (Figure 1) are designed to meet the requirements of collision mitigation measures set out in Section 8 above. The general rationale for the

recommendations is to provide a simple enhancement of current structures which requires no engineering modifications. Changing the colour of the surfaces of wind turbines is unlikely to change the efficacy of their operation.

The principal aim is to make the whole turbine more visible by enhancing its internal pattern of contrast rather than by attempting to enhance the contrast of the structure against its background. The addition of these achromatic contrast patterns should increase the probability of detection of a wind turbine, especially the rotating blades, in a wide range of bird species, and under a wide range of environmental (light and visibility) conditions. The recommended pattern is not designed to be particularly visible to any one species or taxon of the collision vulnerable birds listed in Table 1. Rather, the recommended pattern is a solution which should increase the detectability of turbines to all birds in this collision vulnerable cohort irrespective of the conditions under which they choose to fly. The recommendation is based upon known fundamental properties of avian vision, rather than drawing on specific knowledge of any one collision vulnerable species. It should, therefore, also be applicable to other marine or terrestrial situations involving different cohorts of bird species.

Dividing a blade into thirds lengthways and making it alternately black and white, should serve to increase the probability that there is a flickering contrast pattern set up between the sections of the rotating blades, and between the blades and the pylon. Even though the extremities of the blade may not be visible at high rotation speeds due to the birds' relatively low rates of flicker fusion (Appendix section 10), a flickering pattern generated by the blade sections close to the fulcrum should still be detectable.

The dimensions of the individual elements in the contrast patterns along the blade and on the pylon, should render the patterns detectable at sufficient distance for a bird to change its flight path early enough to avoid collision under a wide range of viewing conditions. For example, it can be assumed that acuity among the collision vulnerable birds is approximately 3 minutes of arc (Appendix section 8, Table 1). To allow for lower light levels and poor visibility under field conditions the effective acuity could be 10 times lower than this. With such acuity (30 minutes of arc) an object or pattern element larger than 8.7 m would be detectable at a viewing distance of 1000 m. This requirement would be met easily within the blade length and pylon heights of current marine wind turbines (e.g., blade lengths ≥ 60 m). A 1000 m detection distance also means that the time between detection and possible collision should be greater than 30 seconds for birds that are approaching within the typical power flight speed range of 13 – 20 m/sec (section 8.3 above).

10. Collision avoidance versus disturbance

The focus of these recommendations is to reduce effects of wind farms on individual birds through collision impacts with turbines (Table 1). However, Furness et al 2013 also considered indirect effects of wind farms through disturbance and/or displacement from key habitats (Table 2). These indirect effects are difficult to observe and quantify but they are presumably the result of birds detecting wind farms and seeking to avoid their general

area. Making individual turbines more readily detectable by collision vulnerable species may therefore have the effect of increasing the disturbance effect on other species which frequent the same area. Reconciling these two effects may only be possible by the careful siting of wind turbine arrays to minimise possible disturbance to those species which are most vulnerable to it. Trials should include monitoring of displacement to understand the degree to which displacement-vulnerable birds respond to the presence of turbines with marked blades.

11. Conclusion

The recommended achromatic patterns applied to the blades and pylons of wind turbines (Figure 1) are a practical and simple solution to enhance the detectability of turbines at sea for a range of bird species which differ in their taxonomy, ecology, behaviour, and visual capabilities. They should serve to enhance the detection of wind turbines under a wide range of natural conditions in which birds choose to fly at sea. The achromatic patterns can be implemented at the production stage of turbines; they would be difficult to retro fit. With the use of suitable surface coatings these patterns should be maintenance free, unlikely to diminish in their efficacy as bird collision mitigation measures, and unlikely to reduce the generation efficiency of wind turbines.

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Appendix: The vision of birds; an overview

1. Introduction

The primary reliance of birds on vision is readily and frequently asserted. Casual observations of birds completing their everyday behaviours is sufficient to convince most observers that birds are using vision to control their key behaviours. This assertion is supported by evidence that in most bird species relatively large portions of their brains are devoted to the analysis of information from vision (Reiner et al. 2005). Also, the so-called intelligent behaviours of birds seem to be based primarily upon visual information (Emery 2006). Thus, gaining information from vision and using it to guide sophisticated behaviours, seems to be the essential function of the brains of most birds.

Only in a handful of extant bird species does vision appear not to be the primary sense. The prime examples of “non-visual” birds are the five species of flightless kiwi (Apterygidae), whose vision seems to have regressed as they evolved in the absence of mammalian predators (Martin et al. 2007). In some bird species these senses play a complementary role to vision. This is found among some species of seabirds, petrels (Procellariidae), shorebirds (Scolopacidae), and owls (Strigidae), in which olfaction, touch, and hearing, respectively, play a key role in finding food items (Martin 2017a). Even in these birds, vision is probably the primary guide for flight. However, as more has been learnt about the sensory ecology of birds, it seems that controlling flight may not be the prime driver of their vision (Martin 2017b).

The key driver of bird senses is now best regarded as stemming from the demands of foraging, that is the detection, acquisition, screening, and ingestion of food items, with vision being driven primarily by the demands of detection and acquisition. The second key driver that has shaped bird vision is the detection of predators. However, the visual tasks of foraging and predator detection can make antagonist demands for information and these demands can be seen played out in the eyes of most birds (Martin 2014). The informational demands for controlling flight can perhaps best be considered as met within the requirements set by the primary sensory challenges of foraging and predator detection.

It has been argued that the essence of birds is best encapsulated in the phrase “a bird is a bill guided by an eye” (Martin 2017b). This is to be juxtaposed with the older phrase which depicted a bird as “a wing guided by an eye”. The change of emphasis from “wing” to “bill” as the prime focus of adaptations of avian vision reflects the idea that bird vision is primarily adapted to the control of the bill as the prime tool with which a bird interacts intimately with its environment. In most species, survival depends upon bringing the bill time and time again to “the right place at the right time”. (Note: for some species, particularly the birds of prey, it might be better to suggest that they are primarily “feet guided by an eye”. This is because it is the feet that do the crucial act of prey acquisition

and so must be positioned accurately in space and time, although even these birds also need to place their bills accurately when manipulating items.)

This change in the short-hand way of describing birds is important because it changes how we might think about birds in an everyday sense. It indicates that the main task of a bird, day-in-day-out is getting its bill (or feet) to the right-place at the right-time, over-and-over again. There is no value in having a tool (bill or feet) that cannot be effectively controlled. Making a sensory based error when flying may be important, but it is not as important as being unable to explore the environment at close range and use the bill to acquire food.

2. What vision does

The essence of vision is simple; it is the determination of the direction from which light has travelled to reach the observer (Land and Nilsson 2012). All aspects of vision, including colour vision, are elaborations and refinements of this basic ability.

Vision in some modern birds is arguably at the pinnacle of eye performance. In some bird species spatial resolution (the ability to differentiate between light arriving at the eye from different directions) is close to the very limits of what is theoretically possible for a vertebrate eye (Land and Nilsson 2012). The highest known spatial resolution (the ability to detect the finest detail) of any animal has been recorded in eagles and vultures (Fischer 1969; Reymond 1985). In these birds resolution reaches close to the limits set by the physical properties of light. However, spatial resolution in most birds is well below this upper limit.

Colour vision enables many birds to differentiate between lights of very similar wavelengths, perhaps giving some species the highest levels of spectral resolution among vertebrates (Wright 1972; Wright 1979). However, even with high spectral resolution the ability to resolve spatial detail using coloured light is below that of spatial resolution involving achromatic patterns (Potier et al. 2018).

Many birds, perhaps the majority of species, achieve spectral resolution across a broad light spectrum, from ultraviolet to far red (Cuthill et al. 2000). However, it should be noted that contrary to popular belief, birds are not exceptional in this, the same broad spectral range of vision is found in many mammals (Douglas and Geffery 2014) and invertebrates (Cronin 2008). Furthermore, vision in the ultraviolet region of the spectrum, is not a property of vision in all birds. The majority of non-passerine species cannot be considered as truly ultraviolet sensitive in that they do not have a retinal photoreceptor that is maximally sensitive in that region (Odeen and Hastad 2013), and in some birds (notably diurnal birds of prey with high spatial resolution) ultraviolet light is filtered out by the lens and cornea and does not reach the retina (Lind et al. 2013; Lind et al. 2014).

The vision of birds can also function within the full range of naturally occurring light levels, a range of 100 million-fold. This allows birds to use visual information in both bright

daylight and in low light level environments, for example, in nocturnal forests and deep-water habitats (Martin 2017a). However, high spatial resolution is achieved only at high light levels, as light levels fall spatial resolution decreases significantly.

A notable feature of the vision of most birds is that they can extract spatial information simultaneously across a wide sector of space about the bird. Most bird eyes have an extensive visual field and because there are always two eyes in the skull, the total visual field is typically very extensive. In some species eye placement and visual fields combine to give complete panoramic vision without blind areas above and behind the head (Martin 2014). However, spatial resolution varies markedly across the field of view and highest performance is usually lateral in the bird's field of view, rather than forwards in the direction of travel.

3. Variations in avian vision

While examples of outstanding visual performance are fascinating and often remarked upon, general descriptions of visual performance in birds must be couched with uncertainty. Qualifications of “most” or “some” when describing the visual performance of bird species are essential. It is not possible to talk about “avian vision” in a unified way, there is much variation between species (Martin 2017a). Differences in visual performance apply especially with respect to resolution, visual fields, and absolute sensitivity.

The ability of eyes to extract accurate and precise information from the world are not without cost. Eyes, and the processing of information by the visual system, are metabolically expensive (Laughlin 2001) and the eyes of no one species can do everything (Land and Nilsson 2012). Like all evolved structures there are compromises and trade-offs and these may be dictated by both physics and biology. For example, it is well understood that the nature of light itself means that adaptations of eye structures that can achieve high resolution run counter to adaptations that enhance high sensitivity (the ability to detect objects at low light levels) (Land and Nilsson 2012).

It is these metabolic and physical limitations that have led to the specialisations of eyes across species. Much of the fascination of avian vision lies in understanding these specialisations. They are perhaps best understood as the result of natural selection for eyes that can extract information which is finely tuned to the sensory challenges presented by the execution of particular tasks in particular environments. Regarding the evolution of eyes as being “task-led” (Nilsson 2009), has provided a valuable explanatory framework with which to account for the diversity of bird eyes found today (Martin 2017a).

Attempting to understand what those tasks are for different species is a valuable way for understanding their vision. All bird eyes are based upon the same basic anatomy and physiology. Variations in visual performance between species are derived from relatively simple differences in structure. These include differences in absolute eye size, differences in optical performance, and differences in the relative numbers and distributions of

photoreceptor types across the retina. These differences can be large but even subtle variations are functionally significant and can be interpreted as specialisations for the extraction of particular information related to the conduct of particular tasks, in particular light environments. However, identifying those tasks and the key environments can be problematic.

4. Bird eyes: Function, structure, and variations

Precise and accurate spatial resolution is achieved in vertebrate eyes through two anatomically linked but functionally separate systems. The *optical system* receives light and creates an image of the world. This image is projected onto a surface, the retina, which is the *image analysis system*. It is here that analysis of the image begins, and information is extracted and sent to the brain for further processing (Figure 2).

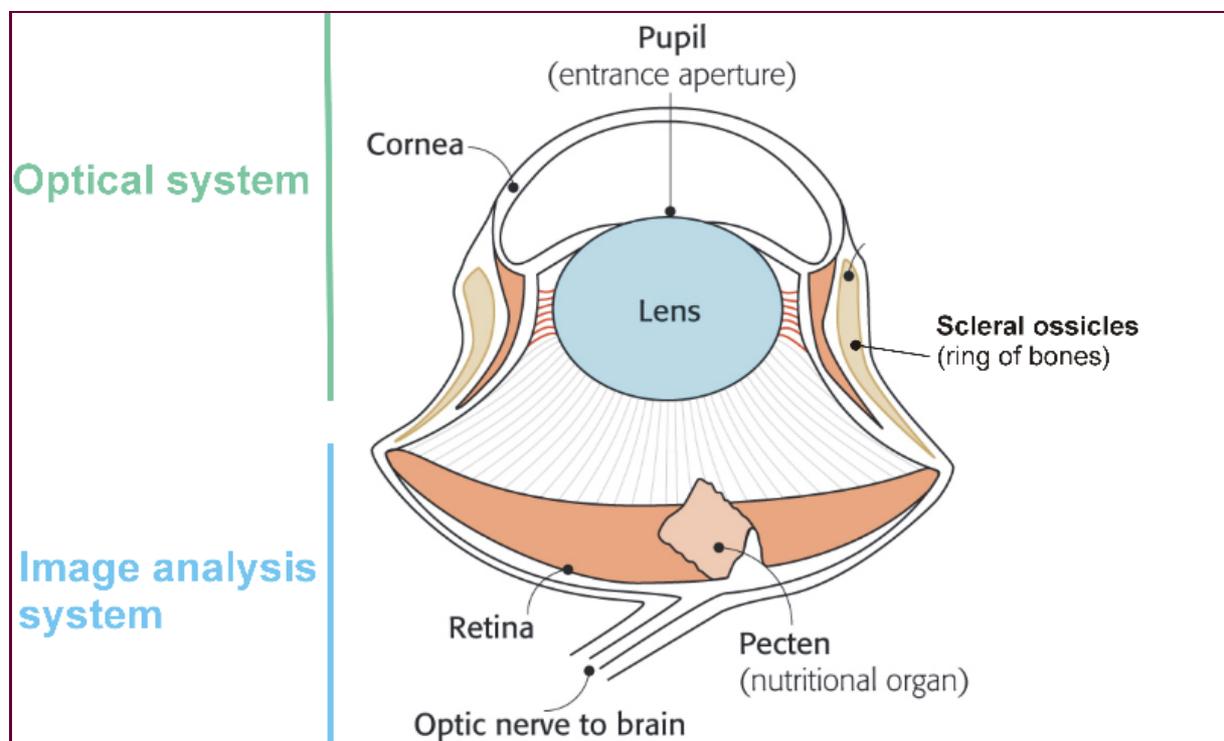


Figure 2: The two main functional systems of a bird's eye illustrated by a sectional diagram of the eye of an owl. The optical system has two components: cornea and the lens. These produce a focused image projected onto the retina which is where the first stage of image analysis begins, and from where information is sent via the optic nerve to the brain. In different eyes the lens and cornea can have different optical properties depending upon their shape and size. These produce images with different properties (size, brightness, contrast) in different eyes. The image analysis system in different species exhibit large variations in the way photoreceptors and ganglion cells are arrayed across the retina, influencing markedly the way that images in different eyes are analysed. Source: Nigel Hawtin, 2019. © 2019, Nigel Hawtin. Reproduced with permission.

Although the two main functional systems of an eye are physically linked, they are subject to independent evolution. Even if the eyes of two different species have similar optical

systems, they may analyse their images in different ways. Similarly, eyes which have the same overall dimensions can have different optical systems which present different images for analysis by their retinas. It seems unlikely that the eyes of any two species are exactly the same. This means that birds of two different species sitting or flying side-by-side will extract different visual information from the environment which they share.

The visual information extracted from the environment by different species can also differ markedly because eyes never occur singly, they are always paired. Although bird eyes are arranged symmetrically in the skull with respect to its median sagittal plane, their positions can differ markedly between species. These differences in eye positions can result in significant differences in the visual fields of birds (Martin 2014). These are the regions of space about the head from which visual information can be retrieved at any one instant. It includes the degree to which there is overlap between the fields of each eye, the binocular field. Differences in visual field configurations have important implications for what information is made available at any one instant and therefore how vision can influence a bird's behaviour.

5. Variation in the optical systems of bird eyes

The relative amount of focusing contributed by the lens and the cornea in forming the image upon the retina can differ quite significantly in different eyes. This is clearly seen when comparing the optical systems of eyes of the same overall size. A good example is provided by comparison of the eyes of rock doves *Columba livia* and Manx shearwaters *Puffinus puffinus* (Figure 3). Although these eyes have the same axial lengths (≈ 12 mm), the curvature of their corneas, and the curvatures of their lens surfaces, differ. Although these are relatively small differences, they result in important differences in the image properties in these two eyes. In shearwaters the shorter focal length of the optical system results in a smaller but brighter image compared with doves (Martin and Brooke 1991). These differences can be interpreted by reference to the frequent night-time activities of shearwaters whereas doves usually go to roost at twilight. The narrower visual field width of shearwater eyes (Figure 3) is a consequence of the shorter focal length of their optics and reduces the space around the head from which shearwaters can gain information, compared with doves.

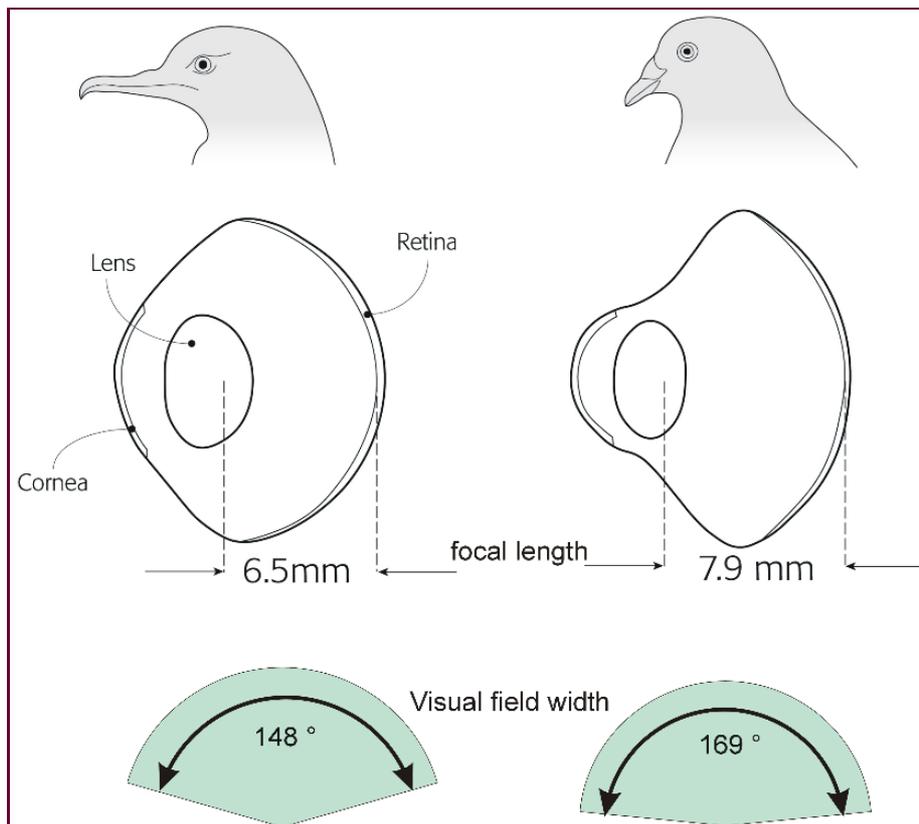


Figure 3: Diagrams of sections through the eyes of Manx shearwaters and rock doves. The eyes of these birds are of the same overall size (both in length and diameter), but their corneas and lenses have quite different characteristics. The result of these differences is that the images produced by them have quite different properties. The image is smaller in shearwaters (indicated by a shorter focal length) and brighter. Also, the visual field of a shearwater's eye is significantly narrower than in a dove. Source: Martin, 2021. © 2021, G R Martin & Pelagic Press. Reproduced with permission of the publisher.

Vertebrate eyes can also vary greatly in size. As in any optical system, absolute size inevitably determines the size of the image that it produces, and a larger sized image of a given scene can contain more detailed spatial information than a smaller image. Furthermore, a large entrance pupil determines the upper limit on the quality of the image, with respect to how sharp the focus of the image can be. This is driven by the wave nature of light and to achieve the sharpest focus requires an absolutely large entrance aperture (Land 1981; Shlaer 1972). However, absolute size also determines the maximum amount of light that can be gathered and hence the brightness of the image, and this is especially important when viewing small discrete sources of light in a scene (Land 1981). A consequence of this is that eyes which have evolved for high sensitivity rather than high resolution also have absolutely large eyes, as is the case in some owl species. Some species of albatross have large eyes, but it is not clear whether their size can be considered as an adaptation for high resolution or sensitivity (Martin 1998). For example, the large size of ostrich eyes is not associated with high resolution and is probably an adaptation associated with vision at low light levels (Boire et al. 2001; Martin et al. 2001) and this may be the case in albatrosses.

6. Variation in the image analysis systems (retinas) of bird eyes

Image analysis in vertebrate eyes begins with the detection of light by the photoreceptors of the retina. These are the familiar rods and cones which are found in all vertebrate eyes. Each photoreceptor signals the absorption of light photons by the photopigment molecules in their outer segment. These signals are collated by ganglion cells which in turn send a signal along the optic nerve to the brain where they are integrated with signals from the many millions of photoreceptors which are distributed across the retina.

Although there is little variation in the suite of photoreceptor types found in the retinas of different bird species, there are known to be very marked differences in the relative abundance of receptor types, and particularly in their distributions, within the retinas of different species (Hart et al. 1998; Hart et al. 2000a; Hart 2001; Hart 2004). The result of this is twofold. First, in any eye, the image projected onto the retina is not analysed in a uniform way across the whole of its area. Second, there can be very marked differences in patterns of analysis between eyes of different species. The result is that an image of the same scene in the eye of one bird species, will be subject to different analysis by the retina of another species.

6.1 Photoreceptors: Rods and Cone types

The rods of bird retinas are of similar structure, and contain a similar photopigment, to those found in the retinas of other vertebrate taxa. The cones, however, differ from those of other vertebrates in respect of both their structure and the wavelengths of light to which their photopigments are maximally sensitive (referred to as their λ_{max}).

In birds two types of cones occur, “single” and “double”, which refers to the number of outer segments (Figure 4). Double cones are not unique to birds, they are widespread in vertebrates but are absent from mammals (Bowmaker and Loew 2008; Cronin 2008; Walls 1942). Double cones contain the same photopigment in both of their outer segments. Single cones in bird retinas are usually of four types, classified according to the λ_{max} of the photopigment they contain (Cserhati et al. 1989; Hart et al. 2000a). Thus, most avian retinas contain a total of six photoreceptor types: double cones, four types of single cones, and rods (Martin and Osorio 2008) (Figure 4). By contrast most mammalian retinas, including humans, have four types of photoreceptors (three single cones, plus rods).

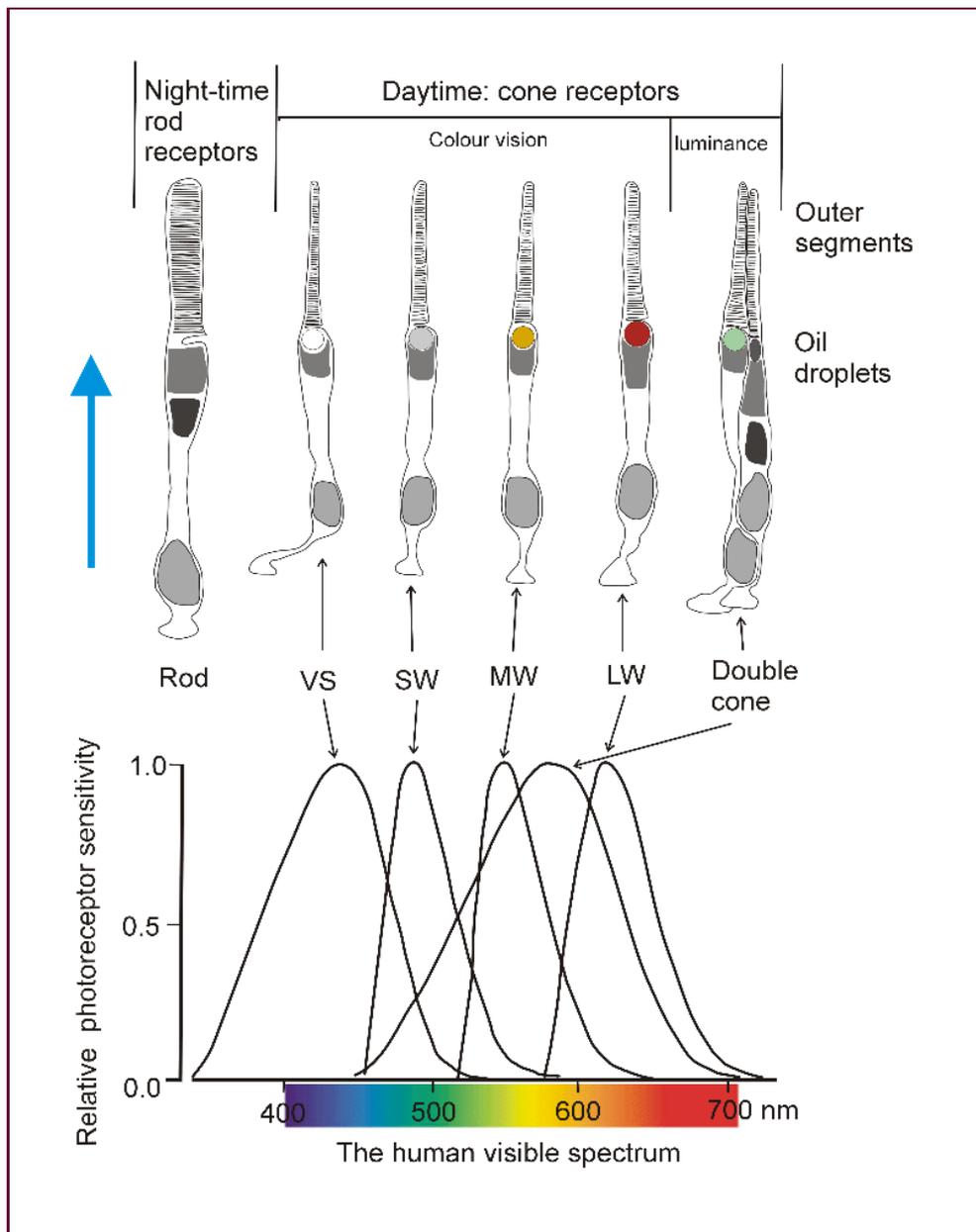


Figure 4: Photoreceptors in birds. The photoreceptors of bird retinas are of few types and are similar in all bird species. What varies between species are the relative numbers and distributions of the different receptor types across the retinas of different species. In birds, rods are of one type, but the cones are of 5 different types: 4 types of single cones and double cones. The different types of single cones are classified by reference to the position in the spectrum of the peak sensitivity of the photopigments that they contain. The top portion of the diagram depicts the types of retinal photoreceptors as they appear when viewed through a light microscope. The outer segments are extremely narrow, generally between 1 and 2 microns in diameter, but they are relatively long. Each outer segment contains many millions of photosensitive pigment molecules. The four types of single cones provide the fundamental mechanism upon which colour vision is based. The double cones provide a neural channel that is thought to signal luminance (brightness) and they are not part of the colour vision system. Within all cone types there is an oil droplet. The arrow on the left indicates the direction in which light travels from the optics of the eye to the focused image on the retina. This means that the light that makes up the retinal image must pass through the oil droplets before it enters the outer segments. Oil droplets that are coloured act as cut-off filters and allow light only above particular wavelengths to pass through to the photopigment

molecules. The combination of photopigment types and oil droplet types result in their being four main types of single cone photoreceptors in birds' retinas with each cone type able to absorb light only within a particular part of the spectrum, although there is overlap between them. The lower section of the diagram shows the resultant photoreceptor sensitivities and the labels used to describe them. These are LW (long wave) which absorb light at the orange-red end of the visible spectrum; MW (middle wave), absorbing light in the green-yellow spectral region; SW (short wave) absorbing light in the blue-green spectral region; VS (violet sensitive) which absorbs light in the violet-ultraviolet spectral region. (Redrawn from illustration provided by Peter Olsson (Lund Vision Group, Sweden, and Daniel Osorio (University of Sussex, UK).) Source: Adapted with permission from Olsson, 2004 and Osorio, 2007. Redrawn by the author, with the original two illustrations combined into a single figure with colour added.

As in other vertebrate retinas the important functional difference between rods and cones is that rods function primarily at low light levels (twilight and below), while cones function at higher light levels (twilight and above).

The types of photopigments found in bird photoreceptor outer segments show a high degree of similarity across species. This suggests that these pigment types arose early in the lineage leading to modern birds and that their properties have been highly conserved. Birds regarded as distantly related (Hackett et al. 2008; Prum et al. 2015) have been shown to have very similar photoreceptor pigments. For example, the visual pigments found in the eyes of a species of pelagic seabird (wedge-tailed shearwaters *Puffinus pacificus*, Procellariiformes) are very similar to those found in a phylogenetically distant species that is terrestrial and lives in open forest habitats (Indian peafowl *Pavo cristatus*, Galliformes;) (Hart 2002; Hart 2004; Hart and Hunt 2007). This suggests that visual pigments in birds have general properties that are not tuned to the performance of specific tasks or to differences in the types of habitats that birds exploit. However, what does differ between species is the number and distributions within the retinas of receptors containing the different photopigment types.

The five types of visual pigments of birds are labelled and characterized by their λ_{max} as follows:

RH1: rhodopsin type 1 (λ_{max} 500 nm), found in the rod receptors

RH2: rhodopsin type 2 (λ_{max} 505 nm), found in single cone receptors

SWS2: short-wave type 2 (λ_{max} 470 nm), found in single cone receptors

LWS: long wave (λ_{max} 565 nm), found in both single and double cone receptors.

SWS1: short-wave type 1. This pigment is also found in single cone receptors but occurs in two types that are found in different species. Pigments with λ_{max} at 365 nm are referred to as ultraviolet sensitive (UVS pigment); those in which λ_{max} is at 410 nm are referred to as violet sensitive (VS pigment) (Wilkie et al. 2000).

Cone receptors containing UVS pigment are found in gulls (Laridae, Charadriiformes), ostriches (Struthioniformes), parrots (Psittaciformes) and oscine passerines (but not in Corvidae) (Odeen et al. 2010; Odeen et al. 2011; Odeen and Hastad 2013). It is only these bird species which have true UV vision. Other species have the VS pigment and although their spectral sensitivity extends into the violet-near UV part of the spectrum, they lack specific UV sensitivity. It is worth noting that human retinas contain a cone pigment

(λ_{\max} in the 420 - 440 nm range) which has peak sensitivity close to that of the avian VS pigment.

The spectral sensitivity characteristics of avian cone receptors are complicated by the presence in each cone of an oil droplet (Figure 4). Each droplet sits in the proximal part of the outer-segment so that light must pass through it before it reaches the photopigment in the outer-segment (Cserhati et al. 1989). Oil droplets are also found in the photoreceptors of reptiles but are absent from most mammal species.

The droplets contain carotenoid pigments that are derived from the bird's diet. These pigments occur at a high density and give the droplets a bright colour when observed using a light microscope. They appear as reds, greens, and yellows, but colourless droplets also occur. The pigments in the oil droplets are not photosensitive they simply absorb and transmit light in different parts of the spectrum and so do not contribute directly to vision. However, because light must travel through the droplets before reaching the outer segment, they serve an important filtering function and sharpen the spectral sensitivity of the LWS, MWS, and SWS cones (Hart and Vorobyev 2005). The resultant spectral sensitivities (photopigment plus oil droplet filtering) of the different receptor types are shown in Figure 3. The peak sensitivities of the four receptor types are spaced approximately equally across the birds' visible spectrum.

Sharpening the spectral sensitivity does not occur in the double cones because their oil droplets are transparent over the wavelengths that the photopigment is sensitive to. However, these droplets do block UV light from reaching the photopigment. The oil droplets in the UV/VS cones are also transparent but they do allow UV light to reach the photopigments.

The key function of the single cone types lies in providing the foundation of colour vision; the ability to differentiate between light sources based upon their spectral composition, not just upon their brightness. There is good evidence from behavioural investigations, as well as from retinal physiology that bird colour vision should be viewed as based on the four single cone receptor types. It is therefore referred to as a tetrachromatic system, as opposed to the cone system underlying human colour vision, which is based on three cone receptor types, trichromatic vision. A range of investigative techniques (Jones and Osorio 2004; Osorio et al. 1999) have indicated that double cones are not part of the colour vision mechanism and probably constitute a separate channel that signals luminance at daytime light levels.

Because cone photoreceptors do not function at lower twilight and night-time light levels colour vision is functional during higher twilight and daytime only. At lower light levels only the rod receptors are functional and since there is only one type of rod receptor there is no basis for colour vision. Furthermore, the photopigments found in rods, the RH1 pigment, have very similar characteristics across all birds and indeed across other animal taxa. The result is that spectral sensitivity at night is likely to be very similar across all bird species, and indeed is similar across most terrestrial vertebrates, with a peak at around 500 nm.

Such similarity in spectral sensitivity, is however, not the case at higher light levels. Under these conditions spectral sensitivity is determined by the combined functioning of the cone photoreceptors. Although the sensitivity of the cone types does not vary markedly across species their relative numbers in each retina do vary. It was found possible to model overall spectral sensitivity of the eyes of rock doves based upon the relative abundance of cone photoreceptor types found across the whole of the retina (Bowmaker 1977). This produced a close match to behaviourally measured spectral sensitivity in the same species. The technique has been used to predict spectral sensitivities in other species, for example domestic turkeys *Meleagris Gallopavo*, based upon the relative abundance of their different cone types (Hart et al. 1999).

6.2 Variation in the distribution of photoreceptor types

Variations in the distributions of cone receptor types across the retina can be striking, and it seems likely that they result in differences in spectral sensitivity and probably colour vision in different parts of the visual field of a single eye, and there is some evidence to support this (Martin and Muntz 1978). A striking example of variation in the types of receptors within the retina is found in rock doves, in which a large area is dominated by receptors containing red oil droplets (LW-sensitive cones), known as the “red-field” (Galifret 1968). This area looks downward within the visual field, while receptors containing yellow oil droplets (MW-sensitive cones, the “yellow field”) predominate in areas that look laterally and upward. These different areas are obvious even to the naked eye in a trans-illuminated excised retina; there is a very clear boundary between the areas. The visual ecology and function of this striking regional specialization within dove eyes is not understood, although it has been suggested that the yellow field in some way enhances the contrast of objects seen against the blue of the sky (Lythgoe 1979). Other species show systematic differences in the distribution of cone receptor types (Galifret 1968), but there is a gradient in the relative abundance of different receptor types across the retina, rather than clearly demarked fields.

6.3 Variation in the densities of photoreceptor types and retinal ganglion cells

Variations in the relative densities of photoreceptors and ganglion cells are also very striking. These differences in the density of cells may be overlaid on patterns of cone receptor types. Very distinct patterns in ganglion cell density have been discerned with light microscopy across a diverse range of species. For example, clear patterns of ganglion cell distribution have been described in doves (Binggeli and Paule 1969), ostrich (Boire et al. 2001), waterfowl (Fernandez-Juricic et al. 2011; Lisney et al. 2013a), Procellariiform seabirds (Hayes and Brooke 1990; Mitkus et al. 2016), penguins (Coimbra et al. 2012), flamingos (Lisney et al. 2020), new world vultures (Lisney et al. 2013b), passerines (Coimbra et al. 2006; Coimbra et al. 2015), and parrots (Coimbra et al. 2014; Mitkus et al. 2014).

In all species clear patterns of photoreceptor and ganglion cell concentrations occur (Figure 5). These patterns may be roughly circular, with a very high concentration at the centre and a gradual decline of cell density away from the centre. In some species more than one region of high concentration can occur, while in others high densities of receptors may occur in a linear band that is typically arranged so that it projects approximately horizontally when the bird's head is held in its usual resting posture. The usual interpretation of these patterns is that areas of high receptor concentration are regions of heightened spatial resolution within the visual field of the eye. These regions may take the form of an elongated band that projects towards the horizon, or they may indicate a direction of elevated resolution projecting in a particular direction.

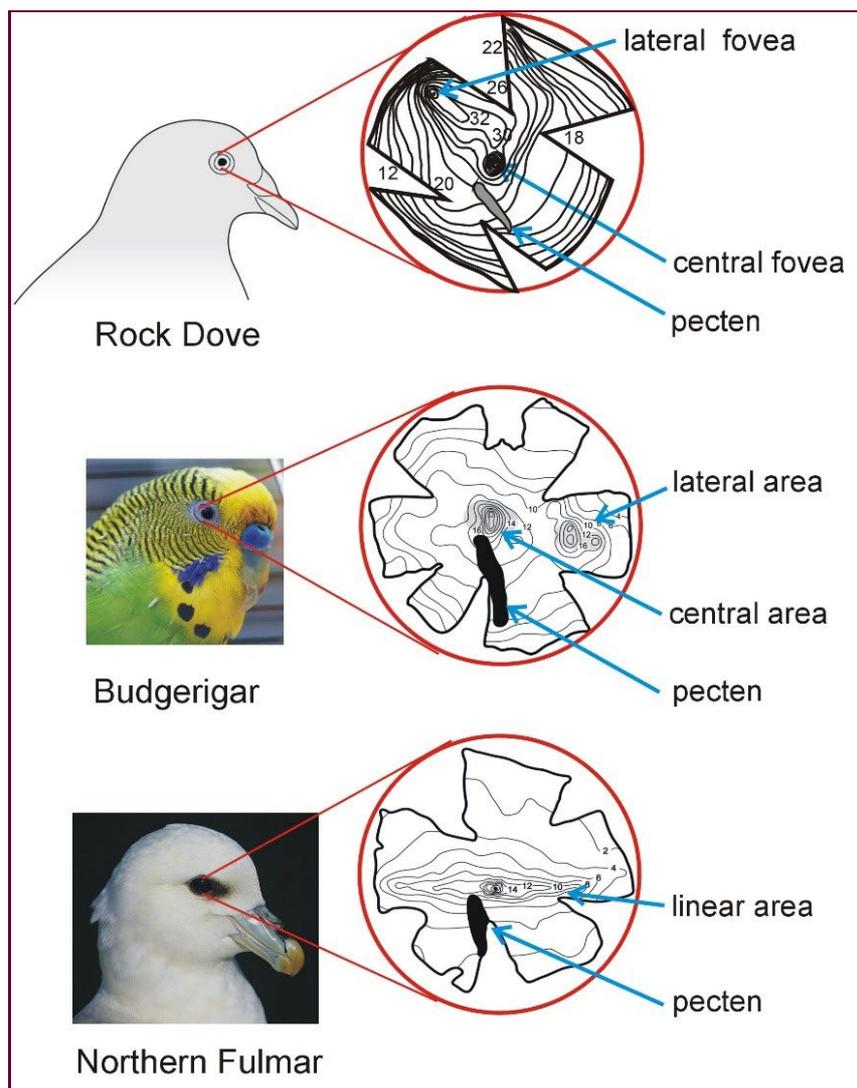


Figure 5: Patterns of ganglion cell distribution in three bird species showing some of the diversity that has been recorded. These are isodensity contour maps and numbers indicate concentrations of receptor in 1000s per mm². Source: Figure compiled by the author from several individual images/diagrams, for which the sources are as follows: Rock dove diagram – © 2019, G R Martin. Budgerigar photo - © Michael Cole, reproduced with permission. Fulmar photo – © Steve Garvie, reproduced with permission. Isodensity contour maps for rock dove – Binggeli & Paule, 1969 © 1969 The Wistar Institute Press, all rights reserved, reproduced with permission from the

publisher John Wiley and Sons. Isodensity contour maps for budgerigar and fulmar – © 2015 Mindaugus Mitkus, reproduced with permission.

Areas of the highest cell density may be associated with a fovea. This is a highly localized region in which the outer layers of the retinal cells are displaced to form a small pit or depression in the surface of the retina (Bringmann 2019) (Figure 6). Displacing the layers of the retina in this way ensures that the highest quality optical image is received directly by the photoreceptors, thus avoiding any image degradation that might be caused by passing through the layers of the retina. A number of hypotheses have been proposed concerning the function of foveas, including image magnification and image fixation mechanisms (Bringmann 2019; Potier et al. 2020b). However, strong evidential support for any of these hypotheses is lacking. Thus, beyond the general observation that displacing the retinal layers enhances spatial resolution by allowing the highest quality image to be received directly at the photoreceptors, it is not clear what the actual form of a fovea does.

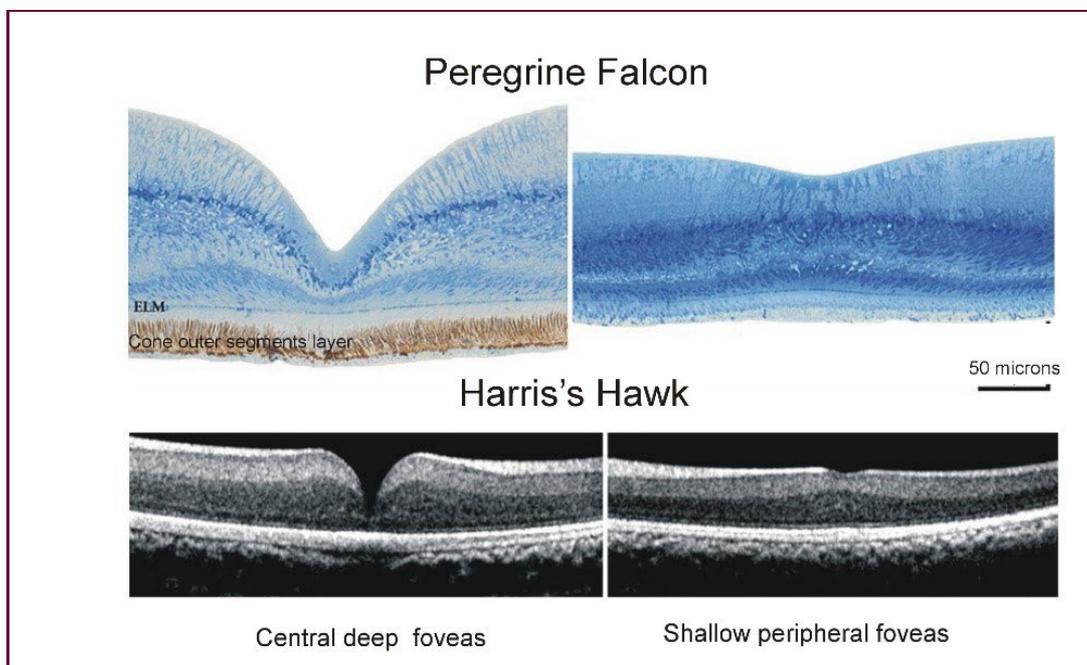


Figure 6: Sections through the retinas of a peregrine and a Harris's hawk showing foveas. In both species there are two foveas. One is placed more-or-less centrally in the retina and looks out laterally in the bird's field of view. The other is placed towards the periphery of the retina and looks more forwards, although it does not look directly forward. The central foveas are deep and have sharply curved sides; they are locations where the highest acuity occurs. The shallow foveas have lower acuity but are still locations where acuity is enhanced compared with the rest of the retina. Note that light making up the image travels from top to bottom in these diagrams and the photoreceptors are in the bottom layers in each illustration. They can be clearly seen in the picture of the peregrine's deep fovea (top left). Source: peregrine - Mindaugus Mitkus, 2015, Harris's hawk – Potier, 2016 (University of Lund Vision Group, Sweden) © 2015, Mitkus/ 2016, Potier. Reproduced with permission.

It is clear that patterns of photoreceptor and ganglion cell distribution can vary not only between species but also between individuals within a species (Mitkus et al. 2014).

Furthermore, differences in cell density and distributions between the eyes of the same individual have also been demonstrated (Hart et al. 2000b) and the shape and size of foveas have been shown to vary between individuals and probably change over an individual's lifetime (Potier et al. 2020b). Such variations provide a very rich substrate for not only interspecific, but also interindividual, differences in analysis of the retinal image. It is upon such differences that natural selection is likely to be continually acting, resulting in visual capacities which can be considered to have become tuned in different species to informational requirements for the conduct of particular tasks in particular environments.

7. The Visual Fields of Birds

Differences in optical structure affect not only the size and brightness of the image but also determine the extent of the world that is imaged (Figure 3). This is important, since it determines the extent of a bird's visual world from which it can gain information. In birds, the field of view of a single eye can be as narrow as 124° (owls) and as wide as 180° (ducks and shorebirds) (Martin 2007).

When the fields of two eyes are combined variations in the birds' total visual field are considerable (Martin 2007) (Figure 7). Thus, in a horizontal plane, the total width of the visual field in owls is about 200° , while in some shorebirds and ducks the field provides a total 360° panorama. Associated with these are marked differences in the extent of visual fields above, behind, and below the head. The axes of the two eyes may diverge by a relatively small amount (e.g., in owls, eyes diverge by about 55°), or they can be almost diametrically opposed (ducks and shorebirds). Thus, the fields of the two eyes have become combined in many ways and so provide a wide range of different total fields of view, as well as markedly different degrees by which the two eyes overlap and provide binocular coverage of part of the total field (Figure 8).

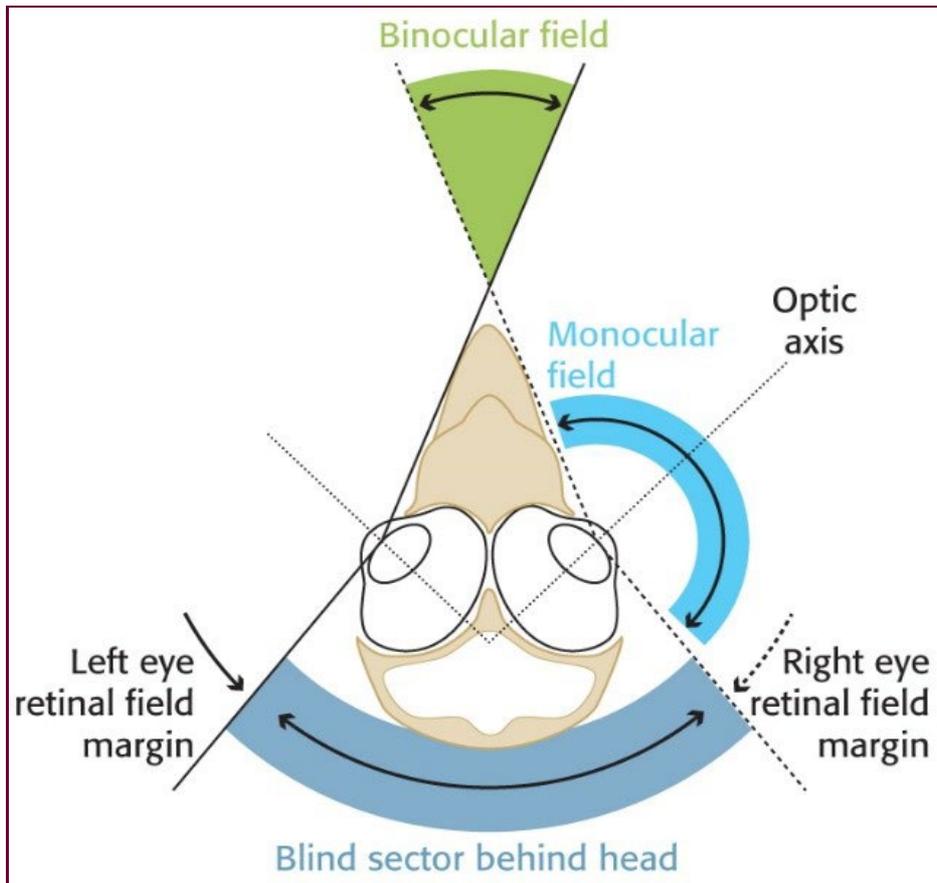


Figure 7: A diagrammatic section through the head of a bird showing a typical arrangement of eyes in the skull and how the visual fields of each eye combine. In all birds the eyes project laterally so that the axes of the eyes always diverge, no birds have forward faced eyes. The field of view of each eye are combined to give the total field of view of the birds and to give a sector in front of the head where the fields of the two eyes overlap to give a binocular field. A wide degree of variation in these basic arrangements are found in birds to give different degrees of overlap, different width blind areas behind the head (but some birds do not have a blind area behind the head). Just small variations in the width of the field of view of each eye, and of eye position in the skull, can result in large differences in visual fields between species. The optic axes indicate the directions each side of the skull in which spatial resolution is usually highest. Source: Hawtin, 2019. © 2019, Hawtin. Adapted from work by the author G R Martin, and reproduced with permission.

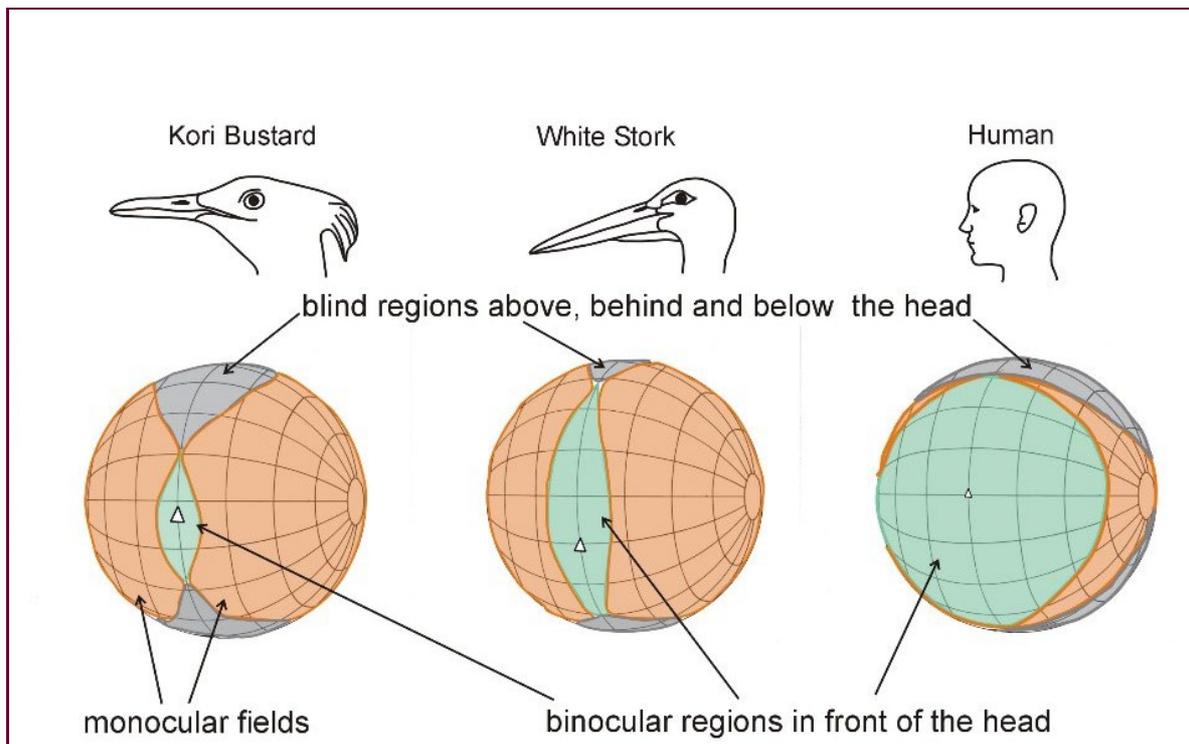


Figure 8: Depictions of the total visual fields of storks, bustards, and humans. The key features of the field are shown as projected onto the surface of a sphere surround the head. This presentation emphasises how different the visual fields of these three species are. This is despite the visual fields of their individual eyes being similar. It is clear that differences in eye position in the skull, as well as differences in the visual fields of individual eyes, can result in quite different ways in which birds can extract information from the world about their heads. Source: G R Martin, 2017 © 2017, G R Martin.

Humans are unusual animals in having two eyes placed on the front of the skull. This results in each eye seeing almost the same sector of space. This arrangement is quite different from that found in birds (Martin 2007; Martin 2012). In most species, eye position is such that each eye sees something different from what is seen by the other eye. Frontal eye placement in humans leaves us with the subjective experience that the world lies in front of us and that we move into it. For most birds, the world surrounds them, and they flow through it. Birds can extract information from a scene receding behind them while simultaneously gaining information from the world into which they are traveling.

Differences in visual field configuration can occur between closely related species suggesting that visual fields can be finely tuned to subtle differences in the perceptual challenges of different foraging tasks. For example, there are significant differences in the visual fields of different species of ibises in the same family (Threskiornithidae) that depend on whether the birds probe their bills into soft substrata or take items from dry surfaces (Martin and Portugal 2011). There are differences in the visual fields of closely related ducks which have been accounted for by whether the species feeds by selective grazing or filter feeding (Guillemain et al. 2002), and differences among sandpipers (Scolopacidae) which have been accounted for by whether the species employs tactile cues from the bill rather than visual cues when foraging (Martin and Piersma 2009; Piersma et al. 1998).

These examples indicate that the vision of different bird species, even within the same family, have been subtly tuned by natural selection primarily to the perceptual challenges of particular foraging tasks. It has been argued that such subtle tuning of visual fields should be considered as important as the fine-tuning of bill structures as a means of meeting the physical challenges posed by the exploitation of different foods in these same species (Martin 2014).

The full range of factors that are considered to play a role in the evolution of visual field configurations in birds have been discussed in some detail (Martin 2014; Martin 2017b). Data is available on visual field configurations in more than 100 species across a wide range of taxa. It is argued that visual field configurations are driven primarily by two competing informational demands posed by the tasks of foraging and predator detection. The primary demand is for the control of bill position during foraging (or in some predatory species, feet position).

The key requirement, regardless of whether a bird forages by pecking, lunging or grabbing items with their feet, is the control of direction of travel and the time to contact with a target. As such it is concerned with objects that lie relatively close to the bird, broadly within its frontal field of view. Predator detection requires the detection of objects that are relatively remote from the bird that lie in its lateral or peripheral field of view. Visual field configurations can thus be considered the result of a trade-off between those demands as they occur in different species. It is thus argued that the configuration of visual fields in birds has been driven primarily by the antagonistic informational demands of foraging and predator detection, and that the control of flight is achieved within limits set by those constraints (Martin 2017b).

8. Spatial resolution in birds

Spatial resolution in vertebrate eyes is determined by the characteristics of both the image producing and image analysing mechanisms. To achieve high resolution requires an image that is of high quality, well focused and large. This requires an optical system which has a long focal length and a large entrance pupil. Pupil size is important since it determines the limit on the quality of the image (Land and Nilsson 2012). Image size is important since it determines the number of photoreceptors/ganglion cells over which the image is spread, and hence are available to analyse the image.

The “best” estimate of an animal’s spatial resolution is gained by interrogating it, using behavioural training psychophysical techniques. These can be used to determine the limits of visual performance under a range of ambient conditions (Lind et al. 2012; Potier et al. 2016; Reymond 1985; White et al. 2007). Such investigations are difficult and laborious, but they can be substituted using data based upon eye anatomy. This provides an estimate of maximum spatial resolution of an eye but only at high light levels. It requires knowledge of the spatial separation of photoreceptors and/or ganglion cells at their maximum density within the retina. This can be combined with a measure or estimate of

the focal length of the eye's optics. The result is an estimate of the maximum resolution of an eye for high contrast stimulus patterns, at high light levels. This anatomical technique has been used to estimate acuity for more than 25 bird species and behavioural data has been gathered on an equal number of species. Some examples of acuity using behavioural and anatomical techniques are given in Table 1. A more comprehensive Table of acuity in over 50 species from 25 avian families can be found in Martin (2017a).

Table 2: Spatial resolution in a sample of bird species and in young humans. Species are arranged in order of their decreasing spatial resolution and includes 7 species (indicated by *) that might encounter wind turbines at sea (Furness et al. 2013). Resolution is shown as both cycle/degree and minutes of arc. The two measures are interchangeable; older studies tended to use acuity while more recent studies prefer to express resolution in cycles per degree. This refers to the number of cycles of alternate black and white stripes in a grating pattern used to estimate acuity. All measures refer to high, day-time light levels and indicate the best performance (finest spatial detail that can be resolved). In all species acuity will decrease with falling light levels. To compare spatial resolution between species simply divide their acuity values. Thus, the eagle's spatial resolution is about 3.5 times higher than that of a fulmar and 21 times higher than a storm petrel. Expressed another way, an eagle should be able to detect a given object 3.5 times further away than a fulmar, and 21 times further away than a storm petrel. Note that acuity of a young human is higher than all the seabirds and is bettered only by the eagle and vulture. A more comprehensive Table of acuity in over 50 species from 25 avian families can be found in Martin (2017a).

Species	Spatial resolution Cycles/degree	Acuity Minutes of arc
*Wedge-tailed eagle <i>Aquila audax</i>	142	0.2
Indian vulture <i>Gyps indicus</i>	135	0.2
Brown falcon <i>Falco berigora</i>	73	0.4
*Northern fulmar <i>Fulmarus glacialis</i>	44.7	0.7
Rock dove <i>Columba livia</i>	18	1.7
*European mallard <i>Anas platyrhynchos</i>	11.9	2.5
*Greater scaup <i>Aythya marila</i>	11.1	2.7
*Lesser scaup <i>Aythya affinis</i>	11.1	2.7
*Red-breasted merganser <i>Mergus serrator</i>	10.7	2.8
*Canada goose <i>Branta canadensis</i>	9.6	3.1
Great horned owl <i>Bubo virginianus</i>	7.5	4
*Leach's storm petrel <i>Oceanodroma leucorhoa</i>	7.1	4.2
European robin <i>Erithacus rubecula</i>	6.0	5.0
House sparrow <i>Passer domesticus</i>	4.8	6.3
House finch <i>Haemorhous mexicanus</i>	4.7	6.4
Human	72	0.4

Crucially, there have been some detailed studies which show that anatomically estimated acuity correlates well with acuity determined at daytime light levels using behavioural psychophysical tests. This was first demonstrated in eagles and falcons (Reymond 1985; Reymond 1987). It should be noted, however, that the anatomical technique cannot provide estimates of spatial resolution at lower levels of illumination, when spatial resolution inevitably decreases (Land and Nilsson 2012). Such decreases in acuity with decreasing light levels have been confirmed using behavioural techniques in a number of bird species including chickens *Gallus gallus* (Gover et al. 2009), doves (Blough 1971), wedge-tailed eagles (Reymond 1985), great horned owls *Bubo virginianus* (Fite 1973), and barn owls *Tyto alba* (Orlowski et al. 2012).

(Table 2) illustrates that maximum spatial resolution across bird species can vary over a range of at least 30-fold. The acuity of an eagle is 8 times higher than that of a dove, and 14 times that of a merganser *Mergus serrator*. Another way to compare these acuities is that an eagle should be able to detect a given object 8 times further away than a dove, and 14 times further away than a merganser.

As shown in (Table 2), acuity provides a useful metric with which to compare vision across species. It is also useful to estimate the distances at which high contrast stimuli can be detected. For example, it is possible to use acuity values to estimate the likely maximum distance at which an obstacle could be detected by a bird under high light levels. This can also be used to estimate the optimum size and positioning of a pattern designed to indicate the presence of a much smaller sized obstacle, such as a power line, that lies ahead of a bird (Martin 2011).

Extrapolations from acuity data to field situations also make it clear that the most conspicuous stimuli are likely to be high contrast (black and white) patterns, rather than coloured patterns. Although particular colours may have salience for particular species in the mediation of specific behaviours (Endler et al. 2005; Endler et al. 2014) acuity for coloured patterns have been shown to be significantly lower than for black and white patterns. This, this has been demonstrated in budgerigars *Melopsittacus undulatus* (Lind and Kelber 2011) and in Harris's hawks *Parabuteo unicinctus* (Potier et al. 2018). Given the phylogenetic distance between these species and their marked differences in ecology, lower acuity for chromatic stimuli is likely to be a feature of the vision of all bird species, probably a feature of all visual systems. It is well established in humans (Mullen 1985).

8.1 Directions of highest spatial resolution

In humans the direction of maximum spatial resolution projects directly to the front of the head, at the centre of the region of binocular overlap (Figure 7). In each eye, the direction of highest acuity coincides with the direction of the eye's optic axes; this is the direction in which image quality is highest. Similarly, in birds the direction of the optic axis of each eye is also the direction of highest image quality and in most birds highest spatial resolution occurs in the direction of the optic axes. However, as described above, and shown in (Figure 7) the optic axes of birds diverge. Furthermore, the regions of elevated

photoreceptor and ganglion cells densities typically project approximately along the optic axes (Figure 2 and Figure 5).

The result of this configuration is that within their visual fields, birds have two regions of highest acuity which project laterally on each side of the head. In birds forward vision is actually peripheral vision with respect to the optical systems (Figure 2). This means that binocular vision in birds is peripheral vision, probably served by lower quality optics than lateral vision. Furthermore, forward vision is served by regions of the retina with relatively lower photoreceptor densities (Figure 7). The upshot is that in the majority of birds forward vision has much lower spatial resolution than lateral vision. There is good evidence that raptors, which have the highest spatial resolution among birds (Table 2) use lateral vision to detect and initially latch-on to the direction of a prey item, only passing transfer of visual control of flight towards a prey item close to the point of capture (Kane and Zamani 2014; Tucker et al. 2000; Tucker 2000).

As described above, acuity measures (Table 2) refer to the highest resolution of an eye based upon behavioural techniques or on anatomical estimates based upon the retinal region in which the highest photoreceptor or ganglion cell densities occur. Therefore, acuity measures of the kind shown in Table 1 do not provide estimates of acuity in the forward direction of a bird's vision, they provide measures of acuity in the lateral field.

That forward resolution is lower than peripheral resolution may seem surprising in that forward vision provides information for the control of flight. However, it is perhaps only surprising if the control of flight (or indeed the control of bill position towards an object) is seen as a static task. In a dynamic situation, in which either the bird or the objects in the scene are moving rapidly, then movement towards them relies upon a different set of information to that used when inspecting a static scene. This information is gained from what is known as the optic flow-field (Gibson 1986), which is regarded as the foundation of perception in both vertebrates and insects (Lee 1980). Information extracted from optic flow-fields are thought to underpin important aspects of dynamic vision in most species, including invertebrates, such as bees and flies, as well as vertebrates, including birds and humans (Bhagavatula et al. 2011; Lee 1980; Srinivasan 1996). All-natural vision is in fact dynamic, caused by the motion of the observer or motion of objects within the world about, only under controlled laboratory conditions can vision be thought of as truly static. In depicting optic flow the important factors is that the images of objects within the field of view flow at different velocities across the retina, depending upon how far away they are from the observer, and where they lie within the field of view.

A key property of optic flow-fields is that when moving directly towards a target the flow-field expands symmetrically about the very point to which an observer is moving and thus the focus of the flow pattern specifies exactly where an animal is heading, that is, it specifies the direction of travel. Furthermore, the rate at which the flow-field, or the image of the world, expands across the retina specifies directly how long it will take to contact the object. There is no need to have information about how far objects are away. If they are far, then the flow-field expands slowly, if they are near it expands rapidly, but both rates of expansion predict how long it will take to reach the target.

An important implication of this is that in bird's frontal vision is not concerned primarily with the detection of detail but with the detection of movement. There is good reason to argue that high sensitivity to movement is facilitated by low resolution vision underpinned by retinal ganglion cells that sum information across relatively large sectors space. In vertebrates a group of retinal cells known as alpha cells may serve this function and indeed there is good evidence that such cells occur specifically in the binocular field (forward vision area) of Manx shearwaters and other procellariiform species (Hayes et al. 1991; Hayes and Brooke 1990). This suggest that vision in these, and probably other birds, in the forward direction is tuned to the detection of relatively large objects moving relative to the bird. High spatial resolution is in the peripheral fields and used to detect objects, while the frontal field is used to detect the relative movements of larger objects towards which the bird is heading.

In a number of birds areas of elevated spatial resolution (indicated by high density patterns of retinal ganglion cells) occur as bands across the retina; an example of this is shown in Northern Fulmars (Figure 4). Such linear areas, which may have a fovea located near their centre, are usually arranged across the retina so that they project horizontally in the field of view. The association of linear areas with their projection laterally towards the horizon has been named the terrain hypothesis (Hughes 1977). This refers to the need to detect objects that either lie in the direction of the horizon or predators that approach from that direction. As such, it is expected that a linear area will be a common feature of the retinas of birds which live in open habitats, such as seascapes and open plains, in which the horizon is ever present. This certainly seems to hold for a number of species including Procellariiform seabirds (Mitkus et al. 2015), open habitat passerines (Tyrrell et al. 2013), and Canada Geese *Branta canadensis* (Moore et al. 2012).

9. Contrast sensitivity

Although it is possible to manufacture high contrast stimuli, natural stimuli are rarely of high contrast. Most avian real-world tasks require the detection of stimuli that are of low contrast. The ability to detect stimuli of low contrast is summarized by the determination of a Contrast Sensitivity Function (Ghim and Hodos 2006). This determines the minimum amount of contrast that can be detected for stripes of different widths when they are presented as gratings of different spatial frequencies. High contrast gratings of the kind used to determine maximum acuity are one extreme of the contrast sensitivity function. To detect very fine detail, high contrast is essential, but coarser patterns can be detected at relatively low contrast (Figure 9). A full contrast sensitivity function indicates how wide stripe patterns (in a set of gratings) must be for the smallest difference in contrast to be visible across a range of grating frequencies.

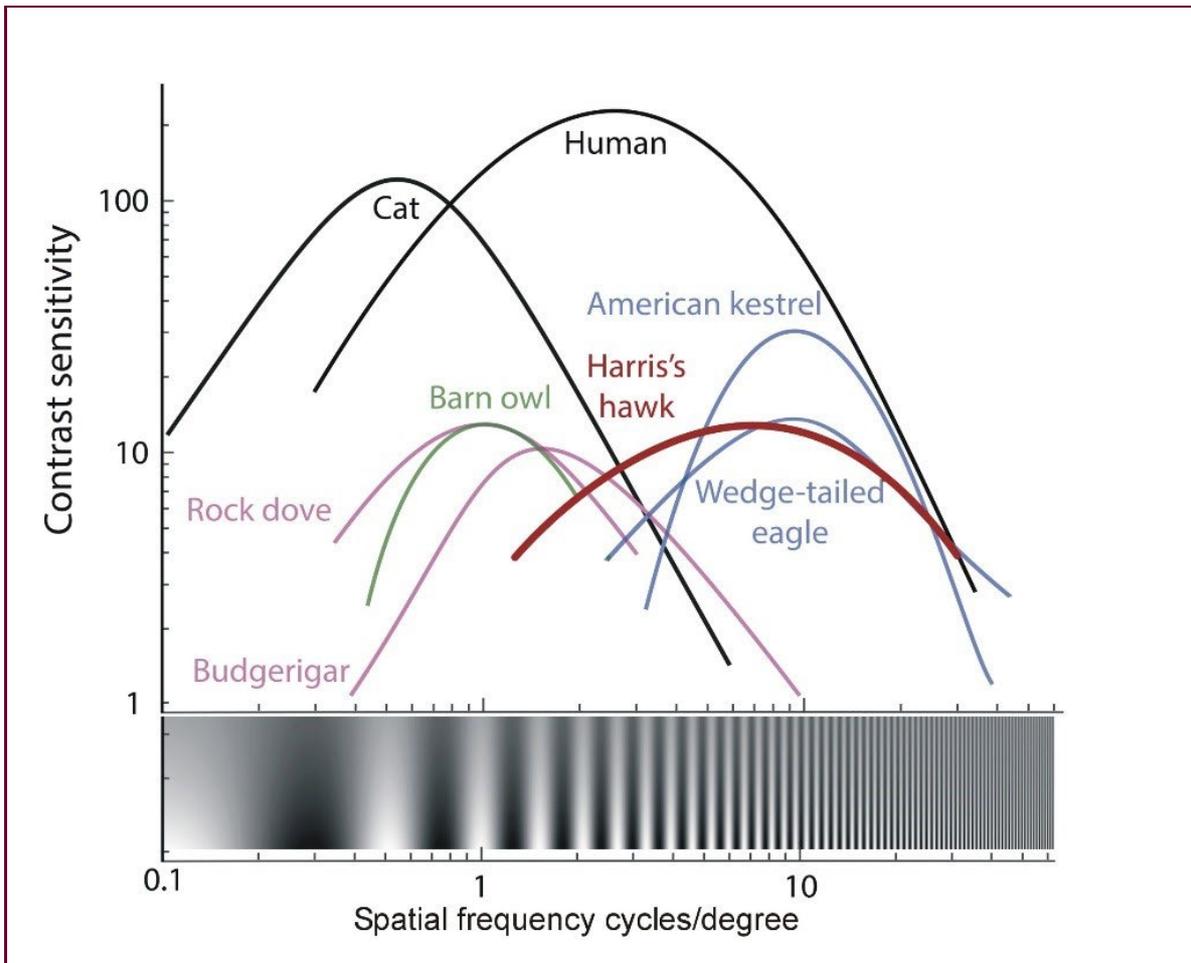


Figure 9: Contrast sensitivity functions of birds, humans, and cats. To determine these functions the animals are presented with grating patterns of different spatial frequency. At each frequency (as indicated across the lower part of the diagram) the contrast of the pattern is varied and the minimum contrast that that the bird can detect at that frequency is determined. The threshold contrast at each frequency tested is then turned into a measure of contrast sensitivity to give an average contrast sensitivity function for the species. It is clear that for each species there is a range of spatial frequencies in which sensitivity to contrast is high. However, sensitivity drops off rapidly at both higher and lower frequencies. It is clear from this diagram that bird species differ markedly in their sensitivity to contrast and that all birds are much less sensitive to contrast than humans and cats. This means that scenes have to have higher degrees of contrast for birds to be able to detect detail within them compared with ourselves. Source: Martin, 2022 © Potier and G R Martin. Adapted with permission from Potier, 2018 (elements of the diagram/graph have been rearranged with the example of spatial frequency moved from above to below the contrast sensitivity functions).

Although contrast sensitivity functions are not available for many bird species, they all indicate that birds have lower contrast sensitivity compared with mammals, including humans. That is, at a given stripe width, contrast has to be higher in birds than in mammals before it can be detected (Harmening et al. 2007; Harmening et al. 2009; Hodos et al. 2002; Lind et al. 2012; Lind and Kelber 2011). In essence this means that there must be greater contrast for a given object to be detected by birds than for it to be detected by mammals, including humans.

In all vertebrate species tested to date, contrast sensitivity declines as stripe widths either increase or decrease away from the widths where contrast sensitivity is highest (Figure 8). Thus, there is a middle range of stripe widths where small amounts of contrast differences are relatively easily detected, and objects or patterns made up of elements of that size can be most easily detected. Most importantly, these studies demonstrate that when stimuli are of low contrast, the optimal size at which they are most likely to be detected is relatively large, much broader than the stripes that are detectable at high contrast. This emphasizes that measures of acuity, of the kind shown (Table 2) may have limited application for understanding what spatial information a bird is able to retrieve from within its natural environment.

10. Temporal Resolution of vision

The temporal resolution of vision is an indication of the ability to resolve rapid changes in a stimulus pattern. It is sometimes referred to as the speed of vision. Temporal resolution is normally investigated by determining the critical flicker fusion frequency (CFF) of a species (Potier et al. 2020a). This is the frequency of a flashing light, at which the eye can no longer distinguish between a flickering light from a constant light of the same brightness. Temporal resolution has been determined behaviourally (an animal choosing between a rapidly changing pattern or light and a fixed one), physiologically (direct recording from the eye using electroretinogram, ERG), or by using the optomotor response (the ability of an animal to follow the lines of a grating pattern that is rotated about its head).

In birds, the highest temporal resolution (mean CFF between 120 - 130 Hz) has been described in some species of small songbirds (Potier et al. 2020a). These CFFs are higher than in humans and have been interpreted as associated with the need for the birds to detect sufficient details to guide flight when moving rapidly in spatially complex environments such as woodlands. However, high CFFs (approximately 100 Hz) have also been reported in Domestic chickens *Gallus domesticus* and Rock Doves suggesting that flight in woodlands is not the driver of high temporal resolution of vision. Also, like spatial resolution, temporal resolution is a function of light level with highest CFFs occurring at high, daytime, light levels and lower CFFs at low light levels, especially when vision is mediated by rod photoreceptors. Temporal resolution of patterns is also a function of contrast within the pattern although this has not been systematically investigated in any species of birds.

The flicker fusion frequency of diurnally active parrots (Budgerigars) and of diurnal active raptors (Harris's hawk) have not been found to be as high as in songbirds (mean CFF of approximately 80 Hz) (Bostrom et al. 2017; Potier et al. 2020a), although the CFF of peregrine falcons *Falco peregrinus* were found to be similar to those of some passerines. Much lower CFFs of between 40 and 50 Hz have been found in great horned owls and little owls *Athene noctua* (Ault and House 1987; Porciatti et al. 1989) and this is thought to be correlated with their vision being primarily adapted to achieve enhanced sensitivity at

lower light levels which is gained by integrating the responses of rod photoreceptor over time (Warrant 2008).

Comparative analysis of temporal resolution in 17 species of birds (Potier et al. 2020a) has not found a consistent pattern that can be correlated with behavioural and ecological variables across species, except that the lowest CFFs are found in nocturnally active species. Among birds which are active during the day a consistent relationship between speed of vision and flight in spatial complex habitats has not been found. However, it is clear that some birds are better able to discern flicker than others at high day time light levels.

11. Closing remarks: the vision of birds

As outlined in the introduction, vision is fundamentally about spatial information, about detecting where light is coming from in the world that surrounds the observer. The ability to differentiate between lights of different brightness (contrast sensitivity), combined with information on where the light is coming from, underlies the ability to detect objects. The remarkable accuracy and precision of vision in birds is built upon finely tuned optics and image analysis mechanisms. Vision in birds is, however, far from uniform. Natural selection has built upon the inherent flexibility of the vertebrate eye's optical system, the flexibility in the way retinal receptors can be arranged, and the flexibility with which eyes can be placed in the skull, to give each species a different suite of visual information. There is not one "bird's eye view", but many.

Well-founded comparisons between the vision of different bird species are, however, limited. Only for those species for which there is detailed information on physiology and anatomy of the eyes, or the visual capacities of the whole animal have been behaviourally determined, can reliable comparisons be made. Such information is available for only a handful of species compared with the more than 10,000 bird species that exist today.

Even among this handful of species there is good evidence for wide differences in the information that their vision provides. Each species appears to have a unique suite of information that guides them in the execution of different tasks in different light environments; from pecking to lunging at food items, from bright sunlight to woodlands at night, from the open skies to below water. It should also be remembered that visual information is complemented by equally diverse sources of information from other senses, and that information provided by vision and other senses are usually used in complementary ways to guide behaviour (Martin 2017a; Martin 2020). The result of this diversity in sensory information is that while different bird species can share the same environment, they live in different worlds, and they certainly live in different worlds to those of humans who also share the same environment.

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