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# Visual fields, foraging and collision vulnerability in gulls (Laridae)

JENNIFER C. CANTLAY,[†,1] STEVEN J. PORTUGAL[1,2,3] & GRAHAM R. MARTIN*[4]
[1]*School of Biological Sciences, Royal Holloway University of London, Egham, Surrey, TW20 0EX, UK*
[2]*The Natural History Museum, Tring, HP23 6AP, UK*
[3]*Department of Zoology, University of Oxford, Oxford, OX1 3SZ, UK*
[4]*School of Biosciences, University of Birmingham, Edgbaston, Birmingham, B15 2TT, UK*

Wide variation in visual field configuration has been recorded among avian species and it is hypothesized that this variation is driven primarily by foraging ecology and predator detection. It has also been shown that visual field configurations can render some species more vulnerable to collisions with human artefacts that extend into open airspace, such as power lines and wind turbines. Visual fields have three main components: the monocular fields describe the extent of the world seen by each eye, the binocular field describes the region where the monocular fields overlap, and the blind area describes the region in which no vision is provided. Among birds, the topography of the binocular field, and the extent and position of the blind area, show considerable interspecific variation. Although Laridae (gulls, terns, skimmers) are a large and cosmopolitan taxon, visual field characteristics of only one species, Black Skimmer *Rynchops niger*, have been determined. However, skimmers are distinct from other Laridae species because they use a specialized foraging technique based upon tactile cues. We determined visual fields in three species of gulls (European Herring Gulls *Larus argentatus*, Lesser Black-backed Gulls *Larus fuscus*, Black-legged Kittiwakes *Rissa tridactyla*), and found that they show the key characteristics associated with visually guided foraging. However, the binocular field does not extend through the full height of the frontal field. This results in a blind sector, which can project in the direction of flight when gulls pitch their heads sufficiently far forwards to visually search the surface below. This could render gulls vulnerable to collisions with anthropogenic structures (power lines, wind turbines) that extend into the open airspace. Photographs show that gulls in level flight do pitch their heads forward sufficiently to render them almost blind in the direction of travel, and further work on the head positions adopted by gulls in flight are recommended. The visual field of skimmers differs markedly from those of gulls. Their binocular field topography is interpreted as functioning in the control of bill position when skimming (flying just above the water surface with the elongated, blade-like, rhamphotheca of the mandible extending through the water surface). Skimmers also have a blind area, which projects forwards in the direction of travel when skimming. This can be associated with the vulnerability of skimmers to collisions with objects that extend just above the water surface.

**Keywords:** binocular vision, blind areas, collision mitigation, gulls, skimmers, vision.

[†]Present address: Animal Plant and Health Agency, Woodham Lane, Addlestone, Surrey, KT15 3NB, UK

*Corresponding author.
Email: g.r.martin@bham.ac.uk

An animal's visual field is the three-dimensional space around its head from which it can extract visual information at any instant. Among avian species, wide variation in visual field configuration is hypothesized to be driven primarily by foraging ecology and predator detection, rather than the control of flight (Martin 2017b, Cantlay *et al.* 2023). It has also been shown that visual field configurations can render some species vulnerable to collisions with human artefacts that extend into open airspace, such as power lines and wind turbines (Martin & Shaw 2010, Martin *et al.* 2012).

Visual fields have three main components: the monocular fields describe the extent of the world seen by each eye, the binocular field describes the region where the monocular fields overlap, and the blind area describes the region in which no vision is provided. Knowledge of all three components is important in understanding the sensory ecology and behaviour of any animal (Martin 2007).

Among birds, the topography of the binocular field (the size, shape and position of the region of binocular overlap relative to the bill) and the extent and position of the blind area show considerable interspecific variation (Martin 2017a). It has been hypothesized that this variation is influenced primarily by a trade-off between species-specific sensory requirements of foraging and predator detection, rather than the guidance of locomotion, or shared ancestry (Martin 2017a). This has been supported by both comparative analyses using phylogenetically informed statistical techniques in large samples of species within a family (ducks and geese, Anatidae (Cantlay *et al.* 2023); owls, Strigidae (Potier *et al.* 2023); diurnal raptors, Accipitridae and Cathartidae (Potier *et al.* 2018)), and by descriptive analyses of visual fields and their relation to foraging ecology among small numbers of closely related species within taxa, for example among Ardeidae (Martin & Katzir 1994), Bucerotidae (Martin & Coetzee 2004), Threskiornithidae (Martin & Portugal 2011), Alcidae (Martin & Wanless 2015) and Accipitridae (Potier *et al.* 2016).

Visual fields have now been determined in over 180 bird species from 20 orders and 32 families (see appendix 1 of Martin (2017a) plus recent comparative analyses (Potier *et al.* 2018, 2023, Cantlay *et al.* 2023)). Although the Laridae (gulls, terns, skimmers) (Gill *et al.* 2024) are a large taxon (approximately 100 species), and are found worldwide (Burger & Gochfeld 1996, Gochfeld & Burger 1996), the visual field characteristics of only one species, Black Skimmers *Rynchops niger*, have been described (Martin *et al.* 2007b). However, the foraging behaviour of skimmers is highly specialized (Zusi 1996) and is not representative of the majority of Laridae. The three species of skimmers probably rely upon tactile information in their foraging; all other Laridae are observed to use visually guided foraging, targeting a wide range of individual food items at the water surface, on harder surfaces, or taking items in mid-air during kleptoparasitism, or in the pursuit of insects, flying fish and birds (Burger & Gochfeld 1996, Gochfeld & Burger 1996).

Tactile cues play a key role in the foraging of skimmers, but it has been argued that vision also plays a specialized role in their foraging (Martin *et al.* 2017b). Prey items are detected at or just below the water surface when a bird 'skims', i.e. flies just above the water surface with the elongated, blade-like, rhamphotheca of the mandible extending through the water surface (Zusi 1962, 1996). Bill closure about a prey item hit by the mandible is probably triggered by tactile cues from the mandible or from jaw musculature. The binocular field of skimmers is relatively narrow and of short vertical extent, but its position encompasses the visual projections of both the mandible and the maxilla when the mouth is open during skimming. It is argued that the binocular field of skimmers has a specific role in controlling the position of the bill with respect to the water surface when a bird skims rather that directing the bill towards specific objects (Martin *et al.*, 2007b).

The foraging of all other Larid species would appear to be dependent upon accurate bill positioning with respect to target objects and with accurate timing of arrival of the bill at an individual food item (Burger & Gochfeld 1996, Gochfeld & Burger 1996). The visual field configuration required for such precision placement of the bill in space and time requires that the projection of the bill is placed approximately centrally within the binocular field (Martin 2009). This arrangement provides an optic flow-field centred around the projection of the bill. From this, flow-field information on both the direction of bill travel and time-to-contact a target can be extracted, thus enabling items to be seized in the bill with precision (Martin 2014).

The present study examines the visual field configurations of three species of Laridae (European Herring Gulls *Larus argentatus*, Lesser Black-backed Gulls *Larus fuscus* and Black-legged Kittiwakes *Rissa tridactyla*) to determine whether they show the general characteristics of birds that are visually guided foragers. The key characteristics (Martin 2014) are: a relatively narrow and vertically elongated frontal binocular field, maximum binocularity occurring at or above the projection of the bill tip, the projection of the bill tip placed centrally or just below the centre of the binocular field, and the presence of a blind area to the rear of the head.

We also examine the projection of the blind area in the dorsal field to determine whether these species may at times fly blind in their direction of travel when foraging. The presence of a forward-projecting blind area has been described in vultures, bustards and cranes, and is thought to be an important factor in their collision vulnerability with human artefacts (Martin & Shaw 2010, Martin *et al.* 2012). Gulls and kittiwakes are hypothesized to be highly vulnerable to collisions with wind turbines because of their flight characteristics (Furness *et al.* 2013). As such, it is important to determine the characteristics of their visual fields, as this would indicate whether they are likely to be intermittently blind in their direction of travel and hence of increased vulnerability to collisions with artefacts.

## METHODS

### Study locations and species

Visual fields were measured for three gull species at two locations in the UK: Skokholm Island, Pembrokeshire, Wales (May and July 2019; 51°41′52.0″N, 5°16′36.0″W) and the Isle of May, Fife, Scotland (July 2019; 56°11′00.0″N, 2°34′00.0″W). Data were collected from adult birds of three species: European Herring Gulls (four individuals), Lesser Black-backed Gulls (three individuals) and Black-legged Kittiwakes (three individuals). The Skokholm Island wardens captured individual European Herring Gulls in specially devised traps (gull or spring trap) during the daytime, and Lesser Black-backed Gulls were captured individually by dazzling and netting at night (gull-trap capture was unsuccessful for these species). UK Centre for Ecology and Hydrology researchers working on the Isle of May captured individual Black-legged Kittiwakes from cliff ledges using a telescopic pole and noose. Each bird was placed in a bag and carried to a building near the point of capture. In both locations, measurements of visual fields were conducted in a darkened room of the building, and on the completion of measurements, each bird was released near its capture location. Bird capture and data collection were conducted under licences granted by Natural Resources Wales (licence S085854/1) and Scottish Natural Heritage (licence 138 016), respectively.

### Visual field measurements

The ophthalmoscopic reflex technique was used to measure the visual field characteristics, following the standard procedure described in previous studies (Martin & Wanless 2015, Potier *et al.* 2018). The bird was held with its body immobilized in a foam-rubber cradle and its bill was placed in a holder specially designed for each species, with the head of the bird adopting its natural resting position. The bill holder was constructed of aluminium sheet shaped to the bird's bill and the surface was coated with cured silicone sealant. The shape of the holder was based upon calibrated photographs and direct measurements of bills from specimens held at the Natural History Museum, Tring, UK. This arrangement fixed the at-rest head position with respect to the co-ordinate system used to characterize the visual field (Fig. 1). This technique has been consistently applied across a wide taxonomy of avian species and provides a reliable method for interspecific comparisons of visual field topography (Martin & Portugal 2011). The UK Animals (Scientific Procedures) Act 1986 was not applicable because the procedure was non-invasive and bird restraint was for only a short period of time (approximately 30 min) (Martin & Portugal 2011).

Spontaneous eye movements were observed in all three gull species, which refers to the observation that some species have complex rotational eye movements, and the translational effect of these movements can alter the limits of the visual field recorded at each elevation (White *et al.* 2007). Visual field measurements were taken for the positions that the eyes spontaneously adopted when fully rotated forwards, hence when they were converged for the front field, providing an estimate of the maximum binocular field width (Potier

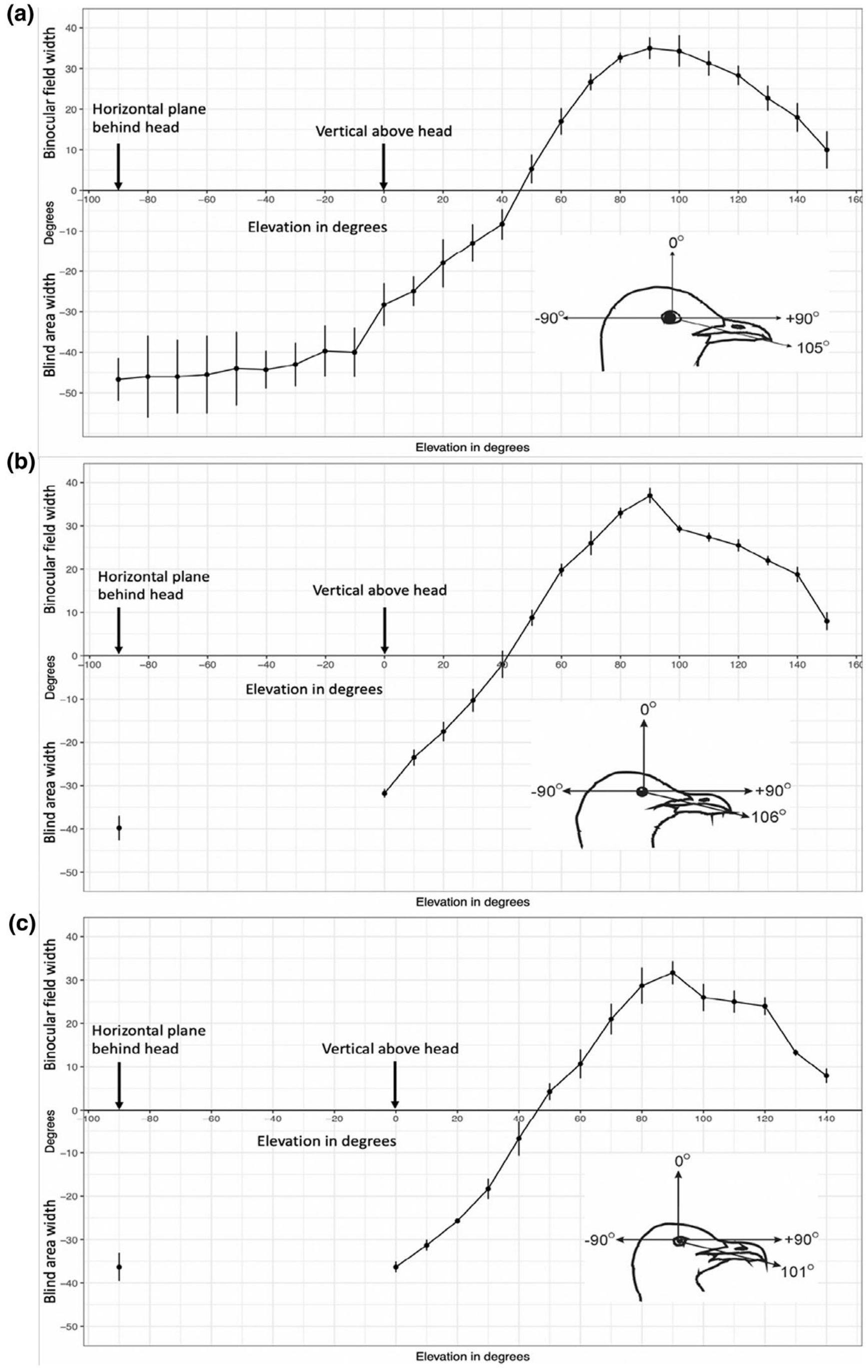


**Figure 1.** The mean ± standard error angular separation of the retinal field margins as a function of elevation in the median sagittal plane for three species of gulls: (a) Black-legged Kittiwakes ($n$ = 3), (b) European Herring Gulls ($n$ = 4) and (c) Lesser Black-backed Gulls ($n$ = 3). Positive values indicate an overlap of the field margins (binocular vision), and negative values indicate the width of the blind area. The co-ordinate system is such that the horizontal plane is defined by the elevations −90° (behind the head) and +90° (in front of the head), and 0° is directly above the head. For each species, there is a drawing of the bird's head in profile with key co-ordinates indicated. The head is shown in the position with respect to the co-ordinate system at which measurements were made. This head position is approximately that spontaneously adopted by a bird held in the hand. The projection of the eye–bill-tip axis is shown.

*et al.* 2016). For European Herring and Lesser Black-backed Gulls, the visual field measurements could not be recorded for most elevations behind the head (except at −90°, i.e. directly behind the head, see Fig. 1) under the field conditions (Tables S2 and S3) because of the licensing requirement for reducing bird restraint time. Examination of three or four individuals provided mean visual field data for each species (Tables S1–S3 and Fig. 1) and these were used to create topographical maps of the visual fields for each species (Fig. 2).

## RESULTS

Visual field data of Black-legged Kittiwakes (three individuals), European Herring Gulls (four individuals) and Lesser Black-backed Gulls (three individuals) were combined for each species (Tables S1–S3) to provide mean values of the angular separation of the retinal field margins at each elevation in the median sagittal plane of the head (Fig. 1). Topographical maps based on the mean values of each species' data illustrate the visual fields in different planes. These are shown as horizontal sections through the visual fields (Fig. 2a), visual fields in the frontal sector (Fig. 2b) and vertical sections through the binocular field in the median sagittal plane (Fig. 2c).

The visual fields of the three species have broadly similar topography. Mean values ± standard error (se) for all species combined are used to summarize key characteristics: (1) the binocular region, from the elevation at which it could be measured below the bill, extends vertically through 111° ± 5.7°, (2) the maximum width of the binocular field has a mean value of 35.1° ± 1.2°, (3) the maximum width of the binocular region projects horizontally when the head is in its resting posture and lies 11.7° ± 1.7°, above the direction of the eye–bill-tip projections, (4) laterally, there are extensive monocular visual fields 142° ± 2.0° wide on either side of the head and (5) there is a blind area that projects into the dorsal anterior of the visual field and extends above and behind the head. The blind area starts at 46° ± 1.3° above the horizontal when the head is in its resting position and has a mean width of 32.1° ± 5.5° directly above the head and broadens to a blind region 40.7° ± 2.3° wide, directly behind the head in the horizontal plane.

## DISCUSSION

Black-legged Kittiwakes, European Herring Gulls and Lesser Black-backed Gulls demonstrate the visual field characteristics of birds whose foraging is visually guided. The key characteristics (Martin 2014) are shown in Figure 2: a relatively narrow and vertically elongated frontal binocular field, maximum binocularity occurring at or above the projection of the bill tip, the projection of the bill tip placed centrally or just below the centre of the binocular field, and the presence of a blind area to the rear of the head.

### Visual field characteristics and visually guided foraging

The type of visual field topography shown in Figure 2 is found across a wide variety of bird species that differ in their ecology and evolutionary relatedness but have in common the use of vision for precise control of the bill or talons to take food items at close range (Martin, 2017b). These features reflect a common requirement for accurate bill placement and timing of bill opening when procuring food items. Taxa in which species show these general characteristics include passerines (Fernandez-Juricici *et al.* 2008), diurnal raptors (Potier *et al.* 2018), auks (Martin & Wanless 2015), herons (Martin & Katzir 1994) and penguins (Martin & Young 1984). Species that do not use visual guidance of bill position when foraging, e.g. some ducks (Guillemain *et al.* 2002, Martin *et al.* 2007a) and shorebirds (Martin 1994), have visual fields in which the bill projection falls outside, or at the lower edge of, the binocular field, a narrow but vertically extensive binocular field, and the absence of a blind area above and behind the head.

Both Lesser Black-backed and European Herring Gulls are opportunistic omnivores, feeding on mobile and sessile food items (fish, marine and terrestrial invertebrates, birds' eggs and chicks, small mammals, berries, fishing boat discards and general edible waste at rubbish tips), and they use varied foraging techniques (foot-paddling, surface-dipping, surface-diving, plunge-diving, pecking, stalking and ambushing) to disturb, detect and take food items (Burger & Gochfeld 1996). Black-legged Kittiwakes mainly feed on marine invertebrates and fish, especially Sandeels *Ammodytes* spp., Herring *Clupea harengus*, European

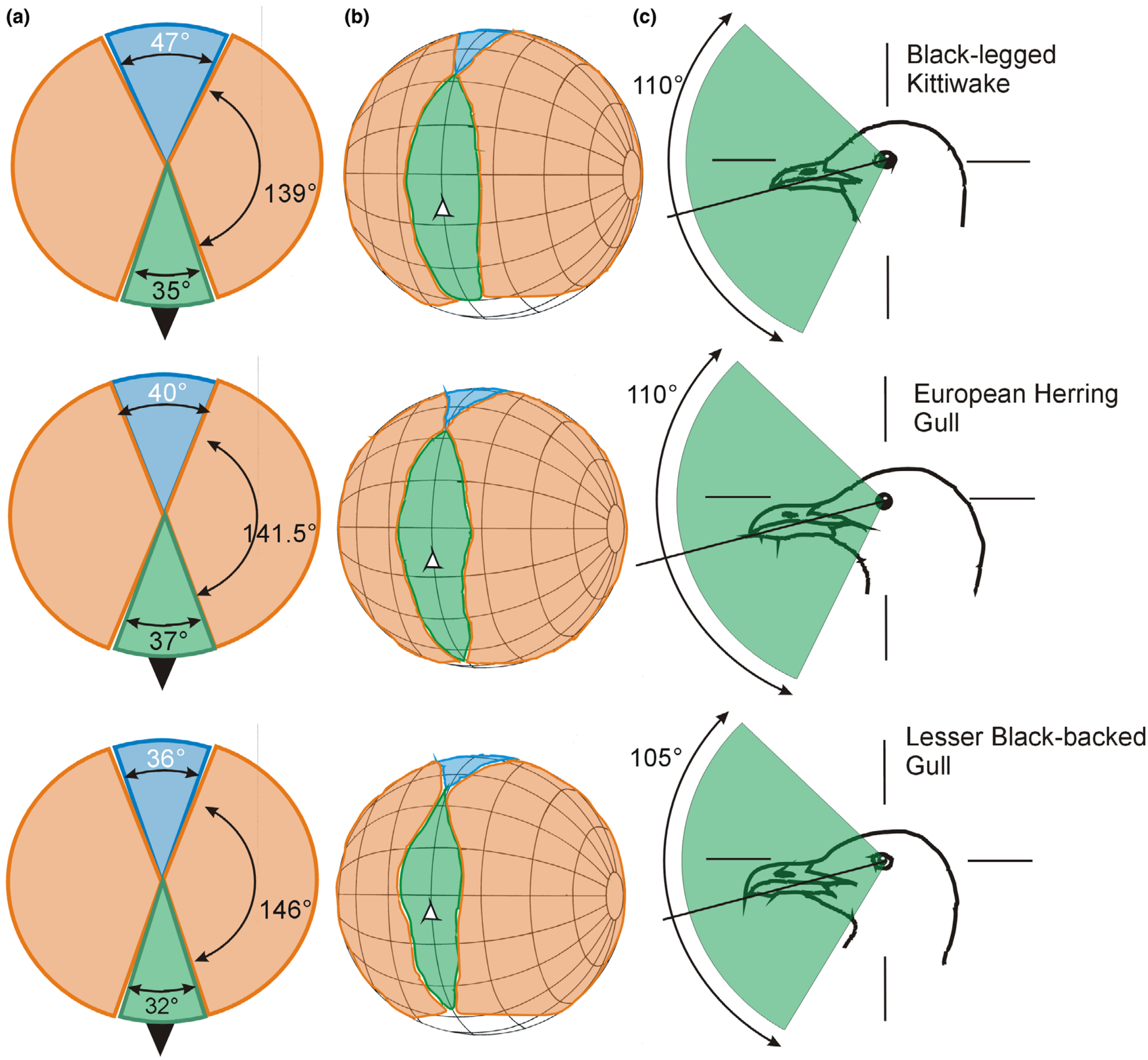


**Figure 2.** Visual fields of three species of gulls. The head of each species is depicted in a lateral view in the right-hand column. The heads are shown in the correct orientation with respect to the co-ordinates used during measurement. The directions of the projection of the eye–bill-tip axes are shown. (a) Section through the visual field in the horizontal plane for each species when the head is in its characteristic resting position. (b) Perspective views of orthographic projections of the boundaries of the retinal fields of the two eyes. (c) Vertical sections through the binocular field in the median sagittal plane of the head. The directions of the eye–bill-tip projections are indicated by white triangles. These orthographic projections use conventional latitude and longitude co-ordinate systems with the equator aligned vertically in the median sagittal plane of the bird (grid at 20° intervals) and values and position of the binocular field in the sagittal plane correspond with those shown in the diagrams in (c). It should be imagined that the bird's head is positioned at the centre of a transparent sphere with the bill tips and field boundaries projected onto the surface of the sphere with the heads in the orientations shown in the right-hand column but with the bill projecting from the centre of the sphere towards the white triangles. Green shading indicates binocular sectors; orange shading monocular sectors; blue shading blind sectors; downward pointing black arrowheads in the diagrams of (a) indicate the direction of the bill.

Sprats *Sprattus sprattus* and Snake Pipefishes *Entelurus aequoreus*, and feeding methods include surface-dipping and plunge-diving (Gochfeld & Burger 1996). The binocular field widths of the three gull species are comparable to those of other non-passerine species, generally falling within the range of 20° to 35° (Martin 2017a), such as Common Guillemots *Uria aalge* (Martin & Wanless 2015), Black-browed and Grey-headed Albatrosses *Thalassarche melanophris* and *Thalassarche chrysostoma* (Martin 1998), and African and Eurasian Spoonbills *Platalea alba* and *Platalea leucorodia* (Martin & Portugal 2011). All of these species have diverse foraging behaviours, but they all require accurate item location and accurate timing of bill arrival to take items in their bills.

## Vertical extent of the binocular field and anterior blind area

The vertical extent of the frontal binocular field is similar across the three Larid species (Fig. 2), with only a 5° difference between Lesser Black-backed Gulls (105°) and the other two species (110°). The vertically long binocular field centred approximately about the bill would enable these birds to view food items in front of them, above and below the bill. The binocular field extends vertically to approximately 55° above the bill (45° above the horizontal when the head is in its resting position). Above the binocular field is the blind area, which projects into the dorsal anterior portion of the visual field and extends behind the head. Such anterior-projecting blind areas are not found in all bird species whose foraging is visually guided. For example, in Cattle Egrets *Bubulcus ibis* and in African Harrier Hawks *Polybroides typus* there is complete visual coverage of the dorsal anterior visual field that is associated with the perceptual challenges of their particular foraging ecology (Martin & Katzir 1994, Portugal *et al.* 2023). However, anterior blind areas have been recorded in other species such as diurnal raptors (Martin *et al.* 2012, Potier *et al.* 2018), bustards (Martin & Shaw 2010) and hornbills (Martin & Coetzee 2004). In these species, such blind areas may function to reduce the probability that the sun is imaged upon the retina and so maintain high spatial resolution under bright natural illumination conditions (Martin & Katzir 2000).

There are two consequences of such blind area configurations. First, the blind area must limit the ability to detect predators approaching from above and behind, thus rendering a bird vulnerable to vertical or posterior attacks from aerial predators. In these gull species, this is likely to be a factor that renders them vulnerable to attack from Great Skuas *Stercorarius skua* and Arctic Skuas *Stercorarius parasiticus* (Oro & Furness 2002), Great Black-backed Gulls *Larus marinus* (Veitch *et al.* 2016) and White-tailed Eagles *Haliaeetus albicilla* (Anker-Nilsen *et al.* 2023). Second, birds in which there is a forward-projecting blind area are likely to be vulnerable to collisions, especially with anthropogenic structures that extend into the open airspace. It is argued that this is the case in vultures, bustards and cranes (Martin & Shaw 2010, Martin *et al.* 2012). These species' vulnerability to collisions with power lines and wind turbines may be a result of them intermittently flying blind as they pitch their head forward to search the ground below when foraging, or when searching for conspecifics.

## Collision vulnerability in gulls and skimmers

Flying blind in the direction of travel occurs in Griffon Vultures *Gyps fulvus* when the head is pitched forward by 40° from its resting position (Martin *et al.* 2012). Pitching the head in this way brings the dorsal anterior blind area to project forwards in the direction of travel. It seems that the same will apply to the gulls in this study. Figure 3 indicates that in these gulls, the head would need to pitch forward by approximately 45° for the blind area to project in the forward direction. That gulls do pitch their heads forward in flight is suggested by casual observations of birds flying over open water, presumably searching the surface below for food items. An internet search for photographs (Google-based search for images using common and scientific names of the three gull species studied) provided some good-quality photographs showing side views of all three species apparently in level flight with the head pitched forward (Fig. 4). Superimposition of the visual projection of the vertical extent of the binocular field onto the photographs (using the eye–bill-tip axis as a co-ordinate) shows that in all three species the blind sector above the binocular field can be brought to project close to the horizontal. This is likely to result in the birds effectively flying blind in their direction of travel. Further forward rotation of the head would certainly render the birds blind in their direction of travel. Further photographs and videos, and field observations, should be collected to confirm this hypothesis.

The situation in skimmers does indicate that foraging birds are flying blind, or nearly so, and

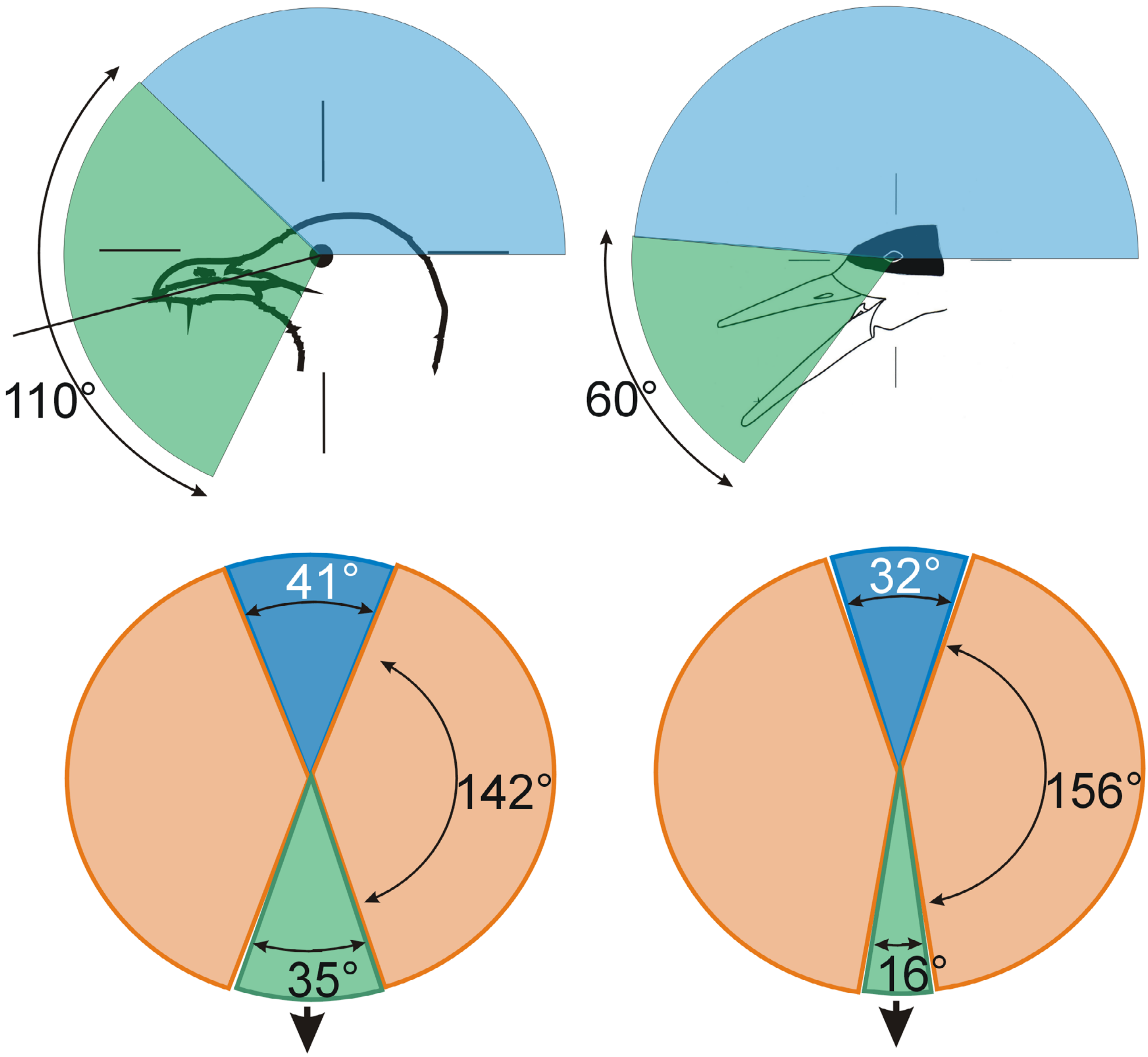


**Figure 3.** Comparison between visual fields in gulls and Black Skimmers. Top diagrams show vertical sections through the binocular field in the median sagittal plane of the head. Bottom diagrams show sections through the visual field in the horizontal plane. For the gulls (left diagrams), the mean of the three species studied here is shown with the head depicted in its typical resting posture. Diagrams for Black Skimmers (right diagrams) are redrawn from Martin *et al.* (2007b) and show the head position when a bird is skimming with the mandible lowered. The water surface would be parallel to and just below the horizontal co-ordinates. Green shading indicates, binocular sectors; orange shading monocular sectors; blue shading blind sectors; downward pointing black arrowheads indicate the direction of the bill.

this could explain their collision vulnerability. Figure 3 shows that the binocular field is about half the width of the gulls' binocular field and that when 'skimming' there is only a very small margin of frontal visual coverage above the horizontal. Hence foraging skimmers are flying blind in their direction of travel, and this can be associated with their known vulnerability to collisions with objects such as piers, logs, boulders and gravel banks, that extend just above the water surface or sit just below it (Zusi 1996). Collisions with such objects can result in breakage of the tip of the mandible. However, an important difference between skimmers and gulls is the elevation at which they fly

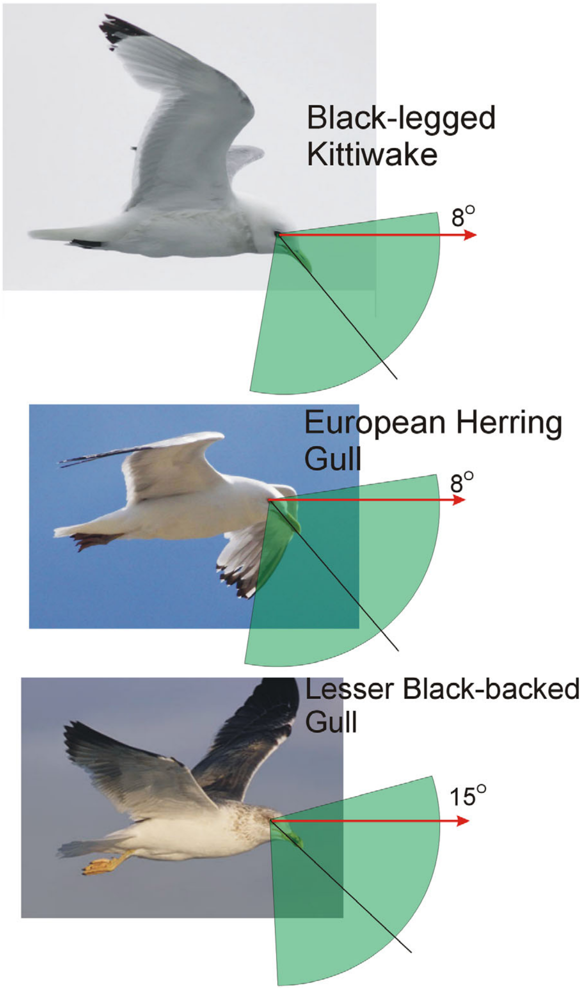


**Figure 4.** Binocular field projections in flight in three species of gulls. Photographs show birds in flight from an approximately lateral view with the head pitched forwards with the birds apparently looking downwards (the eye–bill-tip direction projects approximately 50° below the horizontal/direction of travel). Onto each photograph the projection of the binocular field in the median sagittal plane of the head (Fig. 2c) has been superimposed and aligned on the direction of the eye–-bill-tip projection. Directly above the binocular field is the blind sector. The arrow shows the direction of the horizontal and the numbers above the arrows indicate the angle through which the head would need to be pitched further forward to render the birds blind in the direction of travel. (Photographs are produced with the permission of the authors and have the following attributions: Kittiwake, Terry Sohl (www.sdakotabirds.com); Lesser Black-backed Gull, Phill Swanson (Nebraskabirdlibrary.org; pswanson19@cox.net); European Herring Gull (www.auduboneverglades.org)).

above a water surface when foraging. Skimmers are flying at the water surface and so are not vulnerable to collisions with large structures that extend into the open airspace at that time. Gulls, on the other hand, fly in the open airspace into which human artefacts are introduced. Indeed, it is the propensity of gulls to fly within the sweep zone of wind turbines at sea that has led them to be ranked as the species most vulnerable to collisions with wind turbines at sea (Furness *et al.* 2013). We would suggest that if gulls are flying in the vicinity of wind turbines, their vulnerability to collisions is further increased because they are likely to be flying blind, at least intermittently, when they pitch their heads forward to examine the sea surface below. This is more likely to be the case in locations where gulls forage than in locations through which gulls only transit.

## Collision mitigation

To mitigate vision-based collision vulnerability, measures are necessary to provide birds with information that a hazard lies ahead sufficiently early for them to change flight trajectory and avoid collision. General understanding of avian vision has already led to several recommendations to mitigate the collisions of birds with wind turbines (Martin & Banks 2023). We have shown here that when foraging over open water, gulls may not have available to them a continuous flow of information about what lies ahead. Given that gulls are already regarded as highly vulnerable to collisions with turbines it would seem important that wind turbines at sea are made as conspicuous as possible and that the effectiveness of recommended turbine-blade-marking methods (May *et al.* 2020, Martin & Banks 2023) is trialled. However, increased conspicuousness of turbine blades to gulls could result in habitat loss to other species. Birds may fail to exploit important foraging areas in order to avoid turbines and making turbines more conspicuous is likely to increase the size of the area avoided (Garthe *et al.* 2023, Peschko *et al.* 2024). This potential trade-off between collision reduction and decrease in the size of potential foraging areas will need to be considered in the overall impact of turbine-blade-marking trials.

It is also important to note that both Lesser Black-backed and European Herring Gulls spend a large proportion of their time on land, where they may have relatively high vulnerability to collisions with onshore wind turbines (Thaxter *et al.* 2017, Clewley *et al.* 2023) and possibly with associated energy infrastructures, including power lines (Thaxter *et al.* 2019). It would seem important therefore to investigate whether visual fields and in-flight head position combine to increase the collision vulnerability of gulls in terrestrial, as well as marine situations.

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## AUTHOR CONTRIBUTIONS

**Jennifer C. Cantlay:** Conceptualization; investigation; writing – original draft; methodology; validation; visualization; writing – review and editing; software; formal analysis; project administration; data curation; funding acquisition. **Steven J. Portugal:** Conceptualization; funding acquisition; writing – review and editing; supervision; resources; methodology. **Graham R. Martin:** Methodology; validation; visualization; writing – review and editing; software; supervision; resources; conceptualization.

## CONFLICT OF INTEREST STATEMENT

All authors declare that they have no conflicts of interest.

## ETHICAL NOTE

None.

## DATA AVAILABILITY STATEMENT

The data that support the findings of this study are openly available in the Supporting Information.

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## SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section at the end of the article.

**Table S1.** Visual field data showing binocular field (positive values) and blind area (negative values) widths for three Black-legged Kittiwakes, and mean values ± standard error calculated for this species. This species has a mean bill angle of 105°. NR means not recorded.

**Table S2.** Visual field data showing binocular field (positive values) and blind area (negative values) widths for four European Herring Gulls, and mean values ± standard error calculated for this species. This species has a mean bill angle of 106°. NR means not recorded.

**Table S3.** Visual field data showing binocular field (positive values) and blind area (negative values) widths for three Lesser Black-backed Gulls, and mean values ± standard error calculated for this species. This species has a mean bill angle of 101°. NR means not recorded.