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The visual fields of Common Guillemot *Uria aalge* and Atlantic Puffin *Fratercula arctica*: foraging, vigilance and collision vulnerability

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Running Head: Vision in auks

Significant differences in avian visual fields are found between closely related species that differ in their foraging technique. We report marked differences in the visual fields of two auk species. In air, Common Guillemots *Uria aalge* have relatively narrow binocular fields typical of those found in non-passerine predatory birds. Atlantic Puffins *Fratercula arctica* have much broader binocular fields similar to those that have hitherto been recorded in passerines and in a penguin. In water, visual fields narrow considerably and binocularity in the direction of the bill is probably abolished in both auk species. Although perceptual challenges associated with foraging are similar in both species during the breeding season when they are piscivorous, Puffins (but not Guillemots) face more exacting perceptual

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challenges when foraging at other times when they take a high proportion of small invertebrate prey. Capturing this prey probably requires more accurate, visually-guided bill-placement and we argue that this is met by the Puffin's broader binocular field, which is retained upon immersion; its upward orientation may enable prey to be seen in silhouette. These visual field configurations have potentially important consequences that render these birds vulnerable to collision with human artefacts underwater, but not in air. They also have consequences for vigilance behaviour.

**Key Words:** Alcidae, binocular field, murre, predator detection, vision

It has been hypothesised that the principal drivers of vision in birds are foraging and predator detection, rather than the control of locomotion, and that the principal perceptual challenges of foraging are accurate bill placement and timing of bill contact with an object (Martin 2014). Pecking immobile items from a surface or taking mobile prey both require accurate target location and timing of bill opening, and this can be achieved through the extraction of information from the optic flow-field which expands symmetrically about the direction of travel of the bill (Martin 2009).

To achieve such symmetrical expansion of a flow-field about the direction of bill travel, the visual field of an eye must extend contralaterally, i.e. across the mid-sagittal plane of the bird's head (Martin 2009). Because two eyes are involved the result is that there must be a binocular portion to the total visual field, i.e. a sector in which the two eyes view the same portion of space in front of the head. Surprisingly, the extent of these contralateral projections, and hence the width of the binocular fields, are not extensive in birds. In non-passerine species contralateral projections typically lie between  $10^{\circ}$  -  $15^{\circ}$  (binocular fields of  $20^{\circ}$  -  $30^{\circ}$ ) regardless of whether foraging involves accurate pecking of sessile objects or aerial pursuit of evasive prey caught in the beak or feet. However, in passerine species binocular fields are markedly bigger, typically being  $50^{\circ}$  -  $60^{\circ}$  (Troscianko *et al.* 2012, Martin 2014). The function of this greater contralateral projection is not clear but seems unlikely to be concerned with locomotion and more likely to be associated with accurate bill placement or inspection and manipulation of objects uncovered in foraging (Martin 1986, Fernandez-Juricici *et al.* 2008), or in the case of tool-using species the accurate placement of

the tool's tip (Troschianko *et al.* 2012). There is no evidence that it is involved in stereoscopic vision and the perception of relative depth (Martin 2009).

In some birds whose foraging does not require accurate bill placement, the contralateral projection of the fields may be as small as 5° (10° binocular field) suggesting that such a small binocular field is sufficient for the guidance of bird flight even in complex habitats (Martin 2009). In such birds the total (cyclopean) visual field is enlarged and in some ducks (Anatidae) and sandpipers (Scolopacidae) e.g. Mallard *Anas platyrhynchos*, Northern Shoveler *A. clypeata* and Eurasian Woodcock *Scolopax rusticola* (Guillemain *et al.* 2002), this has resulted in comprehensive visual coverage of the hemisphere around and above the head. These findings suggest a trade-off between gaining sufficient contralateral projection of the frontal fields for the accurate control of bill position and maximising the width of the total field to facilitate the detection of predators and/or conspecifics (Fernandez-Juricic *et al.* 2008, 2010).

Within these twin and antagonistic constraints of accurate bill placement and predator detection, subtle variations in visual field configuration may occur between closely related species, suggesting the fine tuning of vision to subtle differences in the perceptual challenges of different foraging tasks. For example, there are small but significant differences in the visual fields of different ibises (Threskiornithidae) depending upon whether they probe their bills into soft substrates or take items from dry surfaces (Martin & Portugal 2011), differences in the visual fields of congeneric ducks depending upon whether they are selective grazers or filter feeders (Guillemain *et al.* 2002), and differences among sandpipers depending upon the extent to which they rely upon 'remote touch' as opposed to visually guided foraging (Piersma *et al.* 1998, Martin & Piersma 2009). Some birds may switch diet or foraging technique within the annual cycle and it seems that their vision is tuned to the most perceptually challenging of the foraging tasks that they face during the year. For example, the probe-foraging of Red Knot *Calidris canutus* during the winter employs remote touch, which does not require accurate visually-guided bill-placement. However, during the breeding season birds switch to predominantly surface or aerial invertebrates which does require accurate visually-guided bill-placement; it is this task that drives the visual field configuration in this species (Martin & Piersma 2009). Recent analysis of visual fields in seven species of Emberizid sparrows, which are passive prey foragers, has also shown subtle

differences between them and also that their visual field configurations are substantially different from that of a passerine species that forages using a sit-and-wait technique for the capture of aerial insects (Moore *et al.* 2015).

It can be concluded therefore that vision of different bird species within the same family, and even within the same genus, can be subtly tuned to the perceptual challenges of foraging. This subtle tuning of vision may be considered analogous to the fine tuning of bill structures to meet the physical challenges posed by the exploitation of different foods in these same species (Martin 2014).

Here we compare visual fields in two closely related species of marine birds: Atlantic Puffin *Fratercula arctica* and Common Guillemot (Common Murre) *Uria aalge*. Both species are members of the Alcidae (auks), are pursuit-divers and during the breeding season feed almost exclusively on small shoaling fish. As such they would be expected to have visual fields typical of other aquatic predators such as Great Cormorant *Phalacrocorax carbo* (Martin *et al.* 2008), Manx Shearwater *Puffinus puffinus* (Martin & Brooke 1991) and Humboldt Penguin *Spheniscus humboldti* (Martin & Young 1984). Puffins and Guillemots differ with respect to bill morphology: Puffins have convex, laterally compressed bills while Guillemots' bills are long, slim and pointed (Fig. 1). In addition, although information on diet outside the breeding season is more fragmentary, the available data indicate that Puffins take a much higher proportion of very small prey items such as planktonic crustacea and marine worms (Falk *et al.* 1992, Harris *et al.* 2015). Hence Puffins might be expected to have a visual field that is tuned to the more perceptually challenging task of precision-pecking to allow birds to exploit small prey efficiently.

## **METHODS**

The study was carried out on the Isle of May National Nature Reserve (Firth of Forth, Scotland, 56° 11' N, 02° 33' E) in early July 2014. Three adult Puffins, aged by the presence of at least two bill grooves (Harris & Wanless 2011), were caught during a routine mist-netting session. None was carrying fish and thus they were unlikely to be breeding. Three

Guillemots were caught using a soft wire noose attached to a 5-m pole in an area used by prospecting birds, again minimising the risk that birds with chicks were used in the trials. Each bird was held captive for approximately one hour and then released back into the colony. Although the procedures used were non-invasive and not considered to require a licence under the United Kingdom, Animals (Scientific Procedures) Act 1986, all work followed their ethical guidelines for the capture, handling and restraining of birds. All research was conducted under Research Permit (MON/RP/159) issued by Scottish Natural Heritage.

Visual field parameters were determined using an ophthalmoscopic reflex technique. This has been used in a wide range of birds of different phylogeny, ecology and feeding techniques and readily permits interspecific comparisons (Martin 2007). For a detailed description of the apparatus and methods see Martin and Piersma (2009). Briefly, each bird was held with the body resting in a foam rubber cradle secured with Velcro™ straps and the legs held out behind the body. The head was held in position at the centre of a visual perimeter (a device which permits the eyes to be examined from known positions about the head) by a steel and aluminium bill holder specially manufactured to securely hold the bills of each species. The surfaces of the holder were coated in cured silicone to provide a non-slip cushioned surface. Bills were held in place by Micropore™ tape and care was taken to not obstruct the nostrils which in these species are narrow slits, low down on the sides of the maxilla close to the mouth opening (Fig. 1). The perimeter's co-ordinate system followed conventional latitude and longitude with the equator aligned vertically in the median sagittal plane of the birds' head and this co-ordinate system is used for the presentation of visual field data (Figs. 2, 3, 4). The tip of the mandible projected approximately 20° below the horizontal with respect to the eyes (see diagrams of head positions in Fig. 2) and was checked from photographs of the head held in the apparatus taken at the end of each measuring session.

The eyes were examined using an ophthalmoscope mounted against the perimeter arm and its position read to  $\pm 0.5^\circ$ . In both species, eyes were found to be mobile and reported here are the visual fields based upon the maximum forward positions adopted by the eyes. These were determined by making rapid repeated observations at each elevation and the most forward rotated positions of the visual field margins were recorded. The limits of the visual

field were recorded in 10° steps in elevation from 50° - 60° below the horizontal in front of the head, to 10° - 20° below the horizontal behind the head. However, at the elevations 30° below the horizontal, the bill holder intruded into the view of the eyes. Therefore it was not possible to record visual field data at this elevation and binocular field width was estimated as the mean value of the binocular field widths above and below these elevations. The direction of the optic axis of each eye (the axis about which the optical elements of the eye are positioned) was determined by estimating the co-ordinate position at which the alignment of the 1<sup>st</sup> and 2<sup>nd</sup> Purkinje images (reflections from the cornea and the anterior surface of the lens, respectively of a small light source) occurred.

Eye movements were not constrained and we recorded the position of eyes when they had taken up their most forward (converged) positions. These positions were taken up readily but we did not have time (due to bird welfare considerations) to systematically record eye movement amplitude. Anecdotal observations suggested that eye movements had a maximum amplitude of about 20°, sufficient to abolish binocular overlap at some elevations in both species.

From these data (corrected for viewing from a hypothetical viewing point placed at infinity; this correction is based upon the distance between the eyes and the viewing distance used in the perimeter apparatus), a topographical map of the visual field and its principal features was constructed for each species. These features are: monocular fields, the visual field of a single eye; binocular field, the area where monocular fields overlap; cyclopean field, the total visual field produced by the combination of both monocular fields; the blind areas above and behind the head.

## RESULTS

The mean angular separation of the retinal field margins as a function of elevation in the median sagittal plane of the head in each species are shown in Fig. 2. Maps based upon these data show the visual fields in the frontal sector (Figs. 3c, d). Horizontal sections through these fields in the planes containing the optic axes are shown in Figs. 3e, f. These

planes were at the 80° - 260° elevation in Puffins and at the 100° - 280° elevation in Guillemots and are indicated by a dashed line in Figs. 3a, b. Figs. 4a, b show vertical sections through the binocular portions of the visual fields in the media sagittal plane of the head.

### **Visual fields**

Figs. 2, 3 and 4 indicate that the overall topography of the visual fields of these two species is very different.

#### *Binocular fields*

The maximum contralateral projection of each eye in Puffins (24.5°) is twice that in Guillemots (12.5°), resulting in a binocular field whose maximum width in Puffins is twice that in Guillemots. Also the extent of the region of maximum binocular overlap is vertically much longer in Puffins compared with Guillemots (170° and 110°, respectively, in the median sagittal plane of the head, Figs. 4a, b).

#### *Monocular fields*

The monocular retinal fields in the two species are of similar width and equalled 167° in Guillemots and 174° in Puffins in the plane containing the optic axes of the eyes. This suggests that the eyes of the two species are optically similar and that the differences in visual fields result primarily from difference in the placement of the eyes in the skull.

#### *Cyclopean fields and blind areas*

Lateral placement of the eyes in the skull, coupled with the wide monocular fields provide both species with extensive cyclopean fields of 310° and 305° in an approximately horizontal plane in the Puffins and Guillemots, respectively (Figs. 3 e, f). The widths of the blind area above and to the rear of the head are significantly different between the two species with the blind area broader in Puffins but vertically less extensive (Figs. 2 & 3e, f). A result of these differences is that the region about the head from which visual information can be extracted at any one instant is smaller in Guillemots than in Puffins.



## **Optic axes**

In both species the eyes project laterally but the projections of their optic axes differed markedly and further indicate that the differences in visual fields are the result primarily of differences in the placement of eyes in the skull rather than in the optical structures of the eyes. Thus in Puffins the optic axes project  $10^\circ$  above the horizontal but in Guillemots the projection is  $10^\circ$  below the horizontal (Figs. 3 a, b, c, d), and the eyes also project slightly more frontally in the Puffins (separation of optic axes  $103^\circ$  and  $107^\circ$ , respectively, in Puffins and Guillemots, Figs. 3 e, f). These differences in eye position are apparent in the photographs of the birds' heads (Fig. 1).

## **DISCUSSION**

### **Visual field general characteristics**

As measured in air, the visual fields of Puffins and Guillemots exhibit four principal characteristics found in a wide range of bird species that differ in their ecology and phylogeny but have in common pecking or lunging at food items (Martin 2007, 2009): (1) the bill tip projection falls centrally or within the lower half of the binocular area, (2) the binocular field is vertically long, (3) maximum binocularity occurs at or above the projection of the bill tip, and (4) there is a blind area to the rear of the head. In contrast, species that do not employ visual guidance for the control of bill position and timing of its contact have comprehensive visual coverage around the head with the bill projection falling outside or at the periphery of the visual field while the binocular field is very narrow and stretches from directly in front to directly behind the head. These contrasting sets of features suggest that when vision is not required for accurate bill placement and timing, the detection of predators is the principal driver of visual field configuration. They further suggest that in visually guided foragers there is a trade-off between the more frontal placement of the eyes for the control of bill position and their more lateral and more upward facing placement for predator detection (Martin 2014).

## Interspecific visual field differences

Although subtle differences in vision have been described between species in the same family (Martin & Portugal 2011, Moore *et al.* 2015) and even within the same genus (Guillemain *et al.* 2002), the differences in visual fields described here cannot be considered subtle, especially with respect to the width of the binocular overlap, its vertical extent and its position relative to the direction of the bill (Figs. 3 & 4). Thus while Guillemots share the same general characteristics as other aquatic predators, e.g. Great Cormorants (Martin *et al.* 2008) and Manx Shearwaters (Martin & Brooke 1991), which take evasive prey from substrates or in the water column, and herons Ardeidae, which take evasive prey through a water surface (Katzir & Martin 1994), Puffins differed markedly from Guillemots and showed characteristics similar to those of penguins (Martin & Young 1984). Both Puffins and Humboldt Penguins have visual fields in air which achieve a maximum width of about 50° at an elevation of approximately 30° above the bill.

## The effects of immersion

The visual fields described were measured in air. However, it is argued that the driver of visual field characteristics is primarily the perceptual challenges faced when foraging (Martin 2014), which in these birds takes place underwater. Upon immersion, these visual field characteristics will change because the refractive power of the cornea is lost and in consequence the widths of the visual field shrink. When Humboldt Penguins enter water their visual fields are reconfigured quite markedly (Martin & Young 1984). In these birds, visual field shrinkage is sufficient to just abolish underwater the binocular field (which is 30° wide in air) in the direction of the bill. It also reduces the maximum width of the binocular field, which although still positioned 30° above the bill, it reduces from about 50° wide to 30° (Martin & Young 1984). A similar reduction of the visual field is probable in Puffins, although detailed analysis of the optics of the eye are necessary to establish this; it depends upon the radius of curvature of the cornea and the relative position of the lens. It is a possibility that in Guillemots the visual field will also be reduced underwater and that only a small degree of binocularity will be retained.

## Functions of the visual fields

Determining the functions of the visual fields in aquatic foragers is problematic. This is because these birds have to function visually in both air and water. Foraging, which is thought to be the principal driver of vision, takes place underwater, but the birds are probably most vulnerable to predators when in air. In air, the broad binocular field of Puffins showed characteristics that are similar to those of many species of passerine birds. In passerine species binocular fields are markedly bigger than in non-passerines, typically being between  $50^{\circ}$  -  $60^{\circ}$  and their function seems likely to be associated with accurate bill placement or inspection and manipulation of objects uncovered in foraging (Martin 1986, Fernandez-Juricici *et al.* 2008), or in the case of tool using species the accurate placement of the tool's tip (Troscianko *et al.* 2012). There is no evidence that it is involved in stereoscopic vision and the perception of relative depth (Martin 2009). It would not seem that the vision of Puffins would be subject to these types of drivers because much of their behaviour in air does not seem to require subtle or finely controlled bill timing. This would also seem to be the case in Guillemots.

### *Visual fields and foraging*

When foraging underwater, however, accurate bill placement and timing does seem to be required in both species. Accurate bill placement can be achieved using information extracted from the optical flow-field within the binocular field as a target is approached (Martin 2009). This gives both direction of travel and time-to-contact a target but extensive binocularity may not be required for this information to be available in these species. This is because during the breeding season both Puffins and Guillemots take relatively large prey items when they are provisioning chicks. Prey items are shoaling fish generally between 5 and 15 cm in length (Harris & Wanless 2011). Such prey would not seem to set a particularly exacting perceptual challenge no matter how poor the visual acuity of the birds might be underwater. For example, the binocular fields of Great Cormorants are similar to those of Guillemots and their acuity under water (White *et al.* 2007) has been shown to be 60 times lower than the acuity of aerial predatory birds (Reymond 1985), but this acuity and visual field configuration is clearly sufficient to allow evasive prey of various sizes to be taken by Great Cormorants, even in turbid waters (White *et al.* 2007). Therefore, on the basis of foraging tasks carried out during the breeding season even the reduced binocularity that occurs underwater can be

seen to be sufficient for the foraging tasks at that time. But why should Puffins have a wider binocular field, and one that is angled slightly upwards, compared with the Guillemots?

### *Vision and foraging differences in the annual cycle*

Diet and associated foraging methods and hence perceptual challenges can vary markedly over the annual cycle (Piersma *et al.* 1998, Martin & Piersma 2009) and thus interspecific comparisons need to be made at an appropriate time scale. The diet of Guillemots outside the breeding season appears to remain largely piscivorous and includes fish of similar size to those taken during the breeding season (Bradstreet & Brown 1985, Wilson *et al.* 2004). In contrast, there is evidence that the diet of Puffins changes with season (Harris *et al.* 2015). In winter the stomachs of Puffins shot in the Faroe Islands contained the remains of 20 species of fish, six species of crustacea and single species of polychaete, chaetognathid and squid. Thus invertebrates may make up a major component of the Puffin's winter diet, and many of these invertebrates are small crustacea which occur in dense swarms (Falk *et al.* 1992). The perceptual tasks involved in locating and catching such prey appears more challenging since planktonic crustacea are mobile, semi-transparent and distributed in three dimensions.

We speculate that it is this more exacting task of winter foraging that drives visual field configuration in Puffins. There is a need to maintain a wide degree of binocular overlap even when immersed, because the task of taking these small items requires more accurate and subtle bill location, and timing of bill opening, than taking the larger fish prey. Consistent with this is the more upward direction of the eyes (Fig. 1) and the associated upward projection of the binocular region (Fig. 3c), which will facilitate small prey items being seen in silhouette against the down welling light, and once prey are detected above the horizontal they can be grasped in the bill by swinging the head upwards. Although Puffins appear to have large bills they are laterally flattened and the gape width is not large. Therefore trawling for small prey is an unlikely strategy to be used by Puffins and in any case trawling may not be possible without a filter mechanism of the kind found in the bills of some procellariiform species (Klages & Cooper 1992). In Puffins individual items, although small, require detection and selective seizure. The perceptual challenges of taking the larger prey items

which predominate in the breeding season can be met within the parameters set by the challenges of taking smaller prey, but not vice-versa.

### *Predator detection and vigilance behaviour*

A potentially important consequence for Puffins of this visual tuning to meet the requirements of taking small prey items appears to be increased vulnerability to predators due to the broad extent of the blind areas behind the head which results from having the eyes placed more frontally in the skull. This is mitigated to some extent by having the eyes angled upwards, thus extending visual coverage to above and behind the head. However, there is still a large ( $60^\circ$ ) blind sector behind the head and this leaves the birds vulnerable to predatory or kleptoparasitic attack, particularly from gulls (Laridae) and skuas (Stercorariidae) during the breeding period when the birds spend considerable amounts of time on land (Taylor 1982, Harris & Wanless 2011). When attending colonies, Puffins frequently turn their heads in what appear to be saccadic movements. In some situations this ‘head shake’ appears to indicate burrow ownership (Taylor 2011) but saccadic head movements also occur away from burrows and may indicate a high level of vigilance behaviour through which a Puffin scans the total space about it. If this is the function of these head movements then their amplitude should be predicted by the size of the blind sector behind the head; and could be tested by observations in the field. Eye movements could alter the extent of visual coverage behind the head. However, eye movements in birds are complex three dimensional rotations, not just simple translations (Martin 2009), and these complex eye rotations may serve primarily to track the movements of objects in the central part of each eye’s visual field (Land 2015). Thus the ways in which eye movements could alter the visual fields is not clear; they may in fact little alter the extent of the blind area.

### *Vision and vulnerability to collisions*

Amphibious marine bird species are vulnerable to collisions with man-made objects both above and below water, particularly wind and wave driven turbines. Certain groups of birds when in flight are particularly vulnerable to collisions with power lines and turbines due to constraints on their visual fields (Martin 2011, Martin *et al.* 2012). The visual fields of Puffins and Guillemots would suggest that they do not have particular vulnerability when in

flight because the vertical length of their binocular areas mean that they would always maintain visual coverage of the world ahead. This is unlike the situation in vultures whose binocular fields are vertically small and positioned such that when looking downwards in foraging the birds fail to see ahead (Martin *et al.* 2012). Underwater, however, the much reduced visual fields of these auks could well render them vulnerable to underwater obstacles. As argued above, binocularity may well be lost in much of the frontal field. Therefore, small head angle changes could render the birds blind in the direction of travel, at least momentarily. Puffins may well not see very much below them in the frontal field and may not see anything in the direction of the bill since they could rely upon detecting prey items, perhaps in silhouette, using the binocular field that is centred above the horizontal. Clearly the possibility of collision vulnerability underwater is worthy of further investigation.

Both Guillemots and Puffins are also prone to being entangled in gillnets, with Guillemot being one of the most vulnerable species world-wide (Zydalis *et al.* 2013). Analysis of the perceptual reasons for this vulnerability have identified low visual resolution as the primary factor (Martin & Crawford 2015). This is exacerbated by the depths at which Guillemots may forage, as they are sufficient to significantly reduce ambient light levels into the crepuscular-nocturnal range even during daylight. Guillemots may also forage at night, when they may rely upon random encounters with prey rather than visual detection (Regular *et al.* 2011). The reduction and possible loss of binocularity underwater in the direction of travel is another factor which should be considered when accounting for these birds' vulnerability to gillnet bycatch.

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## Figure Captions

**Figure 1.** Photographs of lateral views of the heads of (a) an Atlantic Puffin and (b) a Common Guillemot.

**Figure 2.** Mean ( $\pm$ SE) angular separation of the retinal field margins as a function of elevation in the median sagittal plane in Atlantic Puffins and Common Guillemots.

Positive values indicate overlap of the field margins (binocular vision), negative values indicate the width of the blind areas. The coordinate system is such that the horizontal plane is defined by the elevations 270° (behind the head) and 90° (in front of the head), and 0° is directly above the head, the same co-ordinates are used in

Fig. 3. The drawings show the heads of the birds in profile with key co-ordinates indicated including the direction of the projection of the bill tip (110°). Head orientation for the birds in the drawings are typical for the species when held in the hand and were approximately the positions spontaneously adopted by the birds when placed in the apparatus.

**Figure 3.** Visual fields of Atlantic Puffins and Common Guillemots. (a, b) Drawings of a lateral view of the heads in the positions at which the visual fields were measured and as shown in the diagrams (scale bar 20 mm). (c, d) Perspective views of orthographic projections of the boundaries of the retinal fields of the two eyes. Also shown are the projections of the optic axes and the bill tips. The diagrams use a

conventional latitude and longitude coordinate system with the equator aligned vertically in the median sagittal plane of the bird (grid at 20° intervals). It should be imagined that the bird's head is positioned at the centre of a transparent sphere with the directions of the bill tips and field boundaries projected onto the surface of the sphere. (e, f) Horizontal sections through the visual fields in the planes containing the optics axes. These planes are indicated in the drawing (a, b) by the dashed lines. In the Atlantic Puffins the plane lies at the elevations 260° - 80° (in Fig. 2), and therefore the eyes look slightly upwards, in the Common Guillemots the plane lies at the elevations 280° - 100° and the eyes look slightly downwards with respect to the coordinate system.

**Figure 4.** Vertical sections through the binocular fields of a, Atlantic Puffin and b, Common Guillemot, in the median sagittal plane defined by the vertically oriented equator of the diagrams in Fig. 3 c, d. The line drawings of the heads of the birds show them in the approximate orientations adopted when the visual fields were measured. Scale bars, 20 mm.





