A Comparison of some Aspects of the Retinae of the Manx Shearwater, Fulmar Petrel, and House Sparrow

By JAMES D. LOCKIE

Summary

Most birds are either diurnal or nocturnal. The Manx shearwater is one of the very few that regularly perform such normal activities as feeding, hunting, and flying by day, and other activities, such as homing to the nest, by night. The retinal structure of the Manx shearwater is compared with that of a diurnal passerine (house sparrow) and a diurnal sea-bird (fulmar petrel), in order to determine what features are common to sea-birds and what, if any, may be specific adaptations to vision over a wide range of light intensity. Both sea-birds have a linear area centralis but lack a fovea. The rods of the dark-adapted fulmar and shearwater show great difference of shape from those of the light-adapted. The shearwater has more rods at the area centralis, a larger rod-paraboloid in the dark adapted retina, and a greater ratio of total number of visual cells to ganglion nuclei than has the fulmar.

Introduction

This is a comparison of the retinal structure of the Manx shearwater (P. puffinus (Brünn)), the fulmar petrel (Fulmarus glacialis (L.)), and the house sparrow (Passer domesticus (L.)).

This problem suggested itself while I was studying the breeding habits of the Manx shearwater on the island of Eigg, Inner Hebrides, during 1949. Lockley's observations on Skokholm were confirmed in that, by day, shearwaters were active off-shore, but only at night did they approach or leave the nesting area. Nocturnal activity at the site of the colony in the form of flights about the cliff face was greatest when an overcast sky, mist, or rain reduced light intensity to a minimum (Lockley, 1942). Activity over such a range of light intensity is uncommon in birds, and nothing is known of the visual mechanism by which it is achieved.

No description of the Manx shearwater retina appears to exist, although Wood (1917) shows the fundus of a related species, P. gravis O'Reilly, as seen through the ophthalmoscope. In the initial approach to this problem the shearwater retina is compared with that of a diurnal sea-bird, on one hand, and a diurnal passerine, on the other, in order to determine what features are common to sea-birds and what features, if any, may be specific adaptations to vision over a wide range of light intensity.

Material and Method

The shearwaters, all at least one-year-old birds, were obtained on the island of Eigg in July 1949. The fulmars were taken on Unst, Shetland, in July 1950, and the house sparrows at Edinburgh in February 1951.

A single fulmar and house sparrow were shot by day and were therefore light-adapted. A single shearwater, collected from a nesting burrow by day, was light-adapted in daylight for 30 minutes before killing. One fulmar and one sparrow were collected alive and dark-adapted for one hour in a light-tight box. One dark-adapted shearwater was collected during the night at the nesting colony. This bird was immediately killed and the eyes fixed; the operation was carried out by the indirect light of a small torch.

The retinae were fixed in the following way. The birds that were not shot were first killed with chloroform. A slit was cut round the edge of the cornea and Bouin's fluid pipetted into the eye without delay. The complete bulbus was then excised and placed, whole, in the fixative. Small samples of the retinae were cut with a sharp scalpel: both retina and choroid were readily detached from the sclera in one piece. These selected portions of the retinae were wax-embedded, both paraffin and ester wax giving good results. Sections were cut at 10 μ. Heidenhain's iron haematoxylin was used to stain nuclei, and eosin was used as a counter-stain. Thus both light-adapted and dark-adapted eyes received identical treatment from the moment of fixation.

Retinal pigment was bleached by Mayer's method as given by Gatenby and Painter (1937). All pigment in a 10 μ section was bleached in approximately one hour, with little observable distortion.

Definitions of Some Terms Used

Fovea. The actual pit or depression in the area centralis (Walls, 1942).
Area centralis. A retinal area within which the retina is so constructed as to afford a marked increase in resolving power (Walls, 1942). The area centralis is visible macroscopically as a pale region owing to the thickening of the nuclear layers.
General fundus. The region between the area centralis and the periphery. This region occupies most of the posterior segment of the eye.
Periphery. The extreme edge of the retina near the ora serrata.
Internal convergence of visual cells. Walls (1942) uses this purely anatomical term to describe the convergence of the nervous connexions of many visual cells on one or few ganglion cells. Polyak (1941) and others have shown that whereas only one or few cones connect with one ganglion cell, many rods do so.
Cone. A visual cell possessing an oil droplet situated on the distal side of the ellipsoid.
Rod. A visual cell possessing no oil droplet, and under certain known conditions having a distinct paraboloid, situated on the proximal side of the ellipsoid.

Regions of the Retina

All three species possess a well-defined area centralis, which in both seabirds is ribbon-like and below the horizontal axis of the eye, but which in the sparrow is circular and above the axis. All three species have a pure cone
region, but in both fulmar and shearwater this is restricted to a narrow strip, $60 \times 300 \mu$, along the centre of the area centralis. In the sparrow this region is circular and much more extensive (fig. 1).

The sparrow has, at the centre of the area centralis, a deep convexiciliate fovea with a considerable thinning of the inner nuclear and ganglion layer at this point. Neither fulmar nor shearwater possesses a fovea. In the fulmar there occurs a slight thinning of the ganglion layer at the centre of the area centralis (fig. 2).

![Fig. 1. Plan view of the retina; the broken line indicates the area centralis; the arrow shows the line along which samples were taken for sectioning.](image)

**ANATOMY OF THE VISUAL CELLS**

**Cones**

Selected cone cells of the general fundus for the three species are shown in figs. 3 and 4. They are all similar in form and are typical of the avian cone in possessing a nucleus, myoid, ellipsoid, oil drop, and slim outer segment. The sparrow cones are in general smaller than those of the sea-birds, particularly at the fovea where the outer segments of the cones are rarely preserved in sections. The slimness of the cones at the fovea of the sparrow is to be correlated with the high concentration of visual cells in this region compared with the fulmar and shearwater. In all three retinae the cells tend to become shorter and plumper towards the periphery. This is typical of all retinae (Walls, 1942). Figs. 3 and 4 show a difference in length between dark-adapted and light-adapted shearwater and fulmar cones. Some movement of cones may take place, but this was not seen to occur in any regular way in the retinae examined.

Where cones and rods occur together, the cone nuclei tend to lie nearer the external limiting membrane (figs. 3 and 4). However, at the pure cone region in all three retinae the portion of the cone inside the external limiting membrane tends to be long and filamentous. This is particularly the case in the sparrow fovea where cone nuclei lie some distance from the external limiting membrane (fig. 2).
Rods

Unlike the cones, the rods of each species differ in several respects and, under conditions of light and darkness respectively, assume different shapes within a single species.

In the rods of dark-adapted shearwaters the paraboloid rests almost on the external limiting membrane and the myoid is thick. The paraboloid is large and does not stain with either a nuclear or a cytoplasmic stain (fig. 3). The fulmar rod occupies a similar position to that of the shearwater, relative to the external limiting membrane, but the paraboloid is very much smaller; it also does not stain (fig. 3). Both the shearwater and fulmar paraboloids increase in
size towards the periphery, but the difference between shearwater and fulmar remains roughly constant.

In contrast, the sparrow appears to possess several types of rods. Those at

![Image of visual cells](image)

**FIG. 3.** Selected visual cells from the general fundus of dark-adapted retinae. *m* = myoid, *p* = paraboloid, *o.d.* = oil droplet, *e* = ellipsoid, *o.s.* = outer segment, *n* = nuclei. The two cells on the left in the case of the shearwater and fulmar, and the three on the left in the case of the house sparrow, are rods; the rest are cones. Camera lucida drawings.

![Image of visual cells](image)

**FIG. 4.** Selected visual cells from the general fundus of light-adapted retinae. Lettering as fig. 3. The remarks about rods and cones in the legend to fig. 3 are also applicable here. Camera lucida drawings.

the periphery are the more typical. The paraboloid is usually present and may or may not stain deeply (fig. 3).

Whereas rods are easily identified in the dark-adapted retina, their apparent movement into the pigment layer in the light-adapted retina makes it necessary to bleach the epithelial pigment in order to make the cells visible.

In light-adapted retinae the rods of both shearwater and fulmar change their form greatly. The myoid becomes filamentous, the paraboloid is greatly
reduced in size, and the outer segment is carried deep into the pigment layer, past the cone oil droplet (fig. 4).

In the sparrow, rods occur in similar positions to those in the dark-adapted eye. It is not possible, in the specimens examined, to be sure of the homologies of the structures observed in the light-adapted sparrow rod, nor is it possible to say if movement occurs or not (fig. 4).

![Diagram of visual cells](image)

**Fig. 5**

**Fig. 6**

**Fig. 5.** Double cones from the periphery of the house sparrow.

**Fig. 6.** Anomalous cells from the fulmar retina.

### Anomalous cells

Structures resembling double cones occur in the sparrow retina (fig. 5). They occupy approximately 30 per cent. of the cells at the periphery and are present to a very small extent in the fundus. Cells similar to the accessory member of double cones were observed on either side of the fulmar pure cone region, but none was observed in close union with a cone (fig. 6). They are somewhat intermediate between rod and cone although the oil droplet observed may well be an artifact.

No intermediate cells were found in the shearwater retina. All cells were either distinctly rods or distinctly cones.

### A Numerical Comparison of the Visual Cells

Counts of visual cells and ganglion nuclei were made with a 1/2-inch oil immersion objective and a x9 ocular, in which a slit diaphragm had been introduced between eye- and field-lenses so as expose a strip 50 μ in width. Each section to be counted was orientated under the slit diaphragm so that the visual cells lay parallel to those sides of the diaphragm which were 50 μ apart. All the cells in each field were counted at all focus levels; sections were cut at 10 μ and each count thus indicates the number of cells observed in a portion of retina of area 500 sq. μ.

Tables 1 and 2 show the mean number of visual cells and ganglion nuclei which were counted in an area of 500 sq. μ at the regions of the retina indicated.
The mean values are calculated from several counts made at each region; the standard error of the mean (sx) and the number of counts made, are also listed. When significance is claimed it is at a 0.01 level of probability.

The house sparrow surpasses both sea-birds in the density of cones at comparable parts of the retina, while both sea-birds possess many more rods than the sparrow.

**Table 1. The mean number of rods and cones counted in an area of 500 sq. μ, at the regions of the retina indicated**

<table>
<thead>
<tr>
<th>Regions of retina</th>
<th>Cones</th>
<th>Rods</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Shearwater</td>
<td>Fulmar</td>
</tr>
<tr>
<td>Fovea</td>
<td>37.20</td>
<td>37.80</td>
</tr>
<tr>
<td></td>
<td>1.20</td>
<td>0.69</td>
</tr>
<tr>
<td></td>
<td>5.00</td>
<td>5.00</td>
</tr>
<tr>
<td>Area centralis</td>
<td>25.67</td>
<td>24.57</td>
</tr>
<tr>
<td></td>
<td>0.84</td>
<td>1.13</td>
</tr>
<tr>
<td></td>
<td>6.00</td>
<td>7.00</td>
</tr>
<tr>
<td>Edge of area centralis</td>
<td>20.28</td>
<td>21.50</td>
</tr>
<tr>
<td></td>
<td>0.98</td>
<td>0.71</td>
</tr>
<tr>
<td></td>
<td>18.00</td>
<td>10.00</td>
</tr>
<tr>
<td>General fundus</td>
<td>10.95</td>
<td>17.80</td>
</tr>
<tr>
<td></td>
<td>0.76</td>
<td>0.72</td>
</tr>
<tr>
<td></td>
<td>19.00</td>
<td>15.00</td>
</tr>
</tbody>
</table>

**Table 2. The mean number of ganglion nuclei counted in an area of 500 sq. μ, at the regions of the retina indicated**

<table>
<thead>
<tr>
<th>Regions of retina</th>
<th>Shearwater</th>
<th>Fulmar</th>
<th>House sparrow</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area centralis</td>
<td>28.86</td>
<td>26.00</td>
<td>42.40</td>
</tr>
<tr>
<td></td>
<td>0.46</td>
<td>1.34</td>
<td>1.21</td>
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<tr>
<td></td>
<td>7.00</td>
<td>7.00</td>
<td>10.00</td>
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<tr>
<td>Edge of area centralis</td>
<td>8.89</td>
<td>13.50</td>
<td>22.75</td>
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<tr>
<td></td>
<td>0.72</td>
<td>0.38</td>
<td>0.89</td>
</tr>
<tr>
<td></td>
<td>19.00</td>
<td>10.00</td>
<td>12.00</td>
</tr>
<tr>
<td>General fundus</td>
<td>2.69</td>
<td>6.80</td>
<td>11.40</td>
</tr>
<tr>
<td></td>
<td>0.41</td>
<td>0.67</td>
<td>1.07</td>
</tr>
<tr>
<td></td>
<td>22.00</td>
<td>15.00</td>
<td>5.00</td>
</tr>
</tbody>
</table>

Table 3 shows the internal convergence of visual cells (see definition, p. 348) as measured by the ratio of the total number of visual cells to that of ganglion nuclei in areas of 500 sq. μ. This estimate of the number of visual cells connecting with one ganglion cell is approximate only, owing to horizontal connections in the avian retina, and it does not appear to apply to the fovea of the
sparrow, where the visual cells connect with ganglia situated in the foveal ridge (Ramón y Cajal, quoted by Polyak, 1941). However, apart from the fovea, the degree of convergence measured in this way probably corresponds fairly closely to the true convergence.

Convergence outside the fovea is greatest in the shearwater and least in the sparrow.

**Table 3. The ratio of the total number of visual cells to that of ganglion nuclei**

<table>
<thead>
<tr>
<th>Regions of retina</th>
<th>Shearwater</th>
<th>Fulmar</th>
<th>House sparrow</th>
</tr>
</thead>
<tbody>
<tr>
<td>Area centralis</td>
<td>1.3</td>
<td>1.0</td>
<td>1.0</td>
</tr>
<tr>
<td>Edge of area centralis</td>
<td>3.0</td>
<td>2.5</td>
<td>1.3</td>
</tr>
<tr>
<td>General fundus</td>
<td>8.3</td>
<td>4.3</td>
<td>1.7</td>
</tr>
</tbody>
</table>

**Discussion**

The two sea-birds resemble one another and differ from the passerine in the structure of the area centralis. In both shearwater and fulmar it is linear and lies below the horizontal axis of the eye, whereas in the sparrow it is circular and lies above the axis. This difference may be related to the mode of life of the birds. The circular area is frequently found in tree-dwelling forms (e.g. hoopoe, humming bird, and red-headed woodpecker), whereas the linear area appears to be typical of birds living in a flat and featureless landscape, (e.g. great bustard, flamingo, ostrich (Wood, 1917)). Pumphrey (1948) has suggested that the linear area centralis and fovea appear to be suited to fixation of the horizon and to the preferential increase in sensitivity to vertical movements of objects in relation to the horizon.

The sparrow possesses a deep convexiclavate fovea, whereas neither the shearwater nor fulmar show this structure. The deep fovea is usually associated with strongly diurnal vision, as it is most highly developed in hawks, swallows, and kingfishers. However, the lack of a fovea does not appear necessarily to be universal in sea-birds, for O'Day (1940) records a deep fovea in the albatross Diomedea c. cauta Gould.

It is generally accepted that two main types of visual cells occur in most retinæ, and that these cells, the cones and rods, are concerned with daylight and night vision respectively. The basis for this duplicity theory is the morphological distinctness of the two populations of cells in any one retina. The theory is supported by other evidence. Where an animal possesses only cones or only rods it is invariably found that it is wholly diurnal or wholly nocturnal, respectively. The nerve connexions to each type of cell are different, many rods, but only one or a few cones, being connected to one fibre (Polyak, 1941). The Purkinje phenomenon further suggests that two distinct populations of cells are involved.

The pure cone region of the retinæ examined differs in extent in the three species. This is probably a reflection of the habits of the birds. In the shearwater the pure cone region is small in order to minimize the area which is
non-functional at night and yet large enough to provide a region of accurate
vision for day use. It seems, however, too small to allow the development of a
fovea (see fig. 2). To some extent this may also be true of the fulmar. The exten-
tensive pure cone and cone-rich region of the sparrow is in keeping with the
strongly diurnal habits of this bird.

Considerable change of the rods in dark- and light-adapted retinæ respec-
tively has been observed in the shearwater and fulmar but not in the sparrow.
Garten (1907) showed that movements occurred in the fowl and pigeon, and
Arey (1915) reviewed all reports of photomechanical changes in the retinæ of
vertebrates. His conclusion was that while the movements are probably re-
lated to conditions of light and darkness, their functional significance remains
obscure. The placing of rods near the external limiting membrane in the dark-
adapted eye may have some bearing on sensitivity.

The fulmar and shearwater retinæ are very similar. The anatomical differ-
ences are, in the shearwater, the larger rod paraboloid, the greater number of
rods in the area centralis, and the slightly higher ratio of visual cells to ganglion
nuclei.

Owls show a number of adaptations to the nocturnal habit. Sensitivity is
achieved largely by the sacrifice of features which give acuity in the diurnal
eye. In addition to large numbers of filamentous rods and a high ratio of visual
cells to ganglion nuclei, the structure of the eye as a whole is modified. The
diameter of the lens is increased, it becomes more spherical, and to accom-
modate it the anterior portion of the eye is enlarged. At the same time, the
posterior portion is reduced in size (Walls, 1942). This study has been con-
cerned mainly with visual cells, and accurate measurements of the dimensions
of the eyes of the three species have not been made. However, fig. 7 shows
schematized sections of the eye of owl, shearwater, and pigeon.

No extreme specialization of the eye as a whole, as is evident in the owl
occurs in the shearwater.

Nightjars have large eyes, specialized in much the same manner as those of
the owl, but in addition show 'eyeshine', presumably caused by a tapetum
(Walls, 1942). No 'eyeshine' was observed in any of many shearwaters handled
at night by torchlight, although this was not specifically looked for.
It seems therefore, that sensitivity in the shearwater is achieved in an entirely different manner from that in owls and nightjars. It is, of course, possible that some other sense is used in conjunction with vision. For example, Lockley (1942) suggested that the call is important, in homing to the nest.

Acknowledgements

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References

Wood, Casey A., 1917. The fundus oculi of birds, especially as viewed by the ophthalmoscope. Chicago (Lakeside Press).