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The eyes of oilbirds (*Steatornis caripensis*): pushing at the limits of sensitivity

Abstract An extreme example of a low light-level lifestyle among flying birds is provided by the oilbird, *Steatornis caripensis* (Steatornithidae, Caprimulgiformes). Oilbirds breed and roost in caves, often at sufficient depth that no daylight can penetrate, and forage for fruits at night. Using standard microscopy techniques we investigated the retinal structure of oilbird eyes and used an ophthalmoscopic reflex technique to determine the parameters of these birds' visual fields. The retina is dominated by small rod receptors (diameter 1.3 ± 0.2 μm; length 18.6 ± 0.6 μm) arranged in a banked structure that is unique among terrestrial vertebrates. This arrangement achieves a photoreceptor density that is the highest so far recorded ($\approx1,000,000$ rods mm^{-2}) in any vertebrate eye. Cone photoreceptors are, however, present in low numbers. The eye is relatively small (axial length 16.1 ± 0.2 mm) with a maximum pupil diameter of 9.0 ± 0.0 mm, achieving a light-gathering capacity that is the highest recorded in a bird (f-number ≈1.07). The binocular field has a maximum width of $38°$ and extends vertically through $100°$ with the bill projecting towards the lower periphery; a topography that suggests that vision is not used to control bill position. We propose that oilbird eyes are at one end of the continuum that juxtaposes the conflicting fundamental visual capacities of sensitivity and resolution. Thus, while oilbird visual sensitivity may be close to a maximum, visual resolution must be low. This explains why these birds employ other sensory cues, including olfaction and echolocation, in the control of their behaviour in low-light-level environments.

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Introduction

In all eye types, visual performance is a compromise between the conflicting fundamental capacities of sensitivity and resolution (Land and Nilsson 2002). The balance of these capacities in any one eye is achieved through adaptations of both optical and retinal structures, and is assumed to reflect both the behaviour and the ecology of the species (Archer et al. 1999). In birds, flight is considered to be controlled primarily by vision and requires a high degree of spatial resolution (Davies and Green 1994). However, a small number of birds are active at naturally low light levels, where high sensitivity is required (Martin 1990). The most extreme example of a low-light-level lifestyle among flying birds is provided by the cave-dwelling oilbirds, *Steatornis caripensis*, Steatornithidae, Caprimulgiformes (Thomas 1999).

Oilbirds (see Fig. 1a, b) breed and roost in caves often at sufficient depth that no daylight can penetrate, and this must result in the majority of individuals never experiencing throughout their lifetime (up to 12 years) natural light levels above those of maximum moonlight (Thomas 1999). Within the caves, oilbirds employ echolocation using audible click vocalisations, which provide low spatial resolution, to avoid in-flight collisions (Konishi and Knudsen 1979) although, due to a low wing loading, flight speeds are low (Thomas 1999). However, their nocturnal foraging for fruit is thought to be guided primarily by vision, with olfaction playing a secondary role (Snow 1961).

We investigated the adaptations of oilbird eyes to this lifestyle through the examination of retinal structure,

visual fields and the light-gathering capacity of the eye's optical system.

Methods

We obtained oilbirds under licence from the Instituto de Parques of Venezuela, from the breeding colony, Cueva del Guácharo, in the Parque Nacional El Guácharo near Caripe, north-eastern Venezuela. Eye dimensions (axial length, equatorial diameter, maximum entrance pupil) were determined in freshly excised eyes and the retinas were prepared for histology using standard procedures to produce sections longitudinal to the photoreceptors (Rojas et al. 1999). Photomicrographs of semi-thin sections were prepared using a Hitachi H-600 electron microscope, and from these micrographs cell characteristics and density were determined in sample sectors from across the retina. In order to present interspecific comparisons of the relative densities of photoreceptors, we calculated the number of photoreceptor cells that would occur proportionally in a 1-mm^2 area of retina, assuming symmetry of cellular densities about the sampling points. Visual field parameters were determined in live birds using an ophthalmoscopic reflex technique as used previously with a range of bird species (Martin and Katzir 1995, 1999).

Results

Retinal structure

The rod photoreceptors (diameter 1.3±0.2 μm; length 18.6±0.6 μm) occur at a uniformly high density across all sectors of the retina with an average density of about 1,000,000 rods mm^{-2}, i.e. approximately1 rod μm^{-2}. This high rod density is achieved by the rods being arranged in irregular banks that are three receptors deep (Fig. 1c). Despite this high rod density the retina is not, however, a pure rod retina. It contains clearly distinguishable single cone receptors and some double cones, both of which contain oil droplets in their inner segments. However, cone receptors occur at a very low average density (≈70 mm^{-2}), i.e. 15,000 times less than the rod density.

We found no evidence of a tapetum in either the retina or choroid. Both flash photographs (Fig. 1a, b) and viewing the retina with an ophthalmoscope showed no evidence of eye-shine, and histological preparations showed no evidence of tapetum-like structures, such as guanine crystals or oil droplets, in a layer behind the photoreceptors (Nicol and Arnott 1974).

Optical structure and visual fields

Although oilbirds have a relatively large-eyed appearance (Fig. 1a, b), the eyes are not exceptionally large, having an axial length of 16.1±0.2 mm and a maximum pupil diameter of 9.0±0.0 mm (n=4). Despite the oilbird's apparent frontal-eyed appearance (Fig. 1b), its functional binocular field is relatively small (Fig. 2), with a maximum width of 38° and vertical extent of 100°.
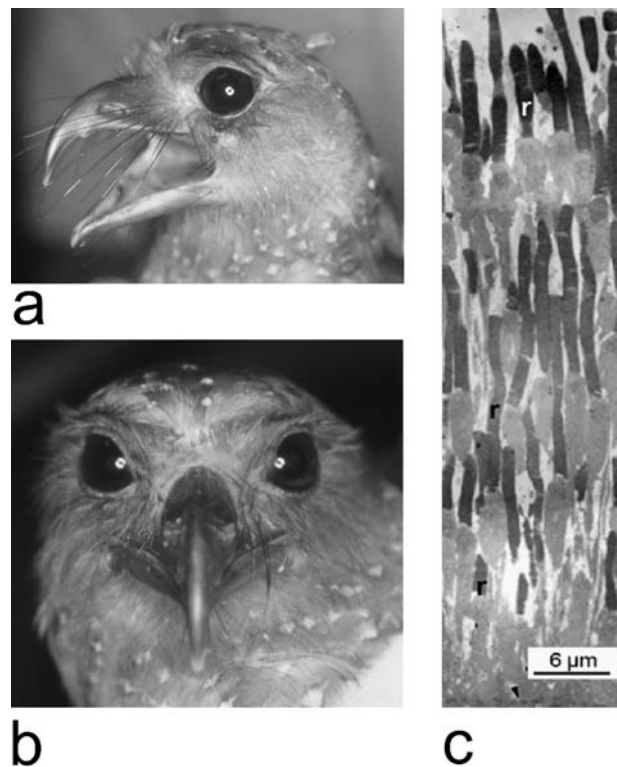

Fig. 1a–c Oilbird (*Steatornis caripensis*) eyes, retina and visual fields. **a** Three-quarter view of the head showing the prominent eyes and long rictal bristles. **b** Frontal view of the head taken from the horizontal plane (as in Fig. 2). **c** Photomicrograph of the outer layer of the retina showing the rod outer segments *r*, distributed on three levels above the external limiting membrane (which is at the bottom of the photograph)
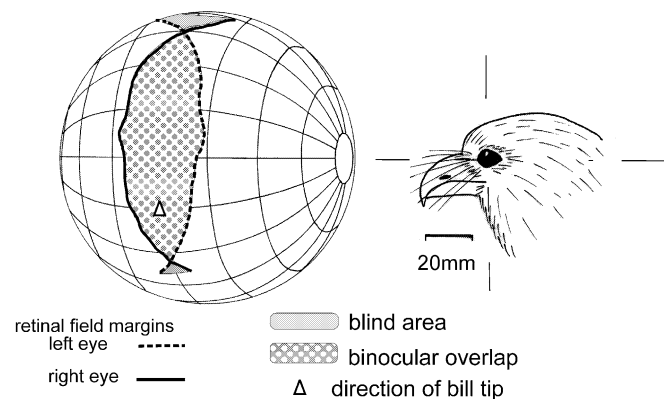

Fig. 2 Perspective view of the projection of the binocular field (mean of three birds). For coordinates the diagram uses the conventional latitude and longitude system but with the equator aligned vertically in the median sagittal plane of the head (grids are at 20° intervals). It should be imagined that the bird's head lies at the centre of a transparent sphere with the features of the field projected onto its surface. The bird's head is looking to the left of the observer, in a position similar to the view shown in Fig. 1a but at a more acute angle. The sketch shows the head in the correct vertical orientation for the coordinate system. This was also the head position employed when measurements were made

Discussion

Retinal adaptations and nocturnal activity

With an average density of about 1,000,000 rods mm^{-2}, the oilbird retina has not only the highest rod density recorded in any vertebrate (Fite and Rosenfield-Wessels 1975; Meyer 1977) but exceeds by approximately ×2.5 the highest density recorded for photoreceptors of any type in bird retinas. The brown falcon, *Falco berigora*, a diurnal raptor, attains a maximum cone density of 380,000 mm^{-2} which is the highest yet recorded in a vertebrate eye (Fite and Rosenfield-Wessels 1975; Miller 1979; Reymond 1987). Furthermore, the oilbird's rod photoreceptor density clearly exceeds the theoretical limit for the packing density of independently functioning photoreceptors in vertebrate retinas (Miller 1979), and the size of oilbird rod photoreceptors (diameter 1.3±0.2 μm, length 18.6±0.6 μm) is close to a theoretical minimum limit on photoreceptor diameter (Miller 1979). Oilbird rods have similar dimensions to those of rods in humans (1.5×25 μm) (Bowmaker and Dartnall 1980) and tawny owls *Strix aluco* (1.5×30 μm) (Bowmaker and Martin 1978), and are smaller than rods in the retina of a diurnal bird, the rock pigeon *Columba livia* (4×30 μm) (Bowmaker 1977). The high packing density of these small rods in the oilbird retina is achieved by their arrangement into a banked structure (Fig. 1c) and this is the first time that such a structure has been reported in a terrestrial vertebrate. Banked retinas of this kind have been described previously only in deep-sea fish, but in these species the rods are typically much larger, with diameters of up to 14 μm and lengths up to 200 μm (Locket 1977). In these species the banked retina is interpreted as an adaptation for the detection of extreme low ambient light levels and of point sources of light produced by the photophores of other fish. The layered arrangement of receptors serves to increase the probability of a photon being captured by the rod outer segments, with the deeper layers catching photons which have either been missed by, or have failed to be absorbed within, the outer segments of the shallower layers, hence enhancing overall sensitivity. However, the banking of the rod receptors in this way must enhance sensitivity at the expense of spatial and temporal resolution (Locket 1977). Clearly, measures of both absolute sensitivity and acuity in oilbirds would help in understanding the function of this apparently unique banked retinal structure.

The very low density of cone photoreceptors ($\approx$70 mm^{-2}), and the very low cone to rod ratio ($\approx$1:123), suggests that vision in oilbirds at high light levels will achieve only very low spatial resolution. Thus, while owls have a maximum cone receptor density well in excess of that of the oilbirds (5,500 mm^{-2}), and a rod:cone ratio of 13:1 (Fite 1973), their wavelength discrimination and spatial resolution at diurnal light levels are poor compared with the vision of diurnal birds in which maximum cone densities in excess of 300,000 mm^{-2} are found (Reymond 1987).

The absence of a tapetum in oilbird retinas is noteworthy. Tapeta are a common feature of mammalian and reptilian retinas in nocturnally active species (Walls 1942) and are also found in deep-sea fish (Locket 1977). A retinal tapetum has been recorded in other species of caprimulgiform birds including the pauraque *Nyctidromus albicollis*, common nighthawk *Chordeiles minor*, and common poorwill *Phalaenoptilus nuttallii* (Nicol and Arnott 1974) but we did not find evidence of such a structure in this caprimulgiform bird.

Optical adaptations and nocturnal activity

The overall dimensions of oilbird eyes (axial length 16.1 mm; maximum pupil diameter 9.0 mm) are considerably smaller than found in some owls, e.g. axial length 28.5 mm, maximum pupil diameter 13.3 mm in tawny owls (Martin 1994a), axial length 38.7 mm in great horned owls (Murphy et al. 1985). However, if it is assumed that the axial length:focal length ratio in oilbirds = 0.6 (as in other bird eyes, including those of owls and pigeons) (Martin 1994a), then the minimum f-number [focal length/maximum entrance pupil diameter; a measure of the maximum light gathering capacity of an optical system when viewing extended light sources (Land 1981)] of oilbird eyes = 1.07. This means that when viewing the same scene the oilbird eye retinal image will be ~1.5, ~3.2, and ~4 times brighter than in tawny owl (f-number = 1.30), rock pigeon (f-number = 1.98) and human (f-number = 2.13) eyes, respectively (Martin 1994a). Thus, optically the oilbird eye can out-perform the light gathering capacity of the eye of a nocturnally active owl as well as that of humans and a diurnally active bird.

The frontal binocular field of oilbirds (maximum width 38°; vertical extent 100°) (see Fig. 2) is broader than in many diurnally active forms (maximum widths of 20–30° are typical) but narrower than in tawny owls (maximum width 47°; vertical extent 80°) (Martin and Katzir 1999). The relatively longer and narrower binocular field of oilbirds is similar to that of a range of bird species that differ markedly in their diets and general ecology (Martin and Katzir 1999). The positioning of the bill at the lower edge of the binocular field in oilbirds is similar to that found in species which exploit non-visual cues in guiding the bill during foraging. These include tawny owls, which employ auditory cues to locate active prey that are captured with the feet (Martin 1990), and some long-billed shorebirds (e.g. woodcock *Scolopax rusticola*, Charadriidae) and dabbling ducks (Anatidae), whose foraging activities are guided primarily by tactile cues from the bill (Martin 1994b; Guillemaine et al. 2002). The similarity of overall frontal visual field topography between the oilbirds and a wide range of bird species that differ markedly in their behavioural ecology is striking. It supports the hypothesis (Martin and Katzir 1999) that the characteristic larger and more frontally positioned eyes of owls are not primarily related in these

species to nocturnal habits, as is frequently supposed (Voous 1988; Welty and Baptista 1988), but may be related to the more specific use of auditory cues for the location of prey items by owls.

Sensitivity versus resolution

The combination in oilbird eyes of an optical structure that achieves high light-gathering power, with a retina packed with small rod receptors arranged at high density in a banked arrangement, suggests that these eyes are at one end of the continuum that juxtaposes the conflicting fundamental visual capacities of sensitivity and resolution (Land and Nilsson 2002). That oilbird eyes are not inherently large suggests that size per se is not primarily related to high visual sensitivity in birds, as is often assumed from casual observation (Voous 1988; Welty and Baptista 1988).

The oilbirds' high visual sensitivity–low resolution retinal structure is combined with a visual field topography that indicates a low reliance upon visual cues for guidance of the bill. This suggests that a range of sensory cues other than vision may be employed by oilbirds in a complementary manner to achieve their nocturnal mobility at low light levels. Within caves, and above the tree canopy at night, oilbirds would seem well equipped to detect the lowest light levels that may occur there and hence be able to use vision for general orientation, but not for tasks involving high spatial resolution. This general orientation is perhaps complemented by tactile cues from the prominent rictal bristles (Fig. 1a) at close range. At an intermediate distance, echolocation and other auditory signals may provide cues for the presence of objects and conspecifics, while olfaction may provide cues to the presence of fruit food sources at greater distances.

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