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# BINOCULAR VISION AND NOCTURNAL ACTIVITY IN OILBIRDS (*STEATORNIS CARIPENSIS*) AND PAURAQUES (*NYCTIDROMUS ALBICOLLIS*): CAPRIMULGIFORMES

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**Resumen. – Visión binocular y actividad nocturna en el Guácharo (*Steatornis caripensis*) y el Chotacabras Pauraque (*Nyctidromus albicollis*). –** Las características del campo visual fueron medidas en el Guácharo (*Steatornis caripensis*) y el Chotacabras pauraque (*Nyctidromus albicollis*) utilizando una técnica de reflejo oftalmoscópico. Aunque los ojos de estas aves dan la apariencia de estar desplazados frontalmente, en la práctica, sus campos binoculares funcionales son relativamente estrechos, con un máximo de 38° de anchura y un alcance vertical de 100° para el Guácharo, y 25° x 110° para el Chotacabras pauraque. La anchura máxima se ubico en 10° arriba del eje horizontal en ambas especies. En el Chotacabras pauraque, el área ciega detrás de la cabeza es igual a 89°, mientras que el campo retiniano monocular es de 148°. El campo binocular aparente (óptico) es de 65° de ancho, en comparación con el campo funcional (retiniano) de 25° aproximadamente. Los campos binoculares de estas aves preponderantemente nocturnas son similares a los de especies de aves primordialmente diurnas. Esto sustenta la hipótesis de que la binocularidad en aves tiene que ver más con la proyección contra-lateral de cada ojo que con la habilidad de lograr imágenes dispares del mismo objeto desde los dos ojos. Tales proyecciones contra-laterales terminan en una sección del campo de cada ojo que proporciona un campo óptico de flujo simétricamente ampliado, en vez de funcionar como una base para la extracción de una información de orden más elevado a partir de imágenes dispares.

**Abstract. –** Visual field characteristics were measured using an ophthalmoscopic reflex technique in Oilbirds (*Steatornis caripensis*) and Pauraques (*Nyctidromus albicollis*). Despite these birds' apparent frontal-eyed appearance, their functional binocular fields are relatively small with a maximum width of 38º and vertical extent of 100º in Oilbirds, and 25º x 110º in Pauraques. Maximum width occurred 10º above the horizontal in both species. In Pauraques, the blind area behind the head equals 89º and the monocular retinal field equals 148º. The apparent (optical) binocular field is 65º wide, compared with the functional (retinal) field approx. 25º. The binocular fields in these highly nocturnal birds are similar to those of strongly diurnal species. This supports the hypothesis that binocularity in birds is concerned with the contra lateral projection of each eye rather than achieving disparate images of the same object from two eyes. These contra lateral projections result in a section of the field in each eye that provides a symmetrically expanding optic flow field, rather than a basis for the extraction of higher order information from disparate images. *Accepted 30 September 2003.*

**Key words**: Oilbird, Pauraques, *Steatornis caripensis*, *Nyctidromus albicollis*, vision, birds, binocular, visual fields, binocularity.

## INTRODUCTION

In all eye types visual performance is a compromise between the conflicting fundamental capacities of sensitivity and resolution (Land & Nilsson 2002). The balance of these capacities in any one eye is achieved through adaptations of both optical and retinal structures, and this balance of sensitivity and resolution is assumed to reflect both the behavior and the ecology of the species (Archer *et al.* 1999). In most birds, flight is considered to be controlled primarily by vision which requires a high degree of spatial resolution (Davies & Green 1994) and that this outweighs the requirements for high sensitivity. However, a small number of birds are active in naturally low light-levels, where high sensitivity is required (Martin 1990). The majority of such nocturnally active species are found among the owls (Strigiformes) and the nightjars and their allies (Caprimulgiformes). It is among birds from these orders that adaptations of optical and retinal structures that have evolved to maximize sensitivity are likely to be found. Some owls live an almost exclusively nocturnal lifestyle under the cover of closed canopy woodlands and must experience some of the lowest naturally occurring natural light levels (Martin 1990). Nightjars, although mainly nocturnal, tend to fly in the open airspace above tree canopies or in sparsely vegetated habitats and hence experience higher night time light levels. However, 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). Recent investigation of the adaptations of Oilbird and nightjar eyes to these nocturnal conditions (Rojas *et al.* 2004) have shown that the retina of Oilbirds exhibits extreme adaptations for sensitivity. Rod photoreceptors occur at a very high density that is achieved by the receptors being arranged irregularly in a various-tiered structure of a kind hitherto described only among deep-sea fish (Locket 1977). However, compared with owl eyes, the overall eye size and entrance pupil diameter of Oilbird eyes are not exceptional.

It has been assumed that large binocular fields are also associated with the nocturnal habit and that this feature of visual topography is typically combined with adaptations of optics and retinal structures to constitute a syndrome of adaptations associated with the nocturnal habit, e.g., Walls 1942, Tansley 1965, Welty & Baptista 1988, Voous 1988). However, investigation of visual fields in Tawny Owls (*Strix aluco*, Strigidae) has already shown the binocular region to be considerably smaller than appears from anecdotal observation with a maximum width of 47º (Martin, 1984). It is also clear than binocular field size is not maximized within constraints imposed by the eye's optics. For example, it has been shown that if full use were made of the optical field of each eye then maximum binocular field width would equal 111º in Tawny Owls. Never-the-less, interspecific comparison has shown that the binocular field of owls are the broadest recorded in birds with the majority of species having a maximum binocular field width between 20º and 30º, and in some species binocular fields are only 10º in maximum width (Martin & Katzir 1999). These interspecific comparisons have lead to the hypothesis that binocularity in birds is not primarily concerned with having two eyes looking at the same scene in order to extract higher order information from their disparate images, but is simply a consequence of placing each eye so as to have a portion of its field facing forward for the extraction of information from an expanding optical flow field (Martin & Katzir 1999). Within this framework, the width of the binocular field of any particular species is

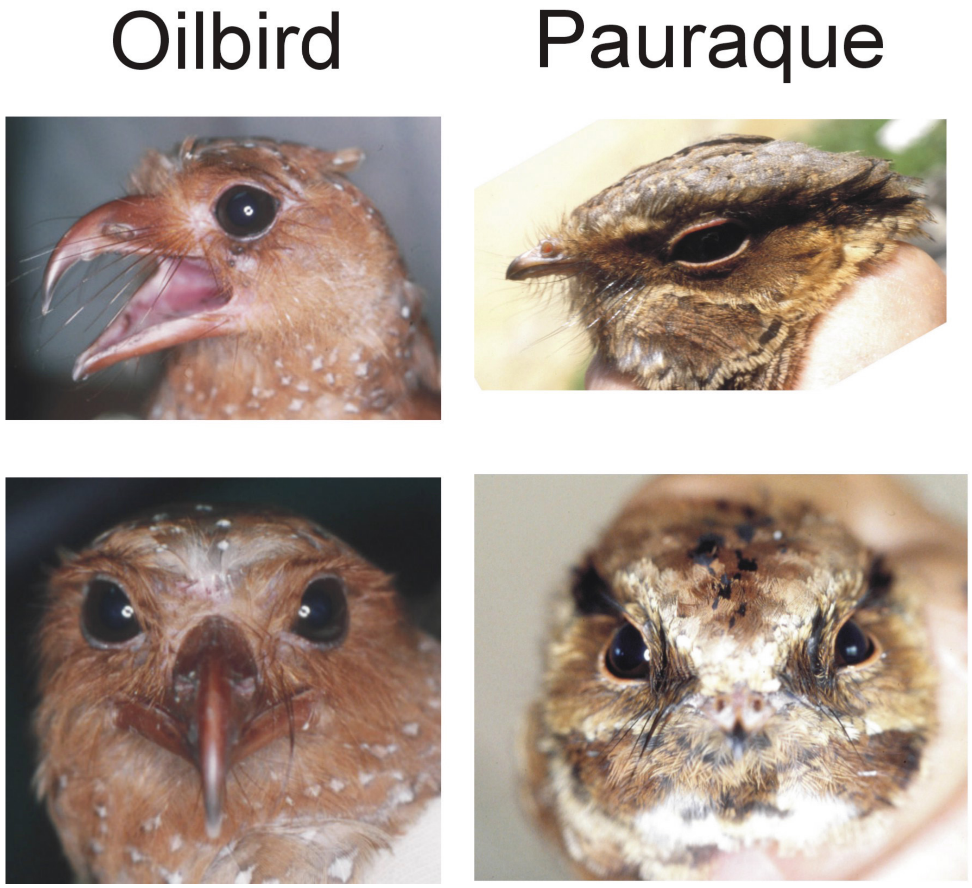

FIG. 1. Oilbird (*Steatornis caripensis*) and Pauraques (*Nyctidromus albicollis*): Top, three quarter views of the heads showing the prominent eyes and long rictal bristles. Bottom, frontal views of the heads taken from the horizontal plane (as defined in Figures 2 and 3).

viewed as determined by the need for an expanding flow field for the control of flight or of head movements. This is balanced against requirements for lateral vision, with the balance moderated by the degree to which other senses are involved in foraging tasks (Martin & Katzir 1999). To test the wider generality of the association of a wider frontal binocular field and nocturnality, and the above hypothesis concerning the general function of binocularity in birds, we have determined the binocular field characteristics of Oilbirds and Pauraques (*Nyctidromus albicollis,* Caprimulgidae).

Oilbirds (Fig. 1) 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 life-time natural light levels above those of maximum moonlight (maximum recorded life-span 12 years) (Thomas 1999). Within caves, Oilbirds employ echolocation using audible click vocalizations which provides low spatial resolution to avoid in-flight collisions (Konishi & Knudsen 1979) although, due to a low wing loading, flight speeds are low (Thomas 1999). However their nocturnal foraging for fruits is thought to be guided primarily by vision, with olfaction playing a secondary role (Snow 1961).

Pauraques (Fig. 1) inhabit more open habitats where they forage on the wing between dusk and dawn for insects flying in the open airspace above vegetation (Cleere 1999). At night they are likely to experience similar light regimes to the Oilbirds, but since they are not cave dwelling they are more likely to be exposed to crepuscular light levels when foraging and may be exposed to high daytime light levels when roosting.

## METHODS

Oilbirds and Pauraques were obtained under license from the Instituto de Parques of Venezuela. Oilbirds were obtained from the breeding colony, Cueva del Guácharo, in the Parque Nacional El Guácharo near Caripe, northeastern Venezuela. Pauraques were obtained in the Mapire region (State of Anzoátegui) in farmland situated within the Venezuelan llanos habitat type. Birds were caught after dusk by the use of spotlights and throw-nets.

Visual field parameters were determined in live birds (three birds of each species) using an ophthalmoscopic reflex technique as used previously with a range of bird species (Martin & Katzir 1995). Each bird was restrained with the body immobilized and the head position fixed by holding the bill. In Oilbirds the bill was held in a specially built metal holder coated with cured silicone sealant to produce a non-slip surface and the bill held in position by tape (Micropore®). In Pauraques, because of the small bill size, the head was held manually in position within a specially designed holder but it was not taped in position. The body was held in a cradle of foam rubber and secured by straps (Velcro®). The bill holder was mounted on an adjustable mechanism and the head positioned so that the mid-point of a line joining the corneal vertices was at the approximate centre of the visual perimeter apparatus. The perimeter's co-ordinate system followed conventional latitude and longitude with the equator aligned vertically in the birds' median sagittal plane and this co-ordinate system is used for the presentation of the visual field data (Fig. 2). Each bird's head was positioned with the plane through the eyes and bill tip pointing at an angle of approximately 20° below the horizontal. Heads in this position are depicted in Figure 2. The projection of the bill tip when measurements were made was determined accurately from photographs and the visual field data corrected for this.

The eyes were examined using an ophthalmoscope mounted on the perimeter arm. The visual projections of the limits of the frontal retinal visual field at elevations above and below the bill for each eye were determined as a function of elevation (10° intervals) in the median sagittal plane. The retinal visual field is the functional visual field. It is defined as that portion of the optical visual field that is served by retina. The optical visual field is the limit of visual field determined by the eye's optical system. It is this optical field that is seen in casual observations of the eye and its limit is defined by the positions from which it is possible to look through the pupil and observe the black pigmentation of the fundus. The retinal field is always smaller than the optical field. In birds, this gives rise to the impression that visual fields, including frontal binocular fields, are more extensive than they functionally are.

In the Pauraques, we were able to determine the limit of the optical field at elevations about the horizontal as well as the limits of the retinal field at all elevations in the frontal

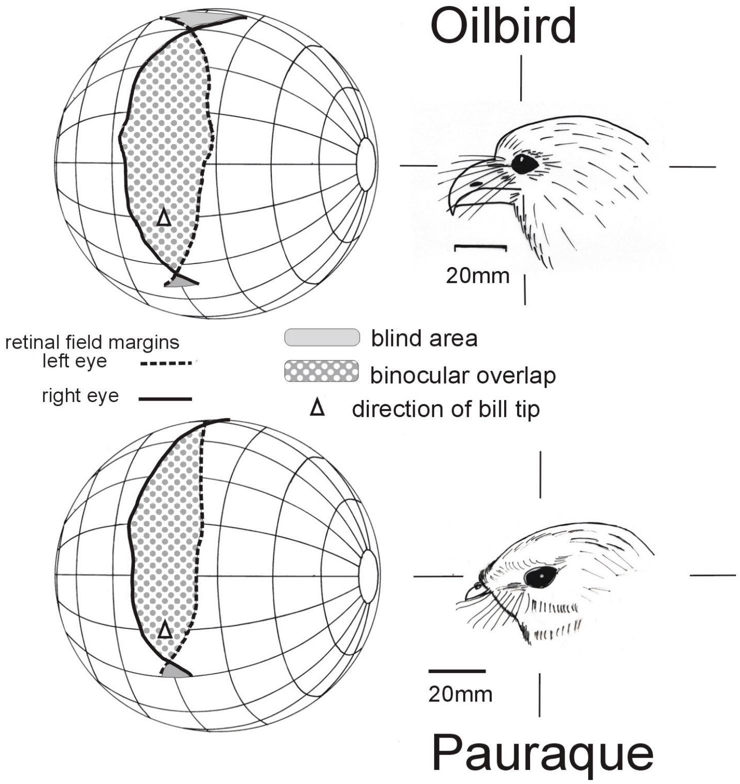

FIG. 2. Perspective views of the projection of the binocular fields in Oilbirds and Pauraques. For co-ordinates the diagram uses the conventional latitude and longitude system but with the equator aligned vertically in the median sagittal plane of the head. Grids are at 20º intervals. It should be imagined that each bird's head lies at the centre of a transparent sphere with the features of the field projected onto its surface. The birds' heads are pointing to the left of the observer in a position similar to the view shown in Figure 1 but at a more acute angle. The sketch (taken from a photograph) shows each head in the correct vertical orientation for the co-ordinate system. This was also the approximate head-bill angle employed when measurements were made.

sector. We also determined the limit of the retinal and optical fields in the horizontal plane directly behind the head in both Oilbirds and Pauraques. By combining these measures with those for the frontal field limit in the same horizontal, plane we were able to determine the total width of each monocular retinal field and the extent of the blind area in the horizontal plane.

Procedures, which in other bird species, e.g., herons (Martin & Katzir 1994), have readily elicited eye movements when birds are positioned in this apparatus (such as light tapping sounds and flashes of light in the periphery of the visual field) were employed to determine whether spontaneous eye movements were present and, if present, to measure their maximum amplitude. This can be achieved by determining the extreme positions at which the limit of the retinal field projects at different elevations. For a detailed description of the apparatus and methods, see

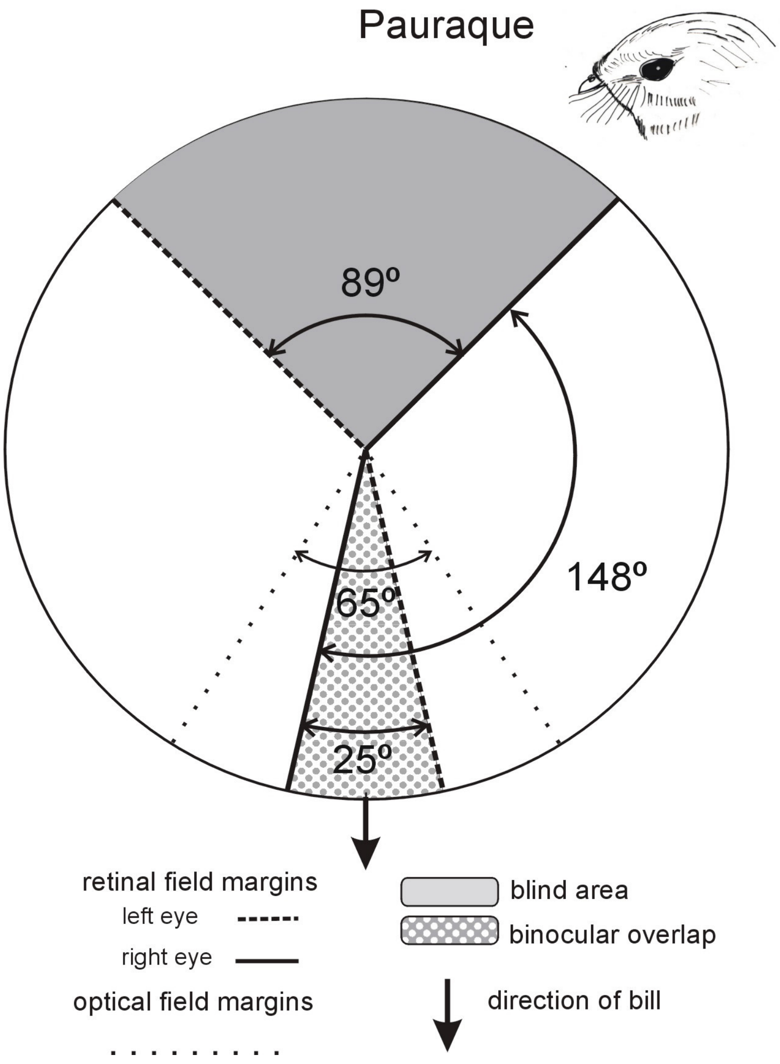

FIG. 3. Horizontal section through the visual field of the Pauraques. The plane of the section is the horizontal of Figure 2. The area of overlap of the optical fields is defined by the positions of the optical field margins. The apparent binocular field equals 65º, compared with the functional (retinal) field of 25º. Each monocular retinal field extends to 148º. The blind sector behind the head equals 89º.

(Martin & Katzir (1994).

From these data, topographical maps of the frontal visual fields (corrected for viewing from an hypothetical viewing point placed at infinity) were constructed for each species.

## RESULTS

Despite these birds' apparent frontal-eyed appearance (Fig. 1), their functional binocular fields are relatively small with a maximum width of 38º and a vertical extent of 100º in

Oilbirds, and a maximum width of 25º and vertical extent of 110º in Pauraques (Fig. 2). Maximum width occurred 10º above the horizontal in our coordinate system in both species. We did not record spontaneous eye movements in either species. A section through the complete visual field in the horizontal plane of Pauraques (Fig. 3) shows that the blind area behind the head is 89º with the monocular retinal field equaling 148º and the monocular optical field equaling 168º. This produces an optical binocular field of 65º, compared with the retinal (functional) field of approximately 25º. Thus although Pauraques appear (Fig. 1) to have a broad binocular field, the functional field has a maximum with of approximately only 40% that of the apparent field (Fig. 3).

## DISCUSSION

Binocularity and nocturnality. The overall binocular field shape of Oilbirds (38º maximum width x 100º height) is broader but shorter than that of Pauraques (25º x 110º). The binocular fields of these species are both narrower and longer than that of Tawny Owls in which binocular fields measure 47º (maximum width) x 80º (vertical extent). Since all three species have in common a highly nocturnal lifestyle, this result does not support the hypothesis that the nocturnal habit in birds results in a convergence upon common visual field topography. Rather it supports the hypothesis that visual field topography is associated with foraging behavior and the extent to which sensory cues other than vision are employed in the location and taking of food items rather than the general level of ambient illumination at which birds are active (Martin & Katzir 1999).

The 20º wide sector at the periphery of the frontal fields that is not served by retina which we found in Pauraques is found also in owls. However, this feature is not associated with the nocturnal habit since it is also found in a wide range of diurnally active species. This suggests that in no bird species is frontal binocular field width maximized within the constraints imposed by the eye's optical system. In all species examined to date, including the Pauraques (Fig. 3), the extent of the retinal visual fields to the rear of the head are maximized within the optical field and there is no blind optical margin to the visual field.

The generally long and narrow nature of the binocular field in the two species of this investigation is similar to the binocular fields of a wide range of mainly diurnally active birds that differ markedly in both phylogeny and behavioral ecology. These species have binocular fields that range in their maximum width of between 20º and 30º, coupled with a vertical extent of between 100º and 180º. Among the diurnally active species showing this topography are Rock Doves (*Columba livia*), various species of herons, albatrosses, penguins, hornbills, and Short-toed Eagles (*Circaetus gallicus*) (Katzir & Martin 1994, 1998; Martin 1998, 1999; Martin & Katzir 1999, Martin & Coetzee in press).

*Projection of the bill tips in relation to the binocular field.* In all of the species discussed immediately above, the projection of the bill tip falls close to the locus of maximum binocular field width, and is located approximately centrally or slightly below centre. However, in Oilbirds and Pauraques, the projection of the bill tip falls towards the lower periphery of the binocular field in a manner similar to that found among owls, ducks and long-billed shorebirds (Martin 1984, 1986b; Martin 1994, Guillemaine *et al.* 2002). These are species that rely mainly upon non-visual cues to locate prey items. The long-billed shorebirds and ducks primarily employ tactile and chemical cues from the bill to locate prey items while the owls employ auditory cues (Martin 1986a). This suggests that, when Oilbirds are foraging, visual cues may play only a general orientation role with the prominent rictal bristles (Fig. 1a) providing close range tactile cues and olfaction providing more distant cues to food sources. The principal sensory cues used by Pauraques when feeding for insects is not known but the anatomical structures associated with feeding among Caprimulgidae includes a wide gape produced by adaptation of the lower jaw (Buhler 1970) and long rictal bristles, and both anatomical features are found in Pauraques. Together these produce an extensive area for trawling small insects from the air space, although it is possible that some Caprimulgiform birds take some items from the ground or through the pursuit of larger individual items that are typically taken in flight from below, e.g. foraging behaviors described in European Nightjars (*Caprimulgus europaeus*) (Schlegel 1967, Cramp 1985, Cleere 1999).

The high degree of specialization of the Oilbirds' and Pauraques' retinal structures for the maximization of sensitivity at the expense of resolution (high densities of rod receptors in both species, which in Oilbirds are arranged in a various banked structure, and the presence of a tapetum in Pauraques) (Rojas *et al.* 2004), also suggests that vision in both of these species is employed primarily for general orientation, rather than pursuit of individual food items which would require high acuity. However, more detailed observations of feeding behavior are clearly required. The positioning of the bill towards the lower edge of the visual field may be indicative that these birds approach larger individual items from below (as reported in European Nightjars), when they would be more easily seen in silhouette against the night sky (Martin, 1990). The eyes appear to be oriented slightly upwards (Fig. 1) but we were unable to determine the projections of the optic axes that would have verified this observation.

*The function of binocularity in Oilbirds and Pauraques.* It has been hypothesized that binocularity in birds is not concerned primarily with the extraction of higher order cues from disparate views of the same scene (Martin & Katzir 1999), although it may play this role in certain granivorous birds when foraging on the ground (McFadden 1994). The presence of a relatively narrow frontal binocular field in both of the strongly nocturnal forms investigated here, coupled with the high sensitivity-low resolution retinal structures, suggests that cues for the detection of the small disparities between the images of the two eyes in these species are likely to be minimal. This supports the hypothesis that binocularity is primarily the result of the contra lateral projection of each eye's visual field in order to achieve a symmetrically expanding optical flow field in each eye, rather than with achieving two views of the same object. The slightly broader binocular fields of these nocturnal species, compared with diurnally active species, may be interpreted as a compensation for a reduced number of optical elements that provide the cues for the optical flow field at reduced spatial resolution associated with lower light levels (Martin & Katzir 1999).

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