

# DIURNAL AND NOCTURNAL VISUAL FUNCTION IN TWO TACTILE FORAGING WATERBIRDS: THE AMERICAN WHITE IBIS AND THE BLACK SKIMMER<sup>1</sup>

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**Abstract.** We compared the diurnal and nocturnal visual function in two tactile foraging waterbird species, the red subspecies of the American White Ibis (*Eudocimus ruber ruber*, formerly the Scarlet Ibis), which is known to feed exclusively during daytime, and the Black Skimmer (*Rynchops niger*), which forages primarily during darkness. Live birds were captured in coastal lagoons of northeastern Venezuela. Electroretinograms (ERGs) were obtained at different light intensities from anesthetized birds, and the retinae were subsequently processed for histological observations. The ERGs of the skimmer were of much larger amplitude than those of the ibis in scotopic (rod-mediated) conditions, but, in contrast, under photopic (cone-mediated) conditions, the amplitude of the ERGs always was significantly larger for the ibis than for the skimmer. The scotopic:photopic b-wave ratio, calculated with b-waves obtained at the highest flash luminance, was 6.82:1 for the skimmer and 0.89:1 for the ibis. The retina of the ibis contained, on the average, 18.8 rods/310  $\mu\text{m}$  and 56.6 cones/310  $\mu\text{m}$ , for a rod:cone ratio of 1:3. The retina of the skimmer contained 90.2 rods/310  $\mu\text{m}$  and 16.8 cones/310  $\mu\text{m}$ , for a ratio of 5:1. The higher density of rods in the skimmer is in some way counterbalanced by their thinness. Compared to the nocturnally active skimmer, the ibis has highly inferior rod function and, consequently, potentially inferior nocturnal visual capabilities. The latter would seem to explain the temporal differences observed in feeding behaviors of the two species.

**Key words:** waterbirds, *Rynchops niger*, *Eudocimus ruber*, *Black Skimmer*, *American White Ibis*, *Scarlet Ibis*, vision, retina, rod, cone, electroretinogram, nocturnal foraging, nocturnal activity.

## INTRODUCTION

Although most bird species feed during daytime only, recent reviews have shown that nocturnal foraging is widespread among coastal, fresh water, and marsh birds, particularly, but not exclusively, in those that are able to forage tactilely (Martin 1990, McNeil et al. 1992, 1993, 1997). Many swimming prey of wetland and marsh birds such as fish, fish larvae, worms, and insects are more active, closer to the water surface, and thus more easily accessible at dusk and night than during daytime (McNeil et al. 1992, 1993, 1995). Direct observations also confirm that polychaetes, isopods, amphipods, decapods, and gastropods, living in the muddy

areas of intertidal habitats where many waterbirds forage, are more active or closer to the sediment surface at night (McNeil et al. 1992, 1993, 1995). Consequently, it might be expected that waterbirds that detect their prey by touch would be able to feed just as fast during darkness as they do during daytime and without having to see the prey on which they feed, whereas birds that detect their prey primarily by sight would be disadvantaged at night (McNeil et al. 1992). In such situations, the tactile method of foraging of skimmers (*Rynchops* spp.) should allow them to feed at night, even under the darkest conditions (Tomkins 1951, Zusi 1962, 1985). Similarly, the blindly probing techniques of ibises also should allow night foraging (Hancock et al. 1992, Matheu and del Hoyo 1992).

Skimmers do in fact feed primarily at night (for review, see Fasola and Canova 1993, McNeil et al. 1993). Usually, skimmers feed in shallow waters in areas containing a high con-

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centration of prey (Erwin 1977, Black and Harris 1983, Zusi 1985). Skimmers are unique in bill structure and feeding behavior: their lower mandible is laterally flattened like a knife blade and it protrudes well beyond the upper one (Tomkins 1951, Zusi 1962, 1985). Skimmers catch their prey by skimming the water surface, i.e., by flying low over the water with the upper jaw raised and the lower jaw open and immersed. When the sharp edge of the lower mandible strikes a prey, the head doubles under the body of the flying bird and the jaws snap shut. The birds fly in a straight path, apparently without seeing individual prey, and are attracted to surface disturbances caused by swarms of fish (Zusi 1985). According to Burger and Gochfeld (1990), Black Skimmers (*Rynchops niger*) may forage primarily at night because fish are feeding more actively on invertebrates near the water surface at that time (see also McNeil et al. 1995). Furthermore, wind is reduced at night and thus the water surface is smoother, which is advantageous to a tactile feeder.

However, contrary to expectation, there is as yet little or no evidence that any ibis species feeds at night with any regularity (McNeil et al. 1993, 1997). For example, the South American race of the American White Ibis (*Eudocimus ruber ruber*), formerly known as the Scarlet Ibis because of its red color, feeds during daytime, primarily by nonvisual probing. It uses its long decurved bill to probe in the shallow waters of marshes, coastal lagoons, and mangrove swamps, but also uses such techniques as head swinging, groping and pecking when appropriate (Kushlan 1977, Hancock et al. 1992). In fact, this ibis appears to be quite blind at night, seldom doing anything but perching after dark. It is possible that ibises do not have the visual capabilities needed to fly safely in the dark, and therefore are unable to access the feeding grounds or escape danger (McNeil et al. 1997).

The retinal receptors of birds, as in all vertebrates, are the rods and cones (Meyer 1977, Tansley and Erichsen 1985). Nocturnal birds have a great preponderance of rods in their retinae, whereas up to 80% of photoreceptors in diurnal birds are cones (see Tansley and Erichsen 1985, Waldvogel 1990). Rods generally are associated with night vision because they are sensitive to low levels of illumination, but rods demonstrate poor discriminative abilities (vi-

sual acuity) and imperfect or no color vision (Tansley and Erichsen 1985). Cones, on the other hand, are associated both with good visual acuity at high light levels and with color vision, but have a low light-sensitivity and poor dark adaptation (Tansley and Erichsen 1985).

If American White Ibises do not forage during nighttime because of poor night vision, then they should have a cone-dominated retina, whereas the retina of the largely nocturnal Black Skimmers should be rod-dominated. We tested this hypothesis by using physiological and morphological techniques that allowed us to verify the rod and cone functions of the retinae of these two bird species.

## MATERIALS AND METHODS

Twelve American White Ibises (scarlet race) and nine Black Skimmers were mist-netted in Laguna de Patos and Chacopata Lagoon, respectively, in northeastern Venezuela. The birds were brought alive to the laboratory of the Universidad de Oriente, in Cumaná, Venezuela.

### ERG RECORDING

The electroretinogram (ERG), widely used in human and veterinary medicine, is the recording of electrical potentials produced by the retina in response to a light stimulus, and which can be recorded at a distance, i.e., at the cornea (see Ikeda 1993 for review). ERGs consist of various waves which arise in different layers of the retina, reflecting light-evoked potentials generated by different retinal cells. The waveform of an ERG and its components exhibit changes depending on the intensity and wavelength of the stimulating flash, as well as the state of retinal adaptation (i.e., photopic or cone-mediated, scotopic or rod-mediated), and thus can be used to compare the retinal sensitivity of different animal species.

ERGs were recorded in a dark room with the use of a LKC EPIC-2000 visual electrodiagnostic system (LKC Technologies Inc., Gaithersburg, MD, USA), comprising a 41-cm diameter Ganzfeld full-field stimulator (LKC Ganzfeld-2503B stimulator), equipped with a Grass PS22 white xenon strobe, allowing maximum luminance flashes of approximately  $3.31 \text{ cd} \cdot \text{m}^{-2} \cdot \text{sec}^{-1}$  and of 20  $\mu\text{sec}$  in duration. A filter wheel assembly provided luminance control in 0.2 log-unit steps over a 4.8 log-units range, with

combinations of 0.0, 0.2, 0.4, 0.6, 0.8, 1.0, 2.0, 3.0, and 4.0 log-units Kodak Wratten neutral density filters. The background light could be controlled between 0 and  $150 \text{ cd} \cdot \text{m}^{-2}$  with a variable aperture.

After a 4-hr period of dark adaptation, birds were anesthetized with a 1:1 mixture of ketamine and xylazine (0.0044 cc/kg injected in the pectoral muscle), immobilized on a home-made recording holder with the head inside the Ganzfeld and the left eye kept open upwards. The eyelids and nictitating membrane were kept retracted with a speculum, the pupil was dilated with 1% tropicamide, and the cornea anesthetized with 0.5% proparacaine hydrochloride. A fine coated conductive yarn (Sauquoit Industries, Scranton, PA) was placed over the cornea and used as the recording electrode (Lachapelle et al. 1993). Subdermal needle electrodes (Grass Instruments, Astro-med Inc., Warwick, RI), inserted under the skin on top of the head and in the pectoral muscle, were used as reference and ground, respectively. Under scotopic (rod mediated) conditions, averages of 6 responses per trial were obtained to flashes of constant luminance delivered at 10.1-sec intervals. These ERGs were obtained, in increasing order of luminance, to light intensities of  $-3.8$ ,  $-3.0$ ,  $-2.6$ ,  $-2.0$ ,  $-1.4$ ,  $-1.0$ , and  $0.0$  log-units, respectively. Thereafter, the birds were light-adapted for 10 min at a background luminance of  $35.7 \text{ cd} \cdot \text{m}^{-2}$ . Under photopic (cone mediated) conditions, averages of 10 responses were obtained to flashes of constant luminance delivered at 4.1 sec. These ERGs were evoked to flashes of decreasing luminance of 0.0,  $-0.6$ ,  $-1.0$ , and  $-1.4$  log-units, respectively. Less stimuli were used in scotopic than in photopic conditions and they were separated by a longer interval to ensure that the retina did not lose its adaptation to darkness and that a sufficient time was given for the rod photopigment to regenerate (Ikeda 1993).

#### HISTOLOGICAL PROCEDURES

Once the ERG recordings were completed, 4 skimmers and 4 ibises were given a lethal dose of sodium pentobarbital. The left eye was injected with 2.5% glutaraldehyde in 0.1 M phosphate buffer (pH = 7.2), dissected out, punctured at the cornea, and placed in the same fixative for 30 min. While the eye was in the fixa-

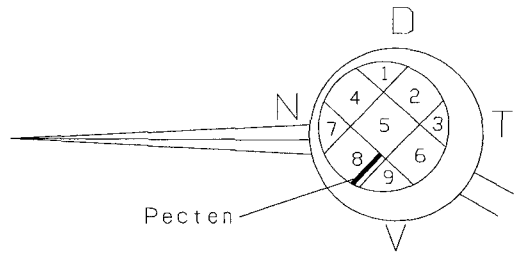


FIGURE 1. Schematic representation of the nine retinal sectors. D, N, T, and V correspond to the dorsal, nasal, temporal, and ventral sectors, respectively.

tive, the retina, still attached to the choroid, was cut into nine sectors, using the pecten as a landmark (Fig. 1). This division is the same as that of Rojas de Azuaje et al. (1993), and corresponds to that of Meyer and May (1973) and Begin and Handford (1987), although the sector numbering is different. While in the fixative, each sector was subdivided into  $2\text{-mm}^2$  portions, of which only two were retained for analysis. After 3 hr in the fixative, the retinal portions, separated from the choroidal layer, were washed with phosphate buffer for 10 min, postfixed in 1%  $\text{OsO}_4$  in 0.1 M phosphate buffer for 1 hr, rinsed in phosphate buffer followed by distilled water, for 10 min each, dehydrated in graded ethanol (10 min per step), and bathed in propylene oxide for 15 min. The tissues were successively infiltrated with a 1:1 mixture of propylene oxide and Epon for 6 hr, and pure Epon medium for another 2 hr. Finally, they were embedded in silicone rubber molds filled with Epon and polymerized at  $60^\circ\text{C}$  for 48 hr.

Sections ( $0.7 \mu\text{m}$ ) were obtained with a Reichert ultramicrotome and 15 of them (one every 30–40 sections) were mounted on glass slides and stained with toluidin blue and examined with a Zeiss-Axiomat photomicroscope. Rods and cones as well as ganglion cells were counted in one field,  $310 \mu\text{m}$  wide, for a total of 15 counts for each of the nine sectors per eye. As in other avian retinae (Meyer and May 1973, Meyer 1977, Tansley and Erichsen 1985, Waldvogel 1990), single and double cones were present in the retinae of both species. Double cones were counted as two cones. In addition, the following parameters were measured: the length and diameter of the outer and inner segments of rods and cones, and the thickness of each retinal layer.

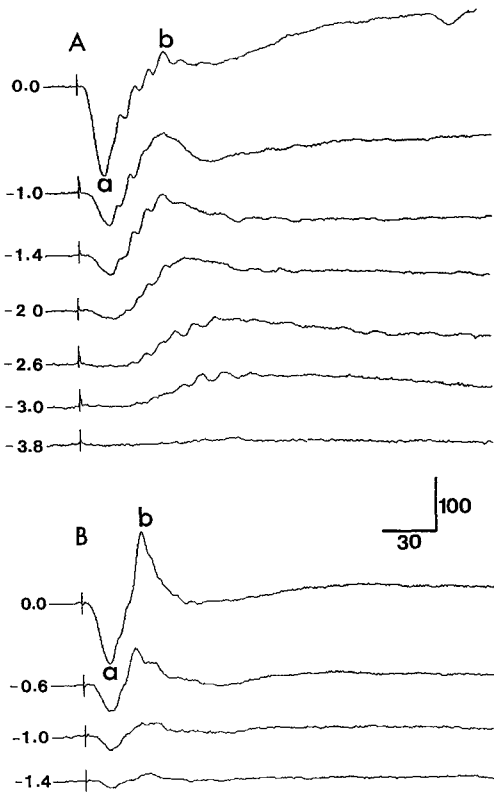


FIGURE 2. ERG responses of the American White Ibis under (A) scotopic and (B) photopic conditions. Nomenclature: a, peak of the a-wave; b, peak of the b-wave. The figures on the left represent light intensity values (Log-units). The amplitude and time scales correspond to 100  $\mu$ V and 30 msec.

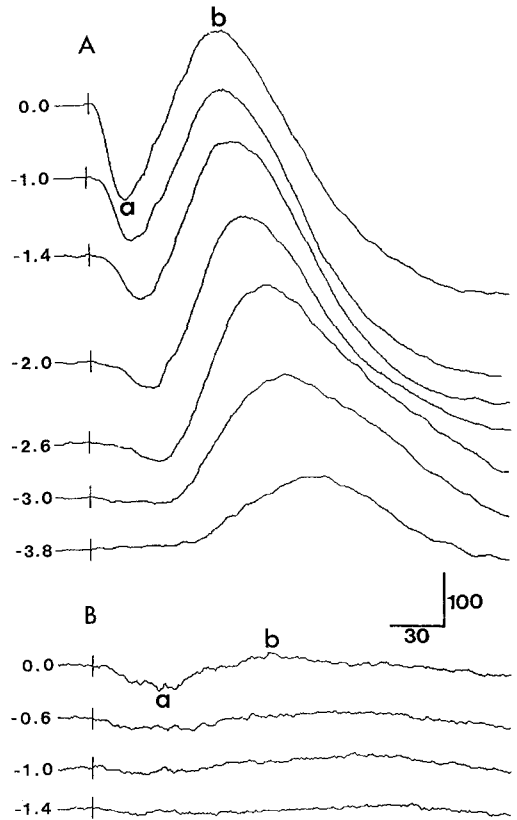


FIGURE 3. ERG responses of the Black Skimmer under (A) scotopic and (B) photopic conditions. Nomenclature as in Figure 2.

RESULTS

ELECTRORETINOGRAPHY

Representative electroretinograms obtained in scotopic and photopic conditions for an American White Ibis and a Black Skimmer are presented in Figures 2 and 3. Comparative luminance-response functions for amplitude (A) and peak time (B) measurements are graphically reported at Figures 4 and 5, respectively. Peak time and amplitude measurements obtained for the brightest stimulus are given in Table 1.

The scotopic ERGs obtained from the ibis are characterized by the presence of small oscillations on the rising phase of the b-wave (Fig. 2A). Such oscillations are not observed in the skimmer (Fig. 3A). Analysis of the intensity-response function (Fig. 4A) reveals, for the skimmer, a rapid growth in the amplitude of the scotopic b-wave from intensity  $-3.8$  to  $-2.6$ ,

which is followed by a saturation from intensity  $-2.6$  to  $0.0$ . In contrast, for the ibis, the amplitude of the scotopic ERGs regularly increases with progressively brighter flashes. It should be noted that the scotopic ERGs of the skimmer are always of larger amplitude than those of the ibis, the difference between the two species reaching significance at flash luminances comprised between  $-3.0$  and  $-1.0$  (Fig. 4A). Similarly, while the peak time of scotopic b-waves of both species shortens with increasing flash luminance, the timing of the scotopic ERG b-waves of the ibis, as shown by the 95% confidence limits for the mean peak time variations (Fig. 5A), is always significantly faster than that of the skimmer.

In the photopic ERG waveforms, a more robust signal is obtained for the ibis, with easily identifiable a- and b-waves at all the flash in-

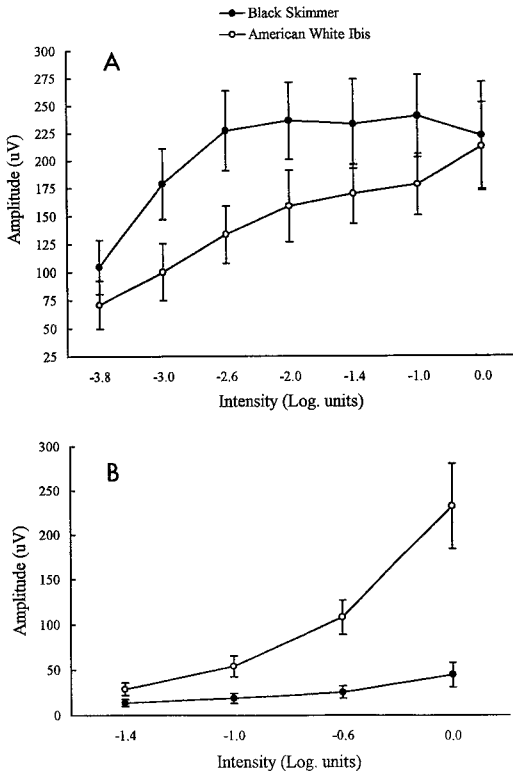


FIGURE 4. Mean amplitude variations ( $\pm 95\%$  confidence limits) in the b-waves of the Black Skimmer and the American White Ibis as a function of light intensity under (A) scotopic and (B) photopic conditions.

tensities used (Fig. 2B), whereas, for the skimmer, identifiable a- and b-waves only are present in responses obtained to the brightest flash (Fig. 3B). The 95% confidence limits of the corresponding luminance-response curves (Fig. 4B) reveal that, for all the intensities used, the amplitude of the cone ERG obtained from the ibis is always significantly larger than that from the skimmer. The peak time of the b-waves does not vary significantly as a function of light intensity (Fig. 5B). However, as under scotopic conditions, as shown by the 95% confidence limits for the mean peak time variations (Fig. 5B), the timing of the photopic ERG b-waves of the ibis is always significantly faster than that of the skimmer. Based on the 95% confidence limits for the means (Table 1), the amplitude of the photopic ERG b-wave obtained at the brightest luminance is significantly lower than that measured under scotopic condi-

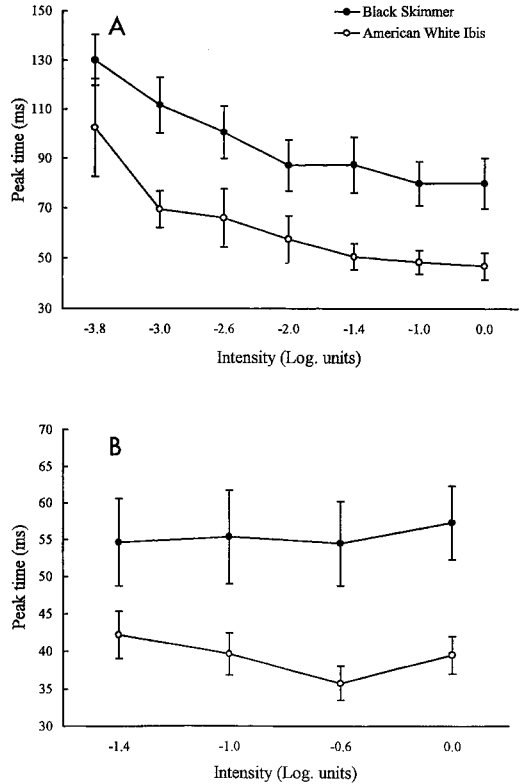


FIGURE 5. Mean peak time variations ( $\pm 95\%$  confidence limits) in the b-waves of the Black Skimmer and the American White Ibis as a function of light intensity under (A) scotopic and (B) photopic conditions.

tions with the same flash luminance in the skimmer, but not in the ibis (Table 1). Indeed, from data of Table 1, the scotopic:photopic b-wave ratio, with b-waves obtained at the brightest luminance, is 6.82:1 for the skimmer, and 0.89:1 for the ibis. Whereas the b:a-wave ratios are similar for the skimmer and the ibis (1.41 vs. 1.28, respectively) under scotopic conditions, they tend to differ in photopic conditions, with values of 2.39 for the ibis and 0.73 for the skimmer.

#### HISTOLOGICAL OBSERVATIONS

Overall, the photoreceptor density of the skimmer is higher than that of the ibis by a factor of 1.4:1, and this difference is due mainly to rod density (Table 2). In the skimmer, rod density is roughly 4.8 times higher than in the ibis, and exceeds that of cones by a factor of 5 to 1. In the ibis, cone density is roughly 3.4 times higher

TABLE 1. Mean amplitude ( $\mu\text{V}$ ) and peak time (msec) and the a- and b-waves of scotopic and photopic ERGs for the 11 Black Skimmers and the 9 American White Ibises.

	a-wave		b-wave	
	Amplitude <sup>a</sup>	Peak time <sup>a</sup>	Amplitude <sup>a</sup>	Peak time <sup>a</sup>
Scotopic				
Skimmer	157.9 $\pm$ 40.7	24.1 $\pm$ 6.8	223.0 $\pm$ 82.3	79.2 $\pm$ 16.0
Ibis	165.3 $\pm$ 41.9	16.5 $\pm$ 1.4	212.9 $\pm$ 67.8	46.9 $\pm$ 8.6
Photopic				
Skimmer	44.2 $\pm$ 13.5	31.4 $\pm$ 8.0	32.7 $\pm$ 15.8	56.9 $\pm$ 7.1
Ibis	99.5 $\pm$ 22.8	17.0 $\pm$ 1.1	238.0 $\pm$ 84.2	39.8 $\pm$ 4.5

<sup>a</sup>  $\bar{x} \pm 95\%$  confidence interval.

than in the skimmer, and exceeds that of rods by a factor of 3 to 1. In the skimmer, rod density and rod:cone ratio tend to be higher in the central (5), dorsal (1 and 4) and temporal (2 and 3) sectors, and lower in the nasal (7) and ventral (6, 8 and 9) sectors, and cone density tends to be higher in the nasal (7), central (5), and lower (6 and 9) sectors than in the dorsal (1 to 4) ones (Table 2, Fig. 1). In the ibis, rod density is higher in sector 5 than in most other ones, but cone density tends to be higher in sector 5 and lower in sector 1 (Table 2).

A section of the retina of each species is shown in Figure 6 and measurements of photoreceptors, average ganglion cell density, and thickness of retinal layers are given in Table 3. For both spe-

cies, there is no clear trend in the sectorial variations of these measurements. However, on the average, the Black Skimmer tends to have longer rod outer segments but thinner rods than the American White Ibis, and the cone outer segment of the ibis almost doubles in length that of the skimmer. Differences between the two species based on the 95% confidence intervals of the means (Table 3), although significant in many cases, are not so striking in other cone measurements. On the other hand, the skimmer has thicker outer nuclear and outer plexiform layers than the ibis. Ganglion cells are more abundant per unit area, and the inner nuclear, inner plexiform, ganglion cell, and optic nerve fiber layers are thicker in the ibis.

TABLE 2. Mean rod and cone relative density in the Black Skimmer and the American White Ibis.  $n = 4$  in all cases.

	Sectors <sup>a</sup>	Rods <sup>b</sup>	Cones <sup>b</sup>	Rods:Cones
Black Skimmer	1	92.8 $\pm$ 14.1	15.0 $\pm$ 0.9	6:1
	2	97.7 $\pm$ 15.4	16.1 $\pm$ 2.6	6:1
	3	92.5 $\pm$ 15.1	16.3 $\pm$ 1.2	6:1
	4	96.1 $\pm$ 14.0	15.7 $\pm$ 0.3	6:1
	5	118.1 $\pm$ 19.4	17.6 $\pm$ 2.3	7:1
	6	81.8 $\pm$ 6.6	17.7 $\pm$ 1.4	5:1
	7	76.1 $\pm$ 16.0	18.7 $\pm$ 3.5	4:1
	8	78.5 $\pm$ 13.5	16.1 $\pm$ 3.1	3:1
	9	77.7 $\pm$ 15.5	18.0 $\pm$ 5.2	4:1
	All	90.2 $\pm$ 8.8	16.8 $\pm$ 0.8	5:1
American White Ibis	1	16.6 $\pm$ 4.0	51.2 $\pm$ 3.4	1:3
	2	21.1 $\pm$ 2.3	59.0 $\pm$ 4.6	1:3
	3	18.6 $\pm$ 2.7	58.9 $\pm$ 6.2	1:3
	4	18.9 $\pm$ 1.8	54.6 $\pm$ 3.9	1:3
	5	23.8 $\pm$ 3.1	60.6 $\pm$ 3.9	1:3
	6	18.0 $\pm$ 2.0	57.4 $\pm$ 2.5	1:3
	7	19.0 $\pm$ 2.5	55.3 $\pm$ 1.7	1:3
	8	17.5 $\pm$ 1.7	56.6 $\pm$ 3.0	1:3
	9	16.0 $\pm$ 3.0	56.1 $\pm$ 5.4	1:4
	All	18.8 $\pm$ 1.7	56.6 $\pm$ 1.8	1:3

<sup>a</sup> Sectors 1 and 4 = dorsal, 2 and 3 = temporal, 5 = central, 7 = nasal, 6, 8 and 9 = ventral.

<sup>b</sup>  $\bar{x}/310 \mu\text{m} \pm 95\%$  confidence interval.

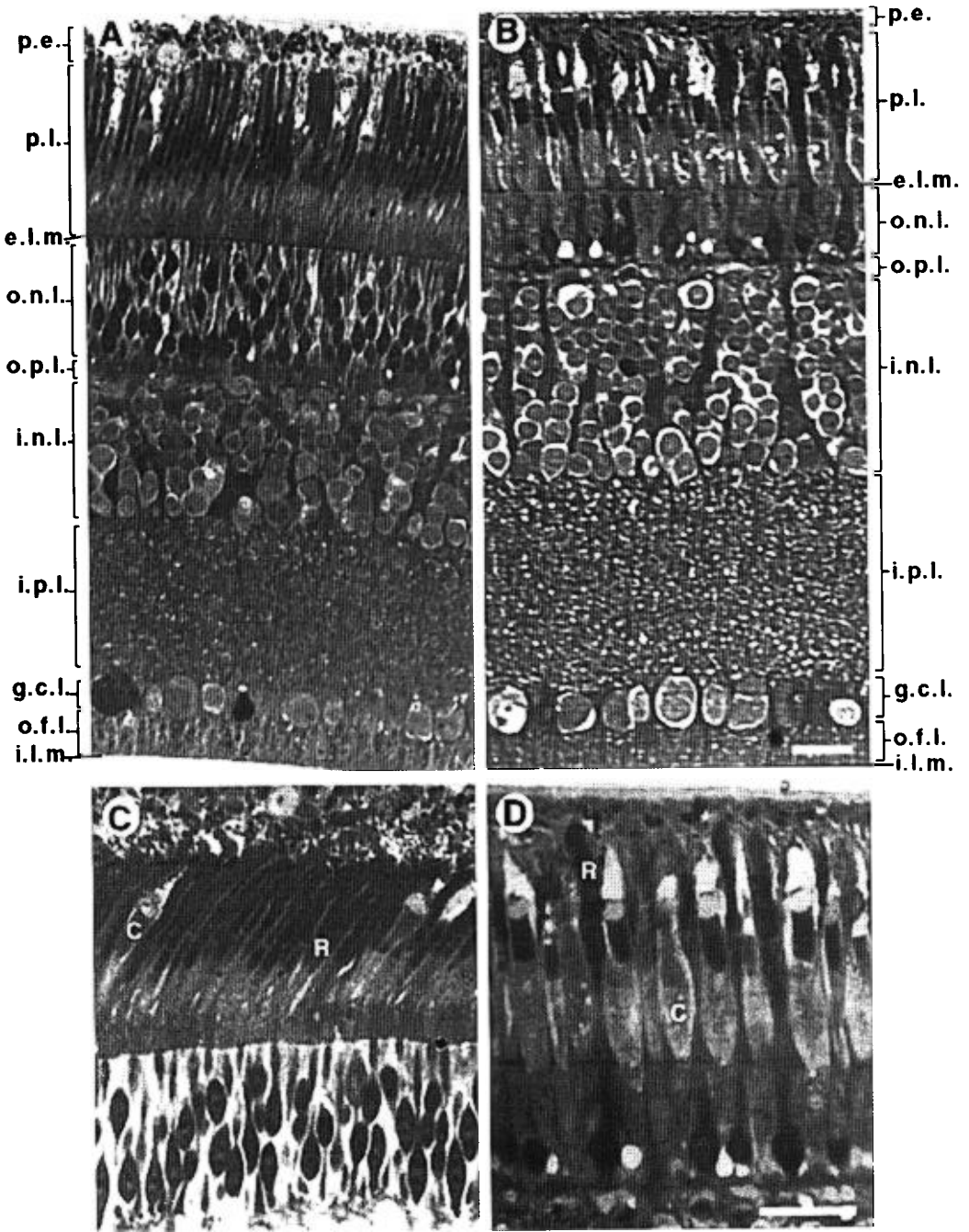


FIGURE 6. Photomicrographs showing the principal layers of the central retina of (A) the Black Skimmer and (B) the American White Ibis. C and D are enlargements of the photoreceptor layer of A and B, respectively. Nomenclature adapted from Kare (1965), Dowling (1970), Fein and Szuts (1982), Ali and Klyne (1985), and Martin (1985): c, cone; e.l.m., external limiting membrane; g.c.l., ganglion cell layer; i.n.l., inner nuclear layer; i.p.l., inner plexiform layer; o.f.l., optic fiber layer; o.n.l., outer nuclear layer; o.p.l., outer plexiform layer; p.e., pigmented epithelium; r, rod; v.c.i.s.l., visual cell inner segment layer; v.c.o.s.l., visual cell outer segment layer. The scale in B equals 20  $\mu\text{m}$  and is valid for A, and that in D also equals 20  $\mu\text{m}$  and is valid for C.

TABLE 3. Overall mean rod and cone measurements ( $\mu\text{m}$ ), mean ganglion cell density ( $\bar{x}/310 \mu\text{m}$ ), and mean thickness ( $\mu\text{m}$ ) of the retinal layers of the Black Skimmer and the American White Ibis (see Fig. 6).  $n = 4$  in all cases.

	Black Skimmer	American White Ibis
	$\bar{x} \pm 95\%$ confidence interval	$\bar{x} \pm 95\%$ confidence interval
<b>Rod</b>		
Outer segment length	25.2 $\pm$ 5.9	20.4 $\pm$ 0.6
Outer segment diameter	1.9 $\pm$ 1.1	4.1 $\pm$ 0.3
Inner segment length	24.9 $\pm$ 2.3	26.4 $\pm$ 1.6
Inner segment diameter	1.9 $\pm$ 1.1	3.9 $\pm$ 0.2
<b>Cone</b>		
Outer segment length	8.2 $\pm$ 0.9	14.0 $\pm$ 1.5
Outer segment diameter	1.3 $\pm$ 0.1	1.3 $\pm$ 0.1
Inner segment length <sup>a</sup>	34.9 $\pm$ 1.4	34.3 $\pm$ 1.1
Inner segment length <sup>a</sup>	27.0 $\pm$ 0.2	28.1 $\pm$ 0.7
Inner segment diameter <sup>a</sup>	4.6 $\pm$ 0.2	3.7 $\pm$ 0.2
Inner segment diameter <sup>b</sup>	4.7 $\pm$ 0.1	6.4 $\pm$ 0.1
Outer nuclear layer	28.8 $\pm$ 1.4	20.8 $\pm$ 0.1
Inner nuclear layer	26.7 $\pm$ 2.0	42.3 $\pm$ 1.8
Outer plexiform layer	6.8 $\pm$ 0.4	5.4 $\pm$ 0.2
Inner plexiform layer	33.5 $\pm$ 2.5	53.4 $\pm$ 1.6
Ganglion cell layer	8.2 $\pm$ 0.3	11.1 $\pm$ 1.0
Ganglion cell density	13.5 $\pm$ 4.6	26.7 $\pm$ 2.4
Optic nerve fiber layer	12.3 $\pm$ 1.1	27.5 $\pm$ 4.6

<sup>a</sup> For all cone types, except accessory cones.

<sup>b</sup> For accessory cones.

## DISCUSSION

Contrary to most studies which were based almost exclusively on morphological observations and lacked physiological data, our study has the advantage of comparing two bird species by considering both morphological and physiological aspects of the retina. Our study shows that the retina of the Black Skimmer is well adapted for night vision, whereas that of the American White Ibis is clearly adapted for daytime vision. Each species exhibits distinct ERG responses which differ from each other under the tested conditions (i.e.,  $-3.8$  to  $0$  log-units). The ERG responses indicate that, under scotopic conditions, the retinal sensitivity of the skimmer to low light intensity (e.g.,  $-3.8$  to  $-2.0$  log-units) is always higher than that of the ibis. This feature can be correlated with the measured differences in the photoreceptor ratios and densities.

The rod:cone ratio of the ibis is roughly comparable to that of the Northern Fulmar (*Fulmarus glacialis*) and the Manx Shearwater (*Puffinus puffinus*), but is higher than that of the strictly diurnal House Sparrow (*Passer domesticus*) (Lockie 1952). Both the fulmar and the shearwater are known to forage at night, and the shearwater is particularly noted for its nocturnal attendance at breeding colonies (McNeil et al. 1993). The ibis rod:cone ratio also is lower than that of the Greater Yellowlegs (*Tringa melanoleuca*) (1.0:1.42), a visual feeder during daytime that mostly switches to tactile foraging (side-sweeping) at night (Robert and McNeil 1989, Rojas de Azuaje et al. 1993). The rod:cone ratio of the Black Skimmer is less than half that of the nocturnal Great Horned Owl (*Bubo virginianus*) where values range from 11.6:1 to 13.4:1 (Fite 1973).

Because of higher rod density, the rod:cone ratio tends to be higher in the central, dorsal and temporal sectors of the skimmer retina. This may play a role in seeing the water surface and lower horizon when the bird is skimming the water surface during darkness.

Rod density in the skimmer is in some way counterbalanced by their thinness. Their outer segments, however, are shorter than those of some shorebirds such as the Grey Plover (*Pluvialis squatarola*), the Short-billed Dowitcher (*Limnodromus griseus*) and the Greater Yellowlegs, which all forage both at night and during the day (Rojas de Azuaje 1991, McNeil et al. 1992). They also may be shorter than those of the nocturnal Tawny Owl, however those measurements were obtained from fresh tissue (Bowmaker and Martin 1978). Contrary to the assertion of Walls (1942) that rods can lower their thresholds during evolution (thus increasing their sensitivity) by lengthening their outer segments, the increased sensitivity exhibited by the Black Skimmer over that of the American White Ibis and the above-mentioned species is probably the result not of exceptionally long rod outer segments, but of a greater area covered by rods. This may be due to their large number and packing (Bowmaker and Martin 1978). However, rod sensitivity is not solely determined by their length or diameter, but also by the density of the visual pigment they contain, a factor not examined in the present study.

In both species, and under both scotopic and photopic conditions, the a- and b-waves in-



crease in amplitude with increasing light intensity. In addition, the peak time of scotopic b-waves decreases with increasing luminance intensity. The same occurs in the Little Owl (*Athene noctua*) (Porciatti et al. 1989), the Common Pigeon (*Columba livia*) (Porciatti et al. 1991), and in humans (Weleber and Eisner 1988).

The small oscillations observed in the rising phase of the ERG b-wave under scotopic conditions, particularly under the highest luminance values in the ibis, but not in the skimmer, are usually referred to as oscillatory potentials (Speros and Price 1981). They are believed to originate either from the amacrine cells in the inner plexiform layer or the optic nerve fibers in the optic fiber layer (Ikeda 1993). Both of these layers were found to be thicker in the ibis than in the skimmer.

Comparison of the rod:cone ratios of the two species, as well as the amplitudes of their photopic ERG responses, which are significantly larger in the ibis than in the skimmer, suggests that the ibis is better suited for daytime vision. This also is indicated by the fact that ganglion cells are twice as abundant per unit area in the ibis as in the skimmer. Accordingly, the optic nerve fiber layer is twice as thick in the ibis as in the skimmer. It has been shown that ganglion cells are found in higher density in the retinal area subserving visual acuity such as the fovea (Binggeli and Paule 1969, Ikushima et al. 1986, Hayes and Brooke 1990, Inzunza et al. 1991, Suburo et al. 1991).

The skimmer's retina is sensitive to low levels of illumination and might need special protection during occasional daytime foraging. Skimmers are the only birds known to close their pupil into the form of a vertical slit (Zusi and Bridge 1981). Zusi and Bridge (1981) found that the Black Skimmer has a relatively larger maximum pupil size than that of the diurnally active Common Tern (*Sterna hirundo*), and accomplish a greater reduction in its pupillary area from darkness to bright light than does the tern. We observed that the skimmer's maximum pupil size, varying between 6 to 9 mm depending on the size of the bird, is roughly half the diameter of the full eye ball. These features of the skimmer's eye may serve to enhance nocturnal vision and to protect the retina during occasional daytime feeding and other activities in bright light.

In conclusion, and in accordance with our initial hypothesis, the retina of the Black Skimmer is rod-dominated and corresponds to that of a nocturnal bird, and that of the American White Ibis is cone-dominated and corresponds to that of a diurnal bird. These features are reinforced by their very distinct ERG responses under scotopic and photopic conditions. As a consequence, the ibis appears to have a night vision capability considerably lower than that of the skimmer, and therefore can be viewed as being less capable of safe flights to access feeding grounds, or escape predators when on foraging ground during darkness.

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#### LITERATURE CITED

- ALI, M. A., AND M. A. KLYNE. 1986. La vision chez les vertébrés. Masson, Paris.
- BEGIN, M. R., AND P. HANDFORD. 1987. Comparative study of retinal oil droplets in grebes and coots. *Can. J. Zool.* 65:2105-2110.
- BINGGELI, R. L., AND W. J. PAULE. 1969. The pigeon retina: quantitative aspects of the optic nerve and ganglion cell layer. *J. Comp. Neur.* 137:1-18.
- BLACK, B. B., AND L. D. HARRIS. 1983. Feeding habitat of Black Skimmers wintering on the Florida Gulf coast. *Wilson Bull.* 95:404-415.
- BLOCH, S., AND H. R. MATURARA. 1971. Oil droplet distribution and colour discrimination in the pigeon. *Nature New Biol.* 234:284-285.
- BOWMAKER, J. K., AND G. R. MARTIN. 1978. Visual pigments and colour vision in a nocturnal bird, *Strix aluco* (Tawny Owl). *Vision Res.* 18:1125-1130.
- BURGER, J., AND M. GOCHFELD. 1990. The Black Skimmer: social dynamics of a colonial species. Columbia Univ. Press, New York.
- DOWLING, J. E. 1970. Organization of vertebrate retinas. *Invest. Ophthalmol.* 9:655-680.
- ERWIN, R. M. 1977. Foraging and breeding adaptations to different food regimes in three seabirds: the Common Tern, *Sterna hirundo*, Royal Tern, *Sterna maxima*, and Black Skimmer, *Rynchops niger*. *Ecology* 58:389-397.
- FASOLA, M., AND L. CANOVA. 1993. Diel activity of resident and immigrant waterbirds at Lake Turkana, Kenya. *Ibis* 135:442-450.

- FEIN, A., AND E. Z. SZUTS. 1982. Photoreceptors, their role in vision. Cambridge Univ. Press, Cambridge.
- FITE, K. V. 1973. Anatomical and behavioral correlates of visual acuity in the Great Horned Owl. *Vision Res.* 13:219–230.
- HANCOCK, J. A., J. A. KUSHLAN, AND M. P. KAHL. 1992. Storks, ibises, and spoonbills of the world. Academic Press, London.
- HAYES, B. P., AND M. DE L. BROOKE. 1990. Retinal ganglion cell distribution and behaviour in procellariiform seabirds. *Vision Res.* 30:1277–1289.
- IKEDA, H. 1993. Clinical electroretinography, p. 115–139. In A. M. Halliday [ed.], *Evoked potentials in clinical testing*. Churchill Livingstone, Edinburgh, Scotland.
- IKUSHIMA, M., M. WATANABE, AND H. ITO. 1986. Distribution and morphology of retinal ganglion cells in the Japanese Quail. *Brain Res.* 376:320–334.
- INZUNZA, O., H. BRAVO, R. L. SMITH, AND M. ANGEL. 1991. Topography and morphology of retinal ganglion cells in falconiforms: a study on predatory and carrion-eating birds. *Anat. Rec.* 229:271–277.
- KARE, M. R. 1965. The special senses, p. 406–446. In P. D. Sturkie [ed.], *Avian physiology*. Cornell Univ. Press, Ithaca, NY.
- KUSHLAN, J. A. 1977. Foraging behavior of the White Ibis. *Wilson Bull.* 89:342–345.
- LACHAPPELLE, P., J. BENOIT, J. M. LITTLE, AND B. LACHAPPELLE. 1993. Recording the oscillatory potentials with the DTL electrode. *Doc. Ophthalmol.* 83:119–130.
- LOCKIE, J. D. 1952. A comparison of some aspects of the retinae of the Manx Shearwater, Fulmar Petrel, and House Sparrow. *Quart. J. Microsc. Sci.* 93:347–356.
- MARTIN, G. 1990. *Birds by night*. Poyser, London.
- MARTIN, G. R. 1985. Eye, p. 311–373. In A. S. King and J. McLelland [eds.], *Form and function in birds*, Vol. 3. Academic Press, London.
- MATHEU, E., AND J. DEL HOYO. 1992. Family Threskiornithidae (ibises and spoonbills), p. 472–506. In J. del Hoyo, A. Elliott, and J. Sargatal [eds.], *Handbook of the birds of the world*, Vol. 1. Lynx Edicions, Barcelona.
- MCCNEIL, R., O. DÍAZ D., I. LIÑERO A., AND J. R. RODRÍGUEZ S. 1995. Day- and night-time prey availability for waterbirds in a tropical lagoon. *Can. J. Zool.* 73:869–878.
- MCCNEIL, R., P. DRAPEAU, AND J. D. GOSS-CUSTARD. 1992. The occurrence and adaptive significance of nocturnal habits in waterfowl. *Biol. Rev.* 67:381–419.
- MCCNEIL, R., P. DRAPEAU, AND R. PIEROTTI. 1993. Nocturnality in colonial waterbirds: occurrence, special adaptations, and suspected benefits. *Current Ornithol.* 10:187–246.
- MCCNEIL, R., F. GENEVOIS, J. A. KUSHLAN, AND G. R. MARTIN. 1997. Foraging and nocturnality in colonial waterbirds. In F. Cézilly, H. Hafner and D. N. Nettleship [eds.], *Colonial breeding in waterbirds: evolutionary causes and functional consequences*. Oxford Univ. Press, Oxford, in press.
- MEYER, D. B. 1977. The avian eye and its adaptations, p. 549–611. In F. Crescitelli [ed.], *The visual system in vertebrates*, Vol. VII/5. Springer Verlag, Berlin.
- MEYER, D. B., AND H. C. MAY. 1973. The topographical distribution of rods and cones in the adult chicken retina. *Exp. Eye Res.* 17:347–355.
- PORCIATTI, V., G. FONTANESI, AND P. BAGNOLI. 1989. The electroretinogram of the Little Owl (*Athene noctua*). *Vision Res.* 29:1693–1698.
- PORCIATTI, V., W. HODOS, G. SIGNORINI, AND F. BRAMANTI. 1991. Electroretinographic changes in aged pigeons. *Vision Res.* 31:661–668.
- ROBERT, M., AND R. MCNEIL. 1989. Comparative day and night feeding strategies of shorebird species in a tropical environment. *Ibis* 131:69–79.
- ROJAS DE AZUAJE, L. M. 1991. Proporción de conos y bastones en la retina de tres especies de aves limícolas y la relación entre visión y estrategia alimenticia. Tesis de M. Sc., Instituto de Investigaciones en Biomedicina y Ciencias Aplicadas, Univ. Oriente, Cumaná, Venezuela.
- ROJAS DE AZUAJE, L. M., S. TAI, AND R. MCNEIL. 1993. Comparison of rod/cone ratio in three species of shorebirds having different nocturnal foraging strategies. *Auk* 110:141–145.
- SPELOS, P., AND J. PRICE. 1981. Oscillatory potentials: history, techniques and potential use in the evaluation of disturbances of retinal circulation. *Surv. Ophthalmol.* 25:237–252.
- SUBURO, A. M., M. V. HERRERO, AND J. A. SCOLARO. 1991. Regionalization of the ganglion cell layer in the retina of the Magellanic Penguin (*Spheniscus magellanicus*). *Colonial Waterbirds* 14:17–24.
- TANSLEY, K., AND J. R. ERICHSEN. 1985. Vision, p. 623–629. In B. Campbell and E. Lack [eds.], *A dictionary of birds*. Poyser, Calton, UK.
- TOMKINS, I. R. 1951. Method of feeding of the Black Skimmer. *Auk* 68:236–239.
- WALDVOGEL, J. A. 1990. The bird's eye view. *Am. Sci.* 78:342–353.
- WALLS, G. L. 1942. *The vertebrate eye and its adaptive radiation*. Cranbrook Institute of Science, Bloomfield Hills, MI.
- WELEBER, R. G., AND A. EISNER. 1988. Retinal function and physiological studies, p. 21–69. In D. A. Newsome [ed.], *Retinal dystrophies and degenerations*. Raven Press, New York.
- ZUSI, R. 1962. Structural adaptations of the head and neck in the Black Skimmer. *Rynchops nigra* L. *Publ. Nuttall Ornithol. Club* 3:1–101.
- ZUSI, R. L. 1985. Skimmer, p. 546–547. In B. Campbell and E. Lack [eds.], *A dictionary of birds*. Poyser, Calton, UK.