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Étude comparative et morpho-fonctionnelle de la capacité de vision diurne et nocturne chez deux groupes d'oiseaux aquatiques

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Sommaire

Le but de cette étude était d'examiner, chez un groupe choisi d'oiseaux aquatiques, si la quête alimentaire diurne ou nocturne et le recours à des stratégies de chasse visuelle ou tactile sont corrélés avec la structure et la fonction de leur rétine. Les espèces retenues pour l'étude comprennent six Ciconiiformes et six Charadriiformes. Les Ciconiiformes sont le Bihoreau violacé (*Nycticorax violaceus*), un chasseur crépusculaire et nocturne, le Grand Héron (*Ardea herodias*), principalement crépusculaire, mais aussi diurne et nocturne, la Spatule rosée (*Ajaia ajaja*), un chasseur principalement crépusculaire qui s'alimente plus de nuit que de jour, le Héron garde-boeufs (*Bubulcus ibis*), l'Aigrette tricolore (*Egretta tricolor*) et l'Ibis rouge (*Eudocimus ruber*) qui s'alimentent uniquement de jour. Les hérons et les aigrettes sont des chasseurs visuels alors que les ibis et les spatules sont des chasseurs tactiles. Le groupe des Charadriiformes étudiés comprend: le Pluvier de Wilson (*Charadrius wilsonia*), chasseur visuel, actif surtout de nuit; le Bécassin roux (*Limnodromus griseus*), chasseur tactile actif de jour et de nuit; la Bécasse d'Amérique (*Scolopax minor*), un chasseur tactile de jour et de nuit, mais qui parfois chasse des insectes à la vue durant le jour; l'Échasse d'Amérique (*Himantopus himantopus*), un chasseur visuel autant de nuit que de jour, mais qui a recours à une stratégie tactile lorsqu'il s'alimente dans des eaux dont la surface est agitée; le Chevalier semipalmé (*Catoptrophorus semipalmatus*) dont les individus détenteurs d'un territoire d'alimentation s'alimentent visuellement de nuit comme de jour, sauf durant les nuits sans lune lors desquelles ils deviennent tactiles; et le Bec-en-ciseaux noir (*Rynchops niger*), un chasseur tactile principalement nocturne.

Des électrorétinogrames (ERGs) ont été obtenus, sous anesthésie, à différentes intensités lumineuses et les rétines ont été préservées et préparées pour l'observation histologique.

Parmi les espèces étudiées, en se basant sur les ERGs, la sensibilité rétinienne, et le rapport bâtonnets:cônes, le Bec-en-ciseaux noir est celle qui semble la mieux adaptée pour la vision nocturne. Parmi les autres Charadriiformes étudiés, le pluvier et l'échasse sont tous deux bien adaptés pour la vision nocturne. En dépit d'une faible densité de bâtonnets, comparés à l'échasse et au pluvier, le Chevalier semipalmé et la bécasse ont une sensibilité

rétinienne scotopique semblable à celle de l'échasse et du pluvier, mais se situent à mi-chemin entre le pluvier et le bécassin en ce qui a trait à l'amplitude de l'onde b. Comparés aux chasseurs tactiles nocturnes et à ceux qui doivent passer de visuels de jour à tactiles de nuit, les chasseurs visuels nocturnes ont une fonction des bâtonnets supérieure et sont, par conséquent, susceptibles d'avoir de meilleures capacités de vision nocturne.

Chez les Ciconiiformes, la vision nocturne est meilleure chez le Bihoreau violacé, suivi du Grand Héron et de la Spatule rosée, puis du Héron garde-boeufs, de l'Aigrette tricolore et de l'Ibis rouge. Les chasseurs visuels qui s'alimentent au crépuscule ou de nuit ont un rapport bâtonnets:cônes plus élevé et, en conséquence, une meilleure capacité de vision nocturne que les chasseurs visuels qui s'alimentent uniquement de jour. Les chasseurs visuels nocturnes ont une capacité de vision nocturne meilleure que celles des chasseurs tactiles diurnes, et que celles des chasseurs tactiles nocturnes. Cependant, compte tenu de l'amplitude maximale de l'onde b scotopique, toutes les espèces étudiées, incluant le Héron garde-boeufs et l'Aigrettre tricolore, ont sensiblement la même capacité de vision nocturne. Parmi les Ciconiiformes, le facteur qui distingue le mieux les espèces semble être la capacité de vision diurne. De ce fait, l'Ibis rouge, le Héron garde-boeufs et l'Aigrette tricolore, tous strictement diurnes, présentent des valeurs comparables quant à la densité des cônes, le rapport cônes:bâtonnets, et l'amplitude de l'onde a photopique, valeurs qui sont plus élevées chez ces oiseaux que chez les deux hérons actifs de nuit.

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1. La nocturnalité chez les oiseaux

Parmi les classes de vertébrés, les oiseaux se distinguent particulièrement par la diversité des espèces, des comportements et des modes de vie. La plupart des oiseaux sont diurnes, cependant il existe un nombre minoritaire d'espèces qui sont actives le jour et la nuit et d'autres qui sont strictement nocturnes. Une espèce d'oiseau est considérée comme strictement nocturne quand elle exécute toutes ses activités pendant la nuit. C'est le cas, par exemple, d'espèces appartenant aux ordres des Caprimulgiformes, Strigiformes, Apodiformes et Apterygiformes, lesquels représentent moins de 3% de l'ensemble des espèces d'oiseaux connues (Martin, 1990; McNeil et al., 1992). Cependant, ces quatre ordres d'oiseaux ne sont pas les seuls à comporter des représentants actifs de nuit. Il existe, en fait, neuf autres ordres comprenant 28 familles d'oiseaux aquatiques incluant des espèces partiellement ou principalement nocturnes. Ces ordres sont les Anseriformes, Charadriiformes, Sphenisciformes, Procellariiformes, Pelecaniformes, Ciconiiformes, Phoenicopterigiformes, Gruiformes et Podicipediformes (McNeil et al., 1992, 1993 a et b, 1998).

2. L'activité nocturne chez les oiseaux aquatiques

La nature des activités nocturnes varie selon les groupes. Néanmoins, à part les tâches d'incubation des œufs, la principale activité répertoriée de nuit est la quête alimentaire (McNeil et al., 1992, 1993 a et b, 1998; McNeil et Rodríguez, 1996). Ainsi, chez plusieurs groupes dont les canards et les oies (Anseriformes: Anatidae), les albatros, puffins, pétrels tempête et puffinures (Procellariiformes: Diomedeidae, Procellariidae, Hydrobatidae, Pelecanoididae), les hérons, bihoreaux, butors et spatules (Ciconiiformes: Ardeidae, Threskiornithidae), les limicoles ou oiseaux de rivage et espèces apparentées (Charadriiformes: Charadriidae, Scolopacidae, Recurvirostridae), les becs-en-ciseau (Charadriiformes: Rynchopidae), la quête alimentaire a lieu, selon les espèces, de jour et de nuit, et dans bien des cas, principalement de nuit.

Chez quelques espèces, d'autres activités peuvent aussi avoir lieu de nuit. Ainsi, certains oiseaux de rivage comme le Pluvier argenté (*Pluvialis squatarola*), le Chevalier semipalmé (*Catoptrophorus semipalmatus*) et le Courlis corlieux (*Numenius phaeopus*) continuent, sur leur aire d'hivernage, à défendre et à utiliser la nuit le territoire d'alimentation qu'ils défendent le jour (Wood, 1986, McNeil et Rompré, 1995, Rompré et McNeil, 1996).

3. Avantages de l'alimentation nocturne chez les oiseaux aquatiques

L'alimentation nocturne a été initialement associée uniquement à un besoin de combler des déficits énergétiques accumulés durant la période d'éclairage restreinte en hiver; c'est l'hypothèse du supplément (voir McNeil et al., 1992). Cela peut se produire quand et là où les oiseaux comme certains chevaliers (*Tringa*) et huîtriers (*Haematopus*) passent l'hiver boréal en région froide ou tempérée (Goss-Custard, 1969; Heppleston, 1971; Goss-Custard et al., 1977; Pienkowski, 1981, 1982; Puttick, 1984). Cela peut aussi se produire quand et là où des oiseaux migrateurs, suite à de l'hyperphagie, accumulent les réserves énergétiques (graisses) qui leur serviront pour le vol de longue distance en migration. C'est le cas par exemple du Chevalier semipalmé sur l'aire d'hivernage dans les lagunes côtières du Venezuela (Rompré et McNeil, 1994).

Une autre hypothèse tente d'expliquer les avantages que peuvent retirer les oiseaux aquatiques de la quête alimentaire nocturne, celle du choix (voir McNeil et al., 1992). Certains oiseaux préfèrent s'alimenter de nuit à cause des conditions plus profitables liées à l'abondance et la disponibilité des proies. De ce fait, la connaissance que nous avons de la quête alimentaire nocturne par les oiseaux de mer comme les Procellariiformes est déduite de la connaissance que l'on a de leur régime alimentaire. Beaucoup d'espèces qui constituent le zooplancton et leurs prédateurs (e.g., poissons) effectuent une migration des profondeurs vers la surface des océans la nuit, souvent en suivant le zooplancton dans sa montée vers la surface (Imber, 1973; Simons, 1985; Harper,1987). De tels organismes ne sont accessibles aux oiseaux comme les pétrels tempête et les puffins que durant la nuit. Un phénomène similaire se produit aussi dans les marais, les plans d'eau douce et les lagunes côtières à cause de la rareté en oxygène qui sévit près des fonds durant la nuit (voir McNeil et al., 1998). Dans de tels milieux, et en particulier dans les marais et les lagunes côtières où des espèces comme les becs-en-ciseau (*Rynchops*) et une grande variété d'échassiers (hérons, bihoreaux) et de canards s'alimentent de nuit, beaucoup d'organismes migrent la nuit tombée près de la surface des eaux. Un telle migration verticale se produit aussi en zone intertidale où une grande variété d'oiseaux de rivage et d'échassiers (hérons, bihoreaux, etc.)

s'alimentent la nuit. De ce fait, beaucoup d'invertébrés dont s'alimentent ces oiseaux montent durant la nuit à la surface des substrats qui se découvrent à marée basse (McNeil et al., 1995). Dans les mêmes milieux, les organismes qui nagent (e.g., crustacés, insectes aquatiques) dans les eaux de moins de 10 cm de profondeur, près de la ligne de marée, sont aussi présents en plus grande densité durant la nuit. Ces organismes sont très exploités par les chevaliers (*Tringa*) et les échasses (*Himantopus*) (McNeil et al., 1995). Selon l'hypothèse du choix, certains oiseaux peuvent aussi s'alimenter de nuit, parce qu'elle leur apporte une meilleure sécurité vis-à-vis des prédateurs, ou moins de dérangement de la part des humains (e.g., chasse, activités récréatives sur les plages, etc.). C'est vraisemblablement le cas pour des oies qui s'alimentent davantage de nuit en période de saison de chasse (McNeil et al., 1992) et pour les Bécasseaux sanderling (*Calidris alba*) qui s'alimentent davantage de nuit dans les périodes où ils sont dérangés de jour par des villégiateurs sur les plages (Burger et Gochfeld, 1991).

4. Adaptations sensorielles permettant l'activité nocturne chez les oiseaux aquatiques

Les adaptations sensorielles permettant l'activité la nuit varient selon les groupes d'oiseaux. En général les oiseaux nocturnes ont les bulbes olfactifs plus développés que les oiseaux diurnes (Healy et Guilford, 1990). Cependant, chez les Procellariiformes le sens de l'olfaction est bien développé peu importe si l'espèce est diurne ou nocturne (Grubb, 1972; Jouventin et Robin, 1983; Hutchison et al., 1984, Healy et Guilford, 1990). Ainsi, les puffins, pétrels tempête et puffinures ont des bulbes olfactifs très développés et semblent réaliser une bonne partie de leurs tâches nocturnes (e.g., quête alimentaire, repérage du terrier où se trouve leur nid) uniquement ou principalement à l'aide de l'odorat (Hutchison et Wensel, 1980). Récemment, en étudiant le comportement alimentaire des Procellariiformes, Nevitt et al. (1995) ont constaté que les pétrels tempête sont fortement attirés en mer par les aires d'émanation d'un produit volatile, le sulfure de diméthyle, un sous-produit de la décomposition métabolique du sulphoniopropionate de diméthyle dans le phytoplancton marin. La production de cette substance est accélérée de façon notable pendant que le phytoplancton est consommé par le zooplancton (Dacey et Wakeham, 1986).

En général, chez les Charadriiformes, les espèces nocturnes ont les bulbes olfactifs plus développés que les espèces diurnes (Healy et Guilford, 1990). Cependant, selon Boire

(1989), les bulbes olfactifs sont plus développés chez les oiseaux dont les proies sont dissimulées. Par exemple, le Bécassin roux (*Limnodromus griseus*) (diurne et nocturne), qui cherche ses proies en sondant le sol, a les bulbes olfactifs plus développés que le Pluvier de Wilson, *Charadrius wilsonia* (principalement nocturne), qui cherche ses proies visuellement. Pienkowski (1983) a suggéré que lors de nuits sans lune, les pluviers sont capables de s'alimenter en détectant leurs proies par le son.

D'autre part, il existe des espèces qui détectent les proies au toucher. C'est le cas, par exemple, de la majorité des oiseaux de rivage de la famille des Scolopacidae, de la plupart des canards et des oies, de même que des représentants des Threskiornithidae (spatules et ibis). Plusieurs de ces espèces ont des récepteurs sensoriels (corpuscules de Herbst et de Grandy) à la surface ou à l'extrémité du bec leur permettant de repérer les proies de manière tactile (Schwartzkopff, 1973, 1985; Gottschaldt, 1974; Berkoudt, 1980; Pettigrew et Frost, 1985; Martin, 1990; McNeil et al., 1992, 1993). Chez d'autres, la chémoréception permettent de détecter les aires riches en proies (Gerritsen et al., 1983; Heezik et al., 1983).

Les espèces actives la nuit doivent voler pour se déplacer d'un site alimentaire à l'autre ou d'un site alimentaire au nid. On peut donc s'attendre à ce qu'elles disposent d'une capacité de vision nocturne appropriée. Durant la nuit et malgré la difficulté de distinguer les détails fins, quelques espèces d'oiseaux aquatiques sont quand même des prédateurs strictement visuels. C'est le cas, par exemple, de certaines espèces de Ciconiiformes comme ceux du genre *Nycticorax* (Meyerriecks, 1962; Kushlan, 1976, 1977, 1978) et les Charadriiformes des genres *Pluvialis* et *Charadrius* (Schneider, 1983; Robert et McNeil, 1989). Par contre, d'autres Charadriiformes, comme les chevaliers (*Tringa*), changent de stratégie selon l'éclairage, i.e., visuels de jour et tactiles de nuit (McNeil et Robert, 1988; Robert et McNeil, 1989; McNeil et Rompré, 1995).

On pourrait s'attendre à ce que l'absence d'activité nocturne chez une espèce, comme par exemple l'Aigrette tricolore (*Egretta tricolor*) appartenant aux Ciconiiformes, puisse s'expliquer par une capacité de vision nocturne déficiente. Par contre, l'absence d'activité diurne chez le Bec en ciseaux (*Rynchops niger*) peut être aussi expliquée par une capacité de vision diurne inappropriée. De la même façon, se pourrait-il que le changement de stratégie de quête alimentaire constaté chez les chevaliers (*Tringa*), de visuelle de jour à tactile selon les conditions d'éclairage, soit explicable par une capacité de vision nocturne inadéquate?

Malgré la grande radiation adaptative chez les oiseaux, aucune étude comparative entre plusieurs espèces, prenant en compte les différentes adaptations du système visuel à leur environnement, n'a été faite auparavant. C'est pourquoi nous avons décidé d'étudier chez un groupe d'oiseaux aquatiques certains aspects du système visuel pouvant nous permettre de répondre à de telles questions.

5. Les yeux chez les oiseaux

S'il est une caractéristique bien marquante qui vient à l'esprit quand on pense aux oiseaux, c'est leurs yeux qui sont très développés (grande taille), tant en termes absolu que relatif. Ils peuvent être globuleux ou allongés, frontaux ou latéraux, et de diverses teintes. Chez plusieurs espèces, les yeux apparaissent petits, mais ceci n'est qu'une illusion due au fait que seule une partie de la surface cornéenne est visible (Waldvogel, 1990). De ce fait, chez les oiseaux, les yeux occupent une proportion importante du volume crânien, dépassant souvent les 50% (Walls, 1942; Waldvogel, 1990). Cette valeur est particulièrement élevée comparée à celle des autres vertébrés. Chez l'homme, par exemple, ce chiffre ne dépasse guère les 5%. Pearson (1972) rapporte que les faucons et les hiboux, entre autres, ont des yeux plus volumineux que ceux de l'homme.

Les yeux des oiseaux ont néanmoins une structure de base identique à celle des autres vertébrés (Walls, 1942). La lumière qui pénètre dans l'oeil traverse la même séquence d'éléments optiques. Elle entre par la cornée, traverse l'humeur aqueuse dans la chambre antérieure, puis l'ouverture pupillaire de l'iris et ensuite l'humeur vitrée avant d'atteindre la rétine. Le stimulus lumineux est transformé en influx nerveux dans la rétine, influx acheminé par le nerf optique au cerveau qui le traite et le transforme en une sensation visuelle. La rétine elle-même est une structure assez complexe. Les deux classes de photorécepteurs, cônes et bâtonnets, sont les principaux éléments responsables de la sensibilité à la lumière et de la perception visuelle.

Une question légitime s'impose quand on aborde les yeux des oiseaux: est-ce que leur taille spectaculaire est le résultat d'une adaptation à un style de vie particulier? Quel est l'impact de l'environnement et de la lumière sur la topologie et la morphologie de l'oeil et ses composantes?

Le pouvoir de perception du système visuel est gouverné par deux types de facteurs. Le premier est la série des éléments optiques qui déterminent la qualité de l'image rétinienne et le second regroupe plusieurs types de processus neurologiques (Snyder et al, 1977). La qualité de l'image (ou l'acuité visuelle) est à son tour régie par trois facteurs: la forme de l'oeil, les milieux transparents, ainsi que la densité cellulaire des éléments de la rétine (Tansley et Erichsen, 1985; Waldvogel, 1990).

On trouve chez les oiseaux une grande diversité de taille, forme et position des yeux dans la boîte crânienne (Rochon-Duvigneaud, 1943; 1950; Walls, 1942; Meyer 1977). Il s'est avéré que ces différences anatomiques entre espèces sont un reflet des divers styles de vie (Tansley, 1965; Ali et Klyne, 1986). Il a été constaté que les oiseaux, tels que certains types de hiboux, qui ont un comportement strictement nocturne, ont des yeux de forme tubulaire (Tansley, 1965; Martin, 1990; Waldvogel, 1990). Des espèces diurnes telles que les pigeons ont des yeux aplanis (Tansley, 1965; Waldvogel, 1990). En revanche, les oiseaux de proie diurnes, qui nécessitent une bonne acuité visuelle, ont des yeux de forme plutôt globuleuse (Tansley, 1965).

5.1. Forme et taille de la pupille

Tel que mentionné plus haut, la forme et la taille de l'oeil ne sont pas les seuls critères qui déterminent la qualité de la vision chez les oiseaux. L'ouverture et la forme de la pupille jouent un rôle clé dans la formation de l'image. La pupille régit la quantité de lumière qui est acheminée vers la rétine, image similaire à celle de l'ouverture du diaphragme de l'appareil photographique qui règle la quantité de lumière atteignant le film.

En comparaison avec d'autres vertèbres la plupart des oiseaux ont une très grande pupille par rapport à la taille des yeux. Par conséquent, la quantité de lumière qui atteint la rétine chez les oiseaux est plus grande que chez les mammifères ayant des yeux de même taille. Ceci améliore la qualité de l'image à différents niveaux de lumière, spécialement sous de faibles intensités lumineuses, permettant aux oiseaux nocturnes de voir même lors des nuits sans lune (Martin, 1986). Non seulement la taille de la pupille chez les oiseaux est impressionante, mais aussi la rapidité exceptionnelle avec laquelle ils l'ajustent. Ainsi, par exemple, la pupille du pigeon biset (*Columba livia*) peut rétrécir à 1/9 de sa taille initiale en une ou deux secondes (Donovan, 1978). En revanche, la pupille de l'homme nécessite deux ou trois secondes pour se rétrécir à 1/6 de sa taille initiale. Ce degré et cette rapidité d'ajustement de la taille de la pupille jouent probablement un rôle important dans la précision et la qualité de l'image (Ali et Klyne, 1986).

Les oiseaux nocturnes ont une pupille plus grande, de forme circulaire ou verticale, qui leur permet de capter la plus grande quantité de lumière possible et leur assure ainsi une meilleure vue (Tansley, 1965; Ali et Klyne, 1986; Martin, 1990; Waldvogel, 1990). Certaines espèces, telles que les représentantes de la famille Rynchopidae, ont une pupille de forme de fente verticale (Zusi et Bridge, 1981) et s'alimentent presque exclusivement durant la nuit et de façon tactile (Tomkins, 1951; Zusi, 1959; Burger and Gochfeld, 1990). On pense que cette capacité d'adaptation chez les Rynchopidae les aide, d'une part, à améliorer leur vision nocturne et, d'autre part, à protéger leur rétine de la lumière plus vive pendant le jour (Zusi et Bridge, 1981). On a relevé qu'en général les oiseaux diurnes ont une pupille circulaire et de petite taille, ce qui leur permet de limiter la forte quantité de lumière qui entre dans les yeux pendant le jour.

5.2. La cornée et le cristallin

Dans l'oeil, la cornée et le cristallin agissent comme des lentilles, projetant une image inversée sur la rétine. La taille, la couleur et la courbure de la cornée et du cristallin jouent un rôle capital dans la qualité des images formées sur la rétine. Ces facteurs varient de façon très sensible selon le type d'habitat et les niveaux d'intensité lumineuse. Ainsi, on note une taille plus grande et une courbure plus prononcée de la cornée chez les oiseaux nocturnes que diurnes. Ceci est une conséquence du fait que les oiseaux nocturnes nécessitent une adaptation cornéenne leur permettant une meilleure réception de la lumière (Waldvogel, 1990). C'est le cas, par exemple, des prédateurs nocturnes, tels que les hiboux et les faucons, chez qui on relève, effectivement, une cornée, une pupille et un cristallin extrêmement développés.

La topologie de la cornée varie aussi avec le milieu de transmission des ondes lumineuses. Ainsi, on note en général une cornée plus petite et aplatie chez les oiseaux aquatiques qui s'alimentent sous l'eau (Walls, 1942, Sivak, 1980, Tansley et Erichsen, 1985). La capacité de vision sous l'eau est régie essentiellement par la réfraction du cristallin alors que chez les espèces terrestres, la réfraction est assurée par la cornée, d'où sa courbure prononcée. La réfraction assurer la convergence des rayons lumineux sur la rétine. En effet, l'indice de réfraction du corps vitré, de la cornée et de l'humeur aqueuse est proche de celui de l'eau (1,33), alors que celui du cristallin est un peu supérieur (entre 1,42 et 1,49) (Ali et Klyne, 1986). Ainsi, la réfraction dans l'eau ne peut se faire qu'à l'aide du cristallin qui a un indice de réfraction différent.

La taille et la forme du cristallin aussi dépendent du besoin de l'espèce (Tansley, 1965). Il est petit et aplati chez les oiseaux diurnes et grand et sphérique chez les oiseaux nocturnes. En plus, les espèces aquatiques sont dotées d'une capacité extraordinaire d'ajustement et de compensation de l'indice de réfraction quand elles passent du milieu aérien au milieu aquatique. Elles réussissent une telle accommodation grâce à un changement rapide de la forme du cristallin pour compenser la planéité de la cornée à l'aide des muscles ciliaires entourant le cristallin (Sivak, 1980). Cette capacité d'adaptation permet à plusieurs espèces d'oiseaux de voir “aussi bien" dans l'eau que dans l'air.

La couleur de la cornée et du cristallin est un élément important qui distingue les espèces diurnes et nocturnes. Les espèces diurnes sont caractérisées par un cristallin et une cornée de couleur jaune, jouant le rôle d'un filtre surtout pour les courtes longueurs d'onde de la lumière (Tansley, 1965). Chez les oiseaux nocturnes, ces éléments sont plutôt transparents.

5.3. La rétine

Parmi les composantes optiques qui déterminent la perception visuelle, la rétine joue un rôle primordial. Ali et Klyne (1986) soutiennent qu'il n'existe pas d'autre structure oculaire aussi "étroitement" reliée au mode de vie des animaux que la rétine.

La rétine des oiseaux est “la plus parfaite et la plus compliquée de toutes” (Ramón y Cajal, 1911). Néanmoins, elle a la même constitution de base que celle des autres vertébrés et sa couche photoréceptrice est composée de cônes et de bâtonnets (Walls, 1942, Tansley, 1965; Ramón y Cajal, 1911; Romer et Parson, 1983). Le nombre, la forme, la structure, la distribution et la proportion des cônes et des bâtonnets sont des paramètres étroitement liés à l'adaptation visuelle des oiseaux. Ils sont souvent utilisés comme points de comparaison pour différencier les espèces selon leur mode de vie.

5.3.1. Morphologie rétinienne

La rétine est composée de dix couches (Fig. 1), qui sont en commençant distalement par rapport à la cornée: 1) l'épithélium pigmentaire, qui consiste en une seule assise de cellules dans lesquelles se trouve la mélanine qui protège les photorécepteurs des fortes intensités lumineuses; 2) la couche des segments externes et internes des photorécepteurs; 3) la membrane limitante externe, qui n'est pas une vraie membrane au sens cellulaire du terme mais qui est constituée des prolongements lamellaires horizontaux qui sortent de l'extrémité distale des cellules de Müller au niveau de la base du segment interne des photorécepteurs; 4) la couche nucléaire externe, qui contient les noyaux des photorécepteurs; 5) la couche plexiforme externe, où les axones des photorécepteurs font synapse avec les dendrites des cellules bipolaires et horizontales dont le corps cellulaires se trouvent dans 6) la couche nucléaire interne; 7) la couche plexiforme interne, où les cellules bipolaires et amacrines font synapse avec les dendrites de cellules de 8) la couche des cellules ganglionnaires; 9) la couche des fibres du nerf optique, composée par les axones des cellules ganglionnaires qui forment le nerf optique et apportent l'information visuelle au cerveau; et 10) la membrane limitante interne, encore des prolongements lamellaires horizontaux qui sortent de l'extrémité proximale des cellules de Müller et qui séparent la rétine du corps vitré.

5.3.1.1. Structure et rôle des cônes

En général, la rétine des oiseaux contient deux types de cônes: les cônes simples et les cônes doubles, ces derniers étant composés de deux membres intimement associés, un cône principal et un cône accessoire (Fig.2). Le cône principal est plus long et contient, comme les cônes simples, une gouttelette lipidique colorée à l'apex du segment externe.

Les gouttelettes lipidiques sont de petites sphères huileuses localisées aux extrémités des segments internes des cônes. Elles sont souvent utilisées comme point de référence pour distinguer les cônes des bâtonnets, ces derniers n'en contenant pas. Généralement, le cône accessoire ne contient pas de gouttelette mais dans le cas où elles sont présentes, elles sont petites et incolores (Cohen, 1963; Morris et Shorey, 1967; Bowmaker et al., 1997). Même si les gouttelettes ne font pas l'objet de cette étude, il est intéressant de noter que chez les espèces diurnes, les gouttelettes sont rouges, orangées ou jaunes, alors que chez les espèces nocturnes, elles sont incolores ou jaune très pâle lorsqu'elles sont présentes (Meyer, 1977).

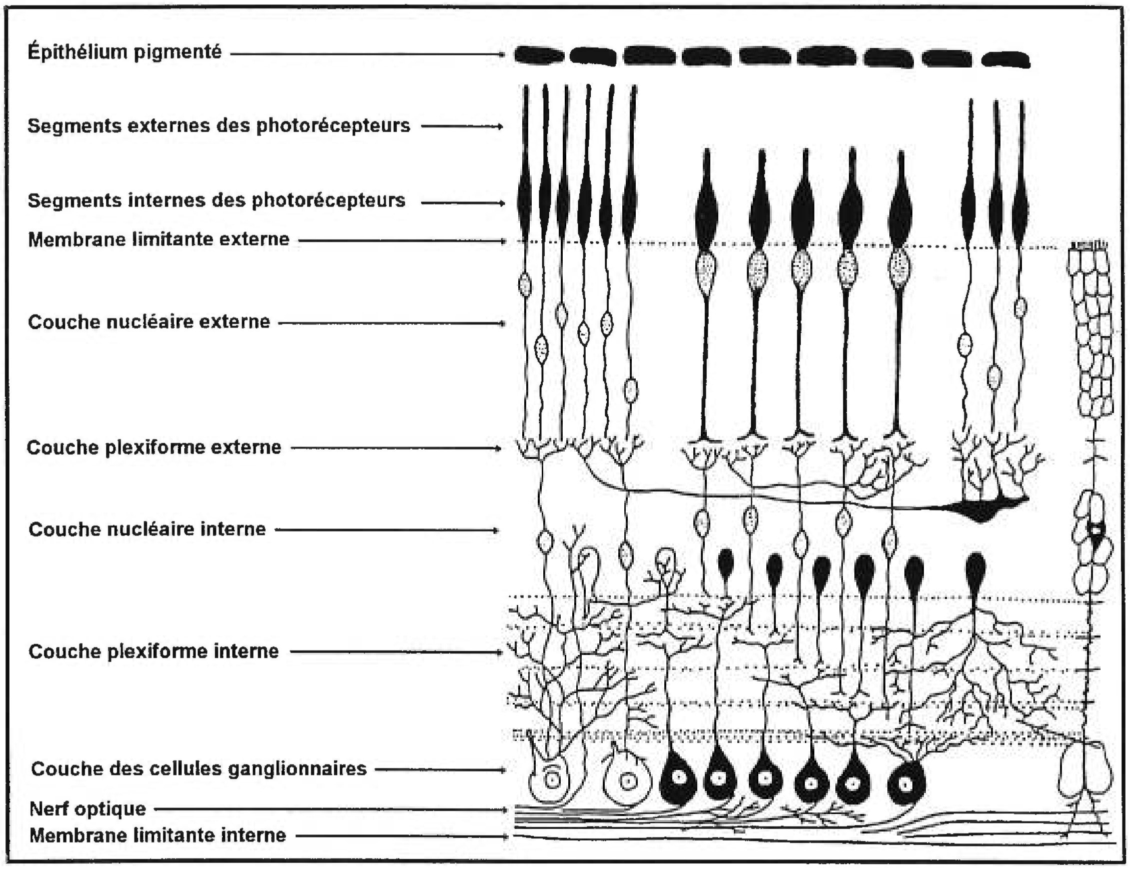

Figure 1. Diagramme de la structure de la rétine chez les vertébrés (Adapté de Kare et Rogers, 1976).

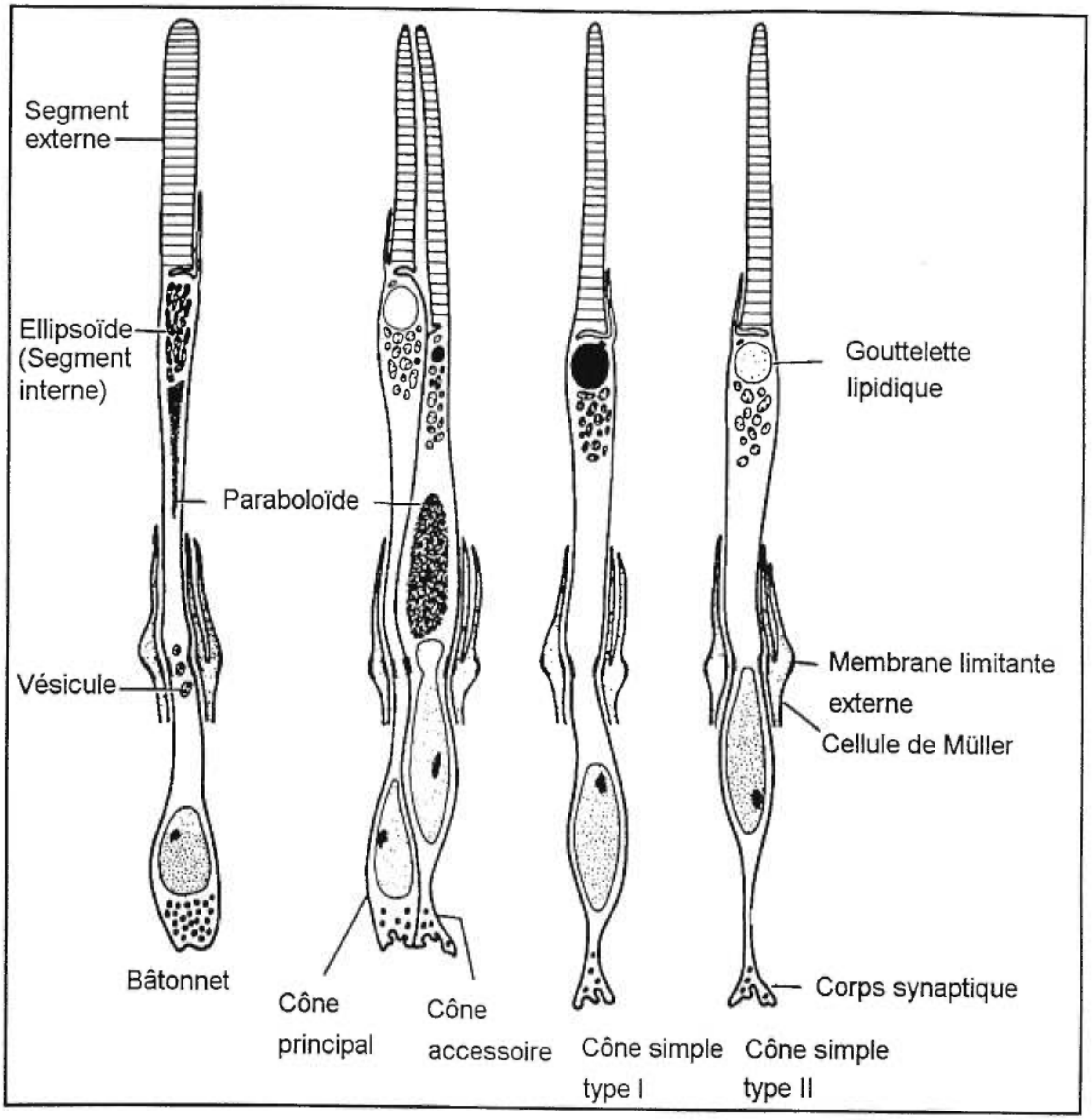

Figure 2. Types de photorécepteurs dans l'oeil du poulet (Adapté de Morris et Shorey, 1967).

La coloration a souvent été attribuée au fait que les gouttelettes constituent un filtre pour certaines longueurs d'onde de lumière, car elles s'interposent entre la lumière incidente et le pigment visuel des cônes. Ainsi, la couleur jaune a été considérée comme un filtre contre les plus courtes longueurs d'onde du spectre visuel. La distribution des gouttelettes dedifférentes couleurs dans la rétine est très variable d'une espèce à une autre (Meyer,1977; Lythgoe,1979; Begin et Handford, 1987). En général, les gouttelettes jaunes sont particulièrement nombreuses au centre de la rétine où la densité des cônes est plus importante. La coloration des gouttelettes lipidiques a été souvent attribuée à la présence de pigments caroténoïdes, qui sont des pigments naturels associés aux lipides (Galifret, 1968; Bowmaker, 1980). C'est pourquoi les gouttelettes sont souvent appelées gouttelettes lipidiques. Il s'est avéré que les gouttelettes lipidiques, conjointement avec le pigment photosensible, jouent un rôle important dans la vision des couleurs chez les oiseaux (Donner, 1953; Bowmaker, 1977, 1980; Bowmaker et Martin, 1977, 1985; Goldsmith et al., 1984; Gondo, 1985; Palacios et Valera, 1992).

L'abondance des cônes dans la rétine est associée à une bonne acuité visuelle (habileté à distinguer les détails très fins) et à une bonne capacité de distinguer les couleurs, mais aussi à une faible sensibilité (Bloch et Maturana, 1971; Cohen, 1972; Bowmaker, 1977; Bowmaker et Martin, 1977; Fein et Szuts, 1982; Waldvogel, 1990; Palacios et Valera, 1992). La rétine des oiseaux diurnes se caractérise par une proportion relativement importante de cônes (Walls, 1942; Morris et Shorey, 1967; Meyer et May, 1973; Meyer, 1977). Les oiseaux strictement diurnes, comme le pigeon, possèdent une rétine composée à 80% de cônes (Meyer, 1977). La rétine des oiseaux diurnes contient une fovéa, parfois deux, région spécialisée où l'acuité est la plus grande. La fovéa se présente comme une dépression où les couchez internes de la rétine sont très minces pour permettre les photorécepteurs de capter mieux la lumière et où la densité de cônes est très grande. Tout autour de la fovéa la densité des cellules bipolaires, horizontales et amacrines est très importante; il y a aussi une augmentation du nombre de cellules ganglionnaires qui, dans certains cas, sont dans une proportion de 1:1 avec les cônes de la fovéa (Tansley, 1965). Cette zone specialisée est fréquemment rencontrée au centre de la rétine, où il y a une plus grande possibilité de capter la lumière (Ramón y Cajal, S. 1911; Walls, 1942; Duijm, 1959; Tansley et Erichsen, 1985), cependant chez certain oiseaux on peu la trouvées dans la rétine temporale. Plusieurs espèces d'oiseaux n'ont pas une fovéa. Ils ont plutôt une région spécialisée où la densité de photorécepteurs et les couches internes de la rétine sont plus épaisses. Cette région spécialisée peu aussi se trouver dans les régions centrale et temporale de la rétine.

5.3.1.2. Rôle des bâtonnets

Les bâtonnets sont très sensibles aux faibles intensités lumineuses et à l'obscurité (vision scotopique). Ils sont associés à une faible acuité visuelle et ne permettent pas de distinguer les couleurs (Walls, 1942; Fein et Szuts, 1982; Ali et Klyne, 1986; Waldvogel, 1990). Leur nombre et leur densité relative par rapport à celle des cônes donne une indication précieuse sur le mode de vie des animaux en général, et celui des oiseaux en particulier. Les yeux des hiboux, par exemple, qui sont considérés parmi les mieux adaptés à la vision nocturne, ont une rétine à dominance de bâtonnets, qui représentent environ 90% de la population totale des photorécepteurs (Fite, 1973). En revanche, chez les oiseaux qui ne sont pas strictement nocturnes, le pourcentage de bâtonnets est un peu plus faible (Lockie, 1952; Rojas de Azuaje, 1993). En comparant la rétine de trois espèces d'oiseaux ayant différents modes de vie, Lockie (1952) a constaté que le Moineau domestique (*Passer domesticus*), qui est complètement diurne, a plus de cônes que le Puffin des Anglais (*Puffinus puffinus*), qui est strictement nocturne, et le Fulmar boréal (*Fulmarus glacialis*), qui montre un comportement diurne dans ses activité au nid (nourrir le jeunes, surveillance) et un comportement nocturne pour chercher son alimentation. D'autre part, il a observé que ces deux derniers ont plus de bâtonnets que le Moineau domestique. La rétine du Puffin des Anglais possède une grande structure paraboloïde dans les bâtonnets de la rétine adaptée à l'obscurité. Le paraboloïde est une grande accumulation de granules de glycogène retrouvés dans le segment interne des bâtonnets, parfois des cônes, de quelques espèces d'oiseaux. Le fonctionnement du paraboloïde n'est pas encore très claire. Selon Lockie (1952), quand des faibles rayons lumineux le traversent pour atteindre le segment externe des photorécepteurs, les granules de glycogène deviennent très serrés, bloquant probablement la lumière du côté du segment externe et augmentant notamment la sensibilité rétinienne. Ceci suggère que la rétine du Puffin des Anglais est mieux adaptée aux conditions de faible luminosité que celle de Fulmar boréal qui ne possède pas telle structure. Lors des travaux précédents (Rojas de Azuaje et al, 1993), nous avons comparé la proportion des bâtonnets et cônes dans les rétines de trois argenté, strictement visuel, le Grand chevalier à pattes jaunes (*Tringa melanoleuca*), visuel de jour et tactile de nuit, et le Bécassin roux, strictement tactile. Nous avons observé que la rétine du Pluvier argenté contient plus de bâtonnets que celle du Grand chevalier à pattes jaunes et celle du Bécassin roux, ce qui suggère qu'elle est mieux adaptée pour la vision nocturne. Par ailleurs, la rétine du Grand chevalier à pattes jaunes possède plus de cônes que celle du Pluvier argenté et celle du Bécassin roux, justifiant ainsi leur alimentation diurne. Le Bécassin roux, qui est typiquement tactile, présente une situation intermédiaire.

5.3.1.3. Rôle des cellules ganglionnaires

Un des paramètres les plus utilisés dans la caractérisation de la rétine est la densité et la morphologie des cellules ganglionnaires. Dans la couche des cellules ganglionnaires, on rencontre aussi une importante quantité de cellules amacrines (Hayes et Holden, 1980). La couche des cellules ganglionnaires est la dernière couche de traitement de l'information visuelle qui est ensuite acheminée, via le nerf optique, vers les centres cérébraux de la vision (tectum opticum, thalamus, wulst ou cortex visuel chez les vertébrés supérieurs). En se basant sur des analyses physiologiques, Maturana et Frenk (1962) ont rapporté différents types de cellules ganglionnaires chez le pigeon. Ils ont constaté que chaque type de cellules répond à une stimulation spécifique de mouvement. La morphologie et la topologie des cellules ganglionnaires sont souvent corrélées avec l'acuité visuelle (Ikushima et al., 1986; Hayes et Brooke, 1990; Hayes et al., 1991; Suburo et al., 1991). La fovéa et les aires centrales chez les oiseaux renferment une densité élevée de ces cellules. Chez le pigeon, Binggeli et Paule (1969) ont trouvé quatre fois plus de cellules ganglionnaires dans la région centrale que dans la périphérie. Inzuza et al. (1991) ont étudié la topologie et la morphologie des cellules ganglionnaires chez les Falconiformes. Ils ont observé deux fovéas dans la rétine: une fovéa temporale composée d'une forte densité de cellules ganglionnaires de taille moyenne et une fovéa nasale avec encore une remarquable densité de cellules ganglionnaires, mais de taille hétérogène. Chez les oiseaux de proies diurnes, la fovéa nasale est utilisée pour la vision panoramique alors que la fovéa temporale est utilisée pour la vision binoculaire (Pettigrew, 1979; Tansley et Erichsen, 1985).

5.3.2. Électrophysiologie de la rétine: l'électrorétinogramme

Pour une meilleure compréhension de l'adaptation visuelle des oiseaux à l'obscurité, il importe de réaliser des études physiologiques. Pour les études de la sensibilité rétinienne, la technique de l'électrorétinographie (ERG) est la plus recommandée (Seggie et al., 1991). En effet, l'oeil stimulé par la lumière manifeste une différence de potentiel de plusieurs microvolts (µV) entre la cornée et la rétine, manifestation électrique enregistrée sous le nom d'électrorétinogramme (ERG) (Jayle et al. 1964; Tansley, 1965; Le Grand, 1967; Brown, 1968; Armington, 1974). En faisant varier l'intensité et/ou la longueur d'onde d'un stimulus lumineux, l'ERG fournit de l'information sur l'activité des cônes et des bâtonnets (Armington, 1974; Ikeda, 1993). Quand la rétine est adaptée à la lumière, on obtient des mesures photopiques et quand elle est adaptée à l'obscurité, on obtient des mesures scotopiques. L'ERG est une réponse globale, très complexe, composée de plusieurs éléments (ondes) séparés. L'identification de chacun de ces éléments et des substrats nerveux qui les engendrent est un exercice très difficile. L'utilisation de microélectrodes intracellulaires a permis de grands progrès dans la compréhension de l'origine de l'ERG, notamment de chacune des ondes constituantes. Selon les conditions d'éclairage ou d'adaptation, on peut distinguer deux types d'ERG: monophasique et polyphasique (Jayle et al., 1964). L'ERG monophasique se manifeste à de faibles intensités lumineuses tandis que l'ERG polyphasique apparaît sous de forts éclairages. L'ERG, autant monophasique que polyphasique, dépend non seulement de la condition du stimulus mais aussi de la structure même de la rétine (nombre et distribution des cônes et des bâtonnets).

5.3.2.1. L'onde a

L'onde a (Fig. 3), la première de l'ERG, a ses origines dans les segments extrenes des photorécepteurs (Brown et Wiesel, 1961; Brown et Watanabe, 1962; Murakami et Kaneko, 1966; Witkovsky et al., 1973; Dick et Miller, 1985). Sa polarité est négative et son amplitude varie en fonction de l'intensité du stimulus, aussi bien pour la lumière monochromatique que polychromatique.

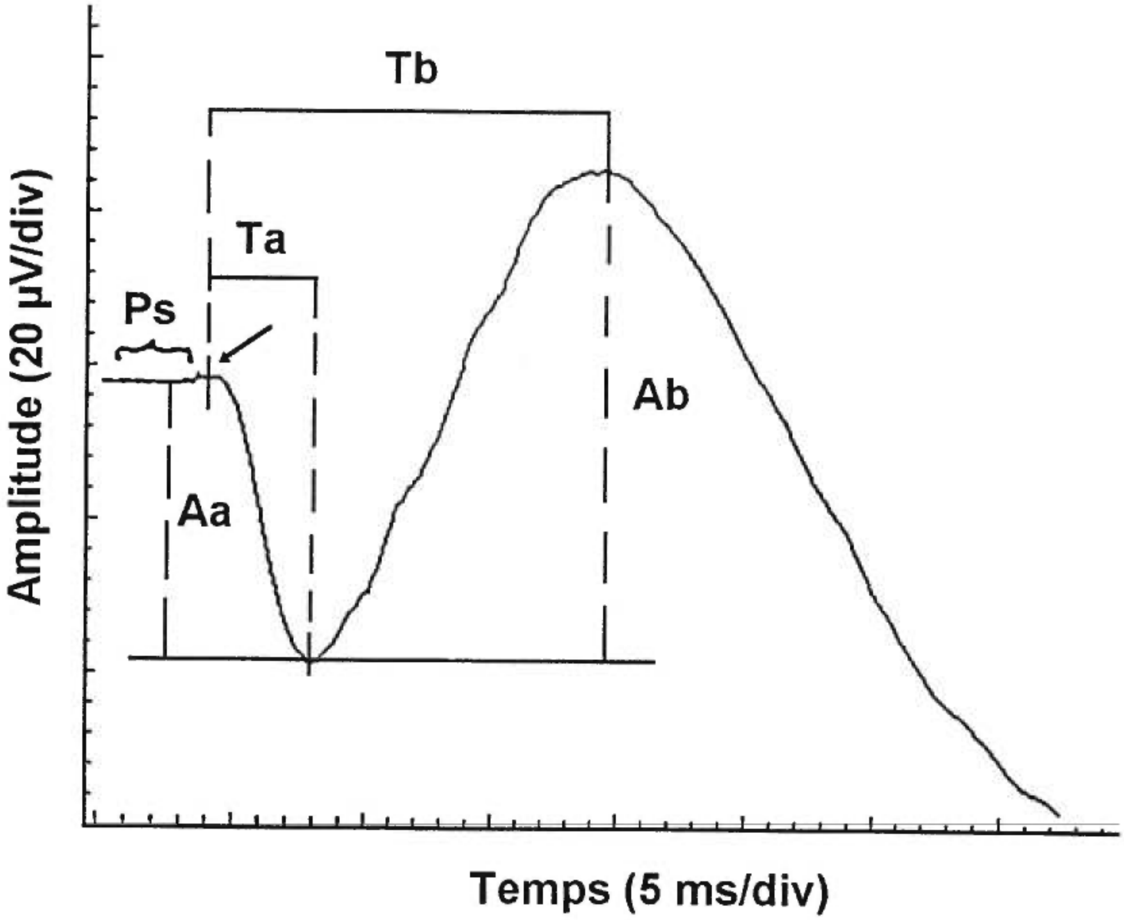

Figure 3. ERG scotopique typique. On note une onde a et une onde b. Les mesures d'amplitude de ces deux ondes ont été effectuées selon les procédures schématisées sur cette courbe. Abrév.: Ps: pré-stimulus; ↓: début du stimulus; Aa: amplitude de l'onde a; Ab amplitude de l'onde b; Ta: temps de culmination de l'onde a; Tb: temps de culmination de l'onde b.

5.3.2.2. L'onde b

L'onde b est une onde positive avec un temps de culmination lent qui décline brusquement lorsque le stimulus cesse (Jayle et al., 1964; Armington, 1974) (Fig. 3).

L'identification des cellules qui génèrent l'onde b a été une tâche très difficile (Dick et Miller, 1978; Newman, 1980; Heckenlively et Arden, 1991). En plaçant des microélectrodes dans la rétine, Brown et Wiesel (1961), Arden et Brown (1965) ainsi que Bysov (1965) ont constaté que l'onde b résulte plutôt de la réponse de la couche nucléaire interne abritant les cellules horizontales et bipolaires. Par contre, en utilisant des microélectrodes intracellulaires, Faber (1969), Miller et Dowling (1970) ainsi que Dick et Miller (1978) ont rapporté que l'onde b prend son origine dans les cellules de Müller. Ces cellules traversent la rétine de la membrane limitante externe jusqu'à la membrane limitante interne.

On a établi que pendant l'adaptation à l'obscurité, l'onde b est très influencée par le degré de régénération de la rhodopsine (Armington, 1974). Il est donc tout à fait acceptable de considérer les valeurs de l'amplitude et du temps de culmination de l'onde b comme des mesures indirectes de sensibilité rétinienne (Armington, 1974).

5.3.2.3. L'ERG chez les oiseaux

Nous avons déjà vu que les yeux des oiseaux présentent une grande variété d'adaptations au niveau structural qui sont en corrélation directe avec le mode de vie des espèces. Une grande partie de ces adaptations peuvent se répercuter dans la réponse électrorétinographique.

La réponse à la lumière a été bien étudiée chez le poulet et le pigeon. Leurs rétines contiennent une prépondérance de cônes et sont, de ce fait, tout à fait adéquates à l'étude des éléments photopiques (pigment visuel des cônes, sensibilité spectrale, gouttelettes lipidiques colorées, etc.) (Ikeda, 1965; Armington, 1974). En revanche, chez les hiboux, la rétine est dominée par les bâtonnets. Le hibou a souvent été considéré comme le modèle de choix pour l'analyse des éléments scotopiques (pigment visuel des bâtonnets, seuil de sensibilité rétinienne, etc.).

En utilisant l'électrorétinographie avec un stimulus de type flicker, Ikeda (1965) a constaté que la courbe de sensibilité photopique, déterminée par cette méthode, présente un maximum de valeur équivalente à celle du pic du spectre d'absorption de l'iodopsine dans les cônes. La sensibilité des cônes à la lumière n'est pas uniforme pour toute la plage du spectre visible. Ikeda a remarqué que les cônes sont plus sensibles aux fortes qu'aux faibles longueurs d'ondes. Ceci peut être expliqué par la présence de gouttelettes lipidiques colorées. Il a aussi noté qu'en utilisant des stimuli très faibles, on obtient des ERGs typiques du spectre d'absorption de la rhodopsine, et par conséquent des bâtonnets. Ces ERGs sont caractérisés par une forme monomodale arrondie et de faible amplitude. Cependant, en augmentant l'intensité du stimulus, on voit apparaître l'onde a et une onde b de grande amplitude.

En enregistrant des ERGs locaux à l'aide de microélectrodes intrarétiniennes, Ogden et Wylie (1971) ont cherché à identifier les maxima d'amplitude pour les ondes a et b chez le pigeon. En plaçant une microélectrode dans les différentes couches, ils ont constaté que l'amplitude de l'onde b présente un maximum dans la limite externe de la couche nucléaire interne et l'onde a au niveau de l'apex des segments externes des photorécepteurs.

Porciatti et al. (1989) ont analysé les réponses photopiques et scotopiques chez un hibou, la Chevêche d'Athéna (*Athene noctua*). Ils ont enregistré les réponses des deux yeux simultanément et ont noté que les deux courbes sont bien superposables, indiquant que les réponses des deux yeux sont identiques. Ils ont aussi constaté la présence des deux ondes dans les deux types d'adaptation. Leur amplitude varie sensiblement avec l'intensité lumineuse. L'onde b augmente avec l'intensité lumineuse aussi bien en condition photopique que scotopique. La différence entre ces deux ondes correspond à la valeur de l'intensité-seuil de réponse, qui est plus faible en conditions scotopiques que en conditions photopiques. La différence est de l'ordre de 8 unités logarithmiques, ce qui est spectaculaire. On conclut d'après ces résultats que la vision de la Chevêche d'Athéna démontre à la fois un caractère photopique et scotopique.

6. Objectifs et choix d'espèces

Ce travail de recherche fait partie d'un vaste projet qui a comme but principal l'étude de la capacité de vision diurne et nocturne chez différents Ordres d'oiseaux aquatiques parmi lesquel figurent: les Procellariiformes, les Anseriiformes, les Charadriiformes et les Ciconiiformes. Pour ce travail de doctorat nous nous sommes limités à deux Ordres: l'Ordre Charadriiformes (groupe des oiseaux de rivage ou limicoles) et l'Ordre Ciconiiformes (groupes des grands échassiers) (Tableau 1). Le choix des espèces a été très influencé par la facilité de la capture, c'est-à-dire, l'accès à des sites de capture et l'abondance des espèces choisies dans la nature et du coût qu'implique la capture d'une espèce en particulier. On a choisi des espèces dont le comportement alimentaire a déjà été rapporté dans la littérature. Dans ce travail, nous voulons montrer de façon aussi bien qualitative que quantitative les liens existant entre le mode de vie de certaines espèces d'oiseaux et la structure et la physiologie de leur rétine. Le choix des espèces tient compte de leur mode de vie (diurne et/ou nocturne) et de leur stratégie de quête alimentaire (visuelle et/ou tactile). Dans le groupe des limicoles, nous nous sommes intéressés à six espèces appartenant à quatre familles: Recurvirostridae, Charadriidae, Scolopacidae et Rynchopidae. Dans le groupe des Ciconiiformes, nous avons porté notre intérêt sur six espèces appartenant à deux familles: Ardeidae et Threskiornithidae. En général, le but de cette étude est de réaliser une analyse comparative et aussi complète que possible de différentes espèces d'oiseaux bien ciblées, appartenant aux deux groupes distincts mentionnés. Nous proposons une démarche qui consiste à modéliser en laboratoire la réponse des yeux à des conditions de lumière bien contrôlées, puis à les corréler à la structure rétinienne. Nous avons focalisé notre attention sur un seul élément pouvant servir de critère pour différencier les espèces: la rétine. Les objectifs spécifiques de cette étude sont les suivants:

i. vérifier expérimentalement s'il existe un lien entre le mode de vie des espèces étudiées (nocturne et / ou diurne, chasseur tactile et / ou visuel) et la morphologie de leur rétine;

ii. vérifier expérimentalement s'il existe un lien entre le mode de vie des espèces étudiées et l'électrophysiologie de leur rétine;

iii. examiner s'il existe des corrélations entre la structure rétinienne et les caractéristiques électrorétinographiques de chaque espèce.

Ce travail comprend quatre articles dont les objectifs et les liens entre eux sont brièvement rapportés ici:

Table 1. Caractéristiques comportementales des oiseaux sélectionnés.

Espèces	Période de quête alimentaire	Stratégie de quête alimentaire	Références
Ciconiiformes: Ardeidae			
Bihoreau violacé (*Nycticorax violaceus*)	Crépusculaire et nocturne	Chasseur visuel passif	1-6
Héron garde-boeufs (*Bubulcus ibis*)	Strictement diurne	Chasseur visuel actif	1-6
Grand Héron (*Ardea herodias*)	Principalement crépusculaire, mais aussi diurne et nocturne	Chasseur visuel passif	2,7,8
Aigrette tricolore (*Egretta tricolor*)	Strictement diurne	Chasseur visuel actif	1-6
Ciconiiformes: Threskiornithidae			
Ibis rouge (*Eudocimus ruber*)	Strictement diurne	Chasseur tactile	9-11
Spatule rosée (*Ajaia ajaja*)	Principalement crépusculaire et plus nocturne que diurne	Chasseur tactile	2,12
Charadriiformes: Scolopacidae			
Chevalier semipalmé (*Catoptrophorus semipalmatus*)	Diurne et nocturne	Individus territoriaux: visuel lors de nuits avec lune	13-17
Bécasse d'Amérique (*Scolopax minor*)	Hiver: principalement nocturne;	Principalement tactile	18-23
	été: presque exclusivement diurne	occasionnellement visuel durant l'été	24
		tactile lors de nuits sans lune	
Bécassin roux (*Limnodromus griseus*)	Diurne et nocturne	Chasseur tactile	25-27

Tableau 1. Suite.

Espèces	Période de quête alimentaire	Stratégie de quête alimentaire	Références
Charadriiformes: Charadriidae			
Pluvier de Wilson (*Charadrius wilsonia*)	Période de reproduction: diurne et nocturne; période no reproductive: principalement nocturne	Chasseur visuel	25-30
Charadriiformes: Recurvirostridae			
L'Échasse Américaine (*Himantopus himantopus*)	Diurne et nocturne	Généralement visuel excepte de jour lors que l'eau devient trouble et occasionnellement lors de nuits sans lune	25, 26, 27
Charadriiformes: Rynchopidae:			
Bec-en ciseaux noir (*Rynchops niger*)	Nocturne	Chasseur tactile mais besoin de la vision pour voler quand rase la surface de l'eau	31-33

Références

[1] Kushlan, 1978; [2] McNeil et al. 1993b; [3] Meyerriecks 1962; [4] Kushlan 1976; [5] Willard 1977; [6] Rodgers 1983; [7] Horvath et Moholt 1986; [8] McNeil et al. 1993a; [9] Hancock et al. 1992; [10] Matheu et del Hoyo 1992; [11] McNeil et al. 1998; [12] Robert et al. 1989; [13] Llinas G. et Galindo J. 1990; [14] McNeil et Rodríguez S. 1990; [15] Rompré & McNeil 1994; [16] McNeil et Rompré 1995; [17] Rompré et McNeil 1996; [18] Sheldon 1967; [19] Owen et Morgan 1975; [20] Owen 1977; [21] Stribling et Doerr 1985; [22] Sepik et al. 1989; [23] Roberts 1993; [24] Krementz et al. 1995; [25] McNeil et Robert 1988; [26] Robert et McNeil 1989; [27] McNeil et al. 1992; [28] Morrier et McNeil 1991; [29] Thibault et McNeil 1994; [30] Thibault et McNeil 1995; [31] Tomkins 1951; [32] Zusi 1962; [33] Zusi 1985.

1) Diurnal and nocturnal visual function in two tactile foraging waterbirds: the American White Ibis and the Black Skimmer. Rojas, L. M., McNeil, R., Cabana, T. and Lachapelle, P. Condor, 99: 191-200 (1997).

Dans cet article, nous comparons la capacité de vision diurne et nocturne de deux types d'oiseaux chasseurs tactiles ayant des périodes d'activité différentes: le Bec-en-ciseaux noir (*Rynchops niger*; principalement nocturne) et l'Ibis rouge (*Eudocimus ruber*; strictement diurne). Étant donné que ces deux oiseaux adoptent une stratégie tactile pour s'alimenter, nous nous sommes demandé pourquoi l'Ibis rouge, qui est tactile, ne s'alimente pas aussi pendant la nuit, quand la diversité et la disponibilité des proies sont plus favorables?

2) Diurnal and nocturnal visual capabilities in shorebirds as a function of their feeding strategies. Rojas, L. M., McNeil, R., Cabana, T. and Lachapelle, P. Brain, Behavior and Evolution. Accepté, juillet 1998.

Dans cet article, nous comparons 5 espèces de limicoles appartenant à l'ordre Charadriiformes. Ces limicoles, tous actifs de nuit comme de jour, ont différentes stratégies de quête alimentaire. Il s'agit du Pluvier de Wilson (*Charadrius wilsonia*; strictement visuel et principalement nocturne), de l'Échasse d'Amérique (*Himantopus himantopus*; visuelle et tactile, autant le jour que la nuit selon les conditions du milieu), la Bécasse d'Amérique (*Scolopax minor*; tactile, principalement nocturne), le Chevalier semipalmé (*Catoptrophorus semipalmatus*; visuel le jour et durant les nuits éclairées par la lune, tactile lors de nuits sans lune) et le Bécassin roux (*Limnodromus griseus*; strictement tactile, de jour comme de nuit). Étant donné que les stratégies d'alimentation de certains limicoles changent avec les conditions d'éclairage, notre but cette fois-ci était de savoir si les oiseaux ayant une stratégie visuelle la nuit ont une meilleure capacité de vision nocturne que celle des oiseaux strictement tactiles.

3) Behavioral, morphological and physiological correlates of diurnal and nocturnal vision in selected wading bird species. Rojas, L. M., McNeil, R., Cabana, T. and Lachapelle P. Brain, Behavior and Evolution. Soumis, septembre, 1998.

Le but de cet article était de comparer la capacité de vision diurne et nocturne chez 6 espèces de Ciconiiformes appartenant à deux familles différentes: les Ardeidae et les Treskiornithidae. Les Ardeidae sont strictement visuels, tandis que les Treskiornithidae sont strictement tactiles. Chez les Ardeidae, nous avons choisi le Bihoreau violacé *(Nycticorax violaceus*; principalement nocturne), le Héron garde-boeufs (*Bubulcus ibis*; strictement diurne), l'Aigrette tricolore (*Egretta tricolor*; strictement diurne) et le Grand Héron (*Ardea herodias*; diurne, crépusculaire et nocturne). On s'attend, par exemple, à ce que le Bihoreau violacé soit doté d'une sensibilité rétinienne supérieure à celle de l'Aigrette tricolore. Parmi les Treskiornithidae, nous nous sommes intéressés à l'Ibis rouge (*Eudocimus ruber*; strictement diurne) et à la Spatule rosée (*Ajaia ajaja*; principalement crépusculaire et nocturne). Comparée à la Spatule rosée, on s'attend à ce que l'Ibis rouge ait une meilleure acuité visuelle, mais une moins bonne capacité de vision nocturne.

4) Comparative study of the retinal structure and function in two groups of aquatic birds: the Ciconiiformes and the Charadriiformes. Rojas, L. M., McNeil, R., Cabana, T. and Lachapelle P. En préparation.

Dans les articles précédents, nous avons comparé les espèces en utilisant une approche statistique conventionnelle, l'intervalle de confiance 95%. Nous avons observé des différences entre la capacité de vision diurne et nocturne chez les différentes espèces d'oiseaux. Cependant, si ces espèces ont un ancêtre commun, elles ne sont pas indépendantes les unes des autres. Dans cet article, nous avons utilisé une approche phylogénétique pour comparer la structure et la fonction rétinienne des 12 espèces étudiées dans l'ensemble de ce travail. Le but était de savoir si, en tenant compte de la parenté phylogénétique entre les espèces, on continue à observer des différences significatives entre leur structure et leur fonction rétiniennes.

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Chapitre 2

Diurnal and nocturnal visual function in two tactile foraging waterbirds: the American White Ibis and the Black Skimmer

Par

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Abstract This study compares the diurnal and nocturnal visual function in two tactile foraging waterbird species, namely 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 conditions, but, in contrast, under photopic conditions, the amplitude of the ERGs was always 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, is 6.82:1 for the skimmer, and 0.89:1 for the ibis. The retina of the ibis contains, on the average, 18.8 rods/310 µm and 56.6 cones/310 µm, for a rod:cone ratio of 1:3. That of the skimmer contains 90.2 rods/310 µm and 16.8 cones/310 µm, 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 differences observed in feeding behaviors of the two species.

Key words: waterbirds, *Rynchops niger*, *Eudocimus ruber*, *Black Skimmer, American White Ibis,* vision, electroretinogram, retina, rod, cone, 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, 1996). 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 (see 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 (see 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 that without having to see the prey on which they feed, whereas birds that detect their prey primarily by sight would be disadvantaged (see 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 should allow night foraging (see Matheu and del Hoyo 1992, Hancock et al. 1992).

Skimmers do in fact feed primarily at night (for review, see McNeil et al. 1993; see also Fasola and Canova 1993). Usually, skimmers feed in shallow waters, in areas containing a high concentration of prey (Erwin 1977, Black and Harris 1983, Zusi 1985). In bill structure and feeding behavior, skimmers are unique: their lower mandible is laterally flattened like a knife blade and it protrudes well beyond the upper one (Zusi 1985; see also Tomkins 1951, Zusi 1962). 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. Flying in a straight path, apparently without seeing individual prey, the birds 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). Also, wind is reduced 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 (see McNeil et al. 1993, 1996). 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 non-visual 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 found 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 (see McNeil et al. 1996).

The retinal receptors of birds, as of all vertebrates, are the rods and cones (see Meyer 1977, Tansley and Erichsen 1985). Nocturnal birds have a great preponderance of rods in their retinae, while up to 80% of photoreceptors in diurnal birds are cones (see Tansley and Erichsen 1985, Waldvogel 1990). Rods are generally associated with night vision since they are sensitive to low level of illumination, but rods demonstrate poor discriminative abilities (visual acuity) and imperfect or no color vision (Tansley and Erichsen 1985). Cones, on the contrary, are associated with good visual acuity at high light levels and with color vision, but with a low light sensitivity and poor dark adaptation (Tansley and Erichsen 1985).

If non foraging during nighttime because of poor night vision, American White Ibises should have a cone-dominated retina compared to that of the largely nocturnal Black Skimmers which should be rod-dominated. We have thus tested this hypothesis by using physiological and morphological techniques that allowed us to verify the rod and cone functions of the retinae of the 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.

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). It consists 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 $cd \cdot m^{-2} \cdot sec$ and of 20 μsec 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 $cd \cdot m^{-2}$ with a variable aperture.

After a 4-h 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 maintained open upward. The eyelids and nictitating membrane were maintained 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, Pennsylvania) 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 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 $cd \cdot m^{-2}$. Under photopic 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. Working with the eye in the fixative, the retina, still attached to the choroid, was cut into 9 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. Still in the fixative, each sector was subdivided into 2-mm^2 portions, of which only 2 were retained for analysis. After 3 h in the fixative, the retinal portions, separated from the choroidal layer, were washed with phosphate buffer for 10 min, postfixed in 1% OsO_4 in 0.1 M phosphate buffer for 1 h, 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 (15 min). The tissues were successively infiltrated with a 1:1 mixture of propylene oxide and Epon for 6 h, and pure Epon medium for another 2 h. Finally, they were embedded in silicone rubber molds filled with Epon and polymerized at 60°C for 48 h.

Sections (0.7 µm) 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) to be examined with a Zeiss-Axiomat photomicroscope. Rods and cones as well as ganglion cells were counted in one field, 310 µm 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.

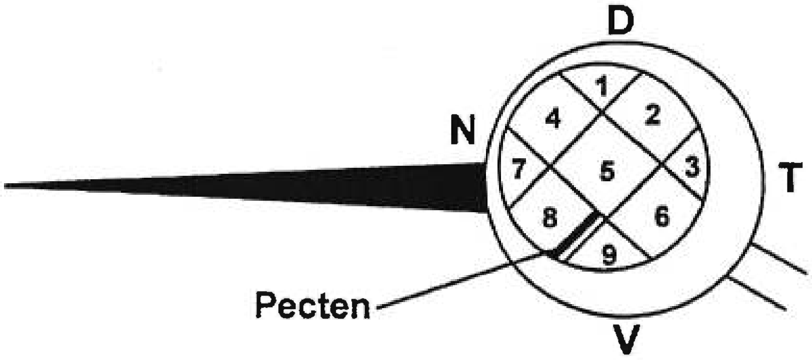


Figure 1. Schematic representation of the nine retinal sectors. **D, N, T**, and **V** correspond to dorsal, nasal, temporal and ventral sectors, respectively.

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 and peak time 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 -1.0 and a small, but not significant, reduction in amplitude at intensity 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 a significant level 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 (Fig. 5A), the timing of the scotopic ERG b-waves of the ibis 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 intensities used (Fig. 2B) while, for the skimmer, identifiable a- and b-waves are only present in responses obtained to the brightest flash (Fig. 3B). Analysis of the corresponding luminance-response curves (Fig. 4B) reveals 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, the timing of the photopic ERG b-waves of the ibis is always significantly faster than that of the skimmer. The amplitude of the photopic ERG b-wave obtained at the brightest luminance is significantly lower than that measured under scotopic conditions with the same flash luminance in the skimmer, but not in the ibis (Table 1). Indeed, from data of

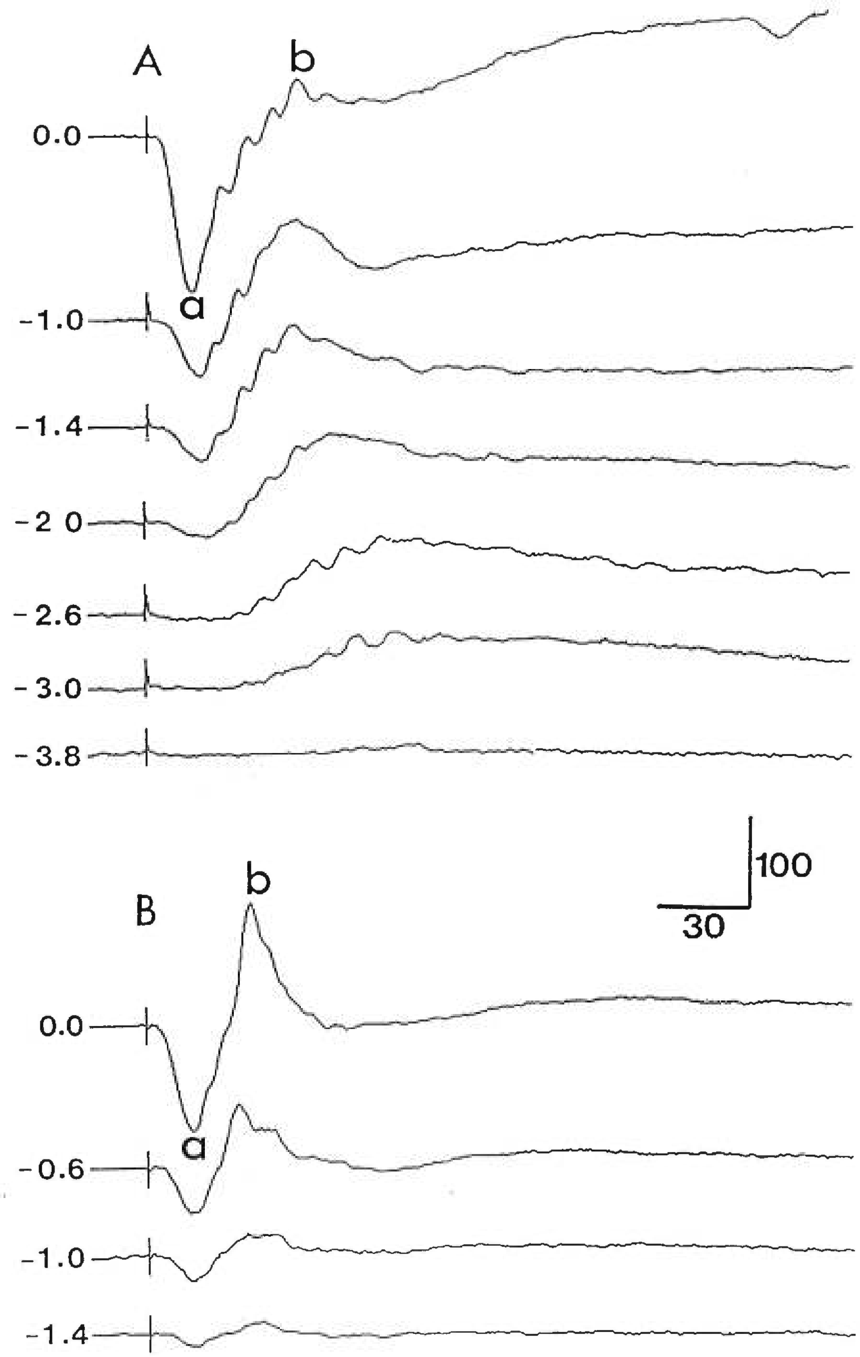


FIGURE 2. ERG responses, under (A) scotopic and (B) photopic conditions, of the American White Ibis. Nomenclature: a, peak of the a-wave; b, peak of the b-wave. The values on the left represent light intensity values (Log. units). The amplitude and time scales correspond to 100 μV and 30 ms.

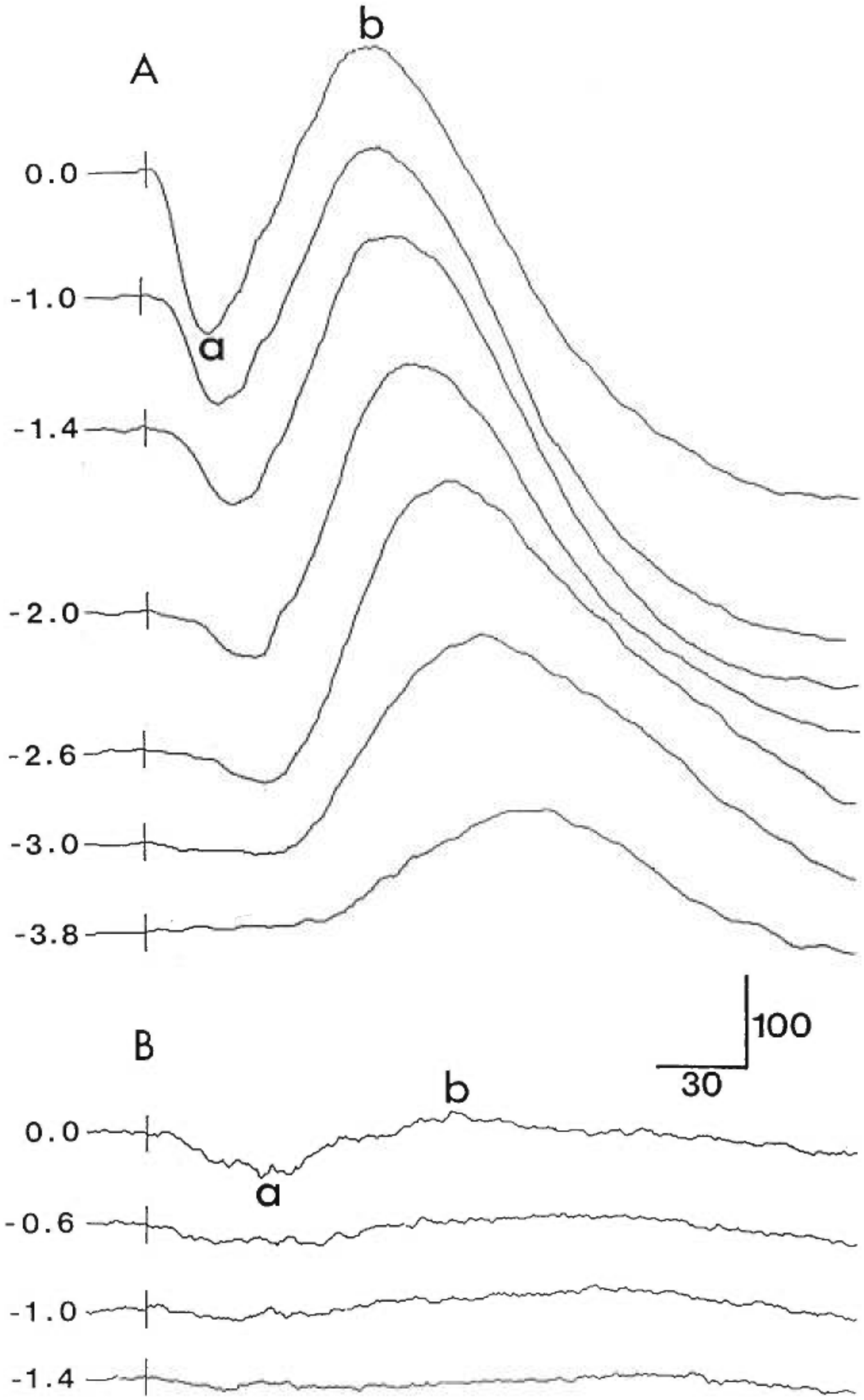


FIGURE 3. ERG responses, under (A) scotopic and (B) photopic conditions, of the Black Skimmer. Nomenclature as in Fig. 2.

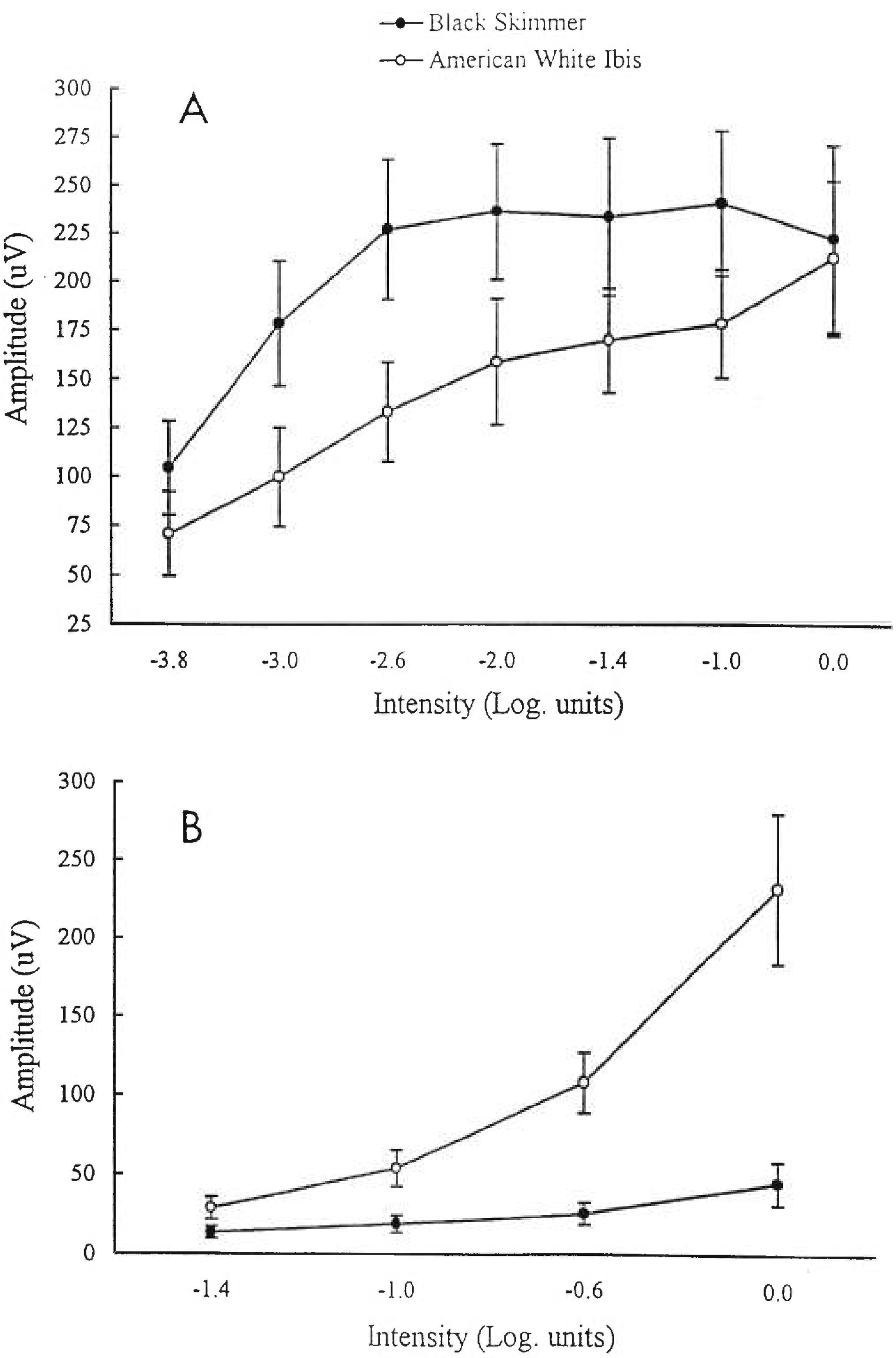


FIGURE 4. Mean amplitude variations (± 95% confidence limits), under (A) scotopic and (B) photopic conditions, in the b-waves of the Black Skimmer and the American White Ibis, as a function of light intensity.

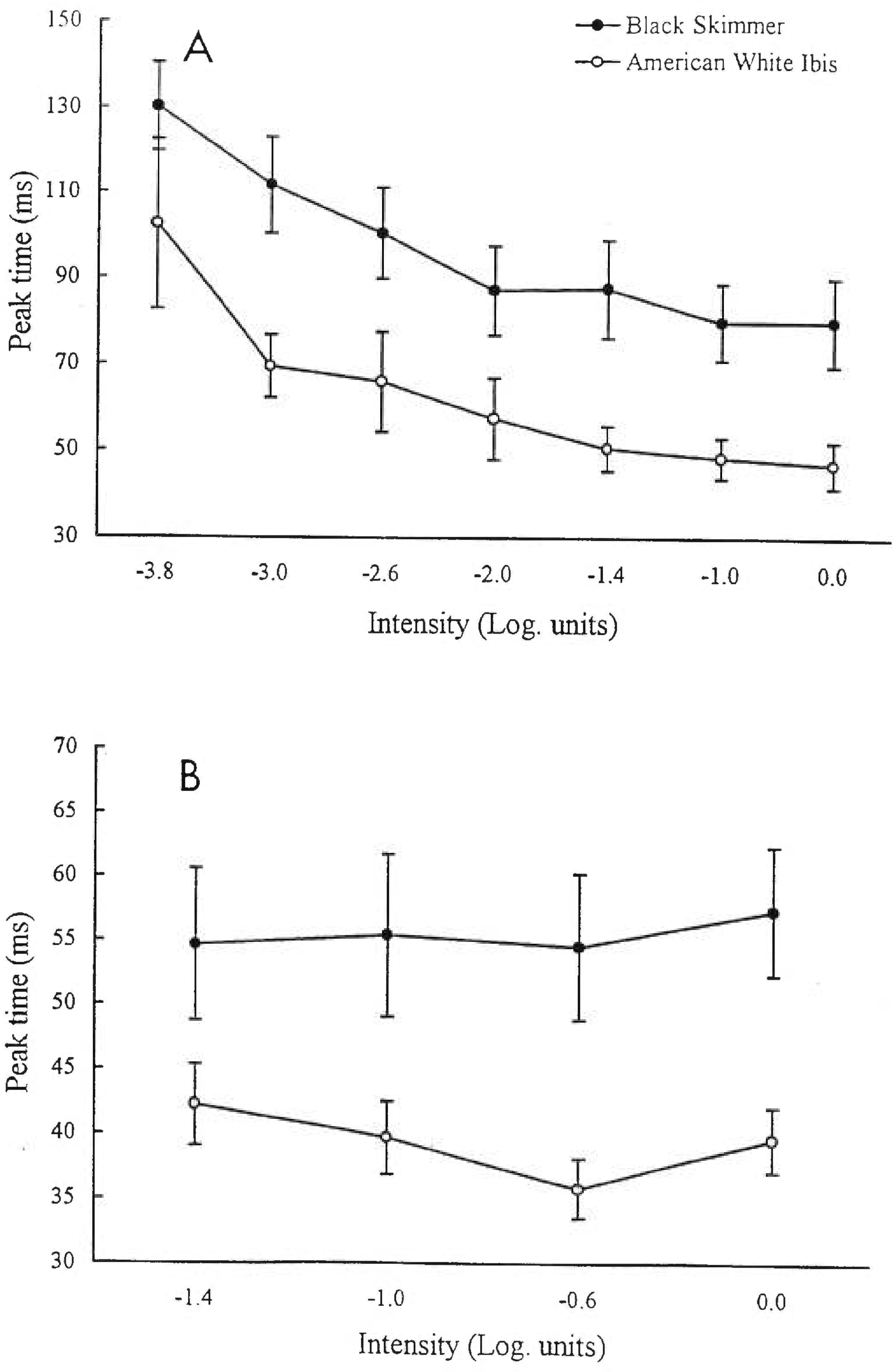


FIGURE 5. Mean peak time variations (± 95% confidence limits), under (A) scotopic and (B) photopic conditions, in the b-waves of the Black Skimmer and the American white Ibis, as a function of light intensity.

TABLE 1. Mean amplitude (μV) and peak time (msec) of 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[a]	Peak time[a]	Amplitude[a]	Peak time[a]
Scotopic				
Skimmer	157.9 ± 40.7	24.1 ± 6.8	223.0 ± 82.3	79.2 ± 16.0
Ibis	165.3 ± 41.9	16.5 ± 1.4	212.9 ± 67.8	46.9 ± 8.6
Photopic				
Skimmer	44.2 ± 13.5	31.4 ± 8.0	32.7 ± 15.8	56.9 ± 7.1
Ibis	99.5 ± 22.8	17.0 ± 1.1	238.0 ± 84.2	39.8 ± 4.5

[a] $\bar{x}$ ± 95% confidence interval.

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 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 either species, 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, 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.

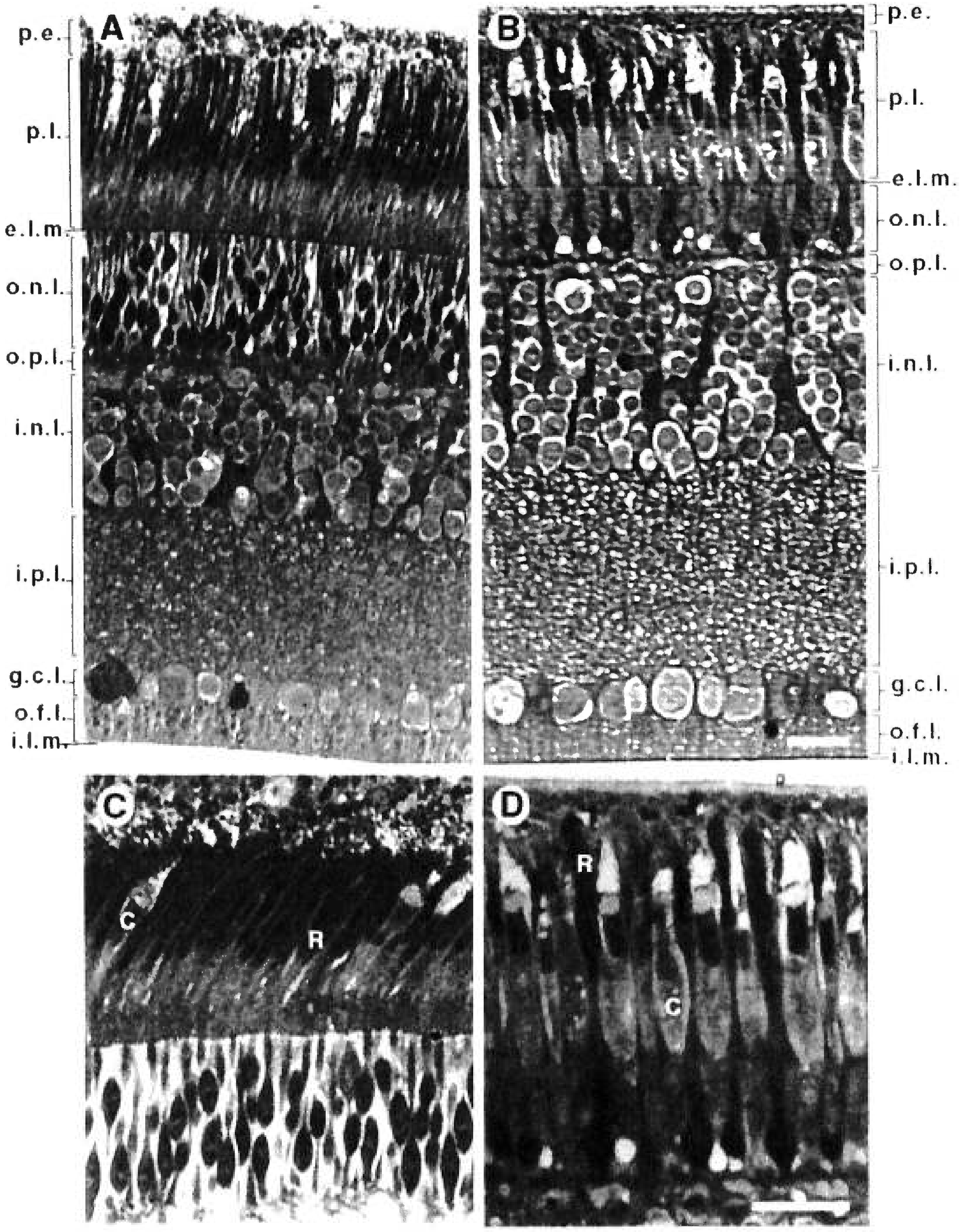
TABLE 2. Mean rod and cone relative density in the Black Skimmer and the American White Ibis. *n* = 4 in all cases.

	Sectors[a]	Rods[b]	Cones[b]	Rods:Cones
Black Skimmer	1	92.8 ± 14.1	15,0 ± 0.9	6:1
	2	97.7 ± 15.4	16.1 ± 2.6	6:1
	3	92.5 ± 15.1	16.3 ± 1.2	6:1
	4	96.1 ± 14.0	15.7 ± 0.3	6:1
	5	118.1 ± 19.4	17.6 ± 2.3	7:1
	6	81.8 ± 6.6	17.7 ± 1.4	5:1
	7	76.1 ± 16.0	18.7 ± 3.5	4:1
	8	78.5 ± 13.5	16.1 ± 3.1	3:1
	9	77.7 ± 15.5	18.0 ± 5.2	4:1
	All	90.2 ± 8.8	16.8 ± 0.8	5:1
American White Ibis	1	16.6 ± 4.0	51.2 ± 3.4	1:3
	2	21.1 ± 2.3	59.0 ± 4.6	1:3
	3	18.6 ± 2.7	58.9 ± 6.2	1:3
	4	18.9 ± 1.8	54.6 ± 3.9	1:3
	5	23.8 ± 3.1	60.6 ± 3.9	1:3
	6	18.0 ± 2.0	57.4 ± 2.5	1:3
	7	19.0 ± 2.5	55.3 ± 1.7	1:3
	8	17.5 ± 1.7	56.6 ± 3.0	1:3
	9	16.0 ± 3.0	56.1 ± 5.4	1:4
	All	18.8 ± 1.7	56.6 ± 1.8	1:3

[a] Sectors 1 and 4 = dorsal, 2 and 3 = temporal, 5 = central, 7 = nasal, 6, 8 and 9 = ventral.

[b] $\bar{x}/310\ \mu m$ ± 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 enlargement of the protoreceptor 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 µm and is valid for A, and that in D also equals 20 µm and is valid for C.


A
B
C
D
p.e.
p.l.
e.l.m.
o.n.l.
o.p.l.
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i.p.l.
g.c.l.
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i.n.l.
i.p.l.
g.c.l.
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C
R
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TABLE 3. Overall mean rod and cone measurements (µm), mean ganglion cell density ($\bar{x}$/310 µm), and mean thickness (µm) of the retinal layer of the Black Skimmer and the American White Ibis (see Fig. 6). $n = 4$ in all cases.

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

[a] For all cone types, except accessory cones.

[b] For accessory cones.

DISCUSSION

Contrary to most studies which were almost exclusively based on morphological observations and lacked physiological data, our study has the advantage of comparing the two bird species by considering both morphological and physiological aspects of the retina. It 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. Under the tested conditions (i.e., -3.8 to 0 log units), each species exhibits distinct ERG responses which differ from each other. These show 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 (see McNeil et al. 1993). The ibis rod:cone ratio is also 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).

Mainly due to 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 vision at 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 may also be shorter than those of the nocturnal Tawny Owl, for whom measurements were obtained from fresh tissue, however (Bowmaker and Martin 1978). As a consequence, contrary to the assertion of Walls (1942) that rods can lower their thresholds in 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 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 (see also 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 which has not been taken into account in the present study.

In both species, and under both scotopic and photopic conditions, the a- and b-waves increase 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 pigeon (*Columba livia*) (Porciatti et al. 1991), and in humans (see 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 (see Ikeda 1993). Both of these layers were found to be thicker in the ibis than in the skimmer.

Comparing 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, suggest that the ibis is better suited for daytime vision. This is also 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 (see Binggeli and Paule 1969, Ikushima et al. 1986, Hayes and Brooke 1990, Inzunza et al. 1991, Suburo et al. 1991).

Being sensitive to low level of illumination, the skimmer's retina 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 effects a greater reduction in its pupillary area from darkness to bright light than does the tern. We observed that the skimmer maximum pupil size, varying between 6 to 9 mm depending on the size of the birds, 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, in accordance with our starting 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.

ACKNOWLEDGMENTS

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Chapitre 3

Diurnal and Nocturnal Visual Capabilities in Shorebirds as a Function of their Feeding Strategies

Par

Luz Marina Rojas, Raymond McNeil, Thérèse Cabana et Pierre Lachapelle

[Brain, Behavior and Evolution. Accepté, juillet, 1998]

Abstract. Some shorebird species forage with the same feeding strategy at night and during daytime, e.g. visual pecking in the Wilson's Plover (*Charadrius wilsonia*) or tactile probing in the Short-billed Dowitcher (*Limnodromus griseus*). The American Woodcock (*Scolopax minor*) uses tactile probing, by day and by night, but sometimes pecks for insects during daytime. The Black-winged Stilt (*Himantopus himantopus*) is a visual pecker both by day and by night, and sometimes forages tactilely on windy (agitated water surface) moonless nights. Territorial Willets (*Catoptrophorus semipalmatus*) are visual peckers during daylight and on moonlight conditions but switch to tactile feeding under lower light conditions. It could be postulated that some shorebird species would switch from visual feeding during daytime to tactile foraging at night because they have poor night vision compared to species which are always sight foragers irrespective of the time of the day. This issue was examined by comparing retinal structures and function in the above species. Electroretinograms (ERGs) were obtained at different light intensities from anesthetized birds, and the retinae were processed for histological observations. Based on ERGs, retinal sensitivity, and rods:cones ratios, both the plover and the stilt are well adapted for nocturnal vision. Albeit with low rod density compared to the stilt and the plover, the Willet and the woodcock have a scotopic retinal sensitivity similar to that of the stilt and the plover, but rank midway between the plover and the dowitcher for the b-wave amplitude. The dowitcher has the lowest scotopic b-wave amplitude and retinal sensitivity and appears as the least well adapted for night vision. Based on photopic ERGs and cone densities, while the stilt, the Willet and the dowitcher appear as well adapted for daytime vision, the plover occupies the last rank of all species. Compared to the nighttime tactile feeders and those which switch from daytime visual pecking to tactile feeding at night, nighttime sight feeders have a superior rod function and, consequently, potentially superior nocturnal visual capabilities.

***Key Words*:** Shorebirds, Nocturnal vision, Diurnal, vision, Retina, Rod,Cone.

INTRODUCTION

Foraging during daytime and nighttime is a characteristic of most shorebird species [McNeil, 1991; McNeil et al., 1992; McNeil and Rodríguez, 1996a, b]. Two basic types of foraging techniques are used by shorebirds: visual searching for prey or indication of their presence on or near the substratum surface, and tactile searching [Schneider, 1983; McNeil et al., 1992]. Some species forage exclusively with the same feeding strategy both during daytime and at night, and even on moonless nights, e.g. visual pecking by the *Charadrius* plovers, and tactile probing by the *Limnodromus* and *Scolopax* species [McNeil and Robert, 1988; Robert and McNeil, 1989; McNeil et al., 1992; Thibault and McNeil, 1994, 1995]. Other shorebird species may vary their foraging strategies according to the feeding habitat conditions, e.g. the Black-winged Stilt (*Himantopus himantopus*), or between night and day depending on light conditions, e.g. the Willet (*Catoptrophorus semipalmatus*) and *Tringa* species [McNeil and Robert, 1988; Robert and McNeil, 1989; McNeil and Rodríguez, 1990; McNeil and Rompré, 1995; Rompré and McNeil, 1994, 1996; see also Llinas and Galindo, 1990].

According to Martin and Brooke [1991], it is believed that "differences in gross anatomy reflect adaptations of the basic structure of vertebrate eyes to differences in the visual problems imposed by different life styles" [see also Walls, 1942; Tansley, 1965], and it "might be expected that the eyes of nocturnally active species would have lower minimum *f*-numbers (higher maximum image brightness) than diurnal species" [Martin, 1994b]. Furthermore, nocturnal birds have a great preponderance of rods in their retinae while, in diurnal birds, up to 80% of photoreceptors are cones [see Tansley and Erichsen, 1985; Waldvogel, 1990]. Rods are generally associated with night vision because they are more sensitive to low levels of illumination, but demonstrate poor discriminative abilities (visual acuity) and allow imperfect or no color vision, while cones are associated 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].

As the feeding strategies of some shorebird species change as a function of light conditions, it can be postulated that species which are always or predominantly sight foragers, irrespective of the time of the day, have a better night vision capability than species which are always tactile feeding or switch from visual feeding during daytime to tactile foraging at night. In other words, do retinal adaptations and light conditions impose constraints on the feeding behavior of those species which change feeding strategies depending on day and night? This issue was examined by comparing the retinal structures and electroretinograms of a selected group of species.

MATERIALS AND METHODS

The original research reported herein was performed under guidelines established by the Canadian Council on Animal Care [1994]. Shorebirds species were selected according to behavioral criteria given in table 1, based on their foraging strategies (visual or tactile) which vary or do not vary with day and night. The Wilson's Plovers (*Charadrius wilsonia*), Black-winged Stilts and Willets were mist-netted in northeastern Venezuela. The Short-billed Dowitchers (*Limnodromus griseus*) and American Woodcocks (*Scolopax minor*) were obtained in the Province of Quebec (Canada), respectively near Rimouski and Montreal. The birds were brought alive to the laboratory at the Universidad de Oriente in Cumaná (Venezuela) or the Université de Montréal.

ERG RECORDING

Five plovers, seven Stilts, four Willets, six dowitchers and two woodcocks were analyzed. Electroretinograms (ERGs) were recorded in a dark room with the use of a LKC EPIC-2000 visual electrodiagnostic system (LKC Technologies Inc., Gaithersburg, MD), which included a 41-cm diameter Ganzfeld full field stimulator (LKC Ganzfeld-2503B stimulator). For a more detailed description of this equipment, see Rojas et al. [1997]. After a 4-h period of dark adaptation for recording in scotopic condition, the birds were anesthetized with a 1:1 mixture of ketamine-xylazine (0.0044 cc/kg injected in the pectoral muscle), and immobilized on a home-made recording holder with the head kept inside the Ganzfeld and the left eye maintained open upward. The left eyelids and nictitating membrane were kept retracted with a speculum, the cornea was anesthetized with 0.5% proparacaine hydrochloride, and the pupil was dilated with 1% tropicamide. The maximum pupil diameter(mm) was measured at the beginning and at the end of the experiment. A fine conductive fiber (Sauquoit Industries, Scranton, PA) was placed over the cornea and used

Table 1. Behavioral characteristics of the selected species and summary of principal results

Species	n[a]	Time of foraging activity	Foraging strategy	Summary of principal results[b]					
				ERG V_{max} amplitudes			Rods	Cones	Rods:Cones
				Scotopic	Photopic				
					a	b			
Wilson's Plover[5,6,10,11,14,17] (*Charadrius wilsonia*)	5	Breeding season: diurnal and nocturnal; non-breeding season: mainly nocturnal	Visual pecking	++	+	+	++++	+++	1.3:1
Short-billed Dowitcher[5,6,11] (*Limnodromus griseus*)	4	Diurnal and nocturnal	Tactile probing	+	+	++	+++	+++	1.0:1
American Woodcock[1,2,3,4,7,12,15] (*Scolopax minor*)	3	Winter: mainly nocturnal; summer: mainly diurnal	Almost only tactile probing, except occasional pecks during summer	+	+	+	+++	++	1.2:1
Black-winged Stilt[5,6] (*Himantopus himantopus*)	4	Diurnal and nocturnal	Generally visual pecking except scythe-like sweeping when water surface is agitated	+++	+	++	++++	+++	1.1:1

Table 1. Continued

Species	n[a]	Time of foraging activity	Foraging strategy	Summary of principal results[b]					
				ERG V_{max} amplitudes			Rods	Cones	Rods:Cones
				Scotopic	Photopic				
								a	b
Willet[8,9,13,16,18] (*Catoptrophorus semipalmatus*)	4	Diurnal and nocturnal	Territorial owners: visual pecking on moonlit nights, and tactile probing on on moonless nights	+	+	+	++	++++	0.7:1

[a] n = number of birds.

[b] ++++, +++, ++, + represent the relative amplitude of ERG V_{max}, and the density of rods or cones.

[1] Sheldon, 1967; [2] Owen and Morgan, 1975; [3] Owen, 1977; [4] Strigling and Doerr, 1985; [5] McNeil and Robert, 1988; [6] Robert and McNeil, 1989; [7] Sepik et al., 1989; [8] Llinas G. and Galindo J., 1990; [9] McNeil and Rodríguez S., 1990; [10] Morrier and McNeil, 1991; [11] McNeil et al., 1992; [12] Roberts, 1993; [13] Rompré and McNeil, 1994; [14] Thibault and McNeil, 1994; [15] Krementz et al., 1995; [16] McNeil and Rompré, 1995; [17] Thibault and McNeil, 1995; [18] Rompré and McNeil, 1996.

as the ERG recording electrode [Lachapelle et al., 1993; Hébert et al., 1996]. Subdermal needles (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 electrodes, respectively. Averages of 6 responses per trial were obtained to flashes of constant luminance under scotopic conditions. These ERGs were obtained, in increasing order of luminance, at light intensities of -3.8, -3.0, -2.6, -2.0, -1.4, -1.0, and 0.0 log units of attenuation. Thereafter,for recording under photopic condition, the birds were light-adapted for 10 min to a background luminance of 35.7 cd $\cdot$ m^{-2}. Averages of 10 responses were obtained to flashes of constant luminance. These ERGs were evoked to flashes of decreasing luminance of 0.0, -0.6, -1.0, and -1.4 log units. Fewer stimuli were used in scotopic (6) than in photopic (10) condition and they were separated by a longer delay to ensure that the retina retained its dark adapted state [Ikeda, 1993].

In order to take into account the fact that pupil size varies with species and consequently the light which actually falls on the retina also varies with the size of the pupil, the light intensity with which ERGs were recorded was transformed in Troland unit. The Troland (T) is defined as the retinal illuminance equal to that produced by viewing a surface whose luminance is 1 cd $\cdot$ m^{-2} through a pupil whose area is 1 mm^2, and is calculated as follows: T = LI x LS, where LI is the light intensity (cd $\cdot$ m^{-2}) and LS the pupil surface (mm^2) [Wyszecky and Stile, 1967].

We calculated the intensity of the stimulus necessary to evoke a b-wave whose amplitude is half (½ V_{max}) the saturated amplitude (V_{max}) of the response evoked by a very bright flash in scotopic condition. This value is generally considered as an adequate measurement of retinal sensitivity under scotopic condition [see Massof et al., 1984; Fulton, 1991].

MORPHOLOGICAL PROCEDURES

Four plovers, four stilts, four Willets, four dowitchers and three woodcocks were analyzed. Once the ERG recordings were completed, the birds were given a lethal dose of sodium pentobarbital. Their left eye was removed and its axial length and equatorial diameter were measured (see Martin, 1986). It was then injected with 2.5% glutaraldehyde in 0.1 M phosphate buffer (pH = 7.2), punctured at the cornea, and placed in the same

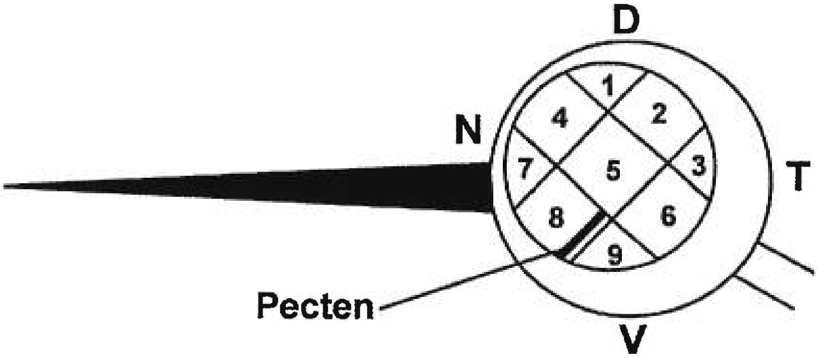


Figure 1. Schematic representation of the nine retinal sectors. **D, N, T**, and **V** correspond to dorsal, nasal, temporal and ventral sectors, respectively.

fixative for 30 min. Working with the eye in the fixative, the retina, still attached to the choroid, was cutinto 9 sectors, using the pecten as a landmark (fig. 1). This division is the same as that of Rojas de Azuaje et al. [1993] and Rojas et al. [1997], and corresponds to that of Meyer and May [1973] and Begin and Handford [1987], although the sector numbering is different. Still in the fixative, each sector was subdivided into 2 mm^2 portions, of which two were retained for analysis. After 3 h in the fixative, the retinal portions, separated from the choroid, were washed with phosphate buffer for 10 min, postfixed in 1% OsO_4 in 0.1 M phosphate buffer for 1 h, rinsed in phosphate buffer followed by distilled water (10 min each), dehydrated in graded ethanol (10 min per step), and bathed in propylene oxide (15 min). The tissues were successively infiltrated with a 1:1 mixture of propylene oxide and Epon for 6 h, and pure Epon medium for another 2 h. Finally, they were embedded in silicone rubber molds filled with Epon and polymerized at 60°C for 48 h.

Semithin (0.7 µm) sections were obtained and 15 of them (one every 30-40 sections) were mounted on glass slides and stained with toluidin blue. Rods, cones and ganglion cells were counted in 310-µm wide fields, for a total of 15 counts for each of the nine sectors. As in other avian retinae [Meyer and May, 1973; Meyer, 1977; Tansley and Erichsen, 1985; Waldvogel, 1990], double cones, in addition to single cones, were present in all five species, and they 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.

RESULTS

ELECTRORETINOGRAPHY

Representative ERGs obtained in scotopic and photopic conditions for each species are presented in figure 2. It can be seen that the ERGs differ in shape and amplitude between species. The luminance-response functions generated from amplitude measurements obtained in scotopic and photopic conditions are graphically represented in figures 3 (b-wave) and 4 (a-wave). Peak time variations as a function of stimulus luminance are shown, for both waves, in figures 5 and 6.

For scotopic responses, analysis of the mean b-wave amplitude variations as a function of luminance (fig. 3A) shows three patterns of intensity response function. The first one is illustrated by the dowitcher where the amplitude of the b-wave increases linearly with luminance. The second one, represented by the stilt and the woodcock, is characterized with an initial rapid growth in the amplitude of the b-wave which is followed by a saturation phase which precedes a moderate but not significant decrease. The third response pattern which is found in the plover and the Willet shows a rapid growth in the amplitude of the b-wave followed by a significant decrease at higher stimulus intensities.

As shown with the 95% confidence intervals, while the maximal amplitudes of the b-wave measured in the stilt and the plover ERGs are significantly higher than those of the other species, they are not significantly different from each other (fig. 3A). As for the temporal parameters, the peak time of the b-wave of all species (fig. 5A) shortens exponentially with increasing luminance. According to the 95% confidence intervals, the timing of the b-wave of the woodcock, the dowitcher and the Willet is generally faster than that of the plover and the stilt. In contrast, while the intensity-response function of the a-wave (fig. 4A) shows a rapid exponential increase in amplitude as a function of luminance, significant interspecific differences appear only at higher luminance intensity where the amplitude of the a-wave of the plover is significantly lower than that of the other four species. Similarly, while the peak time of the a-wave (fig. 6A) shortens as a function of stimulus strength, only that of the woodcock tends to be shorter than that of other species.

For photopic responses, the plover yields ERGs with the lowest a- and b-wave amplitudes, and less sharply defined signals (fig. 2). The amplitude of the b- (fig. 3B) and a-waves (fig. 4B) increases exponentially as a function of luminance. As shown with the 95% confidence intervals, it is only at maximal b-wave values that the lower voltage obtained for the plover and the woodcock can be distinguished from the higher responses recorded for the dowitcher and the stilt (fig. 3B). Interestingly, the lowest a-wave amplitudes are also measured in ERGs recorded from the plover (fig. 4B). The peak time of the b- (fig. 5B) and a-waves (fig. 6B) does not vary significantly as a function of luminance intensity. However,

Figure 2. Representative ERG responses of shorebird species obtained under scotopic and 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).

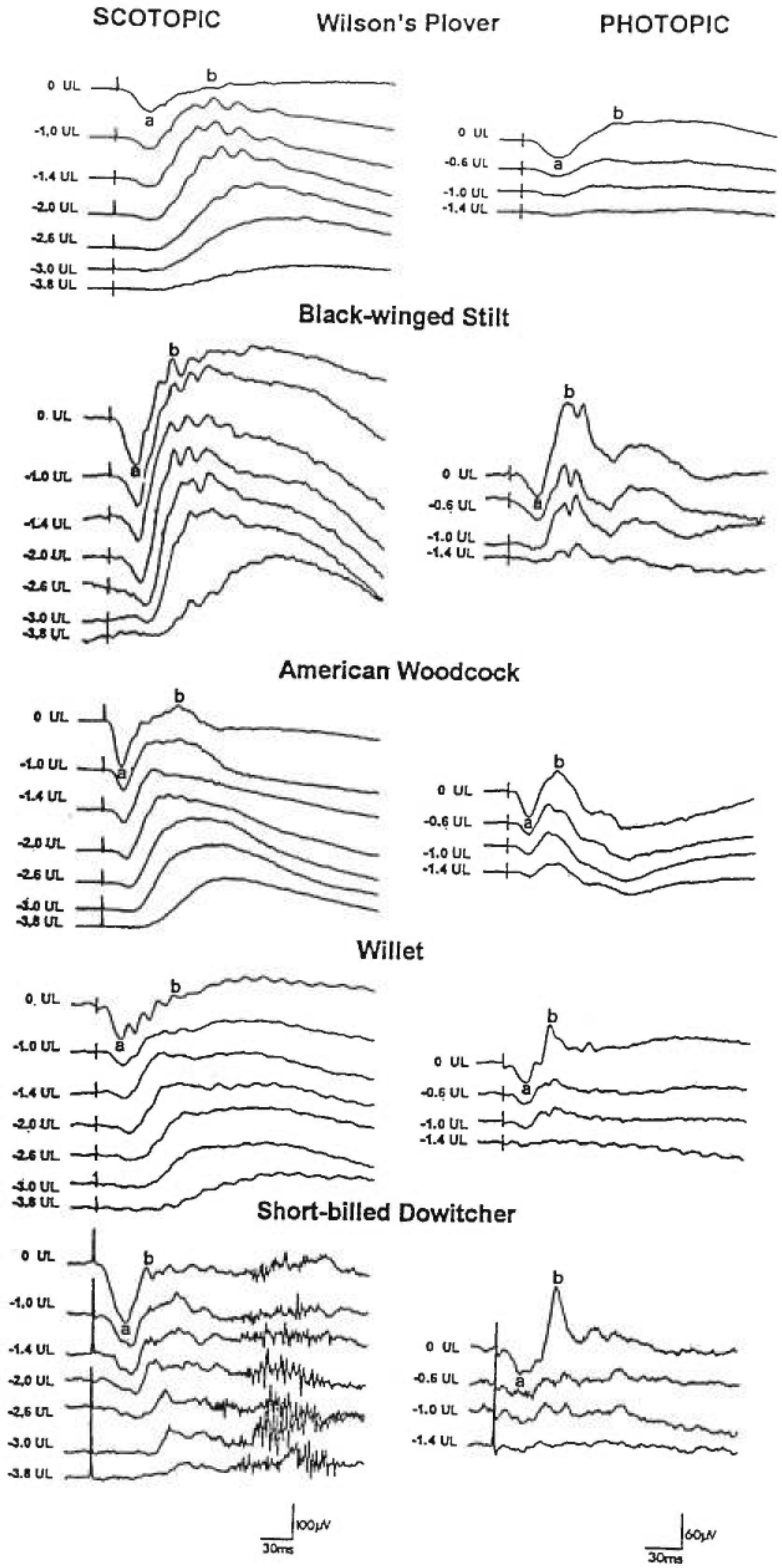

SCOTOPIC
Wilson's Plover
PHOTOPIC
0 UL
-1.0 UL
-1.4 UL
-2.0 UL
-2.6 UL
-3.0 UL
-3.8 UL
a
b
0 UL
-0.6 UL
-1.0 UL
-1.4 UL
Black-winged Stilt
American Woodcock
Willet
Short-billed Dowitcher
100µV
30ms
60µV
30ms

Figure 3. Luminance-response function (± 95% confidence intervals) of the b-wave of shorebird species under **(A)** scotopic and **(B)** photopic conditions. The ordinate represents the b-wave amplitude (μV) and the abscissa the stimulus luminance intensity (Log troland-sec).

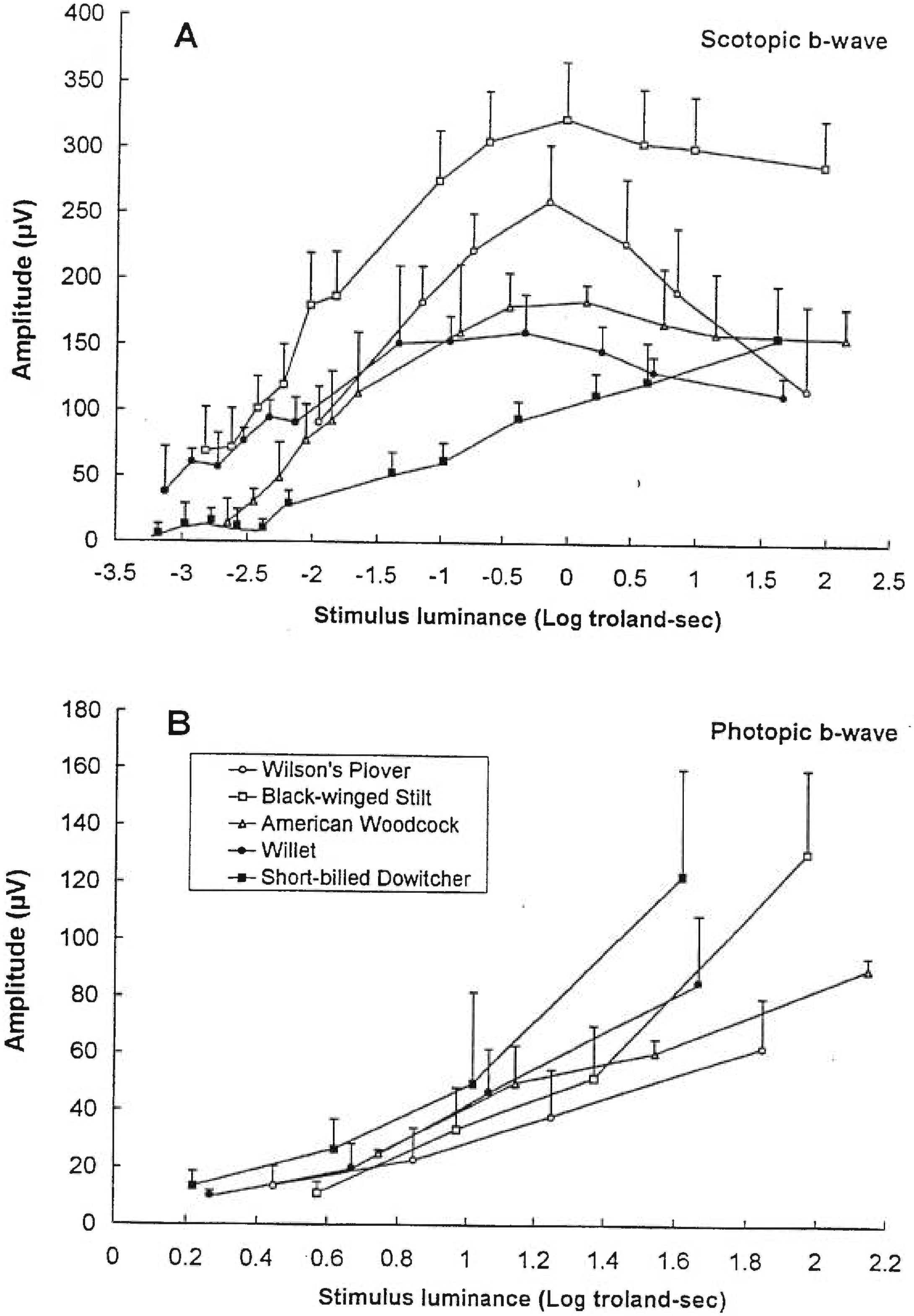

A
Scotopic b-wave
Amplitude (µV)
400
350
300
250
200
150
100
50
0
-3.5
-3
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
2.5
Stimulus luminance (Log troland-sec)
B
Photopic b-wave
Wilson's Plover
Black-winged Stilt
American Woodcock
Willet
Short-billed Dowitcher
Amplitude (µV)
180
160
140
120
100
80
60
40
20
0
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
Stimulus luminance (Log troland-sec)

Figure 4. Luminance-response function (± 95% confidence intervals) of the a-wave of shorebird species under **(A)** scotopic and **(B)** photopic conditions. The ordinate represents the a-wave amplitude (µV) and the abscissa the stimulus luminance intensity (Log troland-sec).

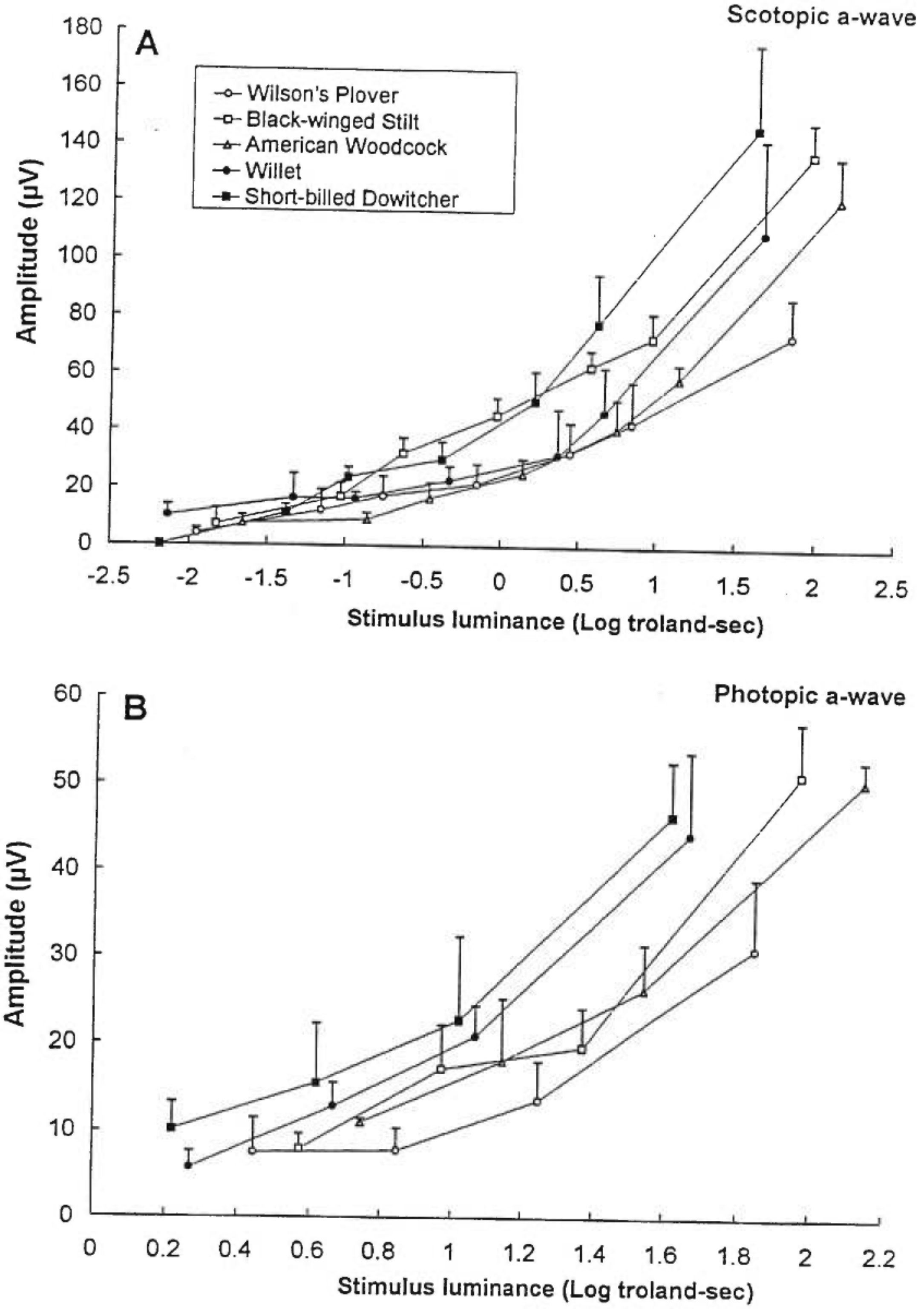

Scotopic a-wave
A
Wilson's Plover
Black-winged Stilt
American Woodcock
Willet
Short-billed Dowitcher
Amplitude (µV)
0
20
40
60
80
100
120
140
160
180
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
2.5
Stimulus luminance (Log troland-sec)
Photopic a-wave
B
Amplitude (µV)
0
10
20
30
40
50
60
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
Stimulus luminance (Log troland-sec)

Figure 5. Mean peak time (ms) variations (± 95% confidence intervals) in the b-wave of shorebird species as a function of the stimulus luminance intensity (Log troland-sec) under **(A)** scotopic and **(B)** photopic conditions.

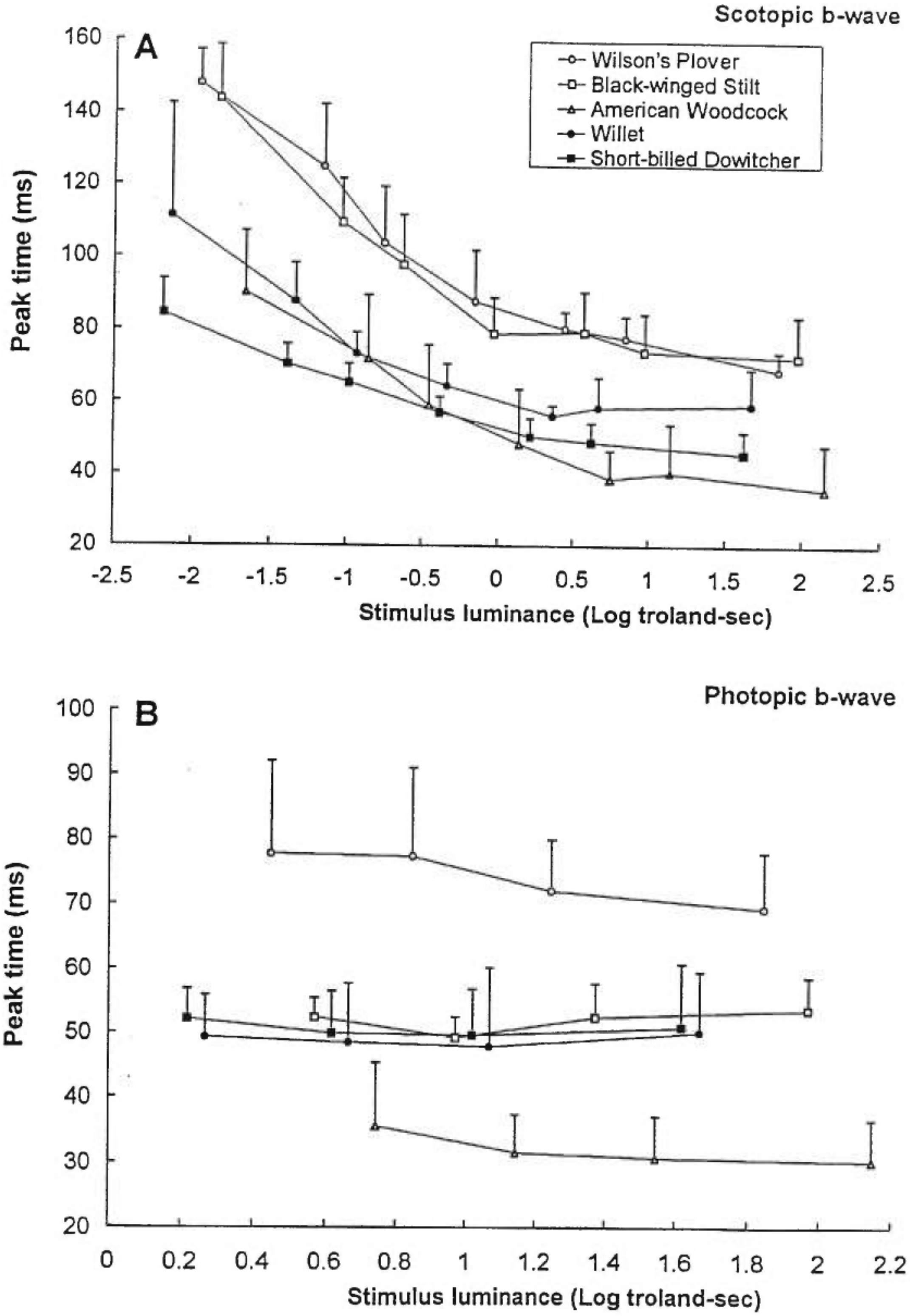
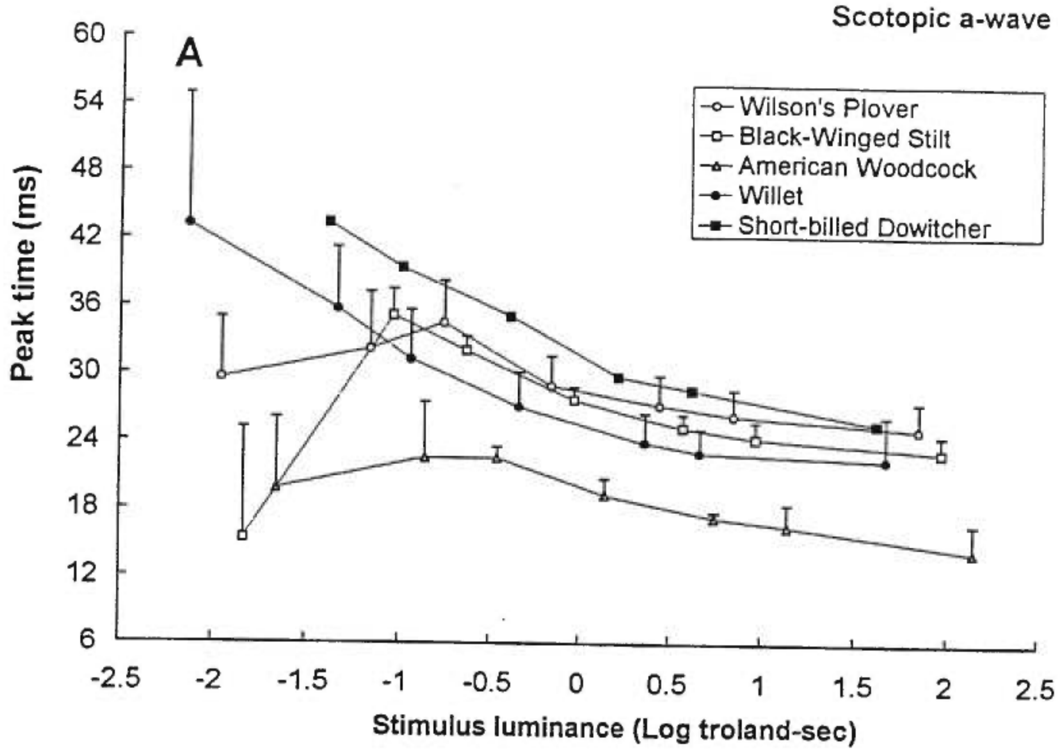
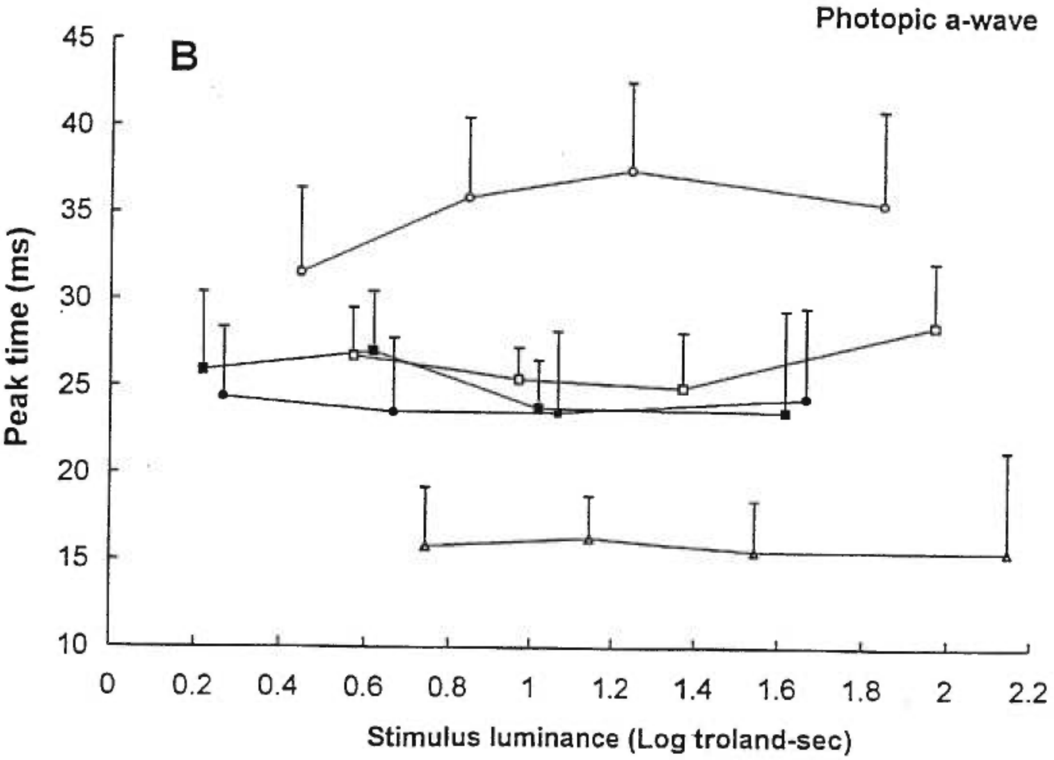

Scotopic b-wave
A
Wilson's Plover
Black-winged Stilt
American Woodcock
Willet
Short-billed Dowitcher
Peak time (ms)
160
140
120
100
80
60
40
20
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
2.5
Stimulus luminance (Log troland-sec)
Photopic b-wave
B
Peak time (ms)
100
90
80
70
60
50
40
30
20
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
Stimulus luminance (Log troland-sec)

Figure 6. Mean peak time (ms) variations (± 95% confidence intervals) in the a-wave of shorebird species as a function of the stimulus luminance intensity (Log troland-sec) under (**A**) scotopic and (**B**) photopic conditions.


Scotopic a-wave
A
Wilson's Plover
Black-Winged Stilt
American Woodcock
Willet
Short-billed Dowitcher
Peak time (ms)
60
54
48
42
36
30
24
18
12
6
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
2.5
Stimulus luminance (Log troland-sec)


Photopic a-wave
B
Peak time (ms)
45
40
35
30
25
20
15
10
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
Stimulus luminance (Log troland-sec)

based on the 95% confidence intervals, the timing of both waves is fastest in the woodcock and most delayed in the plover.The intensity of the stimulus necessary to elicit ½ V_{max} in scotopic condition also varies with the species studied. The dowitcher (-0.76 ± 0.48 Log troland-sec) has considerably and significantly lower retinal sensitivity than the stilt .(-2.11 ± 0.23),. the Willet .(-2.37 ± 0.34), and the plover (-1.44 ± 0.17). Retinal sensitivity of the plover is significantly lower than that of the stilt and the Willet. That of the woodcock is –1.71 ± 0.57 and not significantly different from any of the other four.

MORPHOLOGY

Measurements of the eye are given in table 2. The Wilson's Plover and the Black-winged Stilt tend to have higher axial length:equatorial diameter ratio (AL:ED) than the American Woodcock and the Short-billed Dowitcher.

In the plover, the woodcock and the stilt, rods outnumber cones in all retinal sectors, with overall rods:cones ratios of 1.3:1, 1.2:1, and 1.1:1, respectively (fig. 7). However, in the woodcock, the rods:cones ratio is higher in the dorsal and temporal sectors (1 to 4) than in other sectors; indeed, cone density is particularly low in those sectors. The Willet, on the other hand, has a clearly cone-dominated retina, with an overall rods:cones ratio of 0.7:1, whereas the dowitcher has a mixed retina with similar densities of rods and cones (1.0:1). Based on the 95% confidence intervals, the rod density of the plover and of the stilt significantly exceeds that of the three other species. The Willet has the lowest rod density but its cones outnumber those of the plover, the dowitcher and the woodcock. In all species, but particularly in the plover, the woodcock and the Willet, cones tend to be more numerous in sector 5 than in other sectors (fig. 7). The same is true for rods, but this is less clear in the Willet and the dowitcher.

For each species, the rod and cone measurements generally indicate no clear variations between sectors, and therefore only the overall rod and cone measurements are given in table 3. Rod outer segments tend to be longest in the woodcock, but this is not significant because of important interindividual and intersectorial variations. However, they are significantly longer in the plover and the stilt than in the Willet and the dowitcher. On the other hand, rod inner segments are significantly wider in the dowitcher than in the plover,

Table 2. Eye measurements of the five shorebird species studied, and comparison with other species

	Axial length† (mm) AL	Equatorial diameter† (mm) ED	AL/ED	Dilated pupil diameter† (mm)
Wilson's Plover (*C. wilsonia*)	11.2 ± 0.3 (9)	13.1 ± 0.6 (9)	0.86	5.2 ± 0.3 (5)
Black-winged Stilt (*H. himantopus*)	13.2 ± 0.5 (10)	15.4 ± 0.4 (10)	0.86	6.0 ± 0.4 (8)
American Woodcock (*S. minor*)	10.6 ± 0.2 (6)	15.0 ± 0.3 (6)	0.71	7.3 ± 0.8 (4)
Willet (*C. semipalmatus*)	12.0 ± 0.9 (7)	14.5 ± 0.4 (7)	0.83	4.2 ± 0.2 (4)
Short-billed Dowitcher (*L. griseus*)	7.2 ± 0.1 (4)	9.5 ± 0.1 (4)	0.76	4.0 ± 0.0 (4)
Starling (*S. vulgaris*)[1]	7.9	10.1	0.79	2.5
Manx Shearwater (*P. puffinus*)[2]	11.8	14.3	0.83	3.7
Tawny Owl (*S. aluco*)[3]	28.5	30.1	0.95	13.3
Common Pigeon (*C. livia*)[3,4]	11.0	14.0	0.79	4.0

† $\bar{x}$ ± 95% confidence intervals (n = number of birds).

[1] Martin, 1986; [2] Martin and Brooke, 1991; [3] Martin, 1982; [4] Chard and Gundlach, 1938.

Table 3. Overall mean rod and cone measurements (μm) of shorebird species

	Wilson's Plover (*C. wilsonia*) n[1] = 4	Black-winged Stilt (*H. himantopus*) n = 4	American Woodcock (*S. minor*) n = 3	Willet (*C. semipalmatus*) n = 4	Short-billed Dowitcher (*L. griseus*) n = 4
Rod outer segment length	47.2 ± 4.2	41.2 ± 1.3	48.4 ± 12.3	35.6 ± 4.7	33.5 ± 2.0
outer segment diameter	3.8 ± 0.2	4.1 ± 0.1	3.9 ± 0.1	3.9 ± 0.1	4.1 ± 1.2
inner segment length	27.6 ± 2.3	34.1 ± 7.0	31.3 ± 2.7	30.2 ± 0.9	26.8 ± 2.5
inner segment diameter	3.9 ± 0.2	4.1 ± 0.1	4.0 ± 0.2	4.2 ± 0.2	4.4 ± 0.1
Cone outer segment length	17.6 ± 1.7	18.5 ± 1.0	21.9 ± 3.8	17.5 ± 2.1	15.5 ± 0.9
outer segment diameter	1.3 ± 0.1	1.3 ± 0.1	2.0 ± 0.3	1.3 ± 0.1	1.4 ± 0.1
inner segment length [2]	31.5 ± 5.7	32.3 ± 4.1	31.4 ± 3.3	40.7 ± 6.5	34.3 ± 1.5
inner segment length [3]	24.2 ± 4.4	25.1 ± 1.5	24.7 ± 2.7	32.5 ± 4.3	27.9 ± 0.5
inner segment diameter[2]	3.9 ± 0.3	4.2 ± 0.1	4.6 ± 0.1	3.9 ± 0.1	3.7 ± 0.1
inner segment diameter [3]	4.0 ± 0.1	4.6 ± 0.3	5.3 ± 0.6	4.1 ± 0.2	3.8 ± 0.3

[1] n = number of birds.

[2] All cone types, except accessory cones.

[3] Accessory cones.

Figure 7. Mean rod and cone numbers ($\bar{x}$/310 µm ± 95% confidence intervals) of shorebird species in each of the nine retinal sectors as well as in all sectors averaged. The figures above the «all» columns indicate the overall rods:cones ratio.

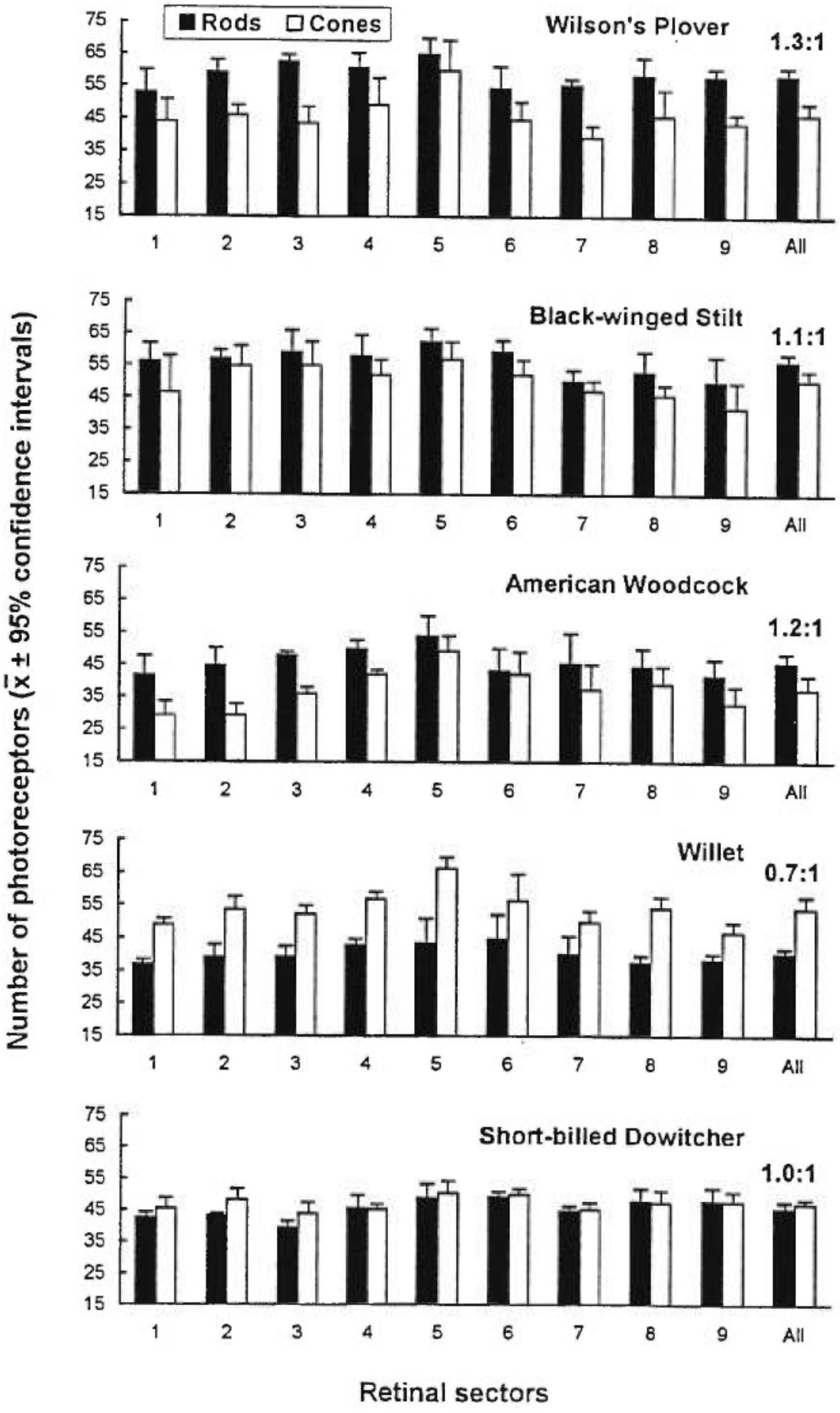

■ Rods □ Cones
Wilson's Plover
1.3:1
Black-winged Stilt
1.1:1
American Woodcock
1.2:1
Willet
0.7:1
Short-billed Dowitcher
1.0:1
75
65
55
45
35
25
15
1
2
3
4
5
6
7
8
9
All
Number of photoreceptors ($\bar{x}$ ± 95% confidence intervals)
Retinal sectors

Figure 8. Photomicrographs showing the principal layers of sector 5 of the retina of shorebird species. Nomenclature: **e.l.m.**, external limiting membrane; **g.c.l.**, ganglion cell layer; **i.l.m.**, inner limiting membrane; **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.l.**, photoreceptor layer. In each photomicrograph, the arrow points to a rod and the triangle to a cone.

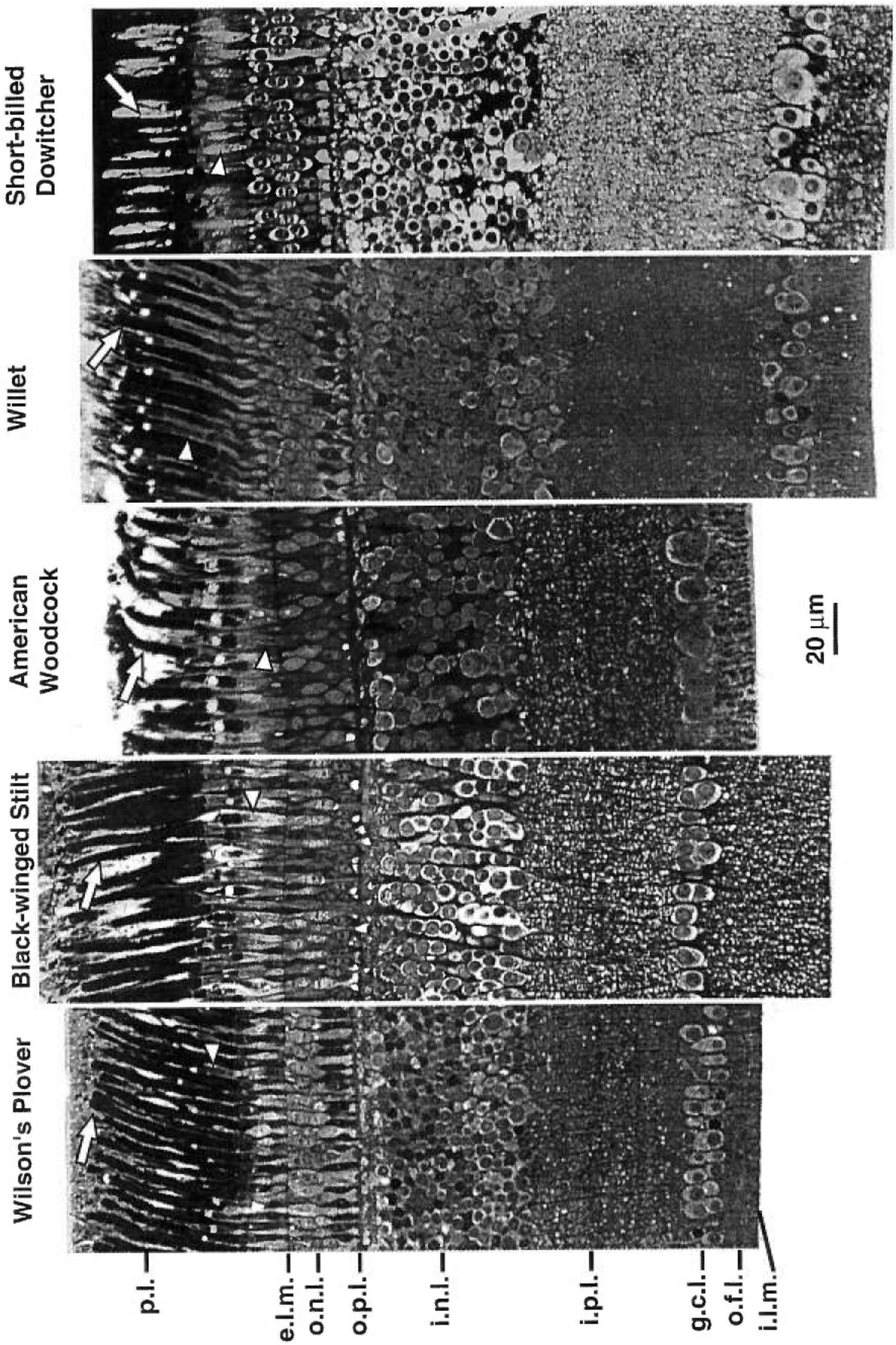

Wilson's Plover
Black-winged Stilt
American Woodcock
Willet
Short-billed Dowitcher
20 µm
p.l.
e.l.m.
o.n.l.
o.p.l.
i.n.l.
i.p.l.
g.c.l.
o.f.l.
i.l.m.

Table 4. Thickness (μm) of retinal layers and ganglion cell number ($\bar{x}$/310 μm) in the different sectors of the retina of the Wilson's Plover (*C. wilsonia*), Black-winged Stilt (*H. himantopus*), American Woodcock (*S. minor*), Willet (*S. semipalmatus*), and Short-billed Dowitcher (*L. griseus*). Values are the means ($\bar{x}$ ± 95% confidence intervals)

	Sector 1	Sector 2	Sector 3	Sector 4	Sector 5	Sector 6	Sector 7	Sector 8	Sector 9	All	n[1]
Outer nuclear layer											
Wilson's Plover	23.0 ± 3.8	25.7 ± 3.3	27.8 ± 5.5	27.5 ± 5.0	37.0 ± 3.7	28.8 ± 7.5	22.5 ± 2.4	30.4 ± 7.3	24.8 ± 1.8	27.5 ± 2.2	4
Black-winged Stilt	25.9 ± 1.3	29.0 ± 0.9	28.1 ± 4.9	27.0 ± 2.2	29.2 ± 1.8	27.3 ± 2.2	21.9 ± 1.5	22.9 ± 2.1	22.4 ± 0.9	26.0 ± 1.3	4
American Woodcock	25.0 ± 0.9	24.1 ± 1.2	25.5 ± 2.9	25.9 ± 4.8	27.9 ± 1.5	26.9 ± 2.1	26.8 ± 1.9	24.8 ± 1.7	23.8 ± 2.1	25.4 ± 1.8	3
Willet	22.8 ± 4.8	27.0 ± 3.3	27.0 ± 2.5	25.7 ± 4.2	32.0 ± 2.5	28.0 ± 1.8	26.2 ± 1.7	26.6 ± 1.8	27.1 ± 4.1	26.9 ± 2.3	4
Short-billed Dowitcher	25.9 ± 2.7	26.2 ± 1.4	24.2 ± 1.6	27.4 ± 2.5	29.0 ± 2.2	27.1 ± 2.9	24.4 ± 1.2	27.4 ± 3.0	25.6 ± 1.1	26.4 ± 0.8	4
Outer plexiform layer											
Wilson's Plover	5.1 ± 0.7	4.9 ± 0.2	5.1 ± 0.2	5.1 ± 0.3	4.9 ± 0.2	4.9 ± 0.2	4.6 ± 0.2	4.4 ± 0.6	4.6 ± 0.9	4.8 ± 0.2	4
Black-winged Stilt	7.8 ± 0.7	9.4 ± 0.7	7.2 ± 0.9	7.6 ± 1.0	6.6 ± 0.3	6.3 ± 0.3	6.5 ± 0.3	5.7 ± 0.3	6.0 ± 0.2	7.0 ± 0.2	4
American Woodcock	4.3 ± 0.7	4.4 ± 0.7	4.6 ± 0.7	4.4 ± 0.7	4.1 ± 0.6	4.2 ± 0.6	3.8 ± 0.3	3.8 ± 0.3	3.9 ± 0.3	4.2 ± 0.5	3
Willet	6.2 ± 0.2	6.2 ± 0.1	6.3 ± 0.1	6.1 ± 0.3	5.9 ± 0.5	5.9 ± 0.2	6.1 ± 0.3	6.3 ± 0.4	6.3 ± 0.2	6.2 ± 0.1	4
Short-billed Dowitcher	6.0 ± 0.1	6.0 ± 0.1	5.9 ± 0.1	5.8 ± 0.2	5.6 ± 0.8	5.4 ± 0.8	5.7 ± 0.3	5.2 ± 0.7	5.9 ± 0.3	5.7 ± 0.1	4

Table 4. Continued

	Sector 1	Sector 2	Sector 3	Sector 4	Sector 5	Sector 6	Sector 7	Sector 8	Sector 9	All	n[1]
Inner nuclear layer											
Wilson's Plover	42.9 ± 8.1	49.1 ± 7.6	56.2 ± 11.3	60.1 ± 13.9	83.8 ± 10.6	56.0 ± 16.1	40.4 ± 8.1	63.4 ± 12.7	43.5 ± 6.0	55.0 ± 4.4	4
Black-winged Stilt	37.9 ± 7.0	51.7 ± 2.8	53.5 ± 4.3	46.5 ± 3.9	52.9 ± 3.0	50.4 ± 9.9	38.4 ± 3.8	42.2 ± 11.1	37.4 ± 4.2	45.7 ± 1.8	4
American Woodcock	37.3 ± 1.8	37.1 ± 4.4	42.8 ± 14.5	53.2 ± 11.4	55.4 ± 6.5	46.6 ± 7.8	52.1 ± 12.6	42.1 ± 11.2	36.2 ± 9.2	48.8 ± 8.2	3
Willet	42.3 ± 7.9	54.9 ± 4.7	53.2 ± 7.0	51.0 ± 13.8	70.5 ± 2.8	59.3 ± 5.3	49.2 ± 5.0	55.2 ± 12.1	45.0 ± 3.8	53.4 ± 4.5	4
Short-billed Dowitcher	43.8 ± 5.4	48.2 ± 2.4	44.6 ± 9.7	54.9 ± 8.2	59.3 ± 6.4	57.6 ± 11.0	43.8 ± 5.8	51.0 ± 10.8	44.6 ± 3.0	49.8 ± 4.5	4
Inner plexiform layer											
Wilson's Plover	46.5 ± 6.4	51.3 ± 10.4	53.5 ± 12.3	56.7 ± 9.6	71.0 ± 14.2	54.6 ± 8.8	40.0 ± 10.4	59.5 ± 12.5	43.2 ± 3.7	52.9 ± 6.0	4
Black-winged Stilt	53.1 ± 5.6	69.3 ± 4.1	67.7 ± 12.8	56.7 ± 7.6	61.8 ± 4.1	59.6 ± 9.2	50.5 ± 3.9	52.2 ± 15.6	44.0 ± 3.5	57.2 ± 4.1	4
American Woodcock	48.2 ± 6.5	47.9 ± 7.5	51.5 ± 13.3	56.0 ± 9.0	59.3 ± 2.3	52.6 ± 6.4	57.2 ± 8.3	50.8 ± 9.9	47.6 ± 7.8	52.4 ± 7.6	3
Willet	51.2 ± 7.1	69.7 ± 10.7	69.0 ± 13.9	59.6 ± 11.8	78.3 ± 5.0	65.6 ± 6.3	57.2 ± 6.9	58.5 ± 11.9	53.2 ± 4.4	62.4 ± 6.1	4
Short-billed Dowitcher	54.4 ± 9.9	55.1 ± 4.2	54.4 ± 6.3	64.8 ± 6.9	64.0 ± 14.8	62.3 ± 5.4	57.7 ± 8.2	53.4 ± 6.4	60.2 ± 9.7	58.5 ± 4.7	4

Table 4. Continued

	Sector 1	Sector 2	Sector 3	Sector 4	Sector 5	Sector 6	Sector 7	Sector 8	Sector 9	All	n[1]
Ganglion cell density											
Wilson's Plover	32.3 ± 8.3	41.3 ± 3.2	42.4 ± 17.3	47.1 ± 9.5	73.2 ± 6.6	53.2 ± 18.2	29.3 ± 6.9	54.3 ± 18.4	34.0 ± 12.9	45.2 ± 5.9	4
Black-winged Stilt	29.4 ± 5.1	36.4 ± 5.3	42.4 ± 7.7	32.8 ± 3.9	42.8 ± 6.6	40.6 ± 10.1	26.4 ± 4.1	30.1 ± 6.8	21.1 ± 4.2	33.6 ± 2.6	4
American Woodcock	21.2 ± 4.2	30.5 ± 4.1	30.0 ± 5.4	32.5 ± 2.9	41.5 ± 7.7	30.3 ± 5.0	32.8 ± 6.7	29.1 ± 5.8	24.9 ± 2.7	30.3 ± 0.9	3
Willet	30.1 ± 4.3	37.4 ± 3.1	36.9 ± 4.2	36.3 ± 6.8	54.3 ± 3.4	51.3 ± 8.4	31.0 ± 5.3	36.1 ± 3.3	31.8 ± 3.3	38.3 ± 2.2	4
Short-billed Dowitcher	30.0 ± 3.7	32.8 ± 2.0	29.4 ± 5.5	36.3 ± 3.1	42.4 ± 5.1	40.5 ± 6.8	29.7 ± 4.4	35.6 ± 11.5	30.1 ± 2.3	34.1 ± 2.6	4
Optic nerve fiber layer											
Wilson's Plover	4.5 ± 1.0	9.3 ± 6.3	25.0 ± 5.6	9.5 ± 3.7	21.5 ± 4.5	14.0 ± 9.7	20.6 ± 7.7	23.0 ± 8.9	33.4 ± 8.7	17.9 ± 2.0	4
Black-winged Stilt	6.6 ± 0.7	8.8 ± 3.6	14.6 ± 5.3	13.7 ± 2.0	23.4 ± 13.1	38.9 ± 10.6	32.7 ± 9.2	57.4 ± 20.3	32.8 ± 25.4	25.4 ± 3.0	4
American Woodcock	6.6 ± 0.8	10.8 ± 4.3	20.7 ± 10.0	15.3 ± 4.3	17.7 ± 5.7	27.2 ± 19.1	20.5 ± 16.3	36.6 ± 13.0	16.9 ± 6.4	19.1 ± 5.1	3
Willet	7.0 ± 2.8	8.5 ± 1.8	11.6 ± 1.9	12.3 ± 7.1	16.2 ± 4.8	22.3 ± 9.2	17.3 ± 9.7	50.8 ± 17.3	40.8 ± 13.7	20.5 ± 3.3	4
Short-billed Dowitcher	7.0 ± 1.1	7.3 ± 1.1	6.8 ± 0.7	12.3 ± 4.4	15.1 ± 6.3	10.9 ± 4.8	10.0 ± 4.1	16.3 ± 6.4	16.3 ± 7.4	11.3 ± 1.9	4

[1] n = number of birds.

the stilt or the woodcock. There is no significant difference between the five species in the other rod parameters measured (outer segment diameter, inner segment length and inner segment diameter). As for the cones, their outer segments tend to be shorter in the dowitcher than in other species and are widest in the woodcock. Their inner segments are longest in the Willet and widest in the woodcock and the stilt. A photomicrograph from sector 5 of the retina of each species is shown in figure 8, and the measurements of the nuclear, plexiform and optic fiber layers as well as ganglion cell counts for each sector are given in table 4. It can be seen that in all species the thickness of the outer nuclear, inner nuclear and inner plexiform layers as well as the density of ganglion cells are or tend to be greater in sector 5, and that the optic nerve fiber layer is thinner in dorsal and temporal sectors (1 to 4) and thicker in ventral ones (8-9; the region of the optic nerve and pecten). The thickness of the outer plexiform layer displays no sectorial trend. It is in the plover and the Willet that sector-5 outer nuclear, inner nuclear, and inner plexiform layers are or tend to be the thickest and that ganglion cells in all sectors are or tend to be most numerous. The outer plexiform and the optic nerve fiber layer are the thickest in the stilt.

DISCUSSION

In contrast with most studies of avian visual system which were almost exclusively based on morphological observations and lacked physiological data, our study compares both morphological and physiological aspects of the retina in bird species from which detailed behavioral and ecological information is known. Our combined results, summarized for discussion purpose in table 1, show that the retina of the five species is differently adapted for night and for day vision.

The Wilson's Plover is a visual pecker both by day and by night, and the Black-winged Stilt also is except on windy moonless nights. These two species which appear to have the best visual adaptation for nocturnal life among the five species studied (see below) have larger dilated pupil diameters than the Willet, the Short-billed Dowitcher, or strictly diurnal species such as the Starling (*Sturnus vulgaris*) and the Common Pigeon (*Columba livia*) (see table 2). Their AL:ED ratios are lower than that of the strictly nocturnal Tawny Owl (*Strix aluco*), but higher than those of the Manx Shearwater (*Puffinus puffinus*), a species particularly noted for its nocturnal attendance at breeding colonies [see McNeil et al., 1993], the American Woodcock, the dowitcher, the Starling and the pigeon (see table 2). Nocturnally active species tend to have more globular eyes, i.e. with higher AL:ED ratios, than diurnal species [Tansley, 1965; Martin, 1990; Waldvogel, 1990].

Both the Wilson's Plover and the Black-winged Stilt are well adapted for vision under low light intensity. The plover has the highest rods:cones ratio of all species, mainly due to the highest rod density, and its rods also have long outer segment which, according to Walls (1942), would increase sensitivity. Furthermore, compared to the other species, the plover's scotopic b-wave considerably decreases in amplitude at high luminance intensity and its a-wave is of lower amplitude than that of the other species, which could be due to saturation of the scotopic response resulting from rod desensitization. As a corollary, based on the photopic ERG luminance-response function, the plover occupies the last rank of all species in daytime visual capability. Based on the scotopic ERG b-wave luminance-response function, retinal sensitivity, and the ratio and densities of rods and cones, the stilt also appears well adapted for nighttime vision, but also for daytime vision. In all five species studied, the peak time of the scotopic b-wave decreases with increasing stimulus luminance. The same occurs in the Little Owl (*Athene noctua*) [Porciatti et al., 1989], the Common Pigeon [Porciatti et al., 1991], and in the human [see Weleber and Eisner, 1988]. However, in both the Black-winged Stilt and the Wilson's Plover, the peak time of the scotopic b-wave is longer than in the other three shorebird species. Such a slow time to peak appears to be a characteristic of species with a rod-dominated retina such as, for example, the nocturnal Black Skimmer (*Rynchops niger*), in which the scotopic b-wave takes significantly longer to peak than in the diurnal American White Ibis (*Eudocimus ruber*) having a cone-dominated retina [Rojas et al., 1997]. Rods are more sensitive to light than are cones, but their responses are somewhat slower and longer lasting [Fain and Dowling, 1973; Dowling, 1987].

Although having a relatively low rod density compared to the stilt and the plover, the Willet and the American Woodcock have a retinal sensitivity under scotopic conditions similar to that of the stilt and the plover, but rank midway between the plover and the dowitcher for b-wave amplitudes. Territorial Willets, with the lowest rod density and rods:cones ratio of all species, forage by sight during daytime and on moonlit nights but need to switch to tactile feeding on moonless nights. With the highest cone density of all species examined, the Willet is with the stilt well adapted for daytime visually guided behavior, including foraging. The high scotopic sensitivity of the woodcock, in accordance with Walls [1942], can result from its longest rod outer segments. This feature, with the rod-dominated retina (1.2:1), can possibly explain the shorter peak time of its scotopic a-wave, compared to the other four species. In adapting the woodcock to vision in low light intensity, longer rod outer segments may compensate for their small number compared to the stilt or the plover. The woodcock forages most often solitarily, either in woodland or in open habitats, and thus is comparatively more vulnerable to both aerial and terrestrial predators than most other shorebird species which, outside the breeding period, generally forage gregariously. According to Connors and Doerr [1982; see also Krementz et al., 1994, 1995], woodcocks have developed anti-predator behaviors in the form of non-random positioning in the fields. Under photopic conditions, the woodcock has higher b- and a-wave luminance-response functions than the plover. By having thicker cones, albeit in lesser density, than the other shorebird species, the woodcock's retina can probably capture more photons, be more sensitive to the different light levels, and provide better vision of contrasts, even though low cone density and increased diameter can reduce visual acuity [Snyder et al., 1977]. However, the woodcock's cone density, although low in the temporal and dorsal sectors, is high in the central one, and this can contribute to increase acuity on the horizontal plane of the visual field. The eyes of the woodcock are placed laterally and high in the skull, giving the animal a comprehensive visual coverage of the hemisphere above itself, but the bill falls outside the visual field [Martin, 1994a]. Not seeing their bill, woodcocks are probably not fitted for visual capture of prey, and indeed this is something they do only rarely, namely when obtaining food by tactile probing of soft surface is not possible. They have a narrow binocular field, but their monocular field in the horizontal plane is the widest of all bird species and facilitates panoramic vision in the horizontal plane [Martin, 1994a]. In birds like the woodcock, freed from the constraint that vision is essential for prey location or for precise control of bill position, a wide visual field would facilitate the surveillance of their environment [Martin, 1994a], and thus help in the detection of aerial predators, particularly in the case of solitary foragers.

With its lowest scotopic ERG b-wave luminance-response function and retinal sensitivity, the daytime and nighttime tactile foraging Short-billed Dowitcher appears as the least well adapted for night vision. It forages and flies safely from one site to another at night but does not need vision to catch its prey. In photopic ERG, it is comparable to the Black-winged Stilt. Taking into account a cone density about the same as the plover, the photopic ERG response of the dowitcher is of greater amplitude and is comparable to or greater than those obtained for the stilt or the Willet, where cone density is or tends to be greater. This stronger response could be due to the rather uniform distribution of the cones in the different sectors of the retina, compared to what is found in the plover, which would optimize the capture of photons [Snyder et al., 1977]. In addition, this larger b-wave response obtained for the dowitcher could in part result from the fact that the eye has a shorter axial length compared to the other four species, but which is roughly comparable to that of the strictly diurnal Starling (table 2). A shorter axial length should results in reduced preretinal absorption and increased retinal illumination from the same flash intensity [Breton et al., 1995].

The rods:cones ratio of the five shorebird species is higher than that of the Northern Fulmar (*Fulmarus glacialis*) and the Manx Shearwater, and especially the strictly diurnal House Sparrow (*Passer domesticus*) and the American White Ibis [Lockie, 1952; Rojas et al., 1997]. Both the fulmar and the shearwater are known to forage at night [see McNeil et al., 1993]. The rods:cones ratio of the Willet is comparable to that of the Greater Yellowlegs (*Tringa melanoleuca*) (0.7:1) [Rojas de Azuaje et al., 1993], a visual feeder during daytime that mostly switches to tactile foraging (side-sweeping) at night [Robert and McNeil, 1989]. In contrast, the rods:cones ratios of shorebirds are considerably lower than that of the nocturnal Great Horned Owl (*Bubo virginianus*) [Fite, 1973] and the Black Skimmer [Rojas et al., 1997] for which the reported ratios are in the order of 12:1 and 5:1, respectively.

The ganglion cell density and the thickness of outer nuclear, inner nuclear, and inner plexiform layers in sector 5 are greater in the Wilson's Plover and the Willet than in other species. It has been reported that increased ganglion cell density is usually found in the retinal regions subserving higher visual acuity [see Binggeli and Paule, 1969; Ikushima et al., 1986; Hayes and Brooke, 1990; Inzunza et al., 1991; Suburo et al., 1991]. High ganglion cell density could provide the plover and the Willet with a better capacity to discriminate details. The inner nuclear layer is composed of the horizontal cells, the bipolar cells, and the amacrine cells [Tansley, 1965]. Ganglion cells are movement- direction- and contrast-sensitive and receive most of their input from bipolar and amacrine cells [see Dowling, 1987]. In addition, complex processing such as movement and direction selectivity occurs in the inner plexiform layer [see Dowling, 1987]. Thicker inner nuclear and inner plexiform layers could result in increased responses of the retina and thus could provide the plover and the Willet with a better vision of contrasts and prey movement.

In conclusion, under the tested conditions, all species are characterized by distinct ERG responses, both under scotopic and photopic conditions, and these physiological responses are in accordance with photoreceptor ratios and densities and other morphological features of the retina. Together, these data can be correlated with the nighttime and daytime activities and foraging strategies of the five shorebird species studied. The swimming prey of the stilts are more active, closer to the water surface, and thus more easily accessible at dusk and night than during daytime, and direct observations also confirm that most invertebrates, living in the muddy areas of intertidal habitats where the dowitchers forage, are more active or closer to the sediment surface at night [McNeil et al. 1992, 1993, 1995]. The same is true for the terrestrial annelids (*Lumbricus*) on which woodcocks mostly feed [Dugan 1981]. Consequently, it is believed that shorebirds that detect prey by touch, without having to see them, would be able to feed as fast during darkness as during daytime, whereas birds that detect prey primarily by sight would be disadvantaged at night, unless having specialized adaptations favoring nocturnal vision [McNeil et al. 1992]. The *Uca* fiddler crabs, the preferred prey of the Wilson's Plover and territorial Willets, contrary to above-mentioned invertebrates, although swarming by thousands on intertidal mudflats both in the day and at night, are more active during daytime [McNeil and Rompré, 1995; Thibault and McNeil, 1995]. On moonless nights, the territorial Willets have impaired vision, abandon their feeding territory, and move to habitats where they feed tactilely with non-territorial individuals [McNeil and Rompré, 1995; Rompré and McNeil, 1996]. Contrary to most other *Charadrius* plovers, the Wilson's Plovers are solitary foragers [Morrier and McNeil, 1991] and thus, while feeding during daylight, suffer higher individual risks of being captured by aerial predators [Thibault and McNeil, 1994]. During the non-breeding season, they congregate in small groups and remain motionless on roosts where substrata offer better concealing than the wide mudflats [Thibault and McNeil, 1994]. Between 20 to 30 min after dusk, the plovers leave diurnal roosting sites and distribute themselves all over the foraging mudflats. The main reason why Wilson's Plovers are largely nocturnal appears to be the avoidance of diurnal predators [Thibault and McNeil, 1994]. Thus, the plover can advantageously trade-off photopic vision for the scotopic one.

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Chapitre 4

Behavioral, morphological and physiological correlates of diurnal and nocturnal vision in selected wading bird species

Par

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Abstract. We examined in selected wading bird species if diurnal or nocturnal foraging and the use of visual or tactile feeding strategies could be correlated with retinal structure and function. The selected species were the Yellow-crowned Night Heron (*Nycticorax violaceus*), a crepuscular and nocturnal forager, the Great Blue Heron (*Ardea herodias*), a mainly crepuscular, but also diurnal and nocturnal feeder, the Roseate Spoonbill (*Ajaia ajaja*), a mainly crepuscular feeder which forages more at night than during the day, the Cattle (*Bubulcus ibis*) and Tricolored (*Egretta tricolor*) egrets and the American White Ibis (*Eudocimus ruber*) which forage only during daytime. Herons and egrets are visual foragers; ibises and spoonbills are tactile feeders. Electroretinograms were obtained from anesthetized birds in photopic and scotopic conditions to a wide range of light intensities, following which the retinae were processed for histological analysis. Based on rod densities and rods:cones ratios, nocturnal vision capability is greater in the Yellow-crowned Night Heron, followed by the Great Blue Heron and the spoonbill, then by the egrets and the ibis. Visual feeders that forage near dawn or dusk or at night have a higher rods:cones ratio, and consequently a greater night vision capability, than visual feeding species which forage only during daytime. Visual nocturnal feeders have a night vision capability greater than tactile diurnal as well as tactile nocturnal feeders. However, based on maximum scotopic b-wave amplitudes, all species studied have roughly comparable night vision capability. The factor that best discriminates between wading bird species appears to be the daytime visual capabilities. Indeed, the diurnal ibis and egrets have similar cone densities, cones:rods ratios, and photopic a-wave amplitudes, values which are greater than those measured in the two nocturnally active heron species.

Key Words: Wading birds, Nocturnal vision, Diurnal vision, Retina, Rod, Cone, Electroretinogram, Feeding strategies

INTRODUCTION

Nocturnal foraging is widespread among wading birds, and some species like the night herons (*Nycticorax*) specialize in this strategy [Kushlan, 1978; McNeil et al., 1993b]. However, most egrets (*Egretta*) are considered as diurnal [see McNeil et al., 1993b]. Others like the Great Blue Heron (*Ardea herodias*) feed during daytime and nighttime, but are mainly crepuscular feeders [see Horvath and Moholt, 1986; McNeil et al., 1993a, b). The spoonbills (*Ajaia* and *Platalea*) feed more actively in the morning, evening and night than during the daytime [see Robert et al., 1989; McNeil et al., 1993b]. Nevertheless, there is as yet little or no evidence that any ibis species feed at night with any regularity [see McNeil et al., 1998].

Visual foraging predominates in herons and egrets, the prey being usually seized in the bill, sometimes impaled [Kushlan, 1978]. Most crepuscular and nocturnal herons use passive foraging methods (stand and wait at the water's edge or in shallow water for prey to appear, peering, walk slowly in shallow water) but, in contrast, most diurnal egrets use more active foraging methods which involve successive and rapid movements (walk quickly, running forward rapidly, hopping and jumping, and open-wing) [Meyerriecks, 1962; Kushlan, 1976; Willard, 1977; Rodgers, 1983; Martínez-Vilalta and Motis, 1992]. Ibises mostly feed in muddy areas by non visual probing with their curved bill [Hancock et al., 1992; Matheu and del Hoyo, 1992]. They also use head swinging, groping and pecking when appropriate [Kushlan, 1977; Hancock et al., 1992]. Spoonbills forage tactilely by wading through shallow water, sweeping the partly open spatulate bill from side to side through water and silt [Kushlan, 1978; Matheu and del Hoyo, 1992].

Many swimming prey of wading birds are more active, closer to the water surface, and thus more easily accessible at dusk and night than during daytime, and direct observations also confirm that most invertebrates, living in the muddy areas of intertidal habitats where many wading birds forage, are more active or closer to the sediment surface at night [McNeil et al., 1992, 1993b, 1995]. Consequently, it can be expected that wading birds that detect prey by touch, without having to see them, would be able to feed as fast during darkness as during daytime, whereas birds that detect prey primarily by sight would be disadvantaged at night, unless having specialized adaptations favoring nocturnal vision [McNeil et al., 1992]. In such situations, the blindly probing techniques of ibises and spoonbills should allow night foraging [Hancock et al., 1992; Matheu and del Hoyo, 1992]. However, contrary to expectation, it appears that ibises do not feed at night [McNeil et al., 1998].

It is generally believed that "differences in gross anatomy reflect adaptations of the basic structure of vertebrate eyes to differences in the visual problems imposed by different life styles" [Martin and Brooke, 1991; see also Walls, 1942; Tansley, 1965], and it "might be expected that the eyes of nocturnally active species would have lower minimum *f*-numbers (higher maximum image brightness) than diurnal species" [Martin, 1994]. Furthermore, nocturnally active species tend to have more globular eyes, i.e. higher axial length:equatorial diameter (AL:ED) ratios, than diurnal species [Tansley, 1965; Martin, 1990; Waldvogel, 1990]. The retinal receptors of birds, as in all other vertebrates, are the rods and cones. Nocturnal birds have a greater preponderance of rods in their retinae while, in diurnal birds, most photoreceptors are cones [see Tansley and Erichsen, 1985; Waldvogel, 1990]. Rods are generally associated with night vision; cones, on the other hand, are associated with good visual acuity at high light levels [Tansley and Erichsen, 1985]. Finally, the retina of many birds is characterized by the presence of areas of circumscribed thickening which result from an increase in photoreceptor density, combined with a concomitant increase in the number of bipolar, horizontal, amacrine, and ganglion cells, the latter occurring in a proportion of 1:1 with cones [Tansley, 1965]. Such areas correspond to the so-called "central" and "temporal" areas of acute vision or fovea found in most vertebrate groups [see Walls, 1942; Meyer, 1977; Martin, 1985] and "attain their greatest perfection in diurnal birds where almost always one, sometimes two, and even three distinct areas may be developed" [Meyer 1977]. Most commonly, this area of greater cell density is located in the central region of the retina (*area centralis*), but diurnal birds which search for their prey while flying have, in addition to this central area that serves for monocular vision, a temporal one (*area temporalis*) for binocular vision [Tansley, 1965; Martin, 1985]. The photoreceptors of such areas are usually cones although the thickened areas of nocturnal birds such as owls contains both rods and cones, the rods being predominant as in the rest of the retina [Meyer, 1977].

The purpose of this study was to examine in a selected group of wading birds if diurnal and nocturnal foraging and the use of visual or tactile feeding strategies could be correlated with the structure and/or function of their retina. The following predictions were tested: 1) visual feeders that predominantly forage near dawn or dusk or at night have a higher rods:cones ratio and, consequently, a greater night vision capability than visual feeding species which forage only during daytime; 2) visual nocturnal feeders have a greater night vision capability not only than tactile diurnal foragers, but also than tactile nocturnal feeders; and finally 3) diurnal visual foragers should have proportionately more cones, and consequently a greater visual acuity, than diurnal tactile foragers.

MATERIALS AND METHODS

Wading bird species were selected according to behavioral criteria given in table 1. The Yellow-crowned Night Herons (*Nycticorax violaceus*), Cattle Egrets (*Bubulcus ibis*), Tricolored Egrets (*Egretta tricolor*), and American White Ibises (scarlet race: *Eudocimus ruber ruber*) were mist-netted in Laguna de Patos and Chacopata Lagoon in northeastern Venezuela. We were unfortunately unsuccessful in capturing live Roseate Spoonbills (*Ajaia ajaja*). As a consequence, three specimens were shot in Chacopata Lagoon and were unfortunately not available for electroretinogram (ERG) recording. The Great Blue Herons were obtained near Montréal, Province of Québec (Canada).

ERG RECORDING

The electroretinogram 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 [for review, see Ikeda, 1993]. A typical ERG consists of two waves which arise in different layers of the retina, reflecting light-evoked potentials generated by different retinal cells [Brown and Wiesel, 1961; Brown and Watanabe, 1962; Murakami and Kaneko, 1966; Witkowsky et al., 1973; Dick and Miller, 1985]. The first one (a-wave), negative, is generated mainly by the photoreceptors; the second one (b-wave), positive and with a slower peak time, takes origin in the inner nuclear layer [Jayle et al., 1965; Armington, 1974]. The waveform of the 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, scotopic), and thus can be used to compare the retinal sensitivity of different animal species.

Seven Yellow-crowned night heron, eight Great blue heron, four Cattle egret, four Tricolored egret and twelve American white ibis were analyzed. Except the spoonbills, the birds were brought alive to the laboratory at the Universidad de Oriente in Cumaná (Venezuela) or the Université de Montréal. ERGs were recorded in a dark room with the use of a LKC EPIC-2000 visual electrodiagnostic system (LKC Technologies Inc., Gaithersburg, MD), which includes a 41-cm diameter Ganzfeld full field stimulator (LKC

Table 1. Behavioral characteristics of the selected species and summary of principal results.

Species	n[a]	Foraging activity[b]	Foraging strategy[c]	Summary of principal results[d]					
				ERG V_{max} wave amplitudes			rods	cones	rods:cones
				scotopic	photopic				
					a	b			
Yellow-crowned Night Heron (*Nycticorax violaceus*)	7	$C + N^{1-2}$	$V + P^{1,3-6}$	+	+	+	++++	+	2.3:1
Great Blue Heron (*Ardea herodias*)	3	Mainly C, but also $D + N^{2,7-8}$	$V + P^{1,3-6}$	+	+	+	++	+++	0.6:1
Cattle Egret (*Bubulcus ibis*)	4	D^{2}	$V + A^{1,3-6}$	++	++	++	+	+++	0.3:1
Tricolored Egret (*Egretta tricolor*)	4	D^{2}	$V + A^{1,3-6}$	+	++	++	+	+++	0.3:1
American White Ibis (Scarlet) (*Eudocimus ruber ruber*)	9	D^{11}	$T^{10,12}$	+	++	++	+	++	0.3:1
Roseate Spoonbill (*Ajaia ajaja*)	3	Mainly C and more N than $D^{2,9}$	$T^{1,10}$	NA	NA	NA	++	++	0.9:1

[a] Number of birds used for ERG recording.

[b] C = crepuscular, D = diurnal, N = nocturnal.

[c] A = active, T = tactile, V = visual, P = passive.

[d] ++++, +++, ++, + represent the relative amplitude of ERG waves, and the density of rods or cones; NA = not available.

[1]Kushlan, 1978; [2]McNeil et al., 1993b; [3]Meyerriecks, 1962; [4]Kushlan, 1976; [5]Willard, 1977; [6]Rodgers, 1983; [7]Horvath and Moholt, 1986; [8]McNeil et al., 1993a; [9]Robert et al., 1989; [10]Matheu and del Hoyo, 1992; [11]McNeil et al., 1998; [12]Hancock et al., 1992.

Ganzfeld-2503B), using a method previously reported [Rojas et al., 1997]. Briefly, after a period of 4 hours of dark adaptation to allow for the recording of scotopic responses, the birds were anesthetized with a 1:1 mixture of ketamine-xylazine (0.0044 cc/kg injected in the pectoral muscle), and immobilized on a home-made recording holder with the head kept inside the Ganzfeld and the left eye maintained open upward. The left eyelids and nictitating membrane were kept retracted with a speculum, the cornea was anesthetized with 0.5% proparacaine hydrochloride, and the pupil was dilated with 1% Tropicamide. The maximum pupil diameter (mm) was measured at the beginning and at the end of the experiment. The active electrode consisted of a DTL® fiber (Sauquoit Industries, Scranton, PA) which was placed on the cornea [Lachapelle et al., 1993; Hébert et al., 1996]. Subdermal needles (Grass Instruments, Astro-med Inc., Warwick, RI), inserted under the skin of the crown and in the pectoral muscle, served as reference and ground electrodes, respectively. ERG responses (average of 6 at 10.1-sec intervals) were evoked to flashes of increasing luminance of -3.8, -3.0, -2.6, -2.0, -1.4, -1.0, and 0.0 log units of attenuation (maximal intensity: 3.31 cd · m^{-2} · sec^{-1}). The birds were then light-adapted for 10 min to a background luminance of 35.7 cd · m^{-2}, following which the photopic ERGs (average of 10 at 4.1-sec intervals) were evoked to flashes of decreasing luminance (0.0, -0.6, -1.0, and -1.4 log units; maximal intensity: 3.31 cd · m^{-2} · sec^{-1}). Our previous studies indicated that the above parameters resulted in adequate and reproducible segregation of rod and cone functions in birds [Rojas et al., 1997, 1998].

In order to take into account the fact that the size of the pupil, and consequently the light which actually falls on the retina, vary with species, the light intensity with which the ERGs were evoked was transformed in troland unit. The troland (T) is defined as the retinal illuminance equal to that produced by viewing a surface whose luminance is 1 cd · m^{-2} through a pupil whose area is 1 mm^2, and is calculated as follows: T = LI x LS, where LI is the light intensity (cd · m^{-2}) and LS the pupil surface (mm^2) [Wyszecki and Stile, 1967].

To facilitate comparison of data between species of birds, luminance-response function curves were generated from the scotopic ERG responses [Naka and Rushton, 1966]. The intensity (σ or k) of the stimulus necessary to evoke a b-wave whose amplitude is half the maximal saturated amplitude (½ V_{max}) was calculated. This value is generally considered as an adequate measurement of the retinal sensitivity under scotopic condition [see Massof et al., 1984; Fulton, 1991; Hébert et al., 1996].

HISTOLOGICAL PREPARATION

Four Yellow-crowned night heron, four Great blue heron, four Cattle egret, four Tricolored egret, four American white ibis and three Spoonbill were analyzed.

Once the ERG recordings completed, four individuals of each species were kept for histological analysis whereas the others were given enough time to recover from anesthesia and were returned to their original habitat. The former were euthanized with sodium pentobarbital. In the case of the Roseate Spoonbill, only three individuals were available. The left eye was removed and the axial length and equatorial diameter were measured [see Martin, 1986]. The eye was then injected with 2.5% glutaraldehyde in 0.1 M phosphate buffer (pH = 7.2), punctured at the cornea, and placed in the same fixative for 30 min. The eyes of the spoonbills were dissected out and placed in the fixative in the field before transportation to the laboratory. Working with the eye in the fixative, the anterior segment was removed and the retina, still attached to the choroid, was cut into 9 sectors, using the pecten as landmark (fig. 1). This division is the same as that used by Rojas de Azuaje et al. [1993] and Rojas et al. [1997, 1998], and corresponds to that of Meyer and May [1973] and Begin and Handford [1987], although the sector numbering is different. Still in the fixative, each sector was subdivided into 2 mm^2 portions, of which two were retained for analysis. After 3 h in the fixative, the retinal portions, separated from the choroid, were washed in phosphate buffer for 10 min, postfixed in 1% OsO4 in 0.1 M phosphate buffer for 1 h, rinsed in phosphate buffer followed by distilled water (10 min each), dehydrated in graded ethanol (10 min per step), and bathed in propylene oxide (15 min). The tissues were successively infiltrated with a 1:1 mixture of propylene oxide and Epon for 6 h, and pure Epon medium for another 2 h. Finally, they were embedded in silicone rubber molds filled with Epon and polymerized at 60°C for 48 h. Semithin (0.7 µm) sections were obtained and 15 of them (one every 30-40 sections) were mounted on glass slides and stained with toluidin blue. Cuts were made perpendicularly to the retina by reorienting the blocks until achieving sections longitudinal to the photoreceptors. Rods, cones and ganglion cells were counted in 310-µm wide fields, for a total of 15 counts for each of the nine sectors. As in

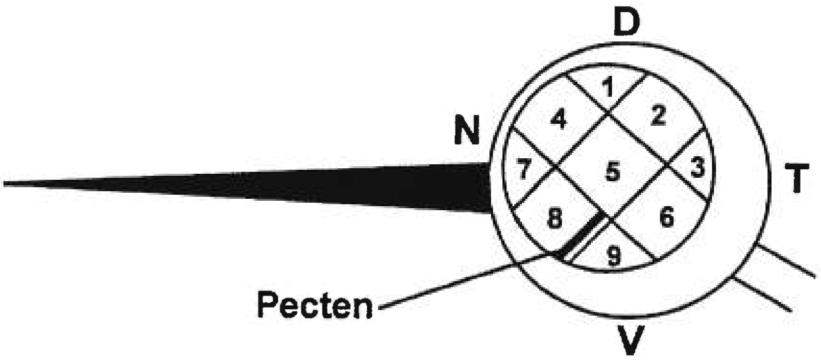


Figure 1. Schematic representation of the nine retinal sectors. **D**, **N**, **T**, and **V** correspond to dorsal, nasal, temporal and ventral sectors, respectively.

other avian retinae [Meyer and May, 1973; Meyer, 1977; Tansley and Erichsen, 1985; Waldvogel, 1990], double cones, in addition to single cones, were present in all five species, and they were counted as two cones. In addition, the length and diameter of the outer and inner segments of rods and cones, and the thickness of each retinal layer were measured. Ganglion cells were identified according to morphology and coloration criteria [Hayes and Brooke, 1990; Inzunza et al., 1991]: rounded or oval large cells with an oval pale nucleus and an easily distinguishable pale blue nucleolus. In most cases, ganglion cell bodies were arranged side by side in a 1-cell thick layer, but in the specialized thickened areas (e.g., central retina), they occurred in two or three layers. Displaced amacrine cells, on the other hand, appeared as small pale stained bodies lying next to the inner plexiform layer.

RESULTS

ELECTRORETINOGRAPHY

Representative ERGs obtained in scotopic and photopic conditions for each species are presented in fig. 2. It can be seen that they differ in shape and amplitude between species. The luminance-response function generated from amplitude measurements obtained in scotopic and photopic conditions are graphically represented in fig. 3 (b-wave) and fig. 4 (a-wave). Peak time variations as a function of stimulus luminance are shown, for both waves, in figs. 5 and 6.

For scotopic responses, analysis of the mean b-wave amplitude variations as a function of luminance (fig. 3A) reveals two patterns of luminance response function. The first one is found in the Cattle Egret, the Tricolored Egret and the American White Ibis where the amplitude of the b-wave increases more or less linearly with luminance. The second pattern is found in the Yellow-crowned Night Heron and the Great Blue Heron, and is characterized by a rapid initial growth in b-wave amplitude followed by a saturation phase, and then by a moderate, not significant decrease. As shown with the 95% confidence intervals, the maximal amplitude of the b-wave measured in the Cattle Egret is significantly higher than that of the Tricolored Egret and the ibis, irrespective of the intensity considered. The b-wave amplitudes measured in these three species are not significantly different from those of the

Figure 2. Representative ERG responses of the species studied obtained under scotopic and 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).

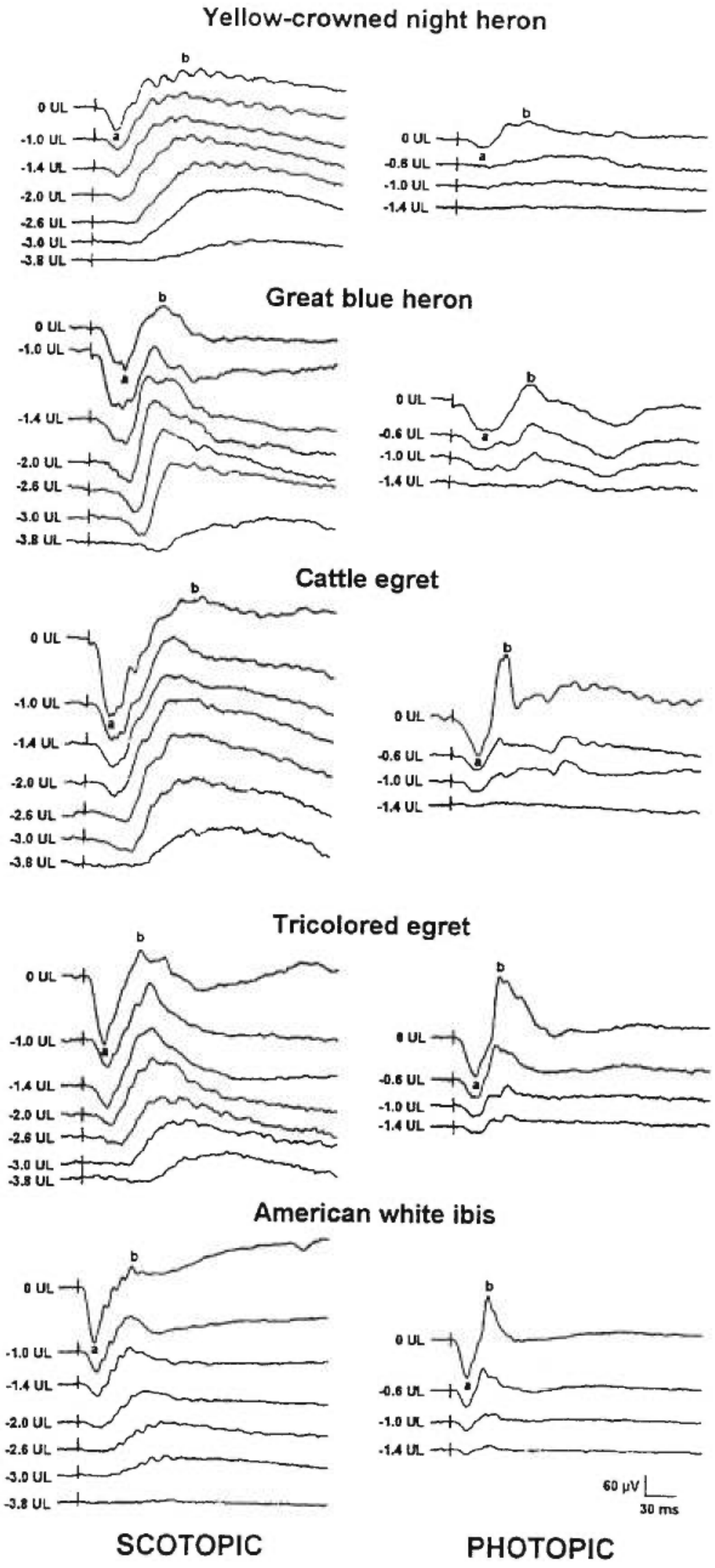

Yellow-crowned night heron
0 UL
-1.0 UL
-1.4 UL
-2.0 UL
-2.6 UL
-3.0 UL
-3.8 UL
0 UL
-0.6 UL
-1.0 UL
-1.4 UL
a
b
Great blue heron
0 UL
-1.0 UL
-1.4 UL
-2.0 UL
-2.6 UL
-3.0 UL
-3.8 UL
0 UL
-0.6 UL
-1.0 UL
-1.4 UL
a
b
Cattle egret
0 UL
-1.0 UL
-1.4 UL
-2.0 UL
-2.6 UL
-3.0 UL
-3.8 UL
0 UL
-0.6 UL
-1.0 UL
-1.4 UL
a
b
Tricolored egret
0 UL
-1.0 UL
-1.4 UL
-2.0 UL
-2.6 UL
-3.0 UL
-3.8 UL
0 UL
-0.6 UL
-1.0 UL
-1.4 UL
a
b
American white ibis
0 UL
-1.0 UL
-1.4 UL
-2.0 UL
-2.6 UL
-3.0 UL
-3.8 UL
0 UL
-0.6 UL
-1.0 UL
-1.4 UL
a
b
60 µV
30 ms
SCOTOPIC
PHOTOPIC

Figure 3. Luminance-response function (± 95% confidence intervals) of the b-wave of the species studied under **(A)** scotopic and **(B)** photopic conditions. The ordinate represents the b-wave amplitude (μV) and the abscissa the stimulus luminance intensity (Log troland-sec).

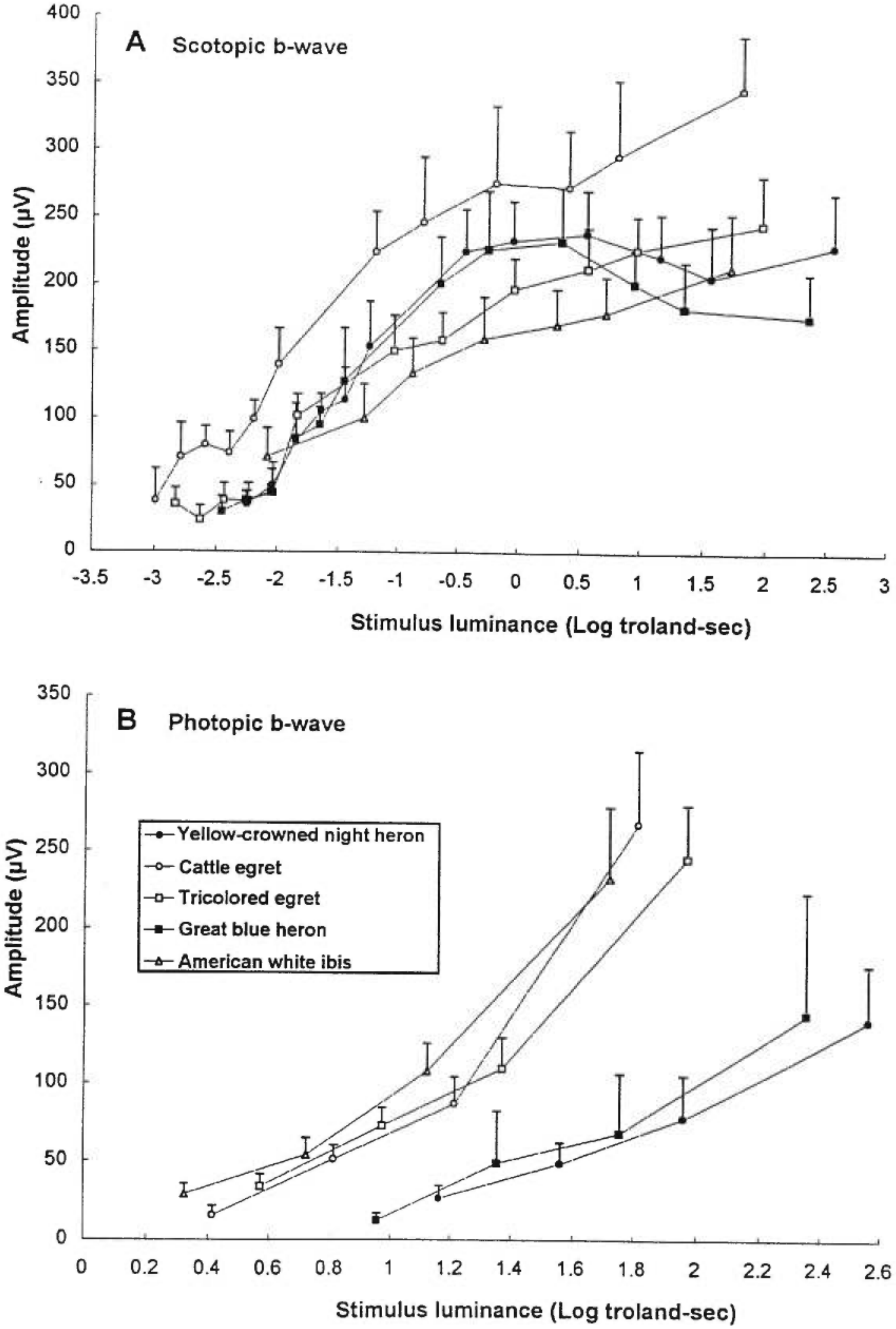
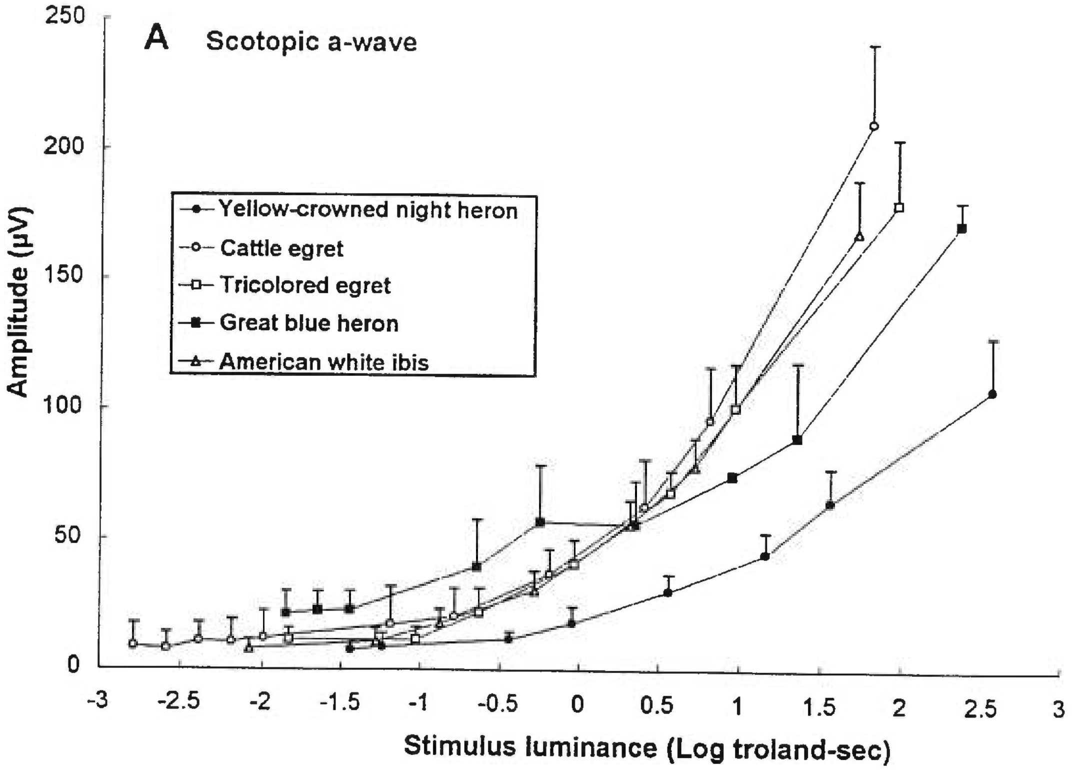

A Scotopic b-wave
Amplitude (µV)
400
350
300
250
200
150
100
50
0
-3.5
-3
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
2.5
3
Stimulus luminance (Log troland-sec)
B Photopic b-wave
Amplitude (µV)
350
300
250
200
150
100
50
0
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
2.4
2.6
Stimulus luminance (Log troland-sec)
Yellow-crowned night heron
Cattle egret
Tricolored egret
Great blue heron
American white ibis

Figure 4. Luminance-response function (± 95% confidence intervals) of the a-wave of the species studied under (**A**) scotopic and (**B**) photopic conditions. The ordinate represents the a-wave amplitude (µV) and the abscissa the stimulus luminance intensity (Log troland-sec).


A
Scotopic a-wave
Amplitude (µV)
250
200
150
100
50
0
-3
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
2.5
3
Stimulus luminance (Log troland-sec)
Yellow-crowned night heron
Cattle egret
Tricolored egret
Great blue heron
American white ibis

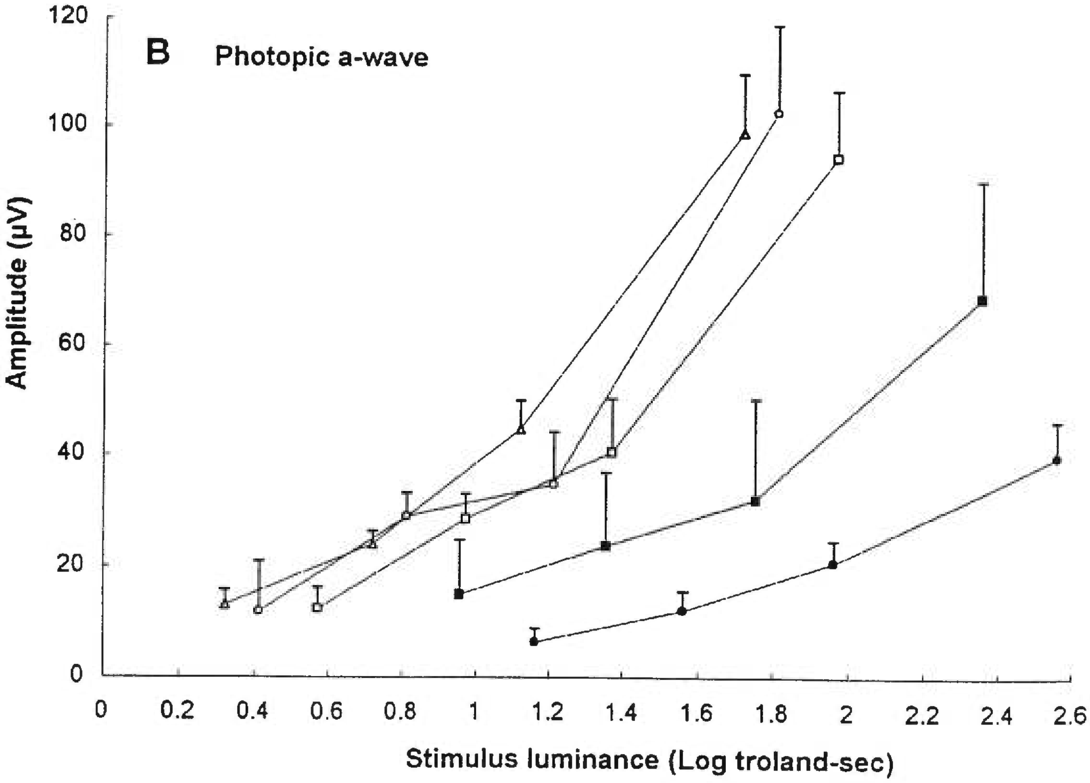
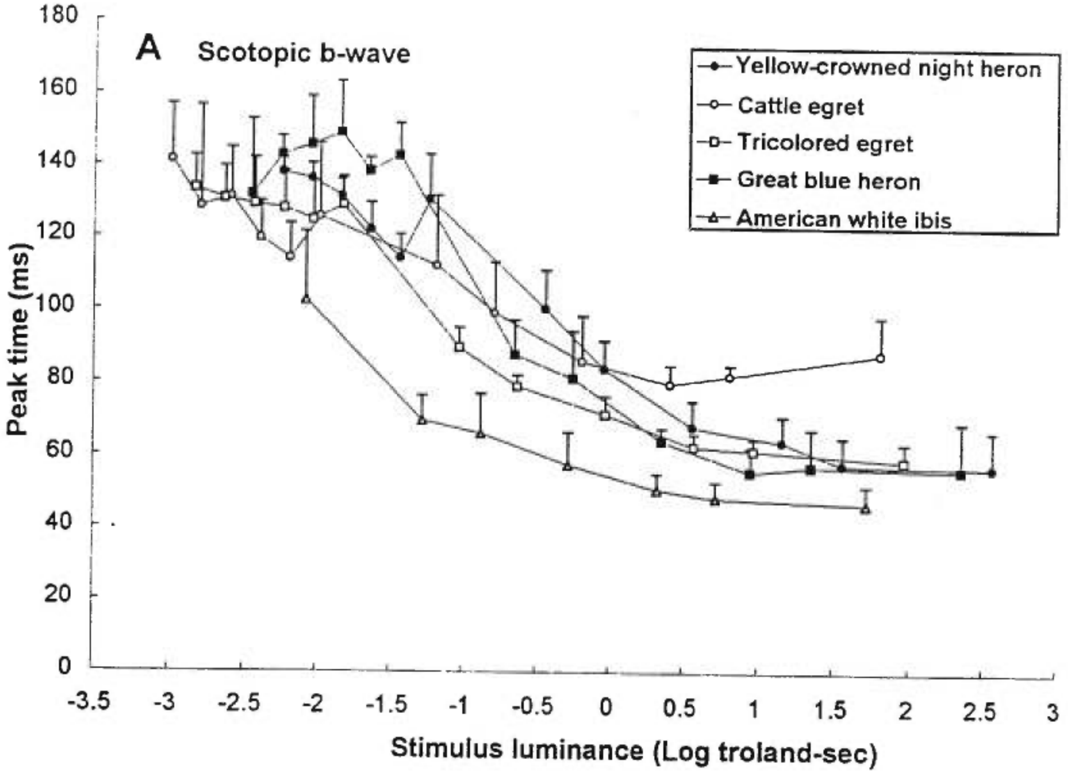
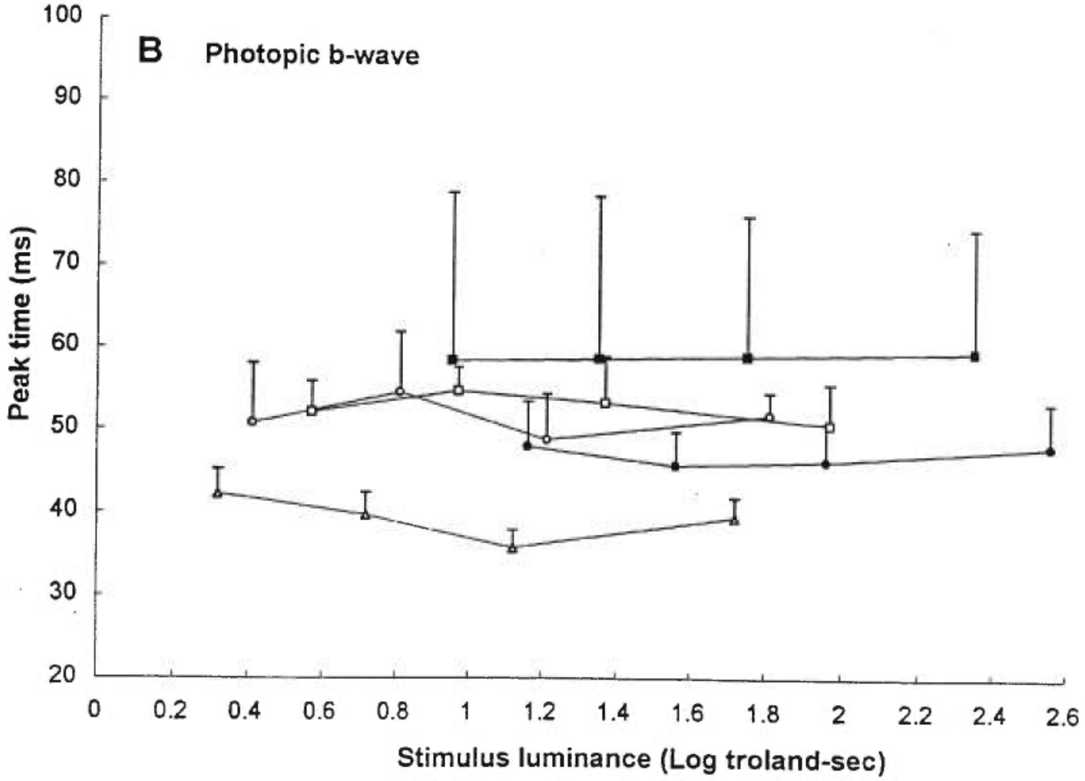

B
Photopic a-wave
Amplitude (µV)
120
100
80
60
40
20
0
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
2.4
2.6
Stimulus luminance (Log troland-sec)

Figure 5. Mean peak time (ms) variations (± 95% confidence intervals) in the b-wave of the species studied as a function of the stimulus luminance intensity (Log troland-sec) under (**A**) scotopic and (**B**) photopic conditions.


A
Scotopic b-wave
Yellow-crowned night heron
Cattle egret
Tricolored egret
Great blue heron
American white ibis
Peak time (ms)
180
160
140
120
100
80
60
40
20
0
-3.5
-3
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
2.5
3
Stimulus luminance (Log troland-sec)


B
Photopic b-wave
Peak time (ms)
100
90
80
70
60
50
40
30
20
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
2.4
2.6
Stimulus luminance (Log troland-sec)

herons. However, the amplitudes recorded for the ibis tend to be lower than those of the heron and egret species at stimulus luminance ranging between –1.5 and 0.5 Log troland-sec. In addition, for intensities above 0.5 Log troland-sec, the Cattle Egret shows a response significantly higher than that of the other species compared. Similarly, as shown with the 95% confidence intervals (fig. 4A), the amplitude of the scotopic a-wave measured in the Yellow-crowned Night Heron is significantly lower than that measured in the other species. The a-wave amplitudes of these four species do not differ significantly from each other. As for the temporal parameters, the peak time of the b-wave (fig. 5A) and a-wave (fig. 6A) of all species shortens exponentially with increasing luminance. According to the 95% confidence intervals, the timing of the b-wave and a-wave of the ibis is generally faster than that of the other species.

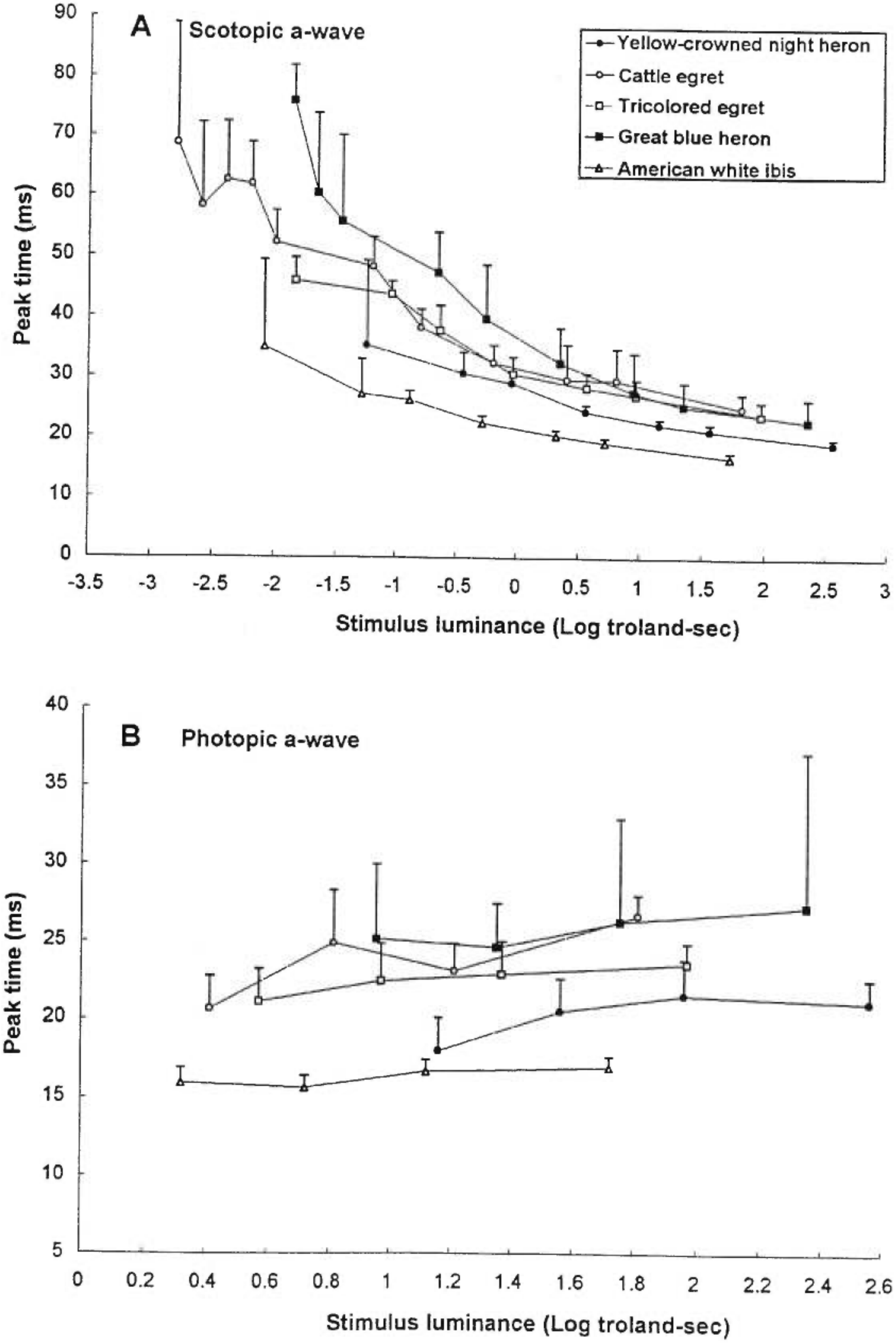
For photopic responses, the amplitude of both b-wave (fig. 3B) and a-wave (fig. 4B) increases exponentially as a function of luminance. As shown with 95% confidence intervals, for all intensities considered, the Yellow-crowned and the Great Blue herons yield photopic responses which are significantly lower than those obtained for the other species (fig. 3B). The lowest a-wave amplitudes are also found in the Yellow-crowned Night Heron (fig. 4B). The peak time of the photopic b-wave (fig. 5B) and a-wave (fig. 6B) does not vary significantly as a function of luminance intensity. However, it would appear that the ERGs of the ibis consistently yield significantly faster a- and b-waves as illustrated by the 95% confidence intervals.

The intensity of the stimulus necessary to elicit $\frac{1}{2}V_{max}$ in scotopic condition also varies with the species studied. The retinal sensitivity of the ibis (-0.89 ± 0.46 log troland-sec) is lower than that of the Great Blue Heron (-1.51 ± 0.14) and tends to be lower than that of the Tricolored Egret (-1.30 ± 0.31), the Yellow-crowned Night Heron (-1.44 ± 0.11), and the Cattle Egret (-1.63 ± 0.35), although differences are not significant.

MORPHOLOGY

Eye measurements are given in table 2. The Yellow-crowned Night Heron has a larger dilated pupil diameter and a greater axial length:equatorial diameter ratio (AL:ED) than the other species.

Figure 6. Mean peak time (ms) variations (± 95% confidence intervals) in the a-wave of the species studied as a function of the stimulus luminance intensity (Log troland-sec) under (**A**) scotopic and (**B**) photopic conditions.


A
Scotopic a-wave
Yellow-crowned night heron
Cattle egret
Tricolored egret
Great blue heron
American white ibis
Peak time (ms)
90
80
70
60
50
40
30
20
10
0
-3.5
-3
-2.5
-2
-1.5
-1
-0.5
0
0.5
1
1.5
2
2.5
3
Stimulus luminance (Log troland-sec)
B
Photopic a-wave
Peak time (ms)
40
35
30
25
20
15
10
5
0
0.2
0.4
0.6
0.8
1
1.2
1.4
1.6
1.8
2
2.2
2.4
2.6
Stimulus luminance (Log troland-sec)

As shown in fig. 7, the Yellow-crowned Night Heron is the only species where the rods outnumber the cones, and that in all retinal sectors. The resulting overall rods:cones ratio is 2.3:1. In contrast, the Great Blue Heron, and particularly the Cattle Egret, the Tricolored Egret and the ibis, have a cone-dominated retina, with overall rods:cones ratios ranging from 0.6:1 to 0.3:1. The spoonbill has a mixed retina (0.9:1) with similar densities of rods and cones in all nine sectors. While in the Great Blue Heron, the spoonbill and the ibis the rods:cones ratio is the same from one sector to another, in the Cattle Egret the cones are more numerous in the central retina (sector 5), and in the Tricolored Egret they are more concentrated in the temporal retina (sector 3) where the rods also show the lowest density. Based on the 95% confidence intervals, rod density is significantly higher in the Yellow-crowned Night Heron than in the five other species; it is also higher in the Great Blue Heron and the spoonbill, compared to the ibis and the Tricolored and Cattle egrets. Cone density is higher in the Cattle Egret, followed by the Tricolored Egret, and then by the ibis; it is lowest in the Yellow-crowned Night Heron.

For each species, the rod and cone morphometric measurements generally indicate no clear variations between sectors, and therefore only the overall data are given in table 3. According to the 95% confidence intervals, the rod outer segments are the longest in the Great Blue Heron, followed by the Yellow-crowned Night Heron and the spoonbill. The rod outer segments of the Great Blue Heron are double in length those of the two egrets and the ibis. There is no significant difference between the six species in the other morphometric parameters of rods (outer segment diameter, and inner segment length and diameter). Similarly, the cone outer and inner segments of the Great Blue Heron significantly exceed in length those of the other species while their cone outer segments are significantly shorter in the ibis than in the other species. In the Cattle Egret, the cone inner segments are significantly shorter than in the other species, except for the Tricolored Egret. The ibis and the Cattle Egret have thinner cone inner segments (except for accessory cones) than the other species. However, the inner segment diameter of accessory cones is wider in the ibis.

A photomicrograph from the central retina (sector 5) of each species is shown in fig. 8. The thickness of the outer plexiform layer displays no sectorial trends. However, in the Yellow-crowned Night Heron, the Cattle Egret and the Roseate Spoonbill, the thickness of

Table 2. Eye measurements of the species studied, and comparison with other species

	Axial length[a] (mm) AL	Equatorial diameter[a] (mm) ED	AL/ED	Dilated pupil diameter[a] (mm)
Yellow-crowned night heron	27.1 ± 4.6 (7)	24.5 ± 0.4 (7)	1.10	11.9 ± 0.3 (6)
Cattle egret	12.3 ± 0.3 (4)	15.1 ± 1.0 (4)	0.81	5.0 ± 0.0 (5)
Tricolored egret	15.0 ± 0.3 (7)	17.2 ± 0.9 (7)	0.87	5.8 ± 0.4 (6)
Great blue heron	18.6 ± 1.3 (8)	23.3 ± 1.8 (8)	0.80	5.3 ± 1.1 (5)
American white ibis	13.4 ± 0.2 (6)	15.9 ± 0.1 (6)	0.84	5.6 ± 0.5 (5)
Black skimmer (*Rynchops niger*)[1]	12.9 ± 0.8 (12)	15.5 ± 0.6 (12)	0.83	7.2 ± 0.5 (19)
Wilson's plover (*Charadrius wilsonia*)[2]	11.2 ± 0.3 (9)	13.1 ± 0.6 (9)	0.86	5.2 ± 0.3 (5)
Black-winged stilt (*Himantopus himantopus*)[2]	13.2 ± 0.5 (10)	15.4 ± 0.4 (10)	0.86	6.0 ± 0.4 (8)
Willet (*Catoptrophorus semipalmatus*)[2]	12.0 ± 0.9 (7)	14.5 ± 0.4 (7)	0.83	4.2 ± 0.2 (4)
Starling (*Sturnus vulgaris*)[3]	7.9	10.1	0.79	2.5
Manx shearwater (*Puffinus puffinus*)[4]	11.8	14.3	0.83	3.7
Tawny owl (*Strix aluco*)[4]	28.5	30.1	0.95	13.3
Common pigeon (*Columba livia*)[5,6]	11.0	14.0	0.79	4.0

[a] $\bar{x}$ ± 95% confidence intervals (*n* = number of birds).

[1]Rojas et al. unpubl.; [2]Rojas et al. submitted; [3]Martin 1986; [4]Martin and Brooke 1991; [5]Martin 1982; [6]Chard and Gundlach 1938.

Figure 7. Mean rod and cone numbers ($\bar{x}$/310 μm ± 95% confidence intervals) of the species studied in each of the nine retinal sectors as well as in all sectors averaged. The figures above the "all" columns indicate the overall rods:cones ratio.

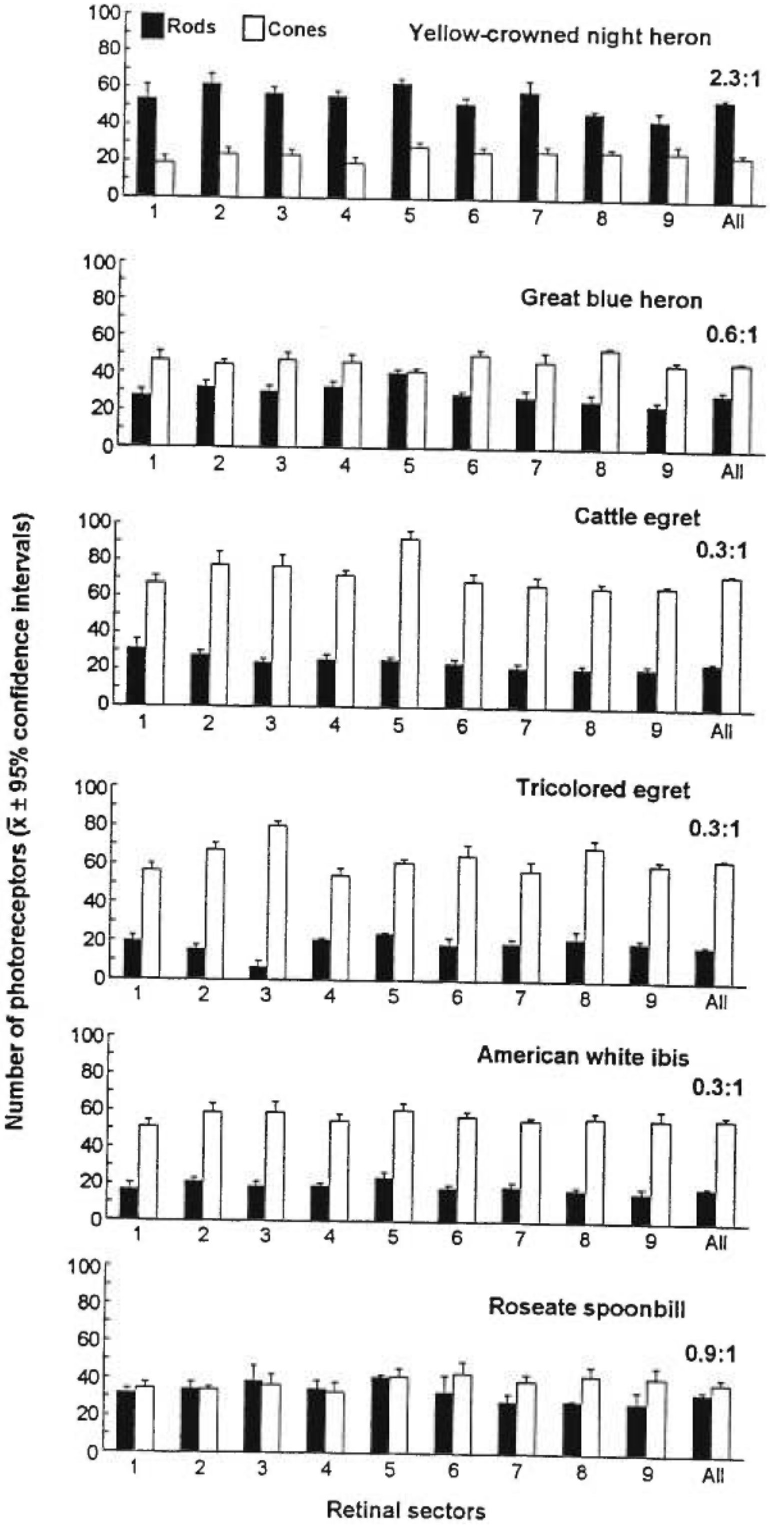

Rods
Cones
Yellow-crowned night heron
2.3:1
Great blue heron
0.6:1
Cattle egret
0.3:1
Tricolored egret
0.3:1
American white ibis
0.3:1
Roseate spoonbill
0.9:1
0
20
40
60
80
100
1
2
3
4
5
6
7
8
9
All
Number of photoreceptors (x̄ ± 95% confidence intervals)
Retinal sectors

Table 3. Overall mean rod and cone measurements (μm) of wading birds species.

	Night heron $n^a = 4$	Cattle egret $n = 4$	Tricolored egret $n = 4$	Great blue heron $n = 4$	American white ibis $n = 4$	Roseate spoonbill $n = 3$
Rod outer segment length	38.0 ± 4.4	20.4 ± 2.6	23.5 ± 1.9	55.2 ± 2.0	20.4 ± 0.6	29.3 ± 1.7
outer segment diameter	3.9 ± 1.2	4.3 ± 0.3	4.1 ± 0.2	4.4 ± 0.3	4.1 ± 0.3	4.5 ± 0.2
inner segment length	27.2 ± 1.9	30.4 ± 1.1	30.9 ± 2.6	28.6 ± 0.9	26.4 ± 1.6	30.1 ± 0.8
inner segment diameter	4.2 ± 0.2	4.4 ± 0.2	4.3 ± 0.1	4.6 ± 0.2	3.9 ± 0.2	4.5 ± 0.1
Cone outer segment length	19.0 ± 0.6	18.2 ± 1.9	20.9 ± 1.7	35.4 ± 1.3	14.0 ± 1.5	17.2 ± 0.8
outer segment diameter	1.5 ± 0.1	1.4 ± 0.0	1.6 ± 0.2	1.7 ± 0.0	1.3 ± 0.1	1.7 ± 0.2
inner segment length[b]	37.7 ± 1.5	31.5 ± 1.4	34.3 ± 2.1	46.8 ± 2.6	34.3 ± 1.1	34.9 ± 1.3
inner segment length[c]	31.8 ± 2.2	26.3 ± 1.2	28.0 ± 1.2	39.5 ± 2.3	28.1 ± 0.7	29.4 ± 0.6
inner segment diameter[b]	4.8 ± 0.2	3.9 ± 0.1	4.6 ± 0.3	4.8 ± 0.1	3.7 ± 0.2	4.5 ± 0.2
inner segment diameter[c]	5.4 ± 0.9	5.7 ± 0.1	6.0 ± 0.5	5.7 ± 0.2	6.4 ± 0.1	5.9 ± 0.1

[a] n = number of birds

[b] All cone types, except accessory cones

[c] Accessory cones

Figure 8. Photomicrographs showing the principal layers of sector 5 of the retina of the species studied. Nomenclature: **e.l.m.**, external limiting membrane; **g.c.l.**, ganglion cell layer; **i.l.m.**, inner limiting membrane; **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.l.**, photoreceptor layer. In each photomicrograph, the arrow points to a rod and the triangle to a cone.

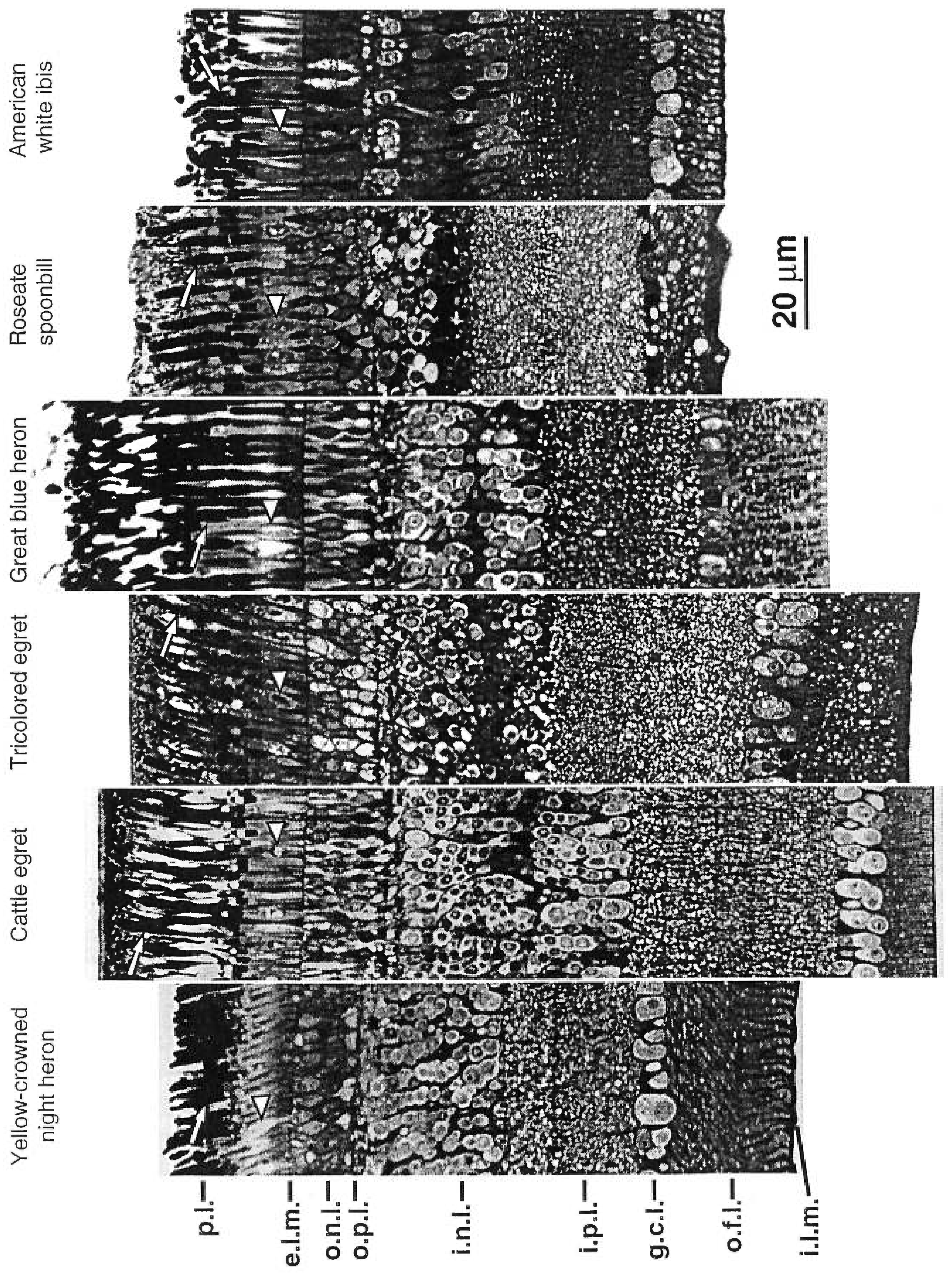
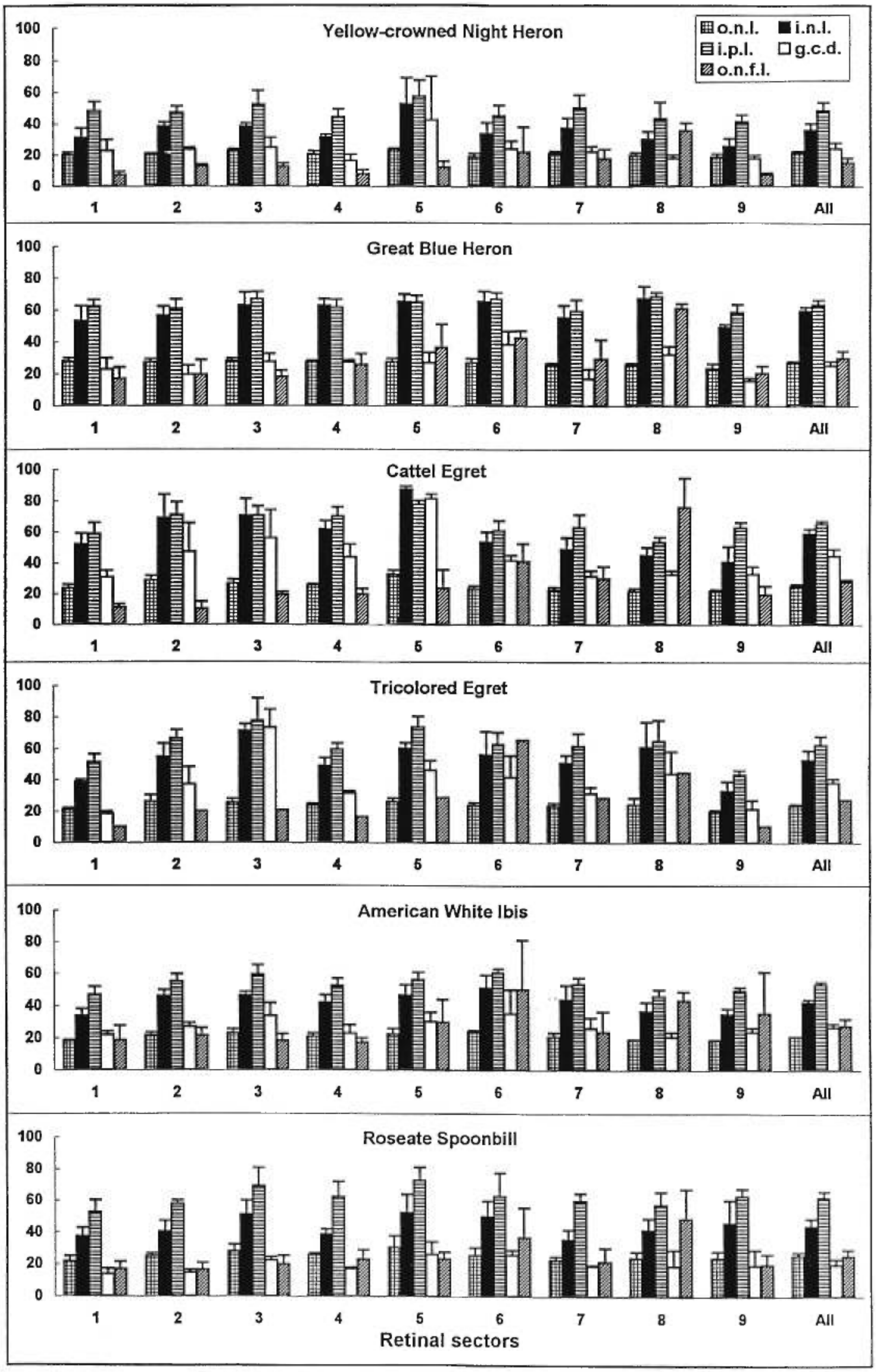

Yellow-crowned night heron
Cattle egret
Tricolored egret
Great blue heron
Roseate spoonbill
American white ibis
p.l.
e.l.m.
o.n.l.
o.p.l.
i.n.l.
i.p.l.
g.c.l.
o.f.l.
i.l.m.
20 μm

Fig. 9. Mean thickness (µm) of retinal layers and mean ganglion cell density ($\bar{x}$/310 µm) in each of the nine retinal sectors of the species studies, as well as in all sectors averaged. Columns represent the means (± 95% confidence intervals). Abbreviations: g.c.l. = ganglion cell density; i.n.l. = inner nuclear layer; i.p.l. = inner plexiform layer; o.n.f.l. = optic nerve fiber layer; o.n.l. = outer nuclear layer. Are represented only those layers which show intersectorial differences. The number of birds is 4 in all cases, except 3 for the Roseate Spoonbill.


Yellow-crowned Night Heron
Great Blue Heron
Cattel Egret
Tricolored Egret
American White Ibis
Roseate Spoonbill
o.n.l.
i.n.l.
i.p.l.
g.c.d.
o.n.f.l.
100
80
60
40
20
0
1
2
3
4
5
6
7
8
9
All
Retinal sectors

the outer nuclear, inner nuclear, and inner plexiform layers, as well as the density of ganglion cells, are or tend to be greater in sector 5, a tendency which was not observed in the other three species (see fig. 9). It is in the Cattle Egret that, in sector 5, the inner nuclear layer is the thickest and the ganglion cells are the most numerous. However, in the Tricolored Egret, the thickness of these layers and ganglion cell density are or tend to be greater in sector 3 (fig. 9). The values for these parameters in sector 3 for the Tricolored Egret are almost as high as they are in sector 5 for the Cattle Egret. As expected, in the six species, the optic nerve fiber layer tends to be thinner in dorsal and temporal sectors (1 to 4) and thicker in sector 8 (fig. 9).

DISCUSSION

In contrast with most studies of avian visual system which were almost exclusively based on morphological observations and lacked any physiological correlates, our study compares both morphological and physiological aspects of the retina in bird species from which detailed behavioral and ecological information is known. Our combined results, summarized for discussion purpose in table 1, show that the retina of the species studied is differently engineered for night and day vision.

The dilated pupil of the Yellow-crowned Night Heron, the crepuscular and nocturnal sight feeder, doubles in diameter that measured for the other species studied and is nearly comparable to that of the strictly nocturnal Tawny Owl (*Strix aluco*) (see table 2). The AL:ED ratio of the night heron, which is greater than those of the ibis, the Great Blue Heron and the two egret species, also exceeds that of the nocturnally active Black Skimmer (*Rynchops niger*; Rojas et al., 1997], the Wilson's Plover (*Charadrius wilsonia*), the Black-winged Stilt (*Himantopus himantopus*) and the Willets (*Catoptrophorus semipalmatus*), shorebirds known to forage at night [see Rojas et al., 1998], as well as the Manx Shearwater (*Puffinus puffinus*), a species particularly noted for its nocturnal attendance at breeding colonies, and is even larger than that of the Tawny Owl (see table 2). The rod density of the Yellow-crowned Night Heron is roughly double that of the other species studied here (see fig. 7) and results in a high rods:cones ratio, which is however lower than that of the Black skimmer [Rojas et al., 1997], but exceeds those of the Wilson's Plover, the Black-winged Stilt and the Willets [Rojas et al., 1998]. The maximal b-wave amplitude of the night heron is slightly lower than that of the Wilson's Plover and the Black-winged Stilt, but exceeds that of the Willets which switches to tactile foraging on moonless nights, and the tactilely foraging American Woodcock (*Scolopax minor*) (Rojas et al., 1998]. Thus, the Yellow-crowned Night Heron appears to be well adapted for vision in poor light environment, which supports our initial predictions that 1) visual feeders that predominantly forage near dawn or dusk or at night have a higher rods:cones ratio and, consequently, a greater night vision capability than visual feeding species which forage only during daytime, and 2) visual nocturnal feeders have a greater night vision capability not only than tactile diurnal foragers, but also than tactile nocturnal feeders.

In contrast, the Great Blue Heron, the mainly crepuscular but also diurnal and nocturnal sight-forager, has a low AL:ED ratio which roughly corresponds to those reported for the strictly diurnal European Starling (*Sturnus vulgaris*) and Common Pigeon (*Columba livia*) (see table 2). Its rods:cones ratio and rod density are much lower than those of the Yellow-crowned Night Heron, but higher than the diurnal ibis and egrets, findings which also support the first initial prediction. In spite of that, compared to the Yellow-crowned Night Heron, the Great Blue Heron has a similar maximum scotopic b-wave amplitude and a slightly higher retinal sensitivity. Its night vision performance can be due, at least in part, to its rod outer segments which are roughly double in length compared to those of the three diurnal species, and significantly exceed in length those of the spoonbill and the night heron (see table 3), as well as those of the Wilson's Plover, the Black-winged Stilt, and the Willets, all of which are nocturnal sight-foragers, at least under moonlit conditions [Rojas et al., 1998].

By comparison, the two strictly diurnal sight-feeding egrets, based on their rods:cones ratios and rod densities, do not appear to be well adapted to execute visual tasks during darkness, in agreement with the first prediction. On the overall, their rod density is lower than in the two heron species (see fig. 7). However, in spite of that, the egrets have comparable (Tricolored Egret) or even higher (Cattle Egret) maximum scotopic b-wave amplitudes than the two herons. In the case of the Tricolored Egret, this could be due in part to its relatively high AL:ED ratio (0.87), the second highest among the species studied, about the same as that of the above-mentioned plover and stilt (see table 2).

The Roseate Spoonbill and the American White Ibis are the two tactilely foraging species, the former predominantly at dawn and dusk, and more at night than during daytime, and the latter strictly diurnal. Our morphological data show that the spoonbill has a rod density and a rods:cones ratio lower than the Yellow-crowned Night Heron, consistent with the second initial prediction, but comparable to the Great Blue Heron. Based on rod densities and rods:cones ratios, the ibis compares to the two egret species. However, its retinal sensitivity (0.89 ± 0.46) is lower than those of the heron and egret species, but comparable to that of the Short-billed Dowitcher (*Limnodromus griseus*) (0.76 ± 0.48), which forages tactilely, both by night and by day [see Rojas et al., 1998]. In addition, its scotopic b-wave responses tend to be lower than those recorded for the heron and egret species at intermediate luminance intensities, and are considerably lower than those of the mainly nocturnal Black skimmer, the differences between the two species reaching significance at flash luminance comprised between –3.0 and –1.0 log-units [Rojas et al., 1997].

Based on maximum scotopic b-wave amplitudes, all the species studied, including the Cattle Egret, appear to have roughly comparable night vision capability. As a consequence, the fact that the two egrets do not forage at night does not appear to result from poor night vision capability. It would seem from our study that the factor which best discriminates between the crepuscular and nocturnal foraging species and the strictly diurnal ones resides in the daytime visual capabilities. Indeed, contrary to the third initial prediction, the strictly diurnal tactile ibis and visual egrets have similar cone densities, cones:rods ratios, and photopic a-wave amplitudes. However, the ibis and the egrets, compared to the nocturnally active heron species, have significantly higher cone densities, and also the highest cones:rods ratios. In addition, for all stimulus luminance intensities tested, the Cattle and Tricolored egrets have photopic b-waves and a-waves which are or tend to be higher than those recorded for the nocturnally active herons.

The scotopic b-waves of both herons are characterized by an initial rapid growth in the amplitude followed by a saturation phase, which could be due to saturation of the scotopic response resulting from rod desensitization. However, in the Yellow-crowned Night Heron, the peak time of the scotopic b-wave is longer than in the ibis. Such a slow time to peak appears to be a characteristic of bird species with a rod-dominated retina such as, for example, the nocturnal Black Skimmer, the Wilson's Plover and the Black-winged Stilt, in which the scotopic b-wave takes longer to peak than in species having a cone-dominated retina [Rojas et al., 1997, 1998]. Rods are more sensitive to light than are cones, but their responses are somewhat slower and longer lasting [Fain and Dowling, 1973; Dowling, 1987].

In the Cattle Egret, the cones:rods ratio, and the thickness of the outer nuclear, inner nuclear, and inner plexiform layers, as well as cone and ganglion cell densities are greater in the central sector 5. The same was observed in the shorebird species, but particularly in the Wilson's Plover and the Willets which forage visually on fast-moving fiddler crabs (*Uca* sp.) [Rojas et al., 1998]. However, in the Tricolored Egret, the values of these parameters are higher in the temporal sector 3. Such thickened areas with higher cone and ganglion cell densities were not found in the ibis, the spoonbill, or the two heron species, but were markedly developed only in the two egrets. Both egret species are considered as active feeders (see Introduction). Such areas correspond to the so-called areas of acute vision or fovea in higher vertebrates and it has been reported that increased ganglion cell density is usually found in the retinal regions subserving higher visual acuity [see Binggeli and Paule, 1969; Ikushima et al., 1986; Hayes and Brooke, 1990; Inzunza et al., 1991; Suburo et al., 1991], and could provide for a greater capacity to discriminate details. Ganglion cells are movement-, direction- and contrast-sensitive, and receive most of their input from bipolar and amacrine cells of the inner nuclear layer; complex processing such as movement and direction selectivity occurs in the inner plexiform layer [see Dowling, 1987]. All these features of the thickened retina in the central sector 5 could provide the Cattle Egret with a greater capacity for monocular perception of contrasts and prey movement on either side of its body [see Smythe, 1975]. This species feeds on insects, locusts, grasshoppers, frogs, tadpoles, fish, lizards, etc., mostly in open grassy areas, meadows and pastures, following cattle and other large mammals, but also in freshwater swamps and rice fields [Siegfried, 1971; Voisin, 1991]. On the other hand, the same features in the temporal sector 3 could provide the Tricolored Egret with a good binocular visual acuity [see Smythe, 1975], for striking at its target fish prey while foraging in shallow water [Meyerriecks, 1962; Martínez-Vilalta and Motis, 1992].

In conclusion, under the tested conditions, all species are characterized by distinct ERG responses, both under scotopic and photopic conditions, and these physiological responses are, in most cases, in accordance with photoreceptor ratios and densities and other morphological features of the retina. Together, these data can be correlated with the nighttime and daytime activities and foraging strategies of the herons, egrets, ibis and spoonbill species studied. The only species which does not concord with this is the Cattle Egret. Indeed, its scotopic response does not correspond to what is expected. Maybe there is a phylogenetic bias (this is a topic in itself that will be considered in another paper) or field-ornithologists may have to come back to the field and see more closely what Cattle Egrets really do at night. We are aware of the fact that vision is a multifactered sense. Some species, e.g. the Wilson's Plover [see Rojas et al., 1998] and the Black-crowned Night Heron, might advantageously trade-off photopic vision and visual acuity for greater scotopic or nocturnal sensitivity.

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Chapitre 5

Comparative study of the retinal structure and function in two groups of aquatic birds: the Ciconiiformes and the Charadriiformes.

Par

Luz Marina Rojas, Raymond McNeil, Thérèse Cabana et Pierre Lachapelle

[Article en préparation]

INTRODUCTION

The idea of a relationship between behavior and the visual system is not recent. In spite of the vast literature on bird vision, few studies compare different species pertaining to the same phylogenetic group. For example, within wading birds, as used in accordance with the North American tradition to apply to the Ciconiiformes (herons, egrets, ibises, spoonbills, etc.), two different foraging strategies can be used: visual searching or tactile probing. The same can be said about the shorebirds (plovers, sandpipers, stilts, etc.). Moreover, within each group, some species use both techniques. According to the feeding periods, they can be classified as diurnal, crepuscular and nocturnal, although most species, particularly among shorebirds, have both daytime and nighttime feeding activities.

In previous studies (Rojas *et al.*, 1997, *in press*, *submitted*), we analyzed the retinal structure and function of 6 wading bird species, 5 shorebird species, as well as Black Skimmer (*Rynchops niger*), selected according to behavioral characters given in Table 1. The objective was to determine if there is a correlation between retinal structure and function, and if the latter two can be directly correlated with the feeding strategies and feeding periods. The results on retinal morphology were obtained by counting and measuring different retinal components on semithin sections, and those on visual function from electroretinograms (ERG) in different light conditions.

Our results showed that, with its high rod density, high rods:cones ratio, and low cone function, the retina of the tactile, mainly nocturnal Black Skimmer is structurally and functionally well adapted for nocturnal vision, but poorly functional for daytime vision (Rojas *et al.*, 1997). In contrast, the wading birds showed different degrees of adaptation to nocturnal vision. Based on photoreceptors density and rods:cones ratio, nocturnal vision is better in the Yellow-crowned Night Heron (*Nycticorax violaceus*; strictly visual and mainly nocturnal), followed by the Great Blue Heron (*Ardea herodias*; strictly visual, but diurnal, crepuscular and nocturnal) and the Roseate Spoonbill (*Ajaia ajaja*; strictly tactile, but mainly crepuscular and nocturnal), the Cattle (*Bubulcus ibis*) and Tricolored (*Egretta tricolor*) egrets (both strictly visual and diurnal) (Rojas *et al.*, *submitted*), the American White Ibis (*Eudocimus ruber*; strictly tactile and diurnal) being the least adapted for

Table 1. Behavioral characteristics of the selected species.

Species	n^a	Foraging activity	Foraging strategy	References
Ciconiiformes: Ardeidae				
Yellow-crowned Night Heron (*Nycticorax violaceus*)	7	Crepuscular and nocturnal	Visual passive forager	1-6
Cattle Egret (*Bubulcus ibis*)	4	Strictly diurnal	Visual active forager	1-6
Great Blue Heron (*Ardea herodias*)	8	Mainly crepuscular, but also diurnal and nocturnal	Visual passive forager	2,7,8
Tricolored Egret (*Egretta tricolor*)	4	Strictly diurnal	Visual active forager	1-6
Ciconiiformes: Threskiornithidae				
American White Ibis (Scarlet) (*Eudocimus ruber*)	12	Strictly diurnal	Tactile probing	9-11
Roseate Spoonbill (*Ajaia ajaja*)	0	Mainly crepuscular and more nocturnal than diurnal	Tactile sweeping	2,12
Charadriiformes: Scolopacidae				
Willet (*Catoptrophorus semipalmatus*)	4	Diurnal and nocturnal	Territorial individuals: visual pecking on moonlit nights, and tactile probing on moonless night	13-17
American Woodcock (*Scolopax minor*)	3	Winter: largely nocturnal; summer: almost exclusively diurnal	Almost exclusively tactile probing, except occasional pecks during the summer	18-24

Table 1. Continued.

Species	n[a]	Foraging activity	Foraging strategy	References
Short-billed Dowitcher (*Limnodromus griseus*)	4	Diurnal and nocturnal	Tactile probing	25-27
Charadriiformes: Charadriidae				
Wilson's Plover (*Charadrius wilsonia*)	5	Breeding season: diurnal and nocturnal; non- breeding season: mainly nocturnal	Visual pecking	25-30
Charadriiformes: Recurvirostridae				
Black-winged Stilt (*Himantopus himantopus*)	4	Diurnal and nocturnal	Generally visual pecking except scythe-like sweeping when water surface is agitated	25-27
Charadriiformes: Rynchopidae				
Black Skimmer (*Rynchops niger*)	9	Mainly nocturnal	tactile forager but needs vision for flying while skimming the water surface	31-33

n[a] = number of birds used for ERG recording

Reférences:

[1]Kushlan, 1978; [2]McNeil et al. 1993b; [3]Meyerriecks 1962; [4]Kushlan 1976; [5]Willard 1977; [6]Rodgers 1983; [7]Horvath et Moholt 1986; [8]McNeil et al. 1993a; [9]Hancock et al. 1992; [10]Matheu et del Hoyo 1992; [11]McNeil et al. 1998; [12]Robert et al. 1989; [13]Llinas G. et Galindo J. 1990; [14]McNeil et Rodríguez S. 1990; [15]Rompré & McNeil 1994; [16]McNeil et Rompré 1995; [17]Rompré et McNeil 1996; [18]Sheldon 1967; [19]Owen et Morgan 1975; [20]Owen 1977; [21]Stribling et Doerr 1985; [22]Sepik et al. 1989; [23]Roberts 1993; [24]Krementz et al. 1995; [25]McNeil et Robert 1988; [26]Robert et McNeil 1989; [27]McNeil et al. 1992; [28]Morrier et McNeil 1991; [29]Thibault et McNeil 1994; [30]Thibault et McNeil 1995; [31]Tomkins 1951; [32]Zusi 1962; [33]Zusi 1985.

nocturnal vision (Rojas *et al.*, 1977, *submitted*). Among the wading bird species studied, visual nocturnal feeders have a night vision capability better than tactile diurnal foragers, and also than tactile nocturnal feeders. However, based on maximum scotopic b-wave amplitude of the ERG, all wading bird species studied, including the egrets, have roughly comparable night vision capability. In the shorebirds, albeit having a low rod density compared to the Black-winged Stilt (*Himantopus himantopus*; mainly visual both by day and night, but tactile when the water surface where individuals feed is muddy or agitated) and the Wilson's Plover (*Charadrius wilsonia*; strictly visual and mainly nocturnal), the Willet (*Catoptrophorus semipalmatus*; territorial individuals forage by sight by day and moonlit nights, but are tactile foragers on moonless nights) and the American Woodcock (*Scolopax minor*; tactile, mainly nocturnal) have a scotopic retinal sensitivity similar to that of the stilt and the plover, but rank midway between the plover and the Short-billed Dowitcher (*Limnodromus griseus*; strictly tactile by day and by night) for the b-wave amplitude (Rojas *et al., in press*).

The above results were analyzed by using a conventional statistical method, the 95% confidence interval, for within-group comparisons, i.e., comparing herons with egrets, ibises and spoonbills among the wading birds, on the one hand (Rojas et al., *in press*), and comparing plovers, Willets, dowitchers, stilts and woodcocks, within the shorebirds, on the other hand (Rojas et al., *submitted*). We also compared the skimmer with the ibis (Rojas *et al.,* 1997). In the present study, we compare all 12 species, both within and between groups, using the same method, but also using an additional statistical analysis. Indeed, according to Felsenstein (1985) and Garland et al. (1993), different species cannot be considered as independent points within a distribution if they are descended from common ancestors. For instance, two bird species could have a similar rod density mainly because they are closely related. These hierarchical relationships may lead to an overestimation of the degrees of freedom used in conventional statistical tests and hence to untrustworthy significance levels (Garland et al., 1993 and references therein). In the present study, we thus re-analyze the results on the retinal structure and function of the 12 above-mentioned species using the method of Garland *et al.* (1993) which allows us to correct our data and eliminate bias due to phylogeny.

METHODS

In addition to 95% confidence intervals on the means (see above), we performed conventional ANOVAs to test for among-species differences for each variable studied. These analyses were conducted using STATGRAPHICS Plus for Window 2.1 (Statistical Graphics Corp.). Thereafter, to correct our data for phylogenetic autocorrelation, we modified the method proposed by Garland et al. (1993) to obtain null distributions of F statistics for hypothesis testing that takes the non-independence of the species into account. The modification was necessary because in their original procedure, Garland *et al.* (1993) compared groups of different species to look for differences between groups whereas in our studies we wanted to look for differences between individual species. Therefore, our modification compares groups of individuals of the same species, where individuals are depicted as unresolved polytomies taking root at the node representing the species, based on the phylogenetic hypothesis of Sibley and Ahlquist (1990). Figure 1 presents the phylogenetic tree for the 12 species analyzed here.

With the PDSIMUL software included in the PDAP package (Garland et al., 1993), 1000 empirically scaled computer simulations of evolution along the tree were performed for each of the variables. That is, the evolution of a variable, such as rod or cone relative density, or b-wave amplitude, was started anew and could lead to different results at the tips of the tree in each of the 1000 simulations. As the branch lengths were not comparable because the information came from two sources using different methods, we set all branches (including those representing individuals) equal to 1, and the model of evolutionary change chosen is known as speciational Brownian motion (Garland et al., 1993). In this model, all successive changes are associated with speciation events, are uncorrelated to each other and to the character's starting value, and are equally likely to be negative or positive (Garland et al., 1993). For each variable, we set the starting value equal to its mean for the overall sample (consisting of all species), and the means and variances of the simulated data sets equal to those of the real one. We used the highest and lowest values found in the overall sample as limits to the range of possible states for each variable, and the bounded simulations were performed with the "Hard Bounce" algorithm. That is, if the next move of a trait located, say, 5 units from the lower limit was 12 units towards that limit, it stepped 5 units towards the limit, bounced, and stepped to remaining 7 units away from it, ending up 2

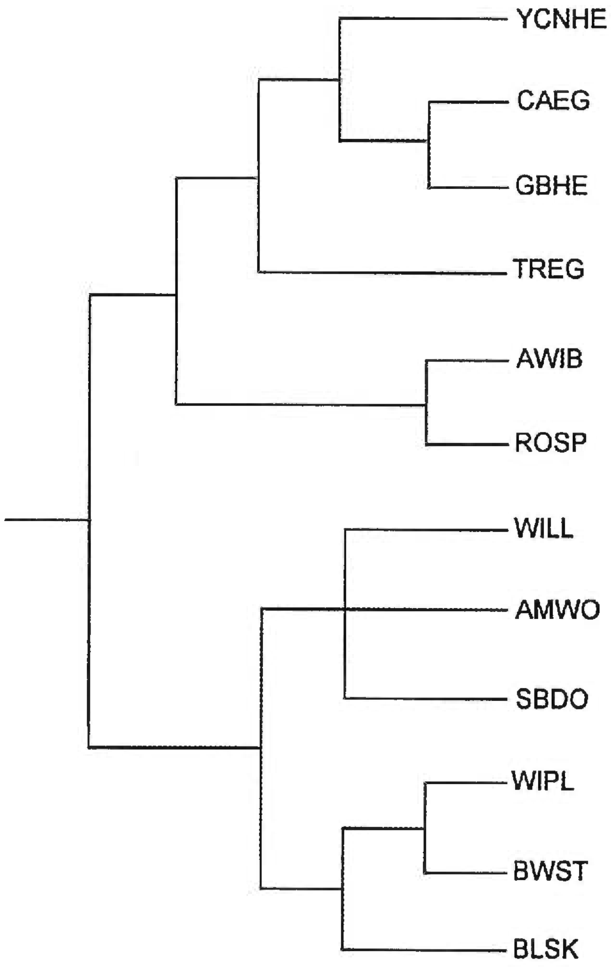

Figure 1. Phylogenetic hypothesis used in this study. Based on Sibley and Ahlquist (1990). AMWO = American Woodcock AWIB = American White Ibis (Scarlet), BLSK = Black Skimmer, BWST = Black-winged Stilt, CAEG = Cattle Egret, GBHE = Great Blue Heron, ROSP = Roseate Spoonbill, SBDO = Short-billed Dowitcher, TREG = Tricolored Egret, WILL = Willet, WIPL = Wilson's Plover, and YCNHE = Yellow-crowned Night Heron.

units further away from the boundary than when it started. Also, since the simulations were performed for two variables at the same time, we fixed the correlation between the two variables in the simulated data sets as equal to that in the real data set. Finally, we used the software PDANOVA, also included in the PDAP package , to compute the *F* ratios of the 1000 simulated data sets for each variable, as in conventional ANOVA tests. We then used STATISTIC version 4.1 (Analytical Software Co.) to read in the ASCII files of *F* ratios output by PDANOVA and calculate the 95 percentile of these distributions. If, for a given variable, the *F* ratio for the real data set exceeded the upper 95 percentile of the null distribution, we could conclude that there was a significant difference in the mean value of this variable among species. In such a case, we then performed pairwise ANOVA tests to find which pairs of species were responsible for the difference, using the same procedure as that described above. However, since individuals would behave as "species" during the simulations, the within-species variation was likely to be greater in the simulated data sets than in the real data set, hence leading to smaller *F* ratios. Therefore, the statistical tests were considered quite liberal.

RESULTS

PHOTORECEPTOR RATIO AND DENSITY

Overall, the 95% confidence intervals for the means and the conventional and corrected ANOVAs present similar results; they show that photoreceptor density varies from a species to another among the 12 species analyzed (Fig. 2, Tables 2 and 3). However, in general, the significance level of the observed differences tend to be lower with the corrected ANOVAs compared to the conventional ones (see Tables 2 and 3).

In the wading birds, the Yellow-crowned Night Heron is the only species where the rods outnumber the cones, with a resulting overall rods:cones ratio of 2.3:1.0. In contrast, the Great Blue Heron, and particularly the Cattle Egret, the Tricolored Egret and the American White Ibis, have a cone-dominated retina, with overall rods:cones ratios ranging from 0.6:1.0 to 0.3:1.0. The spoonbill has a mixed retina (0.9:1.0) with similar densities of rods and cones. Rod density is significantly higher in the Yellow-crowned Night Heron than in the five other wading bird species; it is also higher or tends to be so in the Great Blue Heron and the spoonbill, compared to the ibis and the Tricolored and Cattle egrets. Cone density is higher in the Cattle egret, followed by the Tricolored egret, and then by the ibis; it is lower in the Yellow-crowned Night Heron.

In the shorebirds, rods outnumber cones in the Wilson's Plover, the American Woodcock and the Black-winged Stilt, with overall rods:cones ratios of 1.3:1.0, 1.2:1.0, and 1.1:1.0, respectively. The Willet, on the other hand, has a clearly cone-dominated retina, with an overall rods:cones ratio of 0.7:1.0, whereas the dowitcher has a mixed retina with similar densities of rods and cones (1.0:1.0). Based on both ANOVA types, the Willet has proportionately less rods than the plover and the stilt, but its cones outnumber those of the woodcock.

Overall, in the shorebirds, rod density exceeds rod densities of all wading birds, except the Yellow-crowned Night Heron. In general, except for the Yellow-crowned Night Heron, the cone dominance is stronger in the wading birds than in the shorebirds (Fig. 2). Based on both ANOVA types, the two egret species have or tend to have higher cone density than the American Woodcock and the Short-billed Dowitcher.

Based on the 95% confidence intervals and conventional ANOVAs, the Black Skimmer, with a rods:cones ratio of 5.4:1.0, has the highest rod density and, conversely, the lowest cone density of all species (see Fig. 2). Based on the corrected ANOVAs, the same general tendency is maintained for cones, but not necessarily for rods (Tables 2 and 3). The significance of the differences observed when comparing the rod density of the skimmer with rod densities of the shorebird species, except the Willet, is not maintained (Table 2).

RETINAL PHYSIOLOGY

Overall, the 95% confidence intervals for the means and the conventional ANOVAs present similar results; they show that scotopic and photopic b-wave amplitudes vary from a species to another among all 12 species analyzed (Figs. 3 and 4, Tables 4 and 5).

As shown with the 95% confidence intervals and conventional ANOVAs, the maximal scotopic b-wave amplitudes measured in the Cattle Egret and the Black-winged Stilt are generally significantly higher than in all other species studied, except the Wilson's Plover and the Black Skimmer (Fig. 3, Table 4). The response of the Short-billed Dowitcher is or tends to be the lowest in many cases when compared to that of other species.

For photopic responses, based on 95% confidence intervals and conventional ANOVAs, the maximal b-wave amplitudes measured in the strictly diurnally foraging species (the Cattle

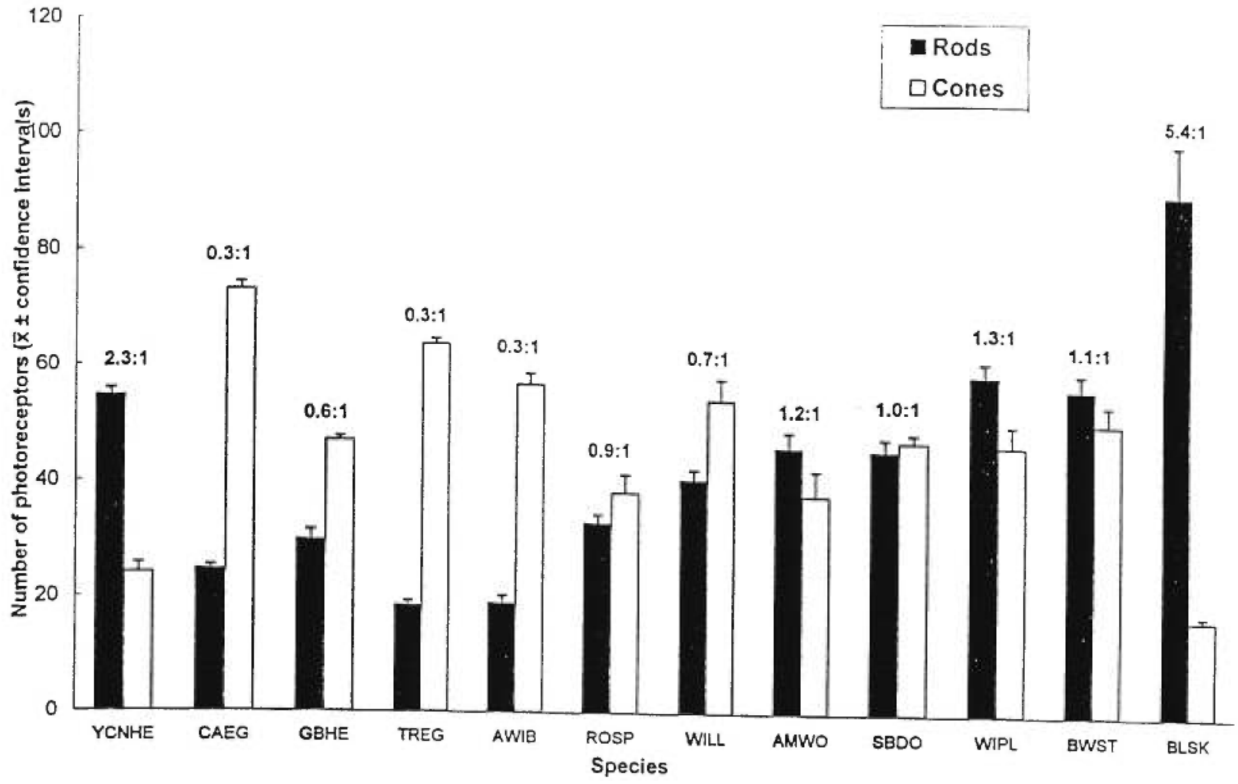

Figure 2. Mean rod and cone numbers (x/310 µm ± 95% confidence intervals) and rods:cones ratios of the species. The figures above the columns indicate the rods:cones ratio. Adapted from Rojas et al. (1997, *in press, submitted*). For species abbreviations, see Figure 1. Number of bird for each species : YCNH= 4; CAEG= 4; GBHE= 4; TREG= 4; AWIB= 4; ROSP= 3; WILL= 4; AMWO= 4; SBDO; 4; WIPL= 5; BWST= 4; BLSK= 4.

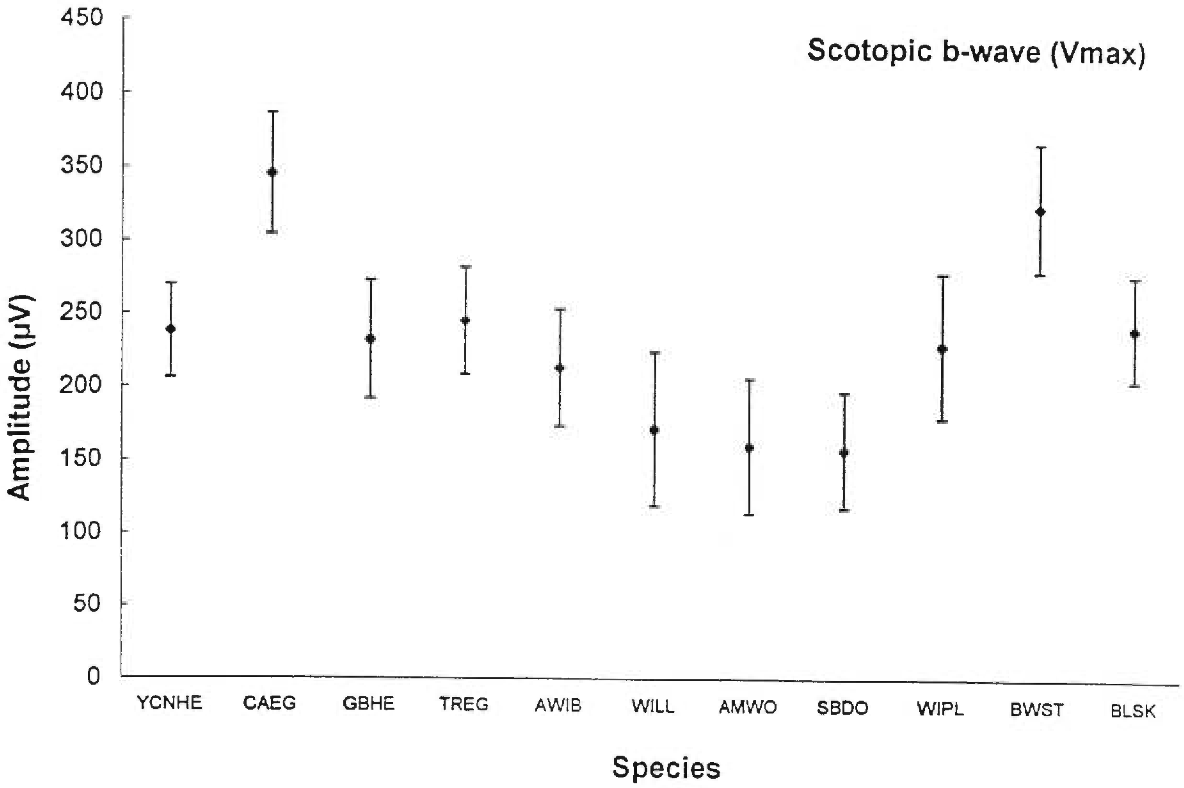

Figure 3. Maximal scotopic b-wave amplitude (V_{max}) of the species studied. For species abbreviations, see Figure 1. Number of birds as in table 1.

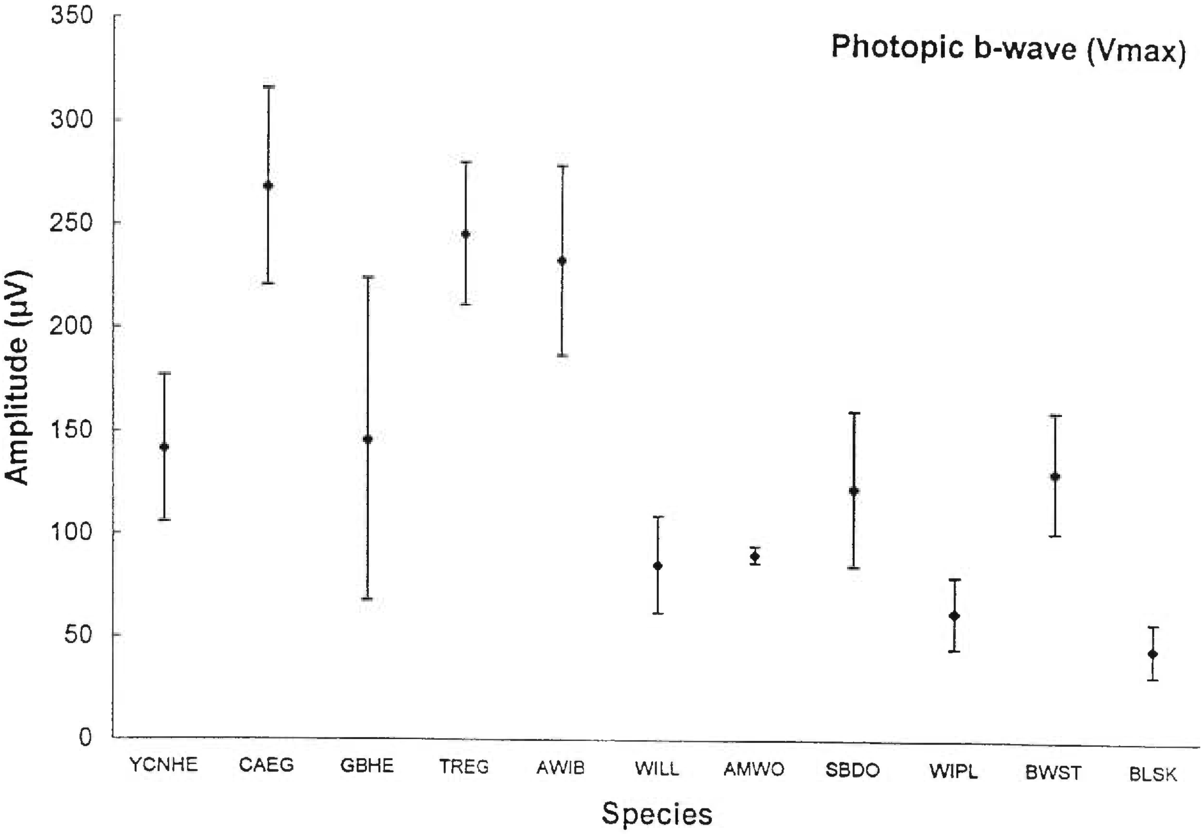

Figure 4. Maximal photopic b-wave amplitude (V_{max}) of the species studied. For species abbreviations, see Figure 1. Number of birds as in table 1.

Table 2. Results of the comparison of mean rod density based on conventional ANOVAs and ANOVAs corrected for taking into account the phylogenetic lineage. For species abbreviations, see Fig. 1 and for species number, see Fig. 2.

		Conventional ANOVA		Corrected ANOVA	
Species	Means (95% Confid. Interv.)	F	P^1	Critical F	P^1
YCNHE	54.6 (53.3 - 55.8)				
- CAEG	24.5 (23.8 - 25.3)	1613.87	0.000***	39.21	0.000***
- GBHE	29.6 (27.8 - 31.4)	482.34	0.000***	42.87	0.000***
- TREG	18.3 (17.4 - 19.2)	2066.45	0.000***	40.35	0.000***
- AWIB	18.8 (17.5 - 20.2)	1437.73	0.000***	58.05	0.000***
- ROSP	32.7 (31.0 - 34.3)	449.78	0.000***	61.89	0.000***
- WILL	40.2 (38.4 - 42.0)	150.89	0.000***	82.96	0.022*
- AMWO	45.8 (43.0 - 48.6)	18.06	0.008**	87.10	0.269ns
- SBDO	45.4 (46.2 - 47.6)	118.66	0.000***	82.67	0.021*
- WIPL	58.4 (55.9 - 60.9)	7.99	0.026ns	86.86	0.480ns
- BWST	56.1 (53.3 - 58.9)	1.06	0.343ns	96.26	0.785ns
- BLSK	90.2 (81.4 - 98.9)	28.26	0.002**	75.98	0.175ns
CAEG	24.5 (23.8 - 25.3)				
- GBHE	29.6 (27.8 - 31.4)	25.23	0.002**	31.12	0.064ns
- TREG	18.3 (17.4 - 19.2)	107.38	0.000***	47.75	0.010**
- AWIB	18.8 (17.5 - 20.2)	53.14	0.000***	63.90	0.071ns
- ROSP	32.7 (31.0 - 34.3)	96.91	0.000***	62.98	0.021*
- WILL	40.2 (38.4 - 42.0)	218.32	0.000***	104.62	0.013*
- AMWO	45.8 (43.0 - 48.6)	115.83	0.000***	93.30	0.039*
- SBDO	45.4 (46.2 - 47.6)	1007.47	0.000***	97.55	0.000***
- WIPL	58.4 (55.9 - 60.9)	717.45	0.000***	113.54	0.001***
- BWST	56.1 (53.3 - 58.9)	560.53	0.000***	78.23	0.000***
- BLSK	90.2 (81.4 - 98.9)	96.76	0.000***	91.80	0.044*
GBHE	29.6 (27.8 - 31.4)				
- TREG	18.3 (17.4 - 19.2)	116.30	0.000***	51.02	0.008**
- AWIB	18.8 (17.5 - 20.2)	86.13	0.000***	69.96	0.035*
- ROSP	32.7 (31.0 - 34.3)	5.47	0.066ns	71.22	0.493ns
- WILL	40.2 (38.4 - 42.0)	59.85	0.000***	101.83	0.097ns
- AMWO	45.8 (43.0 - 48.6)	53.16	0.001***	113.72	0.125ns
- SBDO	45.4 (46.2 - 47.6)	214.15	0.000***	103.16	0.018*
- WIPL	58.4 (55.9 - 60.9)	382.95	0.001***	102.56	0.004**
- BWST	56.1 (53.3 - 58.9)	279.18	0.000***	104.83	0.010**
- BLSK	90.2 (81.4 - 98.9)	81.06	0.000***	78.23	0.048*
TREG	18.3 (17.4 - 19.2)				
- AWIB	18.8 (17.5 - 20.2)	0.38	0.562ns	39.11	0.797 ns
- ROSP	32.7 (31.0 - 34.3)	260.65	0.000***	44.02	0.003**
- WILL	40.2 (38.4 - 42.0)	399.60	0.000***	66.89	0.003*
- AMWO	45.8 (43.0 - 48.6)	188.27	0.000***	67.37	0.011*
- SBDO	45.4 (46.2 - 47.6)	1440.53	0.000***	63.82	0.000***
- WIPL	58.4 (55.9 - 60.9)	969.02	0.000***	96.55	0.000***
- BWST	56.1 (53.3 - 58.9)	769.91	0.000***	85.01	0.001***
- BLSK	90.2 (81.4 - 98.9)	115.75	0.000***	68.76	0.022*

Table 2. Continued.

		Conventional ANOVA		Corrected ANOVA	
Species	Means (95% Confid. Interv.)	F	P[1]	Critical F	P[1]
AWIB	18.8 (17.5 - 20.2)				
- ROSP	32.7 (31.0 - 34.3)	167.37	0.000***	33.36	0.002**
- WILL	40.2 (38.4 - 42.0)	314.28	0.000***	83.93	0.003**
- AMWO	45.8 (43.0 - 48.6)	116.64	0.000***	81.36	0.018*
- SBDO	45.4 (46.2 - 47.6)	926.92	0.000***	89.85	0.000***
- WIPL	58.4 (55.9 - 60.9)	845.08	0.000***	82.80	0.000***
- BWST	56.1 (53.3 - 58.9)	659.19	0.000***	87.70	0.001***
- BLSK	90.2 (81.4 - 98.9)	113.47	0.000***	72.28	0.018**
ROSP	32.7 (31.0 - 34.3)				
- WILL	40.2 (38.4 - 42.0)	30.16	0.003**	75.02	0.151ns
- AMWO	45.8 (43.0 - 48.6)	28.82	0.006**	92.69	0.166ns
- SBDO	45.4 (46.2 - 47.6)	182.47	0.000***	86.88	0.009**
- WIPL	58.4 (55.9 - 60.9)	272.84	0.000***	70.89	0.007**
- BWST	56.1 (53.3 - 58.9)	197.84	0.000***	79.82	0.016*
- BLSK	90.2 (81.4 - 98.9)	52.82	0.001**	57.45	0.063ns
WILL	40.2 (38.4 - 42.0)				
- AMWO	45.8 (43.0 - 48.6)	6.36	0.054ns	32.96	0.275ns
- SBDO	45.4 (46.2 - 47.6)	22.26	0.003**	29.98	0.085ns
- WIPL	58.4 (55.9 - 60.9)	149.35	0.000***	60.63	0.0088**
- BWST	56.1 (53.3 - 58.9)	97.75	0.000***	65.26	0.031*
- BLSK	90.2 (81.4 - 98.9)	55.25	0.000***	46.40	0.038*
AMWO	45.8 (43.0 - 48.6)				
- SBDO	45.4 (46.2 - 47.6)	0.03	0.860ns	30.10	0.939 ns
- WIPL	58.4 (55.9 - 60.9)	32.56	0.001**	59.76	0.105 ns
- BWST	56.1 (53.3 - 58.9)	17.63	0.000***	71.04	0.679 ns
- BLSK	90.2 (81.4 - 98.9)	29.92	0.003**	44.70	0.087 ns
SBDO	45.4 (46.2 - 47.6)				
- WIPL	58.4 (55.9 - 60.9)	98.33	0.000***	57.65	0.020 *
- BWST	56.1 (53.3 - 58.9)	58.98	0.000***	62.72	0.053 ns
- BLSK	90.2 (81.4 - 98.9)	44.84	0.001***	48.47	0.056 ns
WIPL	58.4 (55.9 - 60.9)				
- BWST	56.1 (53.3 - 58.9)	1.98	0.203ns	30.30	0.524 ns
- BLSK	90.2 (81.4 - 98.9)	28.26	0.001**	39.67	0.760 ns
BWST	56.1 (53.3 - 58.9)				
- BLSK	90.2 (81.4 - 98.9)	25.28	0.002**	42.91	0.100 ns

[1] *, $P < 0.05$; **, $P > 0.01$; ***, $P < 0.001$.

Table 3. Results of the comparison of mean cone density based on conventional ANOVAs and ANOVAs corrected for taking into account the phylogenetic lineage. For species abbreviations, see Fig. 1 and for species number, see Fig. 2.

			Conventional ANOVA		Corrected ANOVA	
Species		Means (95% Confid. Interv.)	F	P^1	Critical F	P^1
YCNHE		24.1 (22.4 - 25.8)				
	- CAEG	73.0 (71.6 - 74.3)	1994.00	0.000***	36.89	0.000 ***
	- GBHE	46.9 (46.3 - 47.5)	616.21	0.000***	38.35	0.011 *
	- TREG	63.5 (62.5 - 64.5)	1548.99	0.000***	39.94	0.000 ***
	- AWIB	56.6 (54.7 - 58.6)	617.89	0.000***	70.72	0.000 ***
	- ROSP	38.0 (34.9 - 41.2)	69.66	0.000***	69.54	0.049 *
	- WILL	54.0 (57.7 - 50.3)	342.59	0.000***	92.83	0.004 **
	- AMWO	37.6 (33.3 - 41.9)	115.99	0.000***	94.24	0.033 *
	- SBDO	47.0 (45.6 - 48.4)	663.72	0.000***	91.04	0.001 ***
	- WIPL	46.3 (42.6 - 50.0)	56.11	0.000***	90.88	0.113 ns
	- BWST	50.3 (47.0 - 53.6)	244.09	0.000***	99.24	0.015 *
	- BLSK	16.8 (16.0 - 17.6)	43.48	0.000***	90.81	0.132 ns
CAEG		73.0 (71.6 - 74.3)				
	- GBHE	46.9 (46.3 - 47.5)	1252.59	0.000***	29.68	0.000 ***
	- TREG	63.5 (62.5 - 64.5)	128.54	0.000***	47.42	0.004 **
	- AWIB	56.6 (54.7 - 58.6)	188.31	0.000***	69.33	0.007 **
	- ROSP	38.0 (34.9 - 41.2)	511.15	0.000***	84.44	0.002 **
	- WILL	54.0 (57.7 - 50.3)	156.78	0.000***	106.43	0.022 *
	- AMWO	37.6 (33.3 - 41.9)	1678.06	0.000***	115.09	0.002 **
	- SBDO	47.0 (45.6 - 48.4)	1377.04	0.000***	100.56	0.000 ***
	- WIPL	46.3 (42.6 - 50.0)	82.76	0.000***	111.46	0.072 ns
	- BWST	50.3 (47.0 - 53.6)	205.54	0.000***	109.44	0.018 **
	- BLSK	16.8 (16.0 - 17.6)	3481.94	0.000***	104.72	0.000 ***
GBHE		46.9 (46.3 - 47.5)				
	- TREG	63.5 (62.5 - 64.5)	794.00	0.000***	44.42	0.000 ***
	- AWIB	56.6 (54.7 - 58.6)	89.38	0.000***	74.01	0.042 *
	- ROSP	38.0 (34.9 - 41.2)	41.45	0.001**	72.62	0.126 ns
	- WILL	54.0 (57.7 - 50.3)	25.48	0.002**	113.41	0.251 ns
	- AMWO	37.6 (33.3 - 41.9)	343.77	0.000****	114.96	0.010 **
	- SBDO	47.0 (45.6 - 48.4)	0.09	0.778ns	111.94	0.928 ns
	- WIPL	46.3 (42.6 - 50.0)	0.04	0.841ns	117.27	0.969 ns
	- BWST	50.3 (47.0 - 53.6)	5.22	0.062ns	136.57	0.603 ns
	- BLSK	16.8 (16.0 - 17.6)	1637.00	0.000***	97.33	0.000 ***
TREG		63.5 (62.5 - 64.5)				
	- AWIB	56.6 (54.7 - 58.6)	38.42	0.001***	52.96	0.082 ns
	- ROSP	38.0 (34.9 - 41.2)	306.57	0.000***	53.21	0.001 **
	- WILL	54.0 (57.7 - 50.3)	43.04	0.001***	783.12	0.104 ns
	- AMWO	37.6 (33.3 - 41.9)	1422.12	0.000***	80.98	0.011 *
	- SBDO	47.0 (45.6 - 48.4)	925.53	0.000***	79.29	0.000 ***
	- WIPL	46.3 (42.6 - 50.0)	35.00	0.001***	88.08	0.162 ns
	- BWST	50.3 (47.0 - 53.6)	75.68	0.000***	84.88	0.066 ns
	- BLSK	16.8 (16.0 - 17.6)	3069.47	0.000***	69.62	0.000 ***

Table 3. Continued.

			Conventional ANOVA		Corrected ANOVA	
Species		Means (95% Confid. Interv.)	F	P[1]	Critical F	P[1]
AWIB		56.6 (54.7 - 58.6)				
	- ROSP	38.0 (34.9 - 41.2)	111.12	0.000***	27.92	0.007 **
	- WILL	54.0 (57.7 - 50.3)	2.56	0.161ns	80.83	0.648 ns
	- AMWO	37.6 (33.3 - 41.9)	246.67	0.000***	86.99	0.010 **
	- SBDO	47.0 (45.6 - 48.4)	791.99	0.000***	81.46	0.000 ***
	- WIPL	46.3 (42.6 - 50.0)	11.90	0.011*	98.15	0.940 ns
	- BWST	50.3 (47.0 - 53.6)	13.48	0.010*	86.97	0.374 ns
	- BLSK	16.8 (16.0 - 17.6)	3069.47	0.000***	70.77	0.000 ***
ROSP		38.0 (34.9 - 41.2)				
	- WILL	54.0 (57.7 - 50.3)	58.05	0.001***	81.05	0.082 ns
	- AMWO	37.6 (33.3 - 41.9)	0.08	0.790ns	81.67	0.940 ns
	- SBDO	47.0 (45.6 - 48.4)	44.22	0.001**	76.57	0.108 ns
	- WIPL	46.3 (42.6 - 50.0)	6.47	0.032*	91.92	0.514 ns
	- BWST	50.3 (47.0 - 53.6)	32.10	0.002**	91.47	0.191 ns
	- BLSK	16.8 (16.0 - 17.6)	188.14	0.000***	61.33	0.012 *
WILL		54.0 (57.7 - 50.3)				
	- AMWO	37.6 (33.3 - 41.9)	98.55	0.000***	27.15	0.005 **
	- SBDO	47.0 (45.6 - 48.4)	25.39	0.002**	31.91	0.070 ns
	- WIPL	46.3 (42.6 - 50.0)	6.06	0.043*	68.09	0.498 ns
	- BWST	50.3 (47.0 - 53.6)	3.49	0.111ns	78.11	0.593 ns
	- BLSK	16.8 (16.0 - 17.6)	596.09	0.000***	56.40	0.001 ***
AMWO		37.6 (33.3 - 41.9)				
	- SBDO	47.0 (45.6 - 48.4)	498.53	0.000***	28.55	0.000 ***
	- WIPL	46.3 (42.6 - 50.0)	6.62	0.042*	68.09	0.441 ns
	- BWST	50.3 (47.0 - 53.6)	53.47	0.001***	68.87	0.075 ns
	- BLSK	16.8 (16.0 - 17.6)	566.82	0.000***	54.47	0.000 ***
SBDO		47.0 (45.6 - 48.4)				
	- WIPL	46.3 (42.6 - 50.0)	0.06	0.813ns	65.82	0.930 ns
	- BWST	50.3 (47.0 - 53.6)	5.01	0.067ns	72.13	0.510 ns
	- BLSK	16.8 (16.0 - 17.6)	1823.91	0.000***	46.92	0.000 ***
WIPL		46.3 (42.6 - 50.0)				
	- BWST	50.3 (47.0 - 53.6)	4.91	0.062ns	30.49	0.369 ns
	- BLSK	16.8 (16.0 - 17.6)	101.27	0.000***	38.93	0.010 **
BWST		56.1 (53.3 - 58.9)				
	- BLSK	16.8 (16.0 - 17.6)	444.38	0.000***	42.43	0.000 ***

[1] *, $P < 0.05$; **, $P > 0.01$; ***, $P < 0.001$.

Table 4. Results of the comparison of mean maximal scotopic b-wave amplitude based on conventional ANOVAs and ANOVAs corrected for taking into account the phylogenetic lineage. For species abbreviations, see Fig. 1 and for species number, see Table 1.

		Conventional ANOVA		Corrected ANOVA	
Species	Means (95% Confid. Interv.)	F	P^1	Critical F	P^1
YCNHE	238.0 (206.1 - 269.9)				
- CAEG	345.1 (303.8 - 386.3)	12.68	0.004**	44.03	0.249ns
- GBHE	231.7 (191.3 - 272.1)	0.04	0.854ns	36.93	0.949ns
- TREG	244.6 (208.1 - 281.2)	0.07	0.797ns	57.06	0.949ns
- AWIB	212.9 (173.0 - 252.8)	0.89	0.357ns	88.64	0.836ns
- WILL	171.3 (119.1 - 223.5)	3.95	0.070ns	82.63	0.632ns
- AMWO	159.7 (113.5 - 205.8)	1.84	0.202ns	59.34	0.735ns
- SBDO	157.2 (117.8 - 196.5)	12.49	0.003**	113.76	0.513ns
- WIPL	228.0 (178.7 - 277.4)	1.99	0.179ns	143.68	0.802ns
- BWST	322.9 (278.9 - 366.9)	5.76	0.026*	214.40	0.734ns
- BLSK	240.4 (204.6 - 276.3)	0.01	0.924ns	179.86	0.979ns
CAEG	345.1 (303.8 - 386.3)				
- GBHE	231.7 (191.3 - 272.1)	14.00	0.013*	32.21	0.154ns
- TREG	244.6 (208.1 - 281.2)	11.58	0.008**	53.58	0.330ns
- AWIB	212.9 (173.0 - 252.8)	12.82	0.004**	70.58	0.391ns
- WILL	171.3 (119.1 - 223.5)	36.97	0.002**	117.56	0.176ns
- AMWO	159.7 (113.5 - 205.8)	25.51	0.007**	113.00	0.233ns
- SBDO	157.2 (117.8 - 196.5)	38.36	0.000***	105.99	0.212ns
- WIPL	228.0 (178.7 - 277.4)	2.42	0.158ns	119.28	0.755ns
- BWST	322.9 (278.9 - 366.9)	1.38	0.260ns	143.78	0.802ns
- BLSK	240.4 (204.6 - 276.3)	9.73	0.158ns	113.40	0.542ns
GBHE	231.7 (191.3 - 272.1)				
- TREG	244.6 (208.1 - 281.2)	0.16	0.697ns	50.98	0.892ns
- AWIB	212.9 (173.0 - 252.8)	0.21	0.660ns	57.63	0.910ns
- WILL	171.3 (119.1 - 223.5)	5.09	0.087ns	112.80	0.556ns
- AMWO	159.7 (113.5 - 205.8)	3.08	0.177ns	138.93	0.630ns
- SBDO	157.2 (117.8 - 196.5)	6.01	0.040*	87.44	0.537ns
- WIPL	228.0 (178.7 - 277.4)	1.20	0.310ns	107.59	0.778ns
- BWST	322.9 (278.9 - 366.9)	2.66	0.127ns	109.09	0.740ns
- BLSK	240.4 (204.6 - 276.3)	0.05	0.826ns	87.17	0.965ns
TREG	244.6 (208.1 - 281.2)				
- AWIB	232.6 (186.5 - 278.7)	1.11	0.309ns	56.74	0.766ns
- WILL	171.3 (119.1 - 223.5)	5.38	0.489 ns	66.65	0.545ns
- AMWO	159.7 (113.5 - 205.8)	1.36	0.317ns	53.12	0.728ns
- SBDO	157.2 (117.8 - 196.5)	12.61	0.004**	94.58	0.441ns
- WIPL	228.0 (178.7 - 277.4)	1.18	0.300ns	112.78	0.824ns
- BWST	322.9 (278.9 - 366.9)	3.49	0.079ns	142.64	0.747ns
- BLSK	240.4 (204.6 - 276.3)	0.02	0.884ns	118.87	0.975ns

Table 4. Continued

Species		Means (95% Confid. Interv.)	Conventional ANOVA		Corrected ANOVA	
			F	P[1]	Critical F	P[1]
AWIB		232.6 (186.5 - 278.7)				
	- WILL	171.3 (119.1 - 223.5)	0.96	0.348ns	60.56	0.793ns
	- AMWO	159.7 (113.5 - 205.8)	0.33	0.579ns	43.03	0.858ns
	- SBDO	157.2 (117.8 - 196.5)	4.79	0.045*	96.61	0.635ns
	- WIPL	228.0 (178.7 - 277.4)	3.65	0.077ns	108.03	0.695ns
	- BWST	322.9 (278.9 - 366.9)	8.90	0.007**	149.58	0.623ns
	- BLSK	240.4 (204.6 - 276.3)	0.92	0.349ns	116.74	0.8.60ns
WILL		171.3 (119.1 - 223.5)				
	- AMWO	159.7 (113.5 - 205.8)	0.30	0.624ns	35.56	0.789ns
	- SBDO	157.2 (117.8 - 196.5)	0.65	0.444ns	28.94	0.733ns
	- WIPL	228.0 (178.7 - 277.4)	5.92	0.045*	67.46	0.472ns
	- BWST	322.9 (278.9 - 366.9)	9.29	0.009**	65.69	0.410ns
	- BLSK	240.4 (204.6 - 276.3)	3.10	0.104ns	52.63	0.612ns
AMWO		159.7 (113.5 - 205.8)				
	- SBDO	157.2 (117.8 - 196.5)	0.91	0.371ns	24.58	0.641ns
	- WIPL	228.0 (178.7 - 277.4)	3.20	0.124ns	51.47	0.565ns
	- BWST	322.9 (278.9 - 366.9)	5.20	0.042*	48.17	0.469ns
	- BLSK	240.4 (204.6 - 276.3)	1.45	0.254ns	39.37	0.689ns
SBDO		157.2 (117.8 - 196.5)				
	- WIPL	228.0 (178.7 - 277.4)	14.75	0.003**	79.16	0.376ns
	- BWST	322.9 (278.9 - 366.9)	25.34	0.000***	109.69	0.316ns
	- BLSK	240.4 (204.6 - 276.3)	10.63	0.005**	84.39	0.452ns
WIPL		228.0 (178.7 - 277.4)				
	- BWST	322.9 (278.9 - 366.9)	0.30	0.592ns	38.45	0.866ns
	- BLSK	240.4 (204.6 - 276.3)	1.47	0.243ns	55.03	0.743ns
BWST		322.9 (278.9 - 366.9)				
	- BLSK	240.4 (204.6 - 276.3)	4.69	0.042*	84.96	0.625ns

[1] *, $P < 0.05$; **, $P > 0.01$; ***, $P < 0.001$.

Table 5. Results of the comparison of mean maximal photopic b-wave amplitude based on conventional ANOVAs and ANOVAs corrected for taking into account the phylogenetic lineage. For species abbreviations, see Fig. 1 and for species number, see Table 1.

		Conventional ANOVA		Corrected ANOVA	
Species	Means (95% Confid. Interv.)	F	P^1	Critical F	P^1
YCNHE	141.3 (105.5 - 177.0)				
- CAEG	267.9 (220.2 - 315.6)	14.01	0.025*	43.78	0.249ns
- GBHE	145.4 (67.4 - 223.5)	0.01	0.919ns	33.93	0.981ns
- TREG	245.3 (210.7 - 280.0)	14.93	0.001***	61.94	0.259ns
- AWIB	232.6 (186.5 -278.7)	8.87	0.007**	92.27	0.511ns
- WILL	85.2 (61.6 - 108.9)	3.12	0.100ns	99.34	0.690ns
- AMWO	90.1 (86.0 -94.2)	1.33	0.273ns	62.83	0.735ns
- SBDO	122.4 (84.6 - 160.1)	0.44	0.518ns	120.37	0.896ns
- WIPL	62.1 (44.5 - 79.7)	9.37	0.008**	146.24	0.587ns
- BWST	130.6 (101.3 - 159.9)	0.20	0.660ns	179.98	0.941ns
- BLSK	45.0 (31.9 - 58.0)	26.04	0.000***	175.21	0.425ns
CAEG	267.9 (220.2 - 315.6)				
- GBHE	145.4 (67.4 - 223.5)	7.74	0.039*	25.59	0.208ns
- TREG	245.3 (210.7 - 280.0)	0.57	0.469ns	50.90	0.808ns
- AWIB	232.6 (186.5 -278.7)	0.64	0.438ns	9.23	0.818ns
- WILL	85.2 (61.6 - 108.9)	45.28	0.001***	97.25	0.137ns
- AMWO	90.1 (86.0 -94.2)	23.69	0.008**	94.24	0.226ns
- SBDO	122.4 (84.6 - 160.1)	22.33	0.002**	99.49	0.296ns
- WIPL	62.1 (44.5 - 79.7)	85.43	0.000***	128.09	0.099ns
- BWST	130.6 (101.3 - 159.9)	23.77	0.000***	135.95	0.340ns
- BLSK	45.0 (31.9 - 58.0)	141.27	0.000***	125.00	0.035*
GBHE	145.4 (67.4 - 223.5)				
- TREG	245.3 (210.7 - 280.0)	7.40	0.026*	39.82	0.354ns
- AWIB	232.6 (186.5 -278.7)	2.81	0.119ns	57.13	0.639ns
- WILL	85.2 (61.6 - 108.9)	2.76	0.158ns	94.24	0.680ns
- AMWO	90.1 (86.0 -94.2)	1.16	0.361ns	82.99	0.747ns
- SBDO	122.4 (84.6 - 160.1)	0.36	0.567ns	86.80	0.882ns
- WIPL	62.1 (44.5 - 79.7)	8.15	0.025*	106.71	0.527ns
- BWST	130.6 (101.3 - 159.9)	0.19	0.673ns	110.28	0.920ns
- BLSK	45.0 (31.9 - 58.0)	19.84	0.001***	101.87	0.303ns
TREG	245.3 (210.7 - 280.0)				
- AWIB	232.6 (186.5 -278.7)	0.14	0.713ns	63.80	0.919ns
- WILL	85.2 (61.6 - 108.9)	39.44	0.000***	83.02	0.160ns
- AMWO	90.1 (86.0 -94.2)	11.05	0.007**	48.47	0.333ns
- SBDO	122.4 (84.6 - 160.1)	22.17	0.001***	89.69	0.312ns
- WIPL	62.1 (44.5 - 79.7)	76.66	0.000***	117.44	0.098ns
- BWST	130.6 (101.3 - 159.9)	24.28	0.000***	138.38	0.387ns
- BLSK	45.0 (31.9 - 58.0)	154.77	0.000***	131.24	0.035*

Table 5. continued

			Conventional ANOVA		Corrected ANOVA	
Species		Means (95% Confid. Interv.)	F	P[1]	Critical F	P[1]
AWIB		232.6 (186.5 -278.7)				
	- WILL	85.2 (61.6 - 108.9)	12.06	0.004**	73.50	0.402ns
	- AMWO	90.1 (86.0 -94.2)	5.65	0.368ns	44.74	0.460ns
	- SBDO	122.4 (84.6 - 160.1)	9.07	0.009**	91.61	0.513ns
	- WIPL	62.1 (44.5 - 79.7)	24.42	0.000***	117.50	0.336ns
	- BWST	130.6 (101.3 - 159.9)	11.90	0.003**	159.28	0.561ns
	- BLSK	45.0 (31.9 - 58.0)	57.91	0.000***	139.14	0.182ns
WILL		85.2 (61.6 - 108.9)				
	- AMWO	90.1 (86.0 -94.2)	0.07	0.801ns	30.92	0.668ns
	- SBDO	122.4 (84.6 - 160.1)	2.06	0.189ns	31.46	0.565ns
	- WIPL	62.1 (44.5 - 79.7)	2.48	0.154ns	67.74	0.671ns
	- BWST	130.6 (101.3 - 159.9)	3.23	0.098ns	82.56	0.636ns
	- BLSK	45.0 (31.9 - 58.0)	8.42	0.012*	67.39	0.433ns
AMWO		90.1 (86.0 -94.2)				
	- SBDO	122.4 (84.6 - 160.1)	0.84	0.395ns	22.96	0.674ns
	- WIPL	62.1 (44.5 - 79.7)	2.91	0.139ns	53.31	0.580ns
	- BWST	130.6 (101.3 - 159.9)	1.36	0.271ns	55.60	0.697ns
	- BLSK	45.0 (31.9 - 58.0)	6.59	0.000***	38.94	0.377ns
SBDO		122.4 (84.6 - 160.1)				
	- WIPL	62.1 (44.5 - 79.7)	11.74	0.007ns	74.48	0.403ns
	- BWST	130.6 (101.3 - 159.9)	0.11	0.470ns	102.11	0.947ns
	- BLSK	45.0 (31.9 - 58.0)	21.95	0.000***	80.83	0.273ns
WIPL		62.1 (44.5 - 79.7)				
	- BWST	130.6 (101.3 - 159.9)	10.95	0.005**	35.62	0.264ns
	- BLSK	45.0 (31.9 - 58.0)	2.14	0.163ns	56.64	0.691ns
BWST		130.6 (101.3 - 159.9)				
	- BLSK	45.0 (31.9 - 58.0)	30.26	0.000***	72.28	0.172ns

[1] *, P < 0.05; **, P > 0.01; ***, P < 0.001.

and Tricolored egrets and the American White Ibis) exceed or tend to exceed those recorded for the shorebird species, the two heron species, and the Black Skimmer, which all forage at night (Fig. 4; Table 5). As a consequence, the factor that generally best discriminates between the crepuscular and nocturnal foraging species and the strictly diurnal ones is the photopic V_{max} amplitude. The photopic maximal response of the Black Skimmer is lower than in all the other species, except the Wilson's Plover.

In general, the significance level of the above differences in the b-waves tend to be lower or non significant with the corrected ANOVAs compared to that obtained with the 95% confidence intervals for the means and the conventional ANOVAs (see Tables 4 and 5).

DISCUSSION

Overall, the corrected ANOVAs which take into account the phylogenetic lineage maintain the significance, although generally at a lower level, of the between-species differences in the rod and cone densities previously found using conventional ANOVAs or 95% confidence interval of the means.

Within the group of wading birds, the Cattle Egret presents the highest cone density, higher than that of the Great Blue Heron, a species phylogenetically closely related to it (see Fig. 1). However, the two species have different behaviors. The Cattle Egret is a terrestrial and strictly diurnal sight-forager that feeds mainly on insects and other evasive small preys (Voisin, 1991; Martínez-Vilalta and Motis, 1992). This species has a high cone density in the central retina (Rojas et al., *submitted*) suggesting a good visual acuity and therefore a better visual monocular field (Walls, 1942; Pumphrey, 1948; Smythe, 1975). In contrast, the Great Blue Heron is a crepuscular but also a nocturnal and diurnal sight-forager that feeds in shallow waters, mainly on fish, amphibians and aquatic insects (Martínez-Vilalta and Motis, 1992). Although active at night, this heron has a retinal structure which appears better adapted for diurnal than for nocturnal vision. Indeed, its cone density significantly exceeds that of rods. Our present results show that there is no significant difference in the rod densities of the two species. However, the longer rod outer segments of the Great Blue Heron (2.7 times longer than those of the Cattle Egret (Rojas et al., *submitted*) may be considered as an adaptation to crepuscular and nocturnal life.

The Yellow-crowned Night Heron has a rod density significantly higher than the other wading birds compared. The Yellow-crowned Night Heron is an aquatic and nocturnal sight-feeder which feeds mainly on crustaceans, particularly crabs (Martínez-Vilalta and Motis, 1992). Recently, Katzir and Martin (1998) found that the visual field of the Black-crowned Night Heron is almost identical to that of the diurnal Cattle Egret. They concluded that the visual fields of the two species have no relationship with the fact they are either mainly nocturnal or strictly diurnal feeders but are in direct correlation with the manner with which they catch their prey, guided with their bill tip. According to ours results, the high rod density of the Yellow-crowned Night Heron in comparison with the three diurnal herons is in perfect concordance with the fact that this species is taxonomically placed within the group of nocturnal herons (Hancock and Elliot, 1978; Hanckock and Kushlan, 1984). In addition, cone density of the night heron is lower than in the three diurnal herons studied. Sheldon (1987) and Katzir and Martin (1998) consider that nocturnal herons pertain to a group phylogenetically identical to the diurnal ones.

The Tricolored Egret and the American White Ibis present the lowest rod densities of the 12 species compared. Photoreceptors, in spite of similar density, vary in distribution in the retina from one species to another (Rojas et al., *submitted*). The Tricolored Egret has a high cone density, especially in the temporal sectors of the retina. In this region, the rod density is significantly lower than in other sectors. Such a specialized temporal retina confers to the Tricolored Egret a better visual acuity in its binocular field (Walls, 1942; Pumphrey, 1948; Smythe, 1975). The Tricolored Egret is a sight-feeder and this adaptation could greatly facilitate the capture of highly evasive fish prey while foraging in shallow water (Meyerriecks, 1962; Martínez-Vilalta and Motis, 1992). The American White ibis, in contrast, is strictly tactile and does not necessarily need to see its prey before capturing them (Rojas et al., 1997, *submitted*).

The Roseate Spoonbill is a species phylogenetically close to the American White Ibis in the Threskiornithidae (see Fig. 1). Both are strictly tactile, but the American White Ibis is strictly diurnal and the Roseate Spoonbill rather crepuscular and nocturnal (Robert et al., 1989; McNeil et al., 1993). Our results show that the Roseate Spoonbill, with a rods:cones ratio of 0.9:1.0, has a rod density significantly higher than the American White Ibis, the Tricolored Egret and the Cattle Egret. Its rods:cones ratio and rod density are lower than in the Yellow-crowned Night Heron. However, in accordance with its mainly crepuscular and nocturnal activity, the Roseate Spoonbill, in comparison to the Great Blue Heron, has a higher rods:cones ratio.

The Wilson's Plover presents a rod density higher than other species, except the Yellow-crowned Night Heron, the Black-winged Stilt and the Black Skimmer, the three other species that use sight for their nocturnal foraging activities, independently of the presence or absence of moonlight. Indeed, the Wilson's Plover is mainly a nocturnal sight-feeder, possesses large eyes and has a high rod density (Robert and McNeil, 1989; Rojas et al., *in press*). The Black-winged Stilt is mainly visual at night, but switches to tactile feeding when the water surface where it feeds is turbid or agitated (Robert and McNeil, 1989; McNeil et al., 1992). The Black Skimmer is mainly active during the night. It catches its prey flying near the water with the inferior jaw skimming the surface. This behavior requires a good nocturnal vision. The skimmer's rods:cones ratio equals 5.4:1.0 and thus largely exceeds that of other species, including the other nightly sight-foraging ones such as the Wilson's Plover, the Black-winged Stilt and the Yellow-crowned Night Heron.

The Woodcock, the Willet and the Short-billed Dowitcher are phylogenetically closely-related species in the Scolopacidae (Fig. 1). They roughly have similar rod densities. However, the Willet and the Short-billed Dowitcher have a cone density significantly higher than the American Woodcock (Fig. 2). On the other hand, in the Willet, the cones outnumber the rods (Fig. 2) while the contrary is observed in the American Woodcock. The Willet and the Short-billed Dowitcher are diurnal and nocturnal species. Territorial Willets are sight-feeders during the day and the night, except on moonless nights when they switch to tactile foraging (Llinas and Galindo, 1990; Rompré and McNeil, 1994; McNeil and Rompré, 1995). The Willet has a high cone density in the central retina, suggesting that this species has a good visual acuity in the monocular visual field (Rojas *et al.*, *in press*). The American Woodcock lives in the woods and in open fields and forages tactilely, mainly at night, particularly during the winter (Stribling and Doerr, 1985; Roberts, 1993; Krementz et al., 1995; Rojas et al., *in press*). Because it feeds solitarily, it is more vulnerable to terrestrial and aerial predators than the majority of other shorebirds which are gregarious feeders outside of the breeding period (see Rojas et al., *in press*). The eyes of the Woodcock are placed lateral and high in the skull, giving the animal an effective visual coverage in the hemisphere above itself, but the bill falls outside the visual field (Martin, 1994).

Although phylogenetically quite distant from the Wilson's Plover, the Black-winged Stilt and the Yellow-crowned Night Heron have a comparable rod density. Since in the course of evolution the cones appeared first, the rods being considered as a modification of the cones (Walls, 1942), these common traits in rod density of the three species reflect an evolutionary convergence. Surprisingly, the strong differences observed, based on the conventional ANOVAs and the 95% confidence intervals, between the Black Skimmer and some other nocturnally active species such as the Yellow-crowned Night Heron, the Wilson's Plover and the Black-winged Stilt are not maintained with the ANOVAs corrected for phylogenetic lineage (Tables 2 and 3, Fig. 2). In their adaptation to exploit nocturnal resources, these species developed retinas in which rods outnumber cones. Sight-feeders such as the Yellow-crowned Night Heron and the Wilson's Plover have large eyes and their large pupil allow a better retinal illumination in low light conditions (Rojas et al., *in press, submitted*). The Skimmer' eyes are relatively small, which is typical of tactile birds. By contrast, its rods:cones ratio is the highest among all species studied (Fig. 2). Although having small eyes, the Black Skimmer has relatively large pupils that are vertical during the day and dilate to an almost circular shape at night. This adaptation protects the rods from sunlight and water brilliance during the day and allows for more light on the retina in the low light conditions of the night.

The significance of the differences in the maximal scotopic b-wave amplitude (Vmax) of the 12 species studied found using conventional ANOVAs is, on the overall, not maintained when considering the corrected ANOVAs used here. This can be due to the small size of the samples as well as to important inter-individual differences in the physiological responses while recording ERGs. This may also be due to possible aberrations in the retained phylogenetic hypothesis which is based on information taken from Sibley and Ahlquist (1990). The only exceptions concern the photopic b-wave amplitude of the Black Skimmer. Indeed, the corrected ANOVAs indicate that the skimmer has a diurnal retinal function inferior to that of the Cattle Egret or the Tricolored Egret. These results are directly correlated to the feeding strategy of these species.

In summary, based on the corrected ANOVA, we conclude that the species analyzed in this study have different cones and rods densities because they have different behavioral characteristics and that this is not a consequence of their phylogenetic lineage.

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Chapitre 6

Discussion générale et conclusion

Cette recherche menée sur la capacité de vision diurne et nocturne chez les Ciconiiformes et les Charadriiformes nous a permis de dégager des corrélations intéressantes entre leurs habitudes de vie diurne ou nocturne, leur stratégie de quête alimentaire tactile ou visuelle et quelques caractéristiques structurelles et fonctionnelles de leur oeil.

1. Généralités sur la quête alimentaire des Charadriiformes et des Ciconiiformes

Les Charadriiformes limicoles, oiseaux de rivage, s'alimentent dans des substrats boueux-sableux (sols sablonneux) et boueux-mous (platières vaseuses et zones inondées) (McNeil et Robert, 1988; Rompré, 1993). Les sites de sol sablonneux sont riches en proies. Pour capturer leurs proies, ils utilisent différentes stratégies: visuelle, tactile, ou les deux selon les conditions d'éclairage, l'abondance des proies, les conditions environnementales, etc. (Schneider, 1983; McNeil et Robert, 1988). Les pluviers (*Pluvialis* et *Charadrius*), par exemple, chassent leurs proies de façon visuelle de jour comme de nuit (Pienkowski, 1983). D'autres genres, comme *Limnodromus*, *Scolopax*, *Gallinago* etc., appartenant à la famille des Scolopacidae, sont des chasseurs tactiles aussi bien de jour que de nuit (Godfrey, 1972; Schneider, 1983; McNeil et Robert, 1988). D'une manière générale, les oiseaux strictement tactiles n'ont pas la vision très développée car ils ne l'utilisent pas pour détecter leurs proies. En effet, ils les détectent au toucher et la plupart ont des récepteurs sensoriels tactiles (corpuscules de Herbst et de Grandy) à la surface ou à l'extrémité de leur bec qui leur permettent de repérer les proies (Schwartzkopff, 1973, 1985; Gottschaldt, 1974; Berkoudt, 1980; Gerritsen et al., 1983; Pettigrew et Frost, 1985). Certains chevaliers (*Tringa totanus, T. melanoleuca, T. flavipes*) et les Huîtriers (*Haematopus ostralegus*), qui utilisent la vue pour chasser le jour, changent de stratégie la nuit et chassent plutôt de façon tactile (Goss-Custard, 1969, 1970). De manière semblable, l'Échasse d'Amérique (*Himantopus himantopus*) chasse de façon visuelle durant le jour et les nuits de pleine lune. En revanche pendant les nuits sans lune, elle peut s'alimenter de manière tactile (Robert et McNeil, 1989).

Les Ciconiiformes sont des oiseaux à longues pattes et à long cou qui s'alimentent dans les eaux peu profondes des étangs et des lagunes, de façon visuelle ou tactile. L'alimentation visuelle est généralement utilisée par les hérons et la plupart des cigognes, et l'alimentation tactile par les ibis et les spatules (Meyerriecks 1962; Kushlan, 1978, 1979; Kushlan et al., 1985; Voisin, 1991; Hancock et al., 1992). Les hérons constituent un groupe d'oiseaux hautement spécialisés pour la capture des proies, particulièrement dans l'eau. Cependant, certaines espèces peuvent s'alimenter loin des environnements aquatiques selon la disponibilité des proies (Meyerriecks, 1962; Voisin, 1991; Hancock et al. 1992). Les hérons peuvent être classifiés comme diurnes ou nocturnes. Parmi les hérons nocturnes, on trouve, entre autres, le Bihoreau violacé (*Nycticorax violaceus*) et parmi les diurnes, les aigrettes. On retrouve chez les hérons à peu près 38 méthodes ou stratégies d'alimentation dans lesquelles la vision est hautement impliquée (Kushlan, 1978). Cependant, seules quelques-unes sont quotidiennement utilisées dépendamment de l'espèce et de la disponibilité des proies: l'immobilité et l'attente (stand and wait), le guet (peering), la marche lente (walk slowly), la marche rapide (walk quickly), la course (running) et l'ouverture ou le déploiement des ailes (openwing) (Meyerriecks, 1962; Kushlan, 1976; Willard, 1977; Recher et al., 1983; Rodgers, 1983; Martínez-Vilalta et Motis, 1992). Selon la fréquence d'utilisation de chacune des stratégies les hérons peuvent être classifiés comme prédateurs actifs ou passifs. Les prédateurs actifs utilisent des stratégies d'alimentation impliquant des mouvements rapides et successifs comme la marche rapide, la course et l'ouverture ou le déploiement des ailes. Ils comprennent les hérons strictement diurnes comme l'Aigrette tricolore (*Egretta tricolor*) et le Héron garde-boeufs (*Bubulcus ibis*) (Meyerriecks, 1962; Kushlan, 1976; Willard, 1977; Recher and Holmes, 1982; Rodgers, 1983). Les prédateurs passifs sont ceux qui utilisent une stratégie d'alimentation impliquant l'immobilité et l'attente, le guet et la marche lente, tels le Bihoreau violacé et le Grand Héron (*Ardea herodias*) (Meyerriecks, 1962; Kushlan, 1976; Willard, 1977; Rodgers, 1983). Dotés d'un bec long, mince et courbé, parfaitement adapté pour sonder dans l'eau, dans la boue et explorer des crevasses dans les terrains secs, les ibis et les spatules sont spécialisés pour capturer leurs proies tactilement (Kushland, 1977; Matheu et del Hoyo, 1992). Les stratégies d'alimentation les plus utilisées par ces oiseaux impliquent l'immobilité et la marche lente (Hancock et al., 1992; Kushlan et al., 1985, 1979). Les ibis sont strictement diurnes tandis que les spatules sont principalement crépusculaires et nocturnes.

2. Corrélation entre la taille et la forme des yeux et la quête alimentaire

Dans la littérature, on trouve souvent que les oiseaux nocturnes ont les yeux plus grands que les oiseaux diurnes (Walls, 1942, Rochon-Duvigneaud, 1943; Tansley, 1965, Martin, 1985, 1986; Waldvogel, 1990). Ces observations sont plutôt basées sur des études faites chez les oiseaux strictement ou principalement nocturnes qui cherchent leurs proies visuellement. Par contre, très peu d'études ont porté sur les oiseaux principalement nocturnes qui cherchent leurs proies tactilement. Nous avons remarqué que chez les espèces étudiées ici, la taille des yeux n'est pas liée seulement aux habitudes nocturnes. Elle est aussi corrélée à la stratégie d'alimentation, comme par exemple chez le Bec-en-ciseaux noir (*Rynchops niger*) et le Pluvier de Wilson (*Charadrius wilsonia*), deux Charadriiformes principalement nocturnes (Martin, 1990; McNeil et al. 1992, 1993b), dont le premier, strictement tactile, a les yeux relativement plus petits que le second, strictement visuel. Nous avons aussi noté, chez les Charadriiformes qui s'alimentent autant de jour que de nuit, que le Bécassin roux (*Limnodromus griseus*), strictement tactile (Schneider, 1983; McNeil et Robert, 1988; Robert et McNeil, 1989; McNeil et al., 1992), a les yeux relativement plus petits que le Chevalier semipalmé (*Catoptrophorus semipalmatus*) et l'Échasse d'Amérique, qui peuvent être des chasseurs visuels de jour et lors de nuits éclairées par la lune (McNeil et Robert, 1988; Robert et McNeil, 1989; McNeil et Rodríguez, 1990; Rompré et McNeil, 1994; McNeil et Rompré, 1995). Parmi les Ciconiiformes strictement diurnes analysés dans cette étude, on constate que l'Aigrette tricolore et le Héron garde-boeufs, tous deux strictement visuels (Meyerriecks, 1962; Kushlan, 1976; Willard, 1977; Recher and Holmes, 1982; Rodgers, 1983; Voisin, 1991), ont les yeux relativement plus grands que l'Ibis rouge (*Eudocimus ruber*), strictement tactile (Kushlan, 1979, 1985 et al.; Hancock et al., 1992, Matheu et del Hoyo, 1992).

On a rapporté que les oiseaux nocturnes ont tendance à avoir les yeux plus globulaires, c'est-à-dire avoir un ratio LA:DE (longueur axiale:diamètre équatorial) plus grand que les diurnes (Tansley, 1965; Martin, 1990; Waldvogel, 1990). Cette adaptation permet aux oiseaux nocturnes de collecte un plus grande quantité de lumière. C'est le cas, par exemple, du Pluvier de Wilson et de l'Échasse d'Amérique qui ont un ratio LA:DE plus grand que ceux du Chevalier semipalmé et du Bécassin roux, mais quand même plus petit que celui de la Chouette hulotte (*Strix aluco*), strictement nocturne (Martin et Brooke, 1991). Le Bihoreau violacé, quant à lui, a un ratio LA:DE plus grand que celui de toutes les espèces analysées dans notre étude, et même plus grand que celui de la Chouette hulotte. Paradoxalement le Bec-en-ciseaux noir, strictement nocturne, a un ratio LA:DE comparable à celui de l'Ibis rouge, strictement diurne. La manque des yeux globulaires chez le Bec-en-ciseaux peu être compenser par une très grande pupille dilaté et une rétine qui à surtout des bâtonnets, adaptations qui le permettent une bonne sensibilité.

La pupille dilatée est plus grande chez les oiseaux principalement nocturnes que chez ceux qui sont diurnes. Le Bec-en-ciseaux noir possède une pupille en fente verticale qui reste fermée le jour pour protéger sa rétine qui est très sensible. La pupille de cette espèce devient dilatée et presque circulaire la nuit pour laisser entrer le moindre rayon lumineux (Zusi et Bridge, 1981; Rojas et al., 1997). L'avantage de la pupille en fente verticale pendant le jour c'est que elle peu se contracter complètement en présence de la lumière vive, tandis que une pupille ronde pourrais jamais se fermer complètement (Tansley, 1965). Nous avons observé que le Bec-en-ciseaux noir, le Pluvier de Wilson et le Bihoreau violacé, tous principalement nocturnes, ont une pupille dilatée plus grande que les autres espèces étudiées. Le Bihoreau violacé a une pupille dilatée deux fois plus grande que les autres hérons analysés. La taille de la pupille du Bihoreau est comparable à celle Chouette hulotte (Martin and Brooke, 1991).

3. Corrélation entre la structure et la fonction de la rétine et la quête alimentaire

3.1. Oiseaux actifs la nuit

Les oiseaux principalement nocturnes analysés dans cette étude sont le Bec-en-ciseaux noir, le Pluvier de Wilson et le Bihoreau violacé.

Le Bec-en-ciseaux noir est l'espèce la plus nocturne des Charadriiformes étudiés ici. Dans sa rétine, le nombre de bâtonnets surpasse de 5 fois celui des cônes. Leur distribution n'est pas uniforme, les bâtonnets étant plus abondants dans les secteurs central, dorsal et temporal de la rétine. Cette distribution des bâtonnets peut aider l'oiseau à mieux voir la surface de l'eau et le bas-horizon lorsqu'il rase la surface de l'eau durant la nuit (Tomkins, 1951; Zusi, 1962, 1985); une adaptation qui permettrait d'augmenter la sensibilité visuelle. Chez cette espèce, la réponse photopique est la plus faible de toutes les espèces étudiées, mais sa réponse scotopique est plus grande que celles du Pluvier de Wilson et du Bihoreau violacé. Ces résultats justifie au moins en partie les habitudes nocturnes chez le bec-en-ciseaux.

Le Pluvier de Wilson se caractérise par de grands yeux et un bec court et rigide (Schneider, 1983). Cette espèce est strictement visuelle et principalement nocturne, surtout quand les nuits sont éclairées par la lune, quoique durant la saison de reproduction elle peut s'alimenter autant de nuit que de jour (Thibault et McNeil, 1994, 1995). Sa rétine contient plus de bâtonnets que de cônes, ces derniers étant plus concentrés dans la région centrale (secteur 5). Dans ce même secteur, on observe aussi une augmentation de l'épaisseur moyenne des couches nucléaire et plexiforme internes, combinée avec une forte densité de cellules ganglionnaires, cette caractéristique-ci en particulier conférant une grande acuité visuelle et permettant une meilleure distinction des détails fins (Binggeli and Paule, 1969; Ikushima et al., 1986; Hayes et Brooke, 1990; Hayes et al. 1991, Hayes et Holden, 1980; Inzuza et al., 1991; Suburo et al., 1991). Dowling (1987) rapporte que les cellules ganglionnaires sont sensibles au mouvement, à la direction et au contraste, et reçoivent la plupart des afférences des cellules bipolaires et amacrines qui se trouvent dans la couche nucléaire interne; de plus, un traitement complexe de sélection du mouvement et de la direction est réalisé dans la couche plexiforme interne. Apparemment, la plupart des Pluviers de Wilson sont attirés par des proies en mouvement (principalement les crabes *Uca cumulanta*) (Thibault et McNeil, 1995). Ils surveillent, immobiles, une aire d'alimentation et lorsqu'ils détectent un mouvement, ils courent et capturent leur proie (Schneider, 1983; Pienkowski, 1983). Même si les crabes sont plus abondants et plus actifs le jour que la nuit, le Pluvier de Wilson préfère s'alimenter la nuit. Morrier et McNeil (1991) ainsi que Thibault et McNeil (1995) suggèrent que la nuit donne à ce pluvier qui s'alimente de façon solitaire une excellente protection vis-à-vis des prédateurs aériens. Chez cette espèce, la réponse visuelle en condition scotopique à de faibles intensités lumineuses est plus forte que celles du Chevalier semipalmé et du Bécassin roux. Sa réponse photopique est la plus faible parmi les limicoles étudiés. Sa rétine semble être plus fonctionelle à de faibles qu'à de fortes intensités lumineuses, adaptation qui peut favoriser son alimentation nocturne.

Le Bihoreau violacé est le héron le plus nocturne des Ciconiiformes présentés dans notre étude (Kushlan, 1978; McNeil et al. 1993b) et la densité de ses bâtonnets est deux fois plus grande que celle des autres Ciconiiformes. Il en résulte un grand ratio bâtonnets:cônes qui est toutefois plus faible que celui du Bec-en-ciseaux noir, mais supérieur à ceux du Pluvier de Wilson, de l'Échasse d'Amérique et du Chevalier semipalmé, trois espèces très actives la nuit. De plus, le Bihoreau violacé possède de très grands yeux et une énorme pupille qui l'aide à améliorer sa vision nocturne. Par ailleurs, il possède trois fois moins de cônes que les hérons diurnes, et ses couches nucléaire interne et plexiforme interne sont plus minces. Ses cônes sont distribués de manière homogène dans toute la rétine, résultant en l'absence de d'une zone spécialisée de haute acuité visuelle et de grande perception du mouvement (Smythe, 1975; Tansley, 1965). Les oiseaux qui surveillent leurs proies en volant, tels les aigles, ont deux foveas (Tansley, 1965; voir Buser et Imber, 1987). Par contre, les oiseaux nocturnes comme certains hiboux et les engoulevents n'ont pas de fovea et dépendent plutôt de leurs bâtonnets que de leurs cônes (Smythe, 1975). Chez le Bihoreau violacé, l'alimentation selon une stratégie passive peut être justifiée, en partie, par un manque de cônes, de cellules ganglionnaires et d'autres éléments rétiniens nécessaires à la bonne acuité visuelle et à la sensibilité au mouvement. Spécialiste de la capture des crustacés, principalement des grands crabes et des écrevisses, cet oiseau peut aussi s'alimenter occasionnellement de poissons, d'insectes aquatiques, de mollusques, de grenouilles et de petits serpents (Matheu et del Hoyo, 1992). En général, ses proies sont plus grandes que celles de l'Aigrette tricolore, une aigrette diurne, qui s'alimente de poissons de petite et moyenne taille (Martínez-Vilalta et Moltis, 1992). La réponse visuelle en condition photopique du Bihoreau violacé est caractérisée par des ondes a et b de plus faible amplitude que chez les hérons diurnes. L'amplitude maximale de l'onde b scotopique est légèrement plus petite que celles du Pluvier de Wilson, strictement visuel, et de l'Échasse d'Amérique, strictement tactile. Par contre, elle est plus grande que celles de la Bécasse d'Amérique, strictement tactile, et du Chevalier semipalmé dont les individus défenseurs d'un territoire d'alimentation changent du mode visuel au mode tactile lors de nuits sans lune. Cette bonne performance scotopique du Bihoreau violacé peut être due au fait que les segments externes très longs de ses bâtonnets permettent de mieux capter les faibles rayons lumineux.

3.2. Oiseaux actifs le jour

Les oiseaux strictement diurnes analysés dans cette étude sont le Héron garde-boeufs, l'Aigrette tricolore et l'Ibis rouge.

Chez le Héron garde-boeufs et l'Aigrette tricolore, la densité des cônes dépasse de deux fois celle des bâtonnets, et chez l'Ibis rouge, elle est 2.8 fois celle des bâtonnets. Le ratio cônes:bâtonnets, l'épaisseur des couches nucléaire externe, nucléaire interne et plexiforme interne, ainsi que la densité des cônes et des cellules ganglionnaires sont plus grands dans le secteur central de la rétine (secteur 5) chez le Héron garde-boeufs et le secteur temporal (secteur 3) chez l'Aigrette tricolore. Le Héron garde-boeufs possède une bonne acuité visuelle et une bonne sensibilité aux contrastes et au mouvement dans son champ de vision monoculaire, c'est-à-dire de chaque côté du corps (Smythe, 1975). Cette espèce s'alimente principalement d'insectes (locustes, sauterelles) qu'elle trouve en suivant le bétail ou d'autres grands mammifères dans les aires herbeuses, les prairies et les pâturages; elle s'alimente aussi de poissons et de grenouilles qu'elle trouve la plupart de temps dans les aires inondées d'eau douce et dans les rizières (Siegfried, 1971; Voisin, 1991). Les mêmes caractéristiques dans le secteur temporal peuvent donner à l'Aigrette tricolore une bonne acuité visuelle dans le champ de vision binoculaire, c'est-à-dire en face d'elle (Smythe, 1975), pour capturer des poissons dans des eaux peu profondes (Meyerriecks, 1962; Martínez-Vilalta et Moltis, 1992). La grande densité de cônes lui permet aussi de mieux détecter ses proies lors de journées très ensoleillées. Contrairement au Héron garde-boeufs et à l'Aigrette tricolore, mais à l'instar du Bihoreau violacé et du Grand Héron, l'Ibis rouge ne possède pas une aire spécialisée de grande acuité visuelle, les photorécepteurs étant distribués de manière homogène dans la rétine, expliquant peut-être pourquoi ces espèces-ci ont adopté une technique passive d'alimentation. Les trois espèces strictement diurnes présentent les plus grandes réponses électrorétinographiques dans des conditions photopiques mais montrent en conditions scotopiques des réponses similaires ou plus grandes que celles des oiseaux nocturnes. Le Héron garde-boeufs présente une onde b scotopique significativement plus grande que celle du Bec-en-ciseau noir, du Pluvier de Wilson et du Bihoreau violacé, particulièrement à fortes intensités lumineuses, qui peut s'expliquer par le fait que sa rétine possède un grand ratio cônes:bâtonnets et qu'à de fortes intensités lumineuses, le mécanisme de génération de l'onde b scotopique correspond plutôt à la réponse des cônes qu'à celle bâtonnets.

3.3. Oiseaux actifs le jour et la nuit

Les oiseaux actifs le jour et la nuit analysés dans cette étude sont l'Échasse d'Amérique, la Bécasse d'Amérique (*Scolopax minor*), le Chevalier semipalmé, le Bécassin roux, le Grand Héron et la Spatule rosée (*Ajaia ajaja*).

L'Échasse d'Amérique a presque la même densité moyenne de cônes que de bâtonnets, avec une légère prépondérance des bâtonnets. Sa rétine paraît mieux adaptée à la vision diurne que celle du Pluvier de Wilson; en effet, la longueur moyenne du segment externe des cônes de même que le diamètre moyen des cônes accessoires sont légèrement plus grands chez l'Échasse d'Amérique. Ses longues pattes lui permettent de s'alimenter dans l'eau de 10 à 20 cm de profondeur, de poissons, d'insectes et de crustacés qu'elle capture à la vue pendant le jour et la nuit. Elle peu s'alimenter aussi tactilement en fauchant l'eau de son bec, ou en s'immergeant la tête de façon à sonder avec son bec les substrats boueux pendant le jour dans des eaux turbides et parfois lors de nuits obscures (McNeil et Robert, 1989). SE basant, sur les caractéristiques physiologiques et morphologiques, l'Échasse d'Amérique a montré la plus importante fonction photopique de tous les Charadriiformes analysés dans cette étude. De plus, l'amplitude de l'onde b scotopique de l'ERG de cet oiseau est significativement plus grande que celles du Bec-en ciseaux-noir et du Pluvier de Wilson. Ces résultats indiquent que sa rétine est très fonctionnelle autant le jour que la nuit. Ainsi chez l'Échasse d'Amérique, la bonne performance des visions photopique et scotopique peut être une adaptation lui permettant d'exploiter les ressources alimentaires de son environnement autant le jour que la nuit.

Chez la Bécasse d'Amérique, la période d'activité alimentaire est dépendante de la saison. Elle est principalement diurne l'été et nocturne l'hiver, et sa stratégie est strictement tactile (Sheldon, 1967; Owen et Morgan, 1975; Sepik, et al., 1989; Stribling et Doerr, 1985). La Bécasse d'Amérique a une densité de photorécepteurs plus faible que le Bec-en-ciseaux noir, le Pluvier de Wilson et l'Échasse d'Amérique. Une faible densité de cônes avec des segments externes très larges sur l'ensemble de la rétine suggère une pauvre acuité visuelle (Snyder et al., 1977). Cet oiseau s'alimente seul dans la forêt et dans des milieux ouverts, le rendant plus vulnérable aux prédateurs terrestres que la plupart des limicoles plutôt grégaires en dehors de la période de reproduction. Ses cônes, présents en plus grand nombre dans la rétine centrale, peuvent contribuer à faciliter sa vision panoramique et augmenter sa sensibilité aux contrastes. De plus, ses yeux placés latéralement et haut dans la boîte crânienne lui donnent une bonne couverture visuelle de l'hémisphère au-dessus de lui-même, mais son long bec, adapté pour l'alimentation tactile, tombe hors du champ visuel (Martin, 1994). Ces caractéristiques peuvent permettre à la Bécasse d'Amérique de chercher sa nourriture en même temps qu'elle surveille ses prédateurs aériens. Sa sensibilité rétinienne, similaire à celle du Pluvier de Wilson et de l'Échasse d'Amérique, peut s'expliquer par le fait que sa rétine comprend significativement plus de bâtonnets que de cônes, que les segments externes des bâtonnets sont très longs, et que sa pupille dilatée dans l'obscurité est très grande, aussi grande que celle du Bec-en-ciseaux noir, principalement nocturne.

Tandis que le Bécassin roux est strictement tactile (Schneider, 1983), le Chevalier semipalmé défenseur d'un territoire d'alimentation est tactile et visuel durant le jour et les nuits éclairées par la lune, et uniquement tactile lors des nuits sans lune (McNeil et Rompré, 1995; Rompré et McNeil, 1996). La rétine du Chevalier semipalmé est mieux structurée pour la vision diurne que celle du Bécassin roux et lui confère une meilleure acuité visuelle. Ses cônes, significativement plus nombreux que les bâtonnets dans tous les secteurs de la rétine, sont plus concentrés dans la rétine centrale que périphérique, ce qui lui confère une excellente vision dans le plan horizontal et une excellente acuité visuelle dans le champ visuel monoculaire. Par contre, les photorécepteurs du Bécassin roux sont uniformément distribués dans l'ensemble de la rétine. Les résultats de l'ERG scotopique du Bécassin roux montrent que, parmi tous les Charadriiformes analysés, cet oiseau est le moins adapté à la vision nocturne.

Le Grand Héron est un prédateur principalement crépusculaire mais aussi nocturne. Le ratio bâtonnets:cônes du Grand Héron est beaucoup plus faible que celui du Bihoreau violacé, mais supérieur à celui des hérons strictement diurnes comme l'Aigrette tricolore et le Héron garde-boeufs. Reflétant une adaptation à de faibles intensités lumineuses (crépusculaires), les bâtonnets ont des segments externes très grands permettant au Grand héron d'améliorer sa sensibilité rétinienne. D'autre part, la rétine a moins de cônes que celles du Héron garde-boeufs et de l'Aigrette tricolore. Ce manque d'acuité visuelle et de sensibilité aux contrastes et au mouvement ne facilite pas la quête alimentaire diurne. En étudiant l'impact de la lumière vive du jour chez les hérons, Bovino et Burtt (1979) ont noté que la réflexion sur la surface de l'eau lors des jours très ensoleillés diminue leur habilité à détecter les poissons. Selon ces auteurs, le Grand Héron est plus apte à capturer ses proies lors des jours nuageux qu'ensoleillés. Les oiseaux aquatiques diurnes ayant besoin de regarder à travers l'eau pour s'alimenter possèdent une grande densité de gouttelettes lipidiques de couleurs rouge et orangée (Bowmaker, 1980). Comme nous l'avons déjà expliqué dans l'introduction, ces gouttelettes constituent un filtre pour certaines longueurs d'onde lumineuse car elles s'interposent entre la lumière incidente et le pigment visuel des cônes. En empêchant le passage des ondes courtes elles permettent à l'oiseau de mieux voir à travers la surface de l'eau. La faible densité de cônes dans la rétine du Grand Héron peut être une cause possible de sa faible performance lors de jours très ensoleillés. Bien que l'amplitude maximale de l'onde b scotopique de ce dernier ne soit pas différente de celle du Bihoreau violacé, la sensibilité rétinienne est légèrement supérieure. Les résultats des ERGs photopiques ont montré que le Grand Héron a une capacité de vision diurne inférieure à celle des Ciconiiformes strictement diurnes. Le Grand Héron cherche sa proie de manière plutôt méthodique, en prenant beaucoup de temps et en attendant tranquillement son arrivée (Kushland, 1981; Recher et Recher, 1980). Cette manière passive de chasser exclut les marches rapides et les courses derrière les proies. Le Grand Héron est consideré comme étant un généraliste parce qu'il s'alimente d'une grande variété de proies de différentes tailles, mais il préfère les poissons de taille supérieure à ceux sélectionnés par l'Aigrette tricolore (Recher et Recher, 1980), par exemple. Bien qu'il soit actif le jour, il a aussi une importante activité crépusculaire et nocturne (Horvath et Moholt, 1986; McNeil et al., 1993a 1993b). Selon Kushlan (1972), l'Aigrette neigeuse (*Egretta thula*), par exemple, peut changer de stratégie alimentaire selon la disponibilité des proies. Il affirme que lorsque l'oxygène dissout est faible, par exemple très tôt le matin, les poissons montent à la surface de l'eau où la concentration d'oxygène est plus élevée. À ce moment précis, l'Aigrette neigeuse peut s'alimenter en utilisant une stratégie passive lui permettant d'épargner de l'énergie. Par contre, au fur et à mesure que la journée avance, la concentration en oxygène dissout augmente et les poissons descendent vers le fond. L'Aigrette neigeuse change alors de stratégie et devient un chasseur actif (Kushlan, 1981). Comme l'Aigrette neigeuse, le Grand Héron tire avantage des conditions crépusculaires probablement parce que les proies sont plus abondantes et plus visibles et qu'il dépense donc moins d'énergie pour les capturer.

Nos résultats montrent que la Spatule rosée a une densité de bâtonnets significativement plus importante que l'Ibis rouge. Nous avons noté que la rétine de la Spatule rosée, similaire à celle de l'Ibis rouge, du Bihoreau violacé et du Grand Héron, ne possède pas de fovea ou d'aire spécialisée de grande acuité visuelle.

Malgré tout ce qui vient d'être discuté de la relation entre la morphologie et la physiologie rétinienne et certains éléments de l'activité et du comportement de nos oiseaux, on se doit de constater que la corrélation entre la morphologie et le fonctionnement de la rétine n'est pas parfaite. En effet, s'il existe une étroite relation entre la densité des cônes et leur réponse mesurée dans l'ERG en conditions photopiques, l'on ne peut en dire autant de la relation entre la densité des bâtonnets et les réponses électrorétinographiques obtenues en conditions scotopiques. Par exemple, le Héron garde-boeufs, l'Aigrette tricolore et l'Ibis rouge ont à la fois la meilleure vision photopique et la plus forte densité de cônes des espèces étudiées, et plus la densité de cônes augmente, plus grande est l'amplitude de l'onde a. Au contraire, la corrélation est perdue, chez ces mêmes trois espèces, entre la densité des bâtonnets et la réponse scotopique, ce qui pourrait s'expliquer par le fait qu'à forte intensité lumineuse (en conditions scotopiques) les cônes sont recrutés. Nous enregistrons donc une réponse mixte. Pour éviter ce problème, il aurait fallu effectuer les stimulations en utilisant un filtre bleu qui aurait neutralisé les cônes et permis de n'enregistrer que la réponse des bâtonnets, ce que nous n'avons malheureusement pas fait. Ce phénomène explique peut-être pourquoi la courbe intensité-réponse de l'onde b du Pluvier de Wilson baisse en conditions scotopiques, alors qu'elle forme un plateau chez les onze autres espèces étudiées : on pourrait même être témoin d'une inhibition des bâtonnets par les cônes, comme cela a été signalé chez l'humain (voir Tansley, 1965). De même, le Pluvier de Wilson et l'Échasse d'Amérique ont tous deux à peu près la même densité de bâtonnets et de cônes même si leurs électrorétinogrammes diffèrent significativement.

4. Conclusions

Il ressort de cette étude plusieurs conclusions générales.

1- Les oiseaux principalement nocturnes comme le Bec-en-ciseaux noir, le Pluvier de Wilson et le Bihoreau violacé ont une très faible capacité de vision diurne et montrent une plus grande convergence dans leur rétine que les oiseaux strictement diurnes.

2- Les oiseaux strictement diurnes comme le Héron garde-boeufs, l'Aigrette tricolore et l'Ibis rouge ont la plus forte densité de cônes et la meilleure vision photopique parmi toutes les espèces analysées.

3- Les oiseaux qui s'alimentent de jour et de nuit comme l'Échasse d'Amérique, le Chevalier semipalmé et le Bécassin roux possèdent une rétine structurée différemment selon la stratégie d'alimentation qu'ils utilisent le plus souvent.

4- Les espèces qui s'alimentent visuellement durant le jour comme le Héron garde-boeufs et l'Aigrette tricolore ont une zone rétinienne spécialisée ayant une grande concentration de cônes permettant une meilleure acuité visuelle, contrairement à celles qui sont tactiles ou visuelles nocturnes.

5- La rétine des oiseaux strictement tactiles a une plus faible densité de photorécepteurs que celle des oiseaux visuels, à l'exception du Bec-en-ciseaux noir, strictement nocturne. Malgré cela, la rétine des chasseurs tactiles est autant susceptible à des changements dus à l'adaptation à un style de vie (diurne ou nocturne) que celles des chasseurs visuels.

6- Les Charadriiformes analysés ont une plus grande sensibilité rétinienne que les Ciconiiformes, une caractéristique qu'ils ont developpée probablement au cours de leur adaptation à la vie nocturne. La plupart des limicoles sont actifs le jour et la nuit.

Il serait intéresant de prendre en considération les relations phylogénétiques qui existent entre les espèces qui viennent d'être discutées. Le Pluvier de Wilson, l'Échasse d'Amérique et le Bihoreau violacé sont des espèces phylogénétiquement éloignées (Sibley et Ahlquist, 1990) mais qui montrent une convergence en ce qui concerne la densité des bâtonnets, convergence qui pourrait s'expliquer par une adaptation à l'activité nocturne. Le Bihoreau violacé, notre héron nocturne, diffère des trois hérons diurnes de notre étude par sa grande densité de bâtonnets, justifiant ainsi sa classification par Hancock et Elliot, (1978) et Hancock et Kushlan (1984) parmi les hérons nocturnes, malgré que Sheldon (1987) et Katzir et Martin (1998) considèrent les hérons nocturnes comme appartenant au même groupe phylogénétique que les hérons diurnes.

En résumé, ce travail de doctorat montre de façon aussi bien qualitative que quantitative les liens existant entre le mode de vie (nocturne, diurne), les stratégies d'alimentation (tactile et/ou visuelle), et la structure et fonction rétiniennes de certains limicoles et grands échassiers. Nous avons montré qu'à différentes conditions d'illumination scotopique et photopique les espèces se caractérisent généralement par des ERGs distincts et que leurs réponses physiologiques ont généralement une corrélation avec leur ratio de photorécepteurs et avec d'autres caractéristiques structurelles de leurs rétines. Nous avons constaté aussi que ces résultats ont une corrélation directe avec la période d'activité et la stratégie d'alimentation de ces oiseaux.

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