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Comparison of Rod/Cone Ratio in Three Species of Shorebirds Having Different Nocturnal Foraging Strategies

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Nocturnality, the habit of being active during darkness, is a characteristic of some aquatic birds, particularly those in the shorebird families (McNeil and Robert 1988, Robert and McNeil 1989, Robert et al. 1989; for detailed review concerning aquatic birds,

see McNeil 1991, McNeil et al. 1992, 1993). Two basic types of foraging techniques are used by shorebirds: visual searching for prey or indications of their presence, on or near the surface (e.g. *Pluvialis* and *Charadrius* plovers); and probing with the bill for buried prey that are detected by tactile and taste cues (e.g. Short-billed Dowitcher, *Limnodromus griseus*). Some species feed exclusively with the same foraging technique both by night and by day (e.g. visual searching by *Pluvialis* and *Charadrius* plovers, or tactile probing

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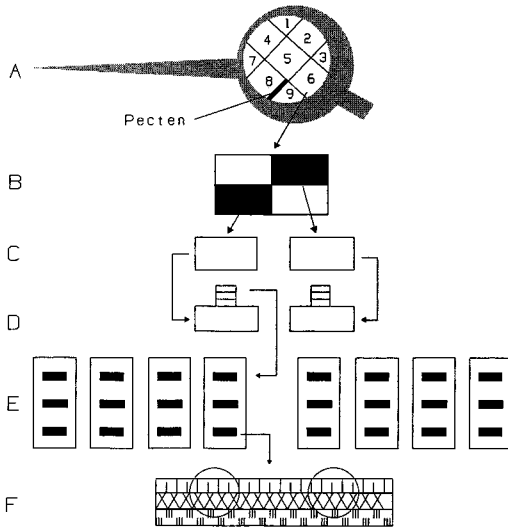


Fig. 1. Schematic representation of sampling methodology for counting rods and cones.

by Short-billed Dowitchers; Evans 1979, Pienkowski 1983a, McNeil and Robert 1988, Robert and McNeil 1989). Some species, such as the Semipalmated Sandpiper (*Calidris pusilla*; Evans 1979), are visual feeders under some conditions and tactile feeders under others (Schneider 1983). Moreover, some shorebirds modify their foraging strategies between night and day. Thus, oystercatchers (*Haematopus*; Hulscher 1976, 1982, Sutherland 1982) and *Tringa* species (Goss-Custard 1969, 1970, Evans 1979, McNeil and Robert 1988, Robert and McNeil 1989) are normally sight feeders during daylight, but switch to tactile foraging at night. During daylight and on bright moonlit nights, Black-winged Stilts (*Himantopus himantopus*) usually are visual peckers, but use scythelike sweeps of the bill (a tactile technique) on moonless nights or under low moonlight conditions (McNeil and Robert 1988, Robert and McNeil 1989).

Compared to visual "plover strategists," shorebirds that feed by touch (e.g. *Limnodromus*) should be relatively unaffected by darkness (Dugan 1981, Pienkowski 1981, Goss-Custard 1983). The presence of numerous touch-sensitive nerve endings (e.g. Herbst's corpuscles) at the bill tip (von Bolze 1968, Schwartzkopff 1973, Pienkowski 1983b; see also Martin 1990), in combination with a trigeminal expansion of the forebrain (Pettigrew and Frost, 1985, Boire 1989), favors touch feeding of many scolopacid species (*Limnodromus*, *Gallinago*, *Calidris*, etc.). In addition, taste (presence of taste buds at tip of beak) may play a role in locating areas rich in prey (Gerritsen et al. 1983, Van Heezik et al. 1983; see also Martin 1990).

Predominantly sight feeders such as *Pluvialis* and *Charadrius* plovers (Pienkowski 1982, 1983a), the Northern Lapwing (*Vanellus vanellus*; Spencer 1953,

Milsom 1984, Milsom et al. 1990), and the Black-winged Stilt (McNeil and Robert 1988, Robert and McNeil 1989) take advantage of the moonlight to forage at night (see also McNeil et al. 1992). According to Pienkowski (1982), Grey Plovers (*Pluvialis squatarola*) have pecking rates lower on very dark moonless nights, compared with daylight, but not on moonlit nights. However, plover strategists, such as the Ringed Plover (*Charadrius hiaticula*), apparently use sight as the main means of prey detection, even on dark nights (Pienkowski 1983a). Spencer (1953) and Hale (1980) reported that visibility of the moon is not required; Northern Lapwings (except under dense clouds in winter; see Milsom et al. 1990) and Eurasian Curlews (*Numenius arquata*) forage on overcast full-moon nights exactly the same as on completely clear nights. Consequently, an important question is: What allows plover strategists to forage visually during darkness?

The relatively large eye in relation to head size of plovers, compared to that of *Calidris* species, can be regarded as an advantage for feeding at night (Dugan 1981, Pienkowski 1983a, b). Crab-plovers (*Dromas*) and stone-curlews (*Burhinus*), which feed at night, and woodcocks (*Scolopax*), which perform acrobatic nocturnal display flights (see McNeil 1991), also have large eyes. According to Pienkowski (1983b), it is thought that plovers are mainly a low-latitude family that evolved under arid semidesert conditions where most prey are active only by night.

The retinal visual receptors of birds, as of all vertebrates, are rods and cones (Meyer 1977, Tansley and Erichsen 1985). Nocturnal birds have a great preponderance of rods in their retinas, while up to 80% of photoreceptors in diurnal birds are cones (Tansley and Erichsen 1985). If plovers are really sight feeders at night, we would expect them to have proportionately more rods than *Haematopus*, *Himantopus*, and *Tringa*—daylight sight feeders that switch to tactile foraging at night. The only reference concerning the rod/cone ratio in shorebirds is that of Rochon-Duvigneaud (1943). He claimed that rod numbers vary with the species in diurnal birds, but are high in *Charadrius hiaticula* and *Calidris alpina*; both species forage at night (Pienkowski 1983a, Batty 1991). The purpose of our study was to compare the rod/cone ratio of the Grey Plover, the Greater Yellowlegs (*Tringa melanoleuca*), and the Short-billed Dowitcher, species that have different foraging strategies.

One adult bird of each species was collected in coastal lagoons (Chacopata and Laguna de Patos) in the state of Sucre, northeastern Venezuela. In the field, within a few minutes of collection, the eyes were injected with 2.5% glutaraldehyde in 0.1 M phosphate buffer (pH = 7.2). In order to enhance the fixation, the eyes were then punctured at the cornea and placed in the same fixative for 30 min, the time needed for their transportation to the laboratory. Following immediate enucleation, the retina, still attached to the choroidal layer, was cut into nine sec-

tors, using the pecten as a landmark (Fig. 1A), according to the procedure of Meyer and May (1973). Each sector was subdivided into four portions (Fig. 1B) of which only two were retained for analysis (Fig. 1C). After 3 h in the fixative, the retinal portions were washed with phosphate buffer for 10 min. The total fixation time was less than 4 h. Tissues were postfixed in 1% OsO₄ in 0.1 M phosphate buffer for 1 h, rinsed in phosphate buffer followed by distilled water, for 10 min each, and dehydrated in grade alcohol series and propylene oxide. The tissues were successively infiltrated with a 1:1 mixture of propylene oxide-epon medium (LX-112) for 12 h, and pure epon medium for another 2 h. Finally, they were embedded in silicone rubber molds filled with epoxide resin (Fig. 1D) and polymerized in an oven (60°C) for 48 h.

Semithin sections of 0.7 μm thick were obtained with an ultramicrotome (Reitner-Jung, Ultracut-E) and stained with toluidin blue. For each retinal portion, 12 sections (one every 30–40 sections) were mounted on glass slides (Fig. 1E), resulting in 24 sections for each of the nine sectors. Sections were examined with a Zeiss photomicroscope. Rods and cones were counted in one or two fields, 238 μm wide (Fig. 1F), for a total of 45 counts per sector, or 405 per eye.

Mean rod and cone densities ($\bar{x}/100 \mu\text{m} \pm \text{SE}$) were calculated for each sector. Results were analyzed using a one-way analysis of variance (ANOVA) and Duncan's *a posteriori* multiple-range test (Nie et al. 1975).

The mean rod and cone densities and rod/cone ratios corresponding to each different retinal sector are given in Table 1. Rod and cone densities differ significantly between species (rods, $F_2 = 11.031$, $df = 2$ and 24 , $P < 0.001$; cones, $F_2 = 7.90$, $df = 2$ and 24 , $P < 0.01$). As indicated by the Duncan's *a posteriori* multiple-range test ($P = 0.05$), the greatest density of rods is found in the Grey Plover, followed by the Short-billed Dowitcher, while the greatest density of cones is in the Greater Yellowlegs, followed by the Grey Plover. Thus, the Grey Plover has the greatest rod/cone ratio, and the Greater Yellowlegs has the lowest. The density of rods and cones tends to be greater in some retinal sectors than in others, but our present objective was not to analyze the significance of such a difference.

Our starting hypothesis was verified; the Grey Plover, a diurnal and nocturnal sight feeder with larger eyes, has more rods and a greater rod/cone ratio than the Greater Yellowlegs, a daylight sight feeder that switches to tactile foraging at night. The Short-billed Dowitcher, a tactile forager both during day and night, is intermediate.

The electron microscope revealed that the outer segment of rods was longer in the Grey Plover than in the Greater Yellowlegs with the Short-billed Dowitcher being intermediate (Rojas de Azuaje 1991). Furthermore, these rods, with longer outer segments, are particularly abundant in some areas of the retina

TABLE 1. Mean rod and cone densities ($\bar{x}/100 \mu\text{m} \pm \text{SE}$, $n = 45$) and rod/cone ratios corresponding to different retinal sectors.

Retinal sectors	Rods	Cones	Rods : cones
Grey Plover			
1	16.9 ± 1.3	12.5 ± 1.5	1.4:1.0
2	17.2 ± 0.7	14.9 ± 0.8	1.2:1.0
3	18.5 ± 0.8	18.6 ± 0.7	1.0:1.0
4	17.1 ± 1.1	13.2 ± 2.2	1.3:1.0
5	19.3 ± 1.3	17.1 ± 1.9	1.1:1.0
6	17.8 ± 1.4	17.4 ± 1.7	1.0:1.0
7	17.0 ± 1.4	17.0 ± 1.7	1.0:1.0
8	16.3 ± 1.0	17.0 ± 1.4	1.0:1.0
9	16.8 ± 0.5	17.1 ± 0.5	1.0:1.0
Greater Yellowlegs			
1	12.3 ± 1.3	19.6 ± 4.6	0.6:1.0
2	13.2 ± 1.3	24.0 ± 1.8	0.6:1.0
3	13.4 ± 1.4	22.5 ± 1.4	0.6:1.0
4	13.8 ± 1.3	17.3 ± 1.8	0.8:1.0
5	14.1 ± 1.6	22.2 ± 1.5	0.6:1.0
6	18.4 ± 2.2	18.8 ± 2.3	1.0:1.0
7	11.6 ± 2.6	13.4 ± 1.8	0.9:1.0
8	12.2 ± 2.7	17.3 ± 1.3	0.7:1.0
9	11.5 ± 0.8	15.8 ± 1.5	0.7:1.0
Short-billed Dowitcher			
1	11.3 ± 1.0	11.6 ± 1.4	1.0:1.0
2	12.3 ± 0.9	14.0 ± 1.4	0.9:1.0
3	13.0 ± 1.0	14.4 ± 1.4	0.9:1.0
4	21.9 ± 1.0	15.9 ± 1.2	1.4:1.0
5	17.2 ± 1.1	16.0 ± 1.2	1.1:1.0
6	15.7 ± 1.7	15.5 ± 1.7	1.0:1.0
7	14.1 ± 1.1	13.9 ± 1.0	1.0:1.0
8	14.0 ± 1.1	14.1 ± 1.4	1.0:1.0
9	14.5 ± 1.0	14.5 ± 1.0	1.0:1.0

(equivalent to sectors 1 to 6 in our study; see Fig. 1) of the Grey Plover (Rojas de Azuaje 1991). According to Meyer (1977), "improved visual acuity in birds may be correlated with the presence" in the retina of areas "housing an extremely dense population of cones and rods." These so-called areas of acute vision "represent circumscribed thickenings of the retina brought about by an increase in the number of visual cells (predominantly cones)" characteristically longer than elsewhere in the retina (see also Walls 1942). The outer segments of the photoreceptors contain the visual pigments that are responsible for the absorption of light incident upon the retina (Meyer 1977). If areas of longer cones favor good visual acuity at high light levels (Meyer 1977), it seems likely that areas of longer rods would be associated with better low-light sensitivity.

From these results, it appears that the Greater Yellowlegs is less well adapted for nocturnal vision than either the Grey Plover or the Short-billed Dowitcher. For this reason, the Greater Yellowlegs may need to abandon its daytime sight-foraging strategy for a tac-

tile one at night, which may still be quite profitable since prey availability may be up to 10 times higher at night (Robert and McNeil 1989, McNeil et al. 1992). The Greater Yellowlegs, thus, uses a tactile side-sweeping strategy that differs from the tactile probing of the Short-billed Dowitcher but, as for the latter, it does not need to see its prey.

Cone density is highest in the Greater Yellowlegs, followed by the Grey Plover and the Short-billed Dowitcher, indicating particularly good visual adaptation in the Greater Yellowlegs, but for daylight only. Both the Greater Yellowlegs and the Grey Plover forage by sight during daylight. However, the Grey Plover feeds on slow-moving or sessile organisms (in coastal habitats on marine worms, small mollusks, crustacea, insects, etc.; in the interior on earthworms, seeds, berries, insects; Bent 1929), while the Greater Yellowlegs forages on fast-swimming prey on most occasions (water insects, small fishes, crustacea; Bent 1927). Consequently, it appears that a higher cone density would give the Greater Yellowlegs a good visual acuity for foraging on fast-moving prey during daylight.

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Extended Parent-Offspring Relationships in Greenland White-fronted Geese (*Anser albifrons flavirostris*)

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Continuing associations between parents and fledged offspring are uncommon among most bird species. They are, however, especially prevalent in territorial species with cooperative breeding (see Brown 1987). Although cooperative breeding has not been recorded in wildfowl, it has long been recognized that juvenile geese remain with their parents for at least part of their first year (Phillips 1916, Elder and Elder 1949, Hochbaum 1955). Guiding offspring

on migration to traditional staging and wintering sites and teaching offspring valuable foraging techniques and social skills, as well as the locations of safe and productive feeding and roosting sites, are common explanations for the prolonged parent-offspring relationships in migratory geese and swans.

Greenland White-fronted Geese (*Anser albifrons flavirostris*; Dalgety and Scott 1948) breed in West Greenland between 64° and 72°N, and winter exclusively