

# Nocturnal foraging in shorebirds

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Members of seven families of shorebirds forage both by day and by night in tropical and temperate latitudes. In some species, foraging takes place principally at dusk and at night. Some species appear to use their daytime territory at night. Some visually guided peckers and some long-billed tactile probers forage by the same preferred method both during the day and during the night. However, some long-billed species change from visual to tactile foraging between day and night. The roles of moonlight and bioluminescence in prey detection are discussed. Two main hypotheses can explain why shorebirds forage at night: (1) night feeding occurs only when the daytime feeding has been inadequate to meet the birds' energetic requirements; this is called the 'supplementary hypothesis'; and (2) birds prefer to feed at night because it provides the most profitable (most available prey), or safest, feeding opportunities. Day and night habitat segregation has been reported for wintering shorebirds.

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Miembros de unas siete familias de chorlos y playeros, tanto de regiones tropicales como templadas, se alimentan de noche y de día. En ciertas especies, el forrajeo ocurre principalmente al atardecer y de noche. Unas especies parecen usar de noche sus territorios de alimentación diurna. Ciertos cazadores visuales y ciertos cazadores táctiles de pico largo se alimentan de la misma manera de noche como de día. Sin embargo, otras especies de pico largo, cazadores visuales de día, cambian su estrategia y se alimentan táctilmente de noche. Se discute el papel jugado por las mareas, el alumbrado lunar y la bioluminescencia. Dos hipótesis principales permiten explicar porque las aves limícolas se alimentan de noche: (1) la alimentación nocturna ocurre únicamente cuando, al alimentarse solo de día, el ave no logra satisfacer sus exigencias energéticas, y así necesita de una alimentación suplementaria de noche; (2) la noche presenta las condiciones alimenticias más provechosas (mayor disponibilidad o actividad de presas) y más seguras y así las aves se alimentan de noche por preferencia. En lugares de invernada en región tropical, ciertas especies parecen alimentarse de noche en lugares diferentes de los que frecuentan de día.

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Les membres de quelque sept familles d'oiseaux de rivage, tant des régions tropicales que tempérées, s'alimentent de nuit et de jour. Chez certaines espèces, la chasse de proies se fait surtout au crépuscule et la nuit. Quelques espèces semblent utiliser de nuit les territoires d'alimentation qu'ils exploitent de jour. Certains chasseurs visuels et quelques chasseurs tactiles à long bec s'alimentent de nuit de la même façon que durant le jour. Cependant, d'autres espèces à long bec, chasseurs visuels de jour, changent leur stratégie et s'alimentent tactilement de nuit. Le cycle de la marée, l'éclairage lunaire et la bioluminescence jouent un certain rôle. Deux hypothèses principales permettent d'expliquer pourquoi les oiseaux de rivage s'alimentent de nuit: (1) l'alimentation nocturne a lieu uniquement quand, à s'alimenter seulement de jour, l'oiseau ne réussit pas à satisfaire ses besoins énergétiques, et ainsi a besoin d'une alimentation supplémentaire de nuit; (2) la nuit offre des conditions plus avantageuses (plus grande disponibilité ou activité des proies) et plus sécuritaires et ainsi les oiseaux s'alimentent de nuit par préférence. Sur les aires d'hivernage en régions tropicales, certaines espèces semblent utiliser de nuit des sites différents de ceux qu'ils fréquentent de jour.

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## Introduction

The habit of being active during darkness has been viewed as characteristic of a minority of bird species, with most considered entirely diurnal. Primary examples of activity in minimal light conditions are found in the Apterygiformes, Strigiformes, Caprimulgiformes and Apodiformes (Martin 1990). In shorebirds of the order

Charadriiformes, members of seven families forage regularly or mainly at night.

The behaviour of shorebirds during darkness is largely unknown. Night activities in shorebirds have been documented by direct observation only on rare occasions (Wood 1986; McNeil & Robert 1988; Robert & McNeil 1989; Robert, McNeil & Leduc 1989; Burger & Gochfeld 1991). This is due particularly to the difficulty of making observations

during darkness; however, with the recent development of night-vision light intensifiers, nocturnal observation of animals has become possible (see McNeil & Robert 1988; Robert & McNeil 1989; Robert, McNeil & Leduc 1989).

Because the main nocturnal activity reported to occur regularly in shorebirds is foraging, the important questions are: why forage at night? and what are the causes of selection for night activity in shorebirds? This paper overviews published information on (1) the occurrence of nocturnal foraging in shorebirds, (2) the special adaptations favouring such habits and (3) the suspected benefits these birds may get from foraging at night.

## Nocturnal foraging activity

### Who forages at night?

There are no reports that any shorebird forages exclusively at night. Yet there are many reports of species regularly foraging both during the day and during the night (Table 1). Such species include oystercatchers (*Haematopus*), plovers (*Pluvialis*, *Charadrius*), many *Calidris* species and most other Scolopacidae, the major family of shorebirds, and stilts (*Himantopus*). Other shorebird species are less likely to forage in full daylight but restrict their activity to twilight and night-time (Table 1). Such species include Painted Snipe *Rostratula benghalensis*, Crab Plover *Dromas ardeola*, Burhinidae (*Esacus*, *Burhinus*), coursers (*Rhinoptilus*), a few lapwing species (*Vanellus*), Inland Dotterel *Peltohyas australis*, woodcocks (*Scolopax*), a few snipe species (*Lymnocyrtus*, *Gallinago*, *Coenocorypha*) and Ruff *Philomachus pugnax*. Pratincoles (*Glareola*) and the Australian Courser *Stiltia isabella* are active mainly at dawn and dusk; the latter and the Common Pratincole *Glareola pratincola* continue foraging at night under moonlight conditions (Ali & Ripley 1981; Cramp & Simmons 1983). Shorebird mist-netting done on staging or wintering areas with better profit at night-time is another indication that some species are very active at night.

### Night-time foraging territories

During the non-breeding season, many species of shorebirds defend foraging territories (Myers, Connors & Pitelka 1979). Wood (1986) has shown that some Grey Plovers *Pluvialis squatarola* continue to use their feeding territories at night. Furthermore, there are indications that territories defended by Eurasian Curlews *Numenius arquata*, Willets *Catoptrophorus semipalmatus* and Whimbrels *Numenius phaeopus* during daylight were occupied by individuals of the same species during darkness (Cramp & Simmons 1983; R. McNeil, unpubl. data).

## Latitude and seasons

Except for the Painted Snipe, Crab Plover, Burhinidae, Glareolidae, lapwings and other species that reside year-round in the tropics, nocturnal activities in shorebirds have been reported almost exclusively for birds staging or wintering in coastal and estuarine habitats in temperate latitudes. Recent studies in Venezuela and Mauritania have shown that some Neotropical residents and Holarctic winter migrants feed at night in tropical environments (McNeil & Robert 1988; Robert & McNeil 1989; Robert, McNeil & Leduc 1989; Zwarts & Dirksen 1990; Zwarts, Blomert & Hupkes 1990; Morrier & McNeil 1991). There seem to be only a few exceptions, and sometimes there are regional variations. For example, the Curlew Sandpiper *Calidris ferruginea* forages at night in Australia (Dann 1981) but not in South Africa (Puttick 1979).

Most accounts of nocturnal feeding in northern Europe report that it is most intense during winter and less intense or absent in the early autumn and the spring (Goss-Custard 1969; Heppleston 1971; Pienkowski 1981a, 1982; Puttick 1984). In southern Portugal, Batty (1991) found that nocturnal feeding is the norm during the migration periods but much less common from November to March. In addition, the woodcocks are known to switch from their winter pattern of feeding at night to feeding only during the day in summer (Dunford & Owen 1973; Hirons 1988).

Almost nothing is known about the occurrence of nocturnal foraging in breeding shorebirds. However, in the tropics, Two-banded Coursers *Rhinoptilus africanus* are known to feed chicks mainly at night (MacLean 1967). In the northern latitudes, breeding Eurasian Dotterels *Charadrius morinellus* and Piping Plovers *Charadrius melodus* forage both during darkness and during daylight (Kalas 1986; K.J. Staine & J. Burger, pers. commun.).

### Foraging behaviour

Shorebirds use two basic types of foraging techniques (Table 1): visual searching (e.g. plovers) for prey items, or indications of their presence, on or near the surface; and probing (e.g. Short-billed Dowitcher *Limnodromus griseus*) with the bill for buried prey, which are detected by tactile and taste cues. While some species may feed exclusively with one of these techniques (e.g. visual searching by most plovers, or tactile probing by Short-billed Dowitchers), other species (e.g. Semipalmated Sandpipers *Calidris pusilla*) use both techniques, being visual in some conditions and tactile in others, according to food items and feeding habitats (see Goss-Custard 1970; Evans 1979; Schneider 1983). Pratincoles are a special group; they feed extensively by aerial hawking for flying insects (Brosset 1979; Hayman, Marchant & Prater 1986).

**Table 1.** Daytime and night-time foraging habits and strategies of shorebirds. DIU = diurnal; CRE = crepuscular; NOC = nocturnal; VIS = visual; TAC = tactile; (+) partly; (++) largely; (-) occasionally. Sequence of genera and nomenclature follow Hayman, Marchant & Prater (1986).

Families & genera	Foraging pattern				Foraging strategy				
	DIU	CRE	NOC	Principal references <sup>a</sup>	Day		Night		Principal references <sup>a</sup>
					VIS	TAC	VIS	TAC	
<b>ROSTRATULIDAE</b>									
<i>Rostratula</i>	-	++	+	1,2,3,4		+		+	1,4
<b>DROMADIDAE</b>									
<i>Dromas</i>	-	++	++	2,3	+		?		5
<b>HAEMATOPODIDAE</b>									
<i>Haematopus</i>	+	+	+	4,5,6,7,8,9	+			+	7,8,9
<b>RECURVIROSTRIDAE</b>									
<i>Himantopus</i>	+	+	+	2,10,11,12	++	+	+	+	10,11,13
<i>Recurvirostra</i>	+	+	+	2,4,13,14	+	+			13
<b>BURHINIDAE</b>									
<i>Burhinus</i>	+	++	++	1,2,3,4,15,16					
<i>Esacus</i>	+	++	++	1,2,16,17	++	-			17
<b>GLAREOLIDAE</b>									
<i>Rhinoptilus</i>	-	+	++	3,4,18			+		3,18
<i>Stiltia</i>	-	++	+	3,16					
<i>Glareola</i>	+	++		2,3,4,16,19				(text)	
<b>CHARADRIIDAE</b>									
<i>Vanellus</i>	+	+	+	1,2,3,4,20,21					
<i>Pluvialis</i>	+	+	+	2,4,22,23,24,25	++		++		26,27
<i>Charadrius</i>	+	+	+	10,11,12,26,28	++		++		1,26,27,28
<i>Thinornis</i>	+	+	+	3,29					
<i>Peltohyas</i>	+	+	++	3,30,31					
<i>Eudromias</i>	+	+	+	4,32,33					
<b>SCOLOPACIDAE</b>									
<i>Limosa</i>	+	+	+	2,22,26		++		++	26
<i>Numenius</i>	+	+	+	2,22,26,34,35	++		++		35
<i>Tringa</i>	+	+	+	2,10,11,12,36,37	++			++	
<i>Catoptrophorus</i>	+	+	+	12,38	++	+	+	+	38,46
<i>Actitis</i>	+	+	+	2					
<i>Arenaria</i>	+	+	?	22,39,40					
<i>Scolopax</i>	+	++	++	2,41,42,43					
<i>Coenocorypha</i>	-	++	++	3,44					
<i>Gallinago</i>	-	++	++	1,2,4,45					
<i>Lymnocyptes</i>	+	++	++	2					
<i>Limnodromus</i>	+	+	+	12,13		++		++	12,13
<i>Calidris</i>	+	+	+	2,12,22,26,40,47	+	+	+	++	26,38
<i>Micropalama</i>	+	+	+	12		++		++	38
<i>Philomachus</i>	+	+	++	1,2,4					

<sup>a</sup> 1, Ali & Ripley (1980–1981); 2, Cramp & Simmons (1983); 3, Hayman, Marchant & Prater (1986); 4, Urban, Fry & Keith (1986); 5, Swennen *et al.* (1987); 6, Heppleston (1971); 7, Hulscher (1976); 8, Sutherland (1982); 9, Goss-Custard (1983); 10, McNeil & Robert (1988); 11, Robert & McNeil (1989); 12, Robert, McNeil & Leduc (1989); 13, Hamilton (1975); 14, Gibson (1978); 15, Glue & Morgan (1974); 16, Pringle (1987); 17, Woodall & Woodall (1989); 18, MacLean (1967); 19, Brosset (1979); 20, Spencer (1953); 21, Milson (1984); 22, Evans (1976); 23, Dugan (1981); 24, Pienkowski (1981a); 25, Wood (1983); 26, Pienkowski (1982); 27, Pienkowski (1983a); 28, Pienkowski (1983b); 29, Phillips (1977); 30, MacLean (1976); 31, McNamara (1980); 32, Kalas (1986); 33, Nethersole-Thompson (1973); 34, Hale (1980); 35, Zwarts (1990); 36, Goss-Custard (1969); 37, Goss-Custard (1970); 38, R. McNeil, unpubl. data; 39, Schneider (1985); 40, Zwarts, Blomert & Hupkes (1990); 41, Hirons & Bickford-Smith (1983); 42, Sheldon (1961); 43, Hirons (1988); 44, Miskelly (1990); 45, Grisser (1988); 46, McNeil & Rodríguez S. (1990); 47, Manseau & Ferron (1991).

Some shorebirds may modify their foraging techniques between night and day. Thus, oyster-catchers (Hulscher 1976) and *Tringa* species (Goss-Custard 1970; McNeil & Robert 1988; Robert & 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* are usually visual peckers, but they use scythe-like sweeps of the bill (a tactile technique) on moonless

nights or under lower moonlight conditions (McNeil & Robert 1988; Robert & McNeil 1989).

### Foraging success

Compared with visual 'plover strategists', shorebirds that feed by touch both by day and by night should be relatively unaffected by darkness (Dugan 1981; Pienkowski 1981b; Goss-Custard 1983). It is very difficult to find out the proportion of attempts to capture prey that are successful at night. Some, but not all, authors have observed or assumed that the rate of prey intake is less at night than by day. For example, Heppleston (1971) and Goss-Custard & Durell (1987) found oystercatchers to be feeding less during darkness, but Hulscher (1976), Swennen, Leopold & De Bruijn (1989) and Swennen (1990) found no difference in average food consumption between hours of daylight and darkness. The case of some plover-like species is surprising. For example, Wood (1984) measured the time budget of a Grey Plover on its territory by day and by night and found no significant difference in the total time spent foraging and in the bird's peck rate in these two periods. Ingestion rates of Northern Lapwings *Vanellus vanellus* at night can be double those achieved during the day (McLennan 1979).

### Sensory adaptations, moonlight and bioluminescence

Shorebirds have visual or tactile adaptations that may enhance foraging at night. According to Dugan (1981) and Pienkowski (1983a, 1983b), the large eye in relation to head size of plovers, compared with that of sandpipers, is assumed to be an advantage for low light intensity. The Crab Plover, Burhinidae, coursers (*Rhinoptilus*) and woodcocks also have large eyes. In addition, the actual visual receptors of birds, as in other vertebrates, are rods and cones. Nocturnal birds have a great preponderance of rods in their retinae (Tansley & Erichsen 1985). The Grey Plover, a diurnal and nocturnal sight feeder, has more rods, a greater rod/cone ratio and longer rod outer segments than the Greater Yellowlegs *Tringa melanoleuca*, a daylight sight feeder that most of the time switches to tactile foraging at night (Rojas de Azuaje 1991). The Short-billed Dowitcher, a tactile forager during both day and night, is intermediate.

The presence of many touch-sensitive nerve endings (e.g. Herbst's corpuscles) in the bill tip favours touch feeding by many scolopacid species (*Limnodromus*, *Gallinago*, *Calidris*, etc.) (Bolze 1968; Schwartzkopff 1973, 1985). In addition, taste or chemoreception (presence of taste buds in the tip of the beak) may play a role in locating areas rich in prey (Gerritsen, Heezik & Swennen 1983; Heezik, Gerritsen & Swennen 1983). Finally, it has been

suggested that plovers may also use acoustic cues to locate prey (Fallet 1962).

Pienkowski (1982, 1983a) concluded that plovers use sight as the main means of prey detection, even on dark nights, and showed that, compared with daylight, Grey Plovers have lower pecking rates on dark moonless nights but not on moonlit nights. In addition, Double-banded Plovers *Charadrius bicinctus* in Australia roost for longer periods (and thus feed for shorter periods) during days that follow moonlit nights, suggesting that their energy intakes were greater on the moonlit nights (Dann 1981). Although the moon seems to influence nocturnal foraging activity for some species, it does not appear that moonlight *per se* is the proximate factor. Thus, for most of the lunar month, Northern Lapwings and Eurasian Curlews forage by day and roost at night. For a few days around the full moon period, the situation is reversed, even if the moon is not visible (Spencer 1953; Hale 1980). The significance of this is not known, but it may reflect an increased activity of prey items influenced by the lunar cycle.

Pienkowski (1983a, 1983b) suggested that shorebirds might take advantage of luminescent organisms at night. In a coastal lagoon of northern Venezuela, no relationship was found between the presence or absence of bioluminescence and the types of nocturnal foraging methods of shorebirds (McNeil & Robert 1988; Robert & McNeil 1989). The relationship could be indirect, if it were shown that prey (e.g. fishes) on which *Tringa* and *Himantopus* species feed at night (Robert & McNeil 1989) are attracted by luminescent organisms.

### Why forage at night?

There are two main hypotheses: (1) the 'supplementary hypothesis', suggesting that night feeding occurs only when the daytime feeding has been inadequate to meet the birds' energy requirements; and (2) the 'preference hypothesis', suggesting that birds prefer to feed at night because it provides the most profitable, or safest, feeding opportunities.

### Supplementary hypothesis

Tides may limit access to feeding sites regardless of prey abundance (Burger 1984), and thus shorebirds might be limited in their diurnal feeding time and need to feed at night to satisfy their energetic needs. However, even species not affected by tides may sometimes feed at night. For example, shorebirds feeding in coastal lagoons in northern Venezuela can feed all of the time, even during most high tides, yet many species feed by both night and day.

Activity patterns of birds are related to energetic needs, which vary during the annual cycle, and nocturnal feeding in temperate zones was first interpreted as a strategy to 'top up' an inadequate daytime energy intake. In temperate latitudes, energy requirements are generally higher during winter, and most accounts of nocturnal feeding by shorebirds in northern Europe report that it is most intense during winter and less intense or absent in early autumn and spring (Goss-Custard 1969; Heppleston 1971; Goss-Custard *et al.* 1977; Pienkowski 1981a, 1982; Puttick 1984). In winter, there is less daylight time available to search for food, and prey availability may decrease because intertidal invertebrates move deeper within the sediment (and sometimes are less active) as temperature falls (Goss-Custard *et al.* 1977; Pienkowski 1982). In the tropics, these factors do not apply, yet several shorebirds feed regularly at night (Robert & McNeil 1989). In some tropical situations, *e.g.* mudflats in Mauritania, daytime prey abundance is low, and feeding in daylight alone is sometimes insufficient for shorebirds to achieve their daily energetic needs (Engelmoer *et al.* 1984).

Finally, we suspect that, even in the tropics, the occurrence of nocturnal feeding may be greater when migratory species have higher energetic demands (Myers & McCaffery 1984) — for instance, during the time of pre-migratory fattening, when refuelling at a stop-over place or when landing after a long oversea flight. The higher incidence of nocturnal feeding during pre-migratory or migration periods in southern Portugal (Batty 1991), Mauritania (Zwarts, Blomert & Hupkes 1990) and northern South America (Morrier & McNeil 1991) provides support to the supplementary hypothesis.

### Preference hypothesis

Some species may take advantage of increased availability and activity of prey at night (Dugan 1981; Pienkowski 1983a, 1983b; Townshend, Dugan & Pienkowski 1984; Evans 1987; Robert & McNeil 1989). It may even be advantageous for shorebirds to feed at night at sites and on prey that are not used during the day (Evans & Dugan 1984; Townshend, Dugan & Pienkowski 1984; Robert & McNeil 1989; Robert, McNeil & Leduc 1989). At some sites, the abundance or activity of prey is higher at night than during daylight (Evans 1987; Robert & McNeil 1989). Black-winged Stilts and *Tringa* species use such sites principally at night and seem to feed then on food items (fishes, Pelecypoda and Hemiptera) at least partly different from those they foraged for during daylight (Robert & McNeil 1989). The use of different day and night habitats might be a fundamental requirement for wintering shorebirds, at least in some regions.

Nocturnal activities in shorebirds may be related to the avoidance of diurnal predators or other kinds of diurnal disturbance. Although the effect of human disturbance has been little studied, Sanderlings *Calidris alba* avoid disturbance by people on Florida beaches, and thus increase the time they feed at low tide, by feeding at night (Burger & Gochfeld 1991). In the Chacopata Lagoon (Venezuela), small bays surrounded by mangrove woodlands are used for feeding by shorebirds much less frequently by day than by night. This is in spite of the fact that they are very rich in prey at all times. During the day, the birds congregate on vast, open mudflats, apparently to avoid predation by Peregrine Falcons *Falco peregrinus* (Robert, McNeil & Leduc 1989). Also in the same lagoon, Wilson's Plovers *Charadrius wilsonia*, in spite of the *Uca* crab abundance, forage very little during daytime; daylight prey intake alone is insufficient to balance their energy budget, and the fact that they forage mainly at night appears related to predator avoidance during daylight (Morrier & McNeil 1991). In north-eastern Africa, Painted Snipes feed at times during the day if the area is undisturbed by humans and other mammals, although only where cover is plentiful (A.J. Tree, *vide* Cramp & Simmons 1983).

During the winter in northern latitudes, Common Snipes *Gallinago gallinago* (Grissler 1988) and woodcocks (Dunford & Owen 1973; Hirons 1988) roost in woodland in daytime but feed on pastures at night. The switch to night feeding in the open habitats may reflect increased vulnerability to predators in these situations during the day. According to Cramp & Simmons (1983), Pintail Snipes *Gallinago stenura* feed mainly at night but may feed during daytime, if undisturbed.

### Conclusions

Nocturnal foraging in shorebirds may be considered as a behaviour that evolved in different groups of species for different reasons and whose occurrence is governed by a variety of factors. For the more terrestrial species, nocturnal foraging occurs regularly and seems to be preferred to feeding by day. For the majority of species and populations, however, foraging at night seems less preferred and probably less efficient than foraging by day. However, the use of open habitats by these species, and their ability to locate prey by tactile cues, have given them the option of feeding at night should energetic demands not be satisfied by daytime feeding. Thus, these birds have a flexibility in foraging strategy that few other avian groups possess. Nocturnal feeding is important for the successful completion of the annual cycle in many populations of shorebirds and so should be taken into account in any conservation measures. The indication that some shorebirds feed nocturnally at sites and on prey that are not used

during the day could demand the protection of some wintering habitats less densely populated by shorebirds during the day but more intensively used at night. Many authors have dealt with time-activity or energy budgets of shorebirds. However, nobody seems to have taken nocturnal activities into account. Most information on the time and energy budgets of shorebirds needs to be revised, bearing in mind their nocturnal activities.

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