Predator avoidance in night-feeding Dunlins *Calidris alpina*: a matter of concealment

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The anti-predator behaviour of night-feeding Dunlins *Calidris alpina* was studied on a tidal flat in the Danish Wadden Sea. The observations indicated that Dunlins at night depress vocalization compared with day-feeding birds. Moreover, when Dunlins were approached by a raptor during day-time almost all took flight. In contrast, when Dunlins were disturbed at night only about 60% took flight, while most of the remaining birds froze. It is suggested that depressed vocalization and freezing at night are means to escape detection by owls. How the behavioural dichotomy (freezing and escape) during nocturnal disturbance is accomplished and how it affects the spacing behaviour of night-feeding Dunlins are discussed.

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Introduction

Shorebirds utilizing tidal areas in the non-breeding season are highly vulnerable to visually hunting predators (mainly raptors) because of the open nature of the habitat. Consequently, shorebirds must rely on their ability to detect a predator and escape before it becomes a threat. In this context, their visual power is of crucial importance, and is the basis for flocking and cooperative vigilance behaviour as predator avoidance in day-feeding shorebirds (for references, see Lima and Dill 1990).

Night-feeding is, however, widespread among shorebirds (Burger 1984, Goss-Custard 1984, Pienkowski et al. 1984, Robert and McNeil 1989, McNeil in press). Most evidence points at inadequate energy intake during daytime, or higher prey availability at night, as factors triggering nocturnal foraging. However, observations also suggest that some waders feed at night to avoid diurnal predators (Robert et al. 1989, McNeil in press). Even if avoidance of raptors could be an additional benefit of nocturnality in some species, night-feeding is not necessarily safe. At night, owls may pose

a serious threat to shorebirds (Page and Whitacre 1975, Kus et al. 1984, Mikkola 1983, Whitfield 1985). Anti-predator behaviour directed against such predators is therefore likely to occur and to differ from daytime behaviour. A difference between methods of diurnal and nocturnal predator avoidance is expected because owls use hunting techniques differing from those of diurnal raptors, and because cooperative vigilance behaviour in shorebirds is impaired at night, due to reduced visual abilities.

During a survey of the nocturnal foraging behaviour of Dunlins *Calidris alpina*, it was noticed that night-feeding Dunlins were more silent than day-feeding birds. Moreover, a considerable proportion of night-feeding Dunlins froze when disturbed. Although freezing in shorebirds has been reported before (Owens and Goss-Custard 1976, Myers 1980), it is very unusual among day-feeding birds (pers. obs., J. Frikke, pers. comm.), and has never been described as a significant nocturnal behaviour.

The aim of this study was to quantify these behavioural traits, and to evaluate possible functional explanations.

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Fig. 1. Calls heard per minute by day (○) and at night (●) as a function of Dunlin density. The daytime regression line is $y = 0.26x - 0.25$ ($r^2 = 0.97$, $t_{19} = 4.30$, $P < 0.001$). The night-time regression line is $y = 0.04x + 1.85$ ($r^2 = 0.32$, $t_{15} = 2.64$, $P < 0.025$). The intercepts do not differ from zero (day: $t_{19} = -0.44$, $P > 0.5$; night: $t_{15} = 1.63$, $P > 0.1$).

Study area and methods

All observations were conducted in September 1989 on a tidal flat near Højer in the southernmost part of the Danish Wadden Sea (54°56' N/8°39' E). An area situated on the border of an 80 ha large *Corophium*-bed (Reise 1978), was selected for study. During low tide, this bed consisted of alternating pools and emerged areas. The latter made up 56% of the entire area, on which the density of the amphipod *Corophium volutator* exceeded 100,000 ind m^{-2} . Throughout the study period, Dunlins were foraging at high densities on the *Corophium*-bed both day and night (Mouritsen unpubl.).

Potential predators on Dunlins recorded in the area included Marsh Harrier *Circus aeruginosus*, Hen Harrier *C. cyaneus*, Montagu's Harrier *C. pygargus*, Peregrine *Falco peregrinus*, Merlin *F. columbarius*, Kestrel *F. tinnunculus*, Eagle Owl *Bubo bubo*, Long-eared Owl *Asio otus* and Short-eared Owl *A. flammeus*.

Behavioural observations were made by frequency sampling of focal birds (Altmann 1974), using a Zeiss Orion image-intensifier (×8) at night and binoculars (×10) during day, both fixed on a tripod. Activity patterns (see Fig. 2) were recorded for periods of 15 minutes until a disturbance occurred and immediately after. Because the exact time at which disturbance occurred was unpredictable, behaviour recorded as *before* corresponded to observations collected within the last 15 minutes before the event actually took place. In addition, the distribution of focal birds in pools and upon emerged areas was recorded at night.

During day-time, disturbance was due to raptors. At night, unfortunately, the source of disturbance was unknown. The observation conditions allowed only a small

area to be surveilled, and during all events the centre of disturbance was located outside the field of vision.

In order to estimate diurnal and nocturnal vocalization in foraging Dunlins, calls that could be heard from the centre of a 1 ha marked square were counted over periods of 1–2 min. Only distinct calls were recorded, excluding the "soft twittering babble" often given by feeding birds (Cramp and Simmons 1983). After each count, the number of Dunlins present in the marked area was recorded, using a lamp at night to highlight the birds. Both day and night, Dunlins were evenly distributed at the study site, foraging at a distance of no more than 5 m from the observer. All data were collected at low tide ± 1 h and in light winds (0–2 Beaufort).

Results

There was, as expected, a positive correlation between the number of calls min^{-1} and the density of Dunlins both during day and night (Fig. 1). At night, however, the density of Dunlins only accounted for a small part of the variance in call rates. A comparison of the regression lines using analysis of covariance (Snedecor and Cochran 1989) revealed no heterogeneity of variance ($F = 1.42$, $df = 15, 19$, $P > 0.05$), but a significant difference between day and night regression coefficients ($F = 322.0$, $df = 1, 34$, $P < 0.001$). Hence, foraging Dunlins somehow depress their vocalization at night compared with during day-time.

The activity pattern of undisturbed Dunlins during the day and at night appeared very similar. However, the response when disturbed differed considerably (Fig. 2). When day-feeding Dunlins were approached by a raptor (in these cases Peregrine Falcon (1), Merlin (2), Kestrel (2) and Marsh Harrier (1)), almost all abandoned the *Corophium*-bed. In contrast, at night only about 60% fled in response to disturbance, and most of the remaining Dunlins froze more or less simultaneously. It was notable that Dunlins situated in pools (on average 22%) always took flight, whereas on the emerged areas only a part fled.

The freezing behaviour was expressed as a quick movement in which the bird flattened itself against the sediment with the head lowered and stretched out, so the tip of the bill rested on the sediment, and remained silent. This behaviour persisted for several seconds before the bird resumed foraging.

Discussion

In coastal areas owls frequently prey upon, and even specialize on, shorebirds (Page and Whitacre 1975, Kus et al. 1984, Mikkola 1983, Whitfield 1985). Page and

Fig. 2. Frequency of different behaviours performed by focal Dunlins by day (light bars) and at night (dark bars) before (A) and immediately after (B) a disturbance. Day: $n = 6$; 50–87 birds per count. Night: $n = 6$; 23–53 birds per count. * denotes significant difference between day and night (Mann-Whitney test, $T = 21$, $P < 0.01$).

Whitacre (1975) reported a high mortality (around 15%) in a wintering population of Dunlins in Bolinas Lagoon, California, due to owls. This is a considerable impact that emphasizes the need for anti-predator behaviour at night.

There is no evidence that Dunlins have visual adaptations to nocturnal light conditions, as suggested for, e.g., plovers (Dugan 1981, Pienkowski 1983a, b). At night, Dunlin vision may be seriously reduced and early detection of predators impossible. Thus, Dunlins must rely on other anti-predator behaviours, and the comparatively lower call rate in night-feeding birds (Fig. 1), could be interpreted as a means of escaping detection by owls. Especially the genera *Asio* and *Bubo* – both recorded in the study area – have morphological modifications enhancing hearing, which is an important means of detecting the prey (Mikkola 1983). It may therefore be selectively advantageous for the individual to minimize vocalization, and thereby the risk of detection. Treisman (1975) has made similar suggestions based upon theoretical predictions. Alternatively, a decreased aggression level in night-feeding Dunlins compared with day-feeding birds may reduce the frequency of “cheerp”-calls, which often occur during intraspecific interactions (Cramp and Simmons 1983). Moreover,

increased tactile foraging (probing) at night could depress vocalization, as birds that have their bill submerged in mud are probably prevented from calling. However, aggression levels neither seemed to differ between day and night, nor to reach a level that would explain the observed difference in vocalization (Fig. 2). Dunlin at night allocate less than 20% of the foraging time to probing (unpubl. data). Even if Dunlins do not probe at all by day (which they do), a 20% reduction in day-time vocalization would preserve the significant difference between day and night regression coefficients shown in Fig. 1.

Obviously, the observed freezing behaviour is an anti-predator strategy directed against nocturnal predators. By using this behaviour Dunlins rely exclusively on concealment and obtain some benefits in relation to owls' ability to detect their prey. Owls' vision is very sensitive to both low light intensities and movements, but visual resolution is comparatively poor (Mikkola 1983). Therefore, to escape owls, a reasonable response would be to lie down thereby concealing the light underparts, freeze and remain silent. During day-time, freezing is probably less advantageous because raptors may be able to see even a sedentary bird very easily. From above the substrate tends to reflect the colour of the sky, which makes the dark upperparts of Dunlins readily detectable (*sensu* Owens and Goss-Custard 1976). However, the freezing behaviour is only an alternative strategy because a large proportion of the Dunlins in fact fled when disturbed (Fig. 2). At night, most Dunlins could not be aged, but by highlighting the birds it was observed that adults, still partly in breeding plumage, occurred both among the freezing and the fleeing birds. This suggests that the behavioural dichotomy is not age-dependent (e.g., juveniles freeze, adults escape). Racial differences are also unlikely since *C. a. alpina* in autumn totally outnumber other subspecies in the Wadden Sea (Boere and Smit 1981). Instead, individual assessment of costs and benefits attached to each strategy may be involved. Dunlins that freeze obtain several energetic benefits compared with those that flee. Freezing birds remain in an optimal feeding habitat (Mouritsen unpubl.), lose only little feeding time, and save energy otherwise used by fleeing. Moreover, it is well established that shorebirds feeding on *Corophium* depress the activity and thereby the accessibility of this food item (Goss-Custard 1970, Selman and Goss-Custard 1987). Because most of their conspecifics leave, the staying Dunlins may experience increased foraging success due to reduced interference. As a counterbalance to these benefits, staying birds are most probably exposed to a comparatively higher predation risk, in defiance of the freezing behaviour due to the proximity of a presumed predator and reduced dilution effect (e.g., Hamilton 1971, Dehn 1990). The freezing behaviour thus optimizes foraging, whereas fleeing optimizes predator avoidance. Contrary to fleeing birds, Dunlins that freeze could be individuals that for various reason

have high energy demands and thus choose the high risk strategy to obtain the forthcoming benefits if they escape predation. Such a difference in priority of conflicting demands (foraging and predator avoidance), has previously been observed in Ruddy Turnstone *Arenaria interpres*, where migratory birds in contrast to resident birds allocate more time to feeding at the expense of anti-predator behaviour during pre-migratory fattening (Metcalf and Furness 1984). Even if the Dunlins are pre-determined for a certain strategy, there must nonetheless be a trade-off between freezing and escape mediated through assessment of the actual predation risk. This could explain why individuals situated in pools always took flight. Because Dunlins often lie down to preen in pools, inconvenience caused by performing the freezing behaviour in water may not be the reason for escape. Instead, reflection and movements of the water surface make birds in pools very conspicuous and thus expose them to a comparatively high predation risk. Consequently they take flight.

Regardless of how these strategies are accomplished, consecutive attacks upon night-feeding Dunlins certainly will break up tight flock structures. The opposite applies to day-feeding birds, in which attacks normally result in flocking (e.g., Caraco et al. 1980, Myers 1980, Elgar 1986, Whitfield 1988). At night, a loose flock structure may be allowed, primarily because concealment as a predator avoidance (freezing, depressed vocalization) does not necessitate large and tight flocks to be efficient, contrary to the cooperative evasive behaviours used in day-time. Secondly, spacing out may enhance predator avoidance per se when animals are hunted by sound (Treisman 1975).

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