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The diurnal and nocturnal foraging behaviour of Dunlins *Calidris alpina* was investigated during their autumn migration in the Danish Wadden Sea. Dunlins fed regularly by both day and night. However, they tended to utilize different habitats during daytime and night-time, with relatively more birds aggregating on soft sediment containing high densities of *Corophium volutator* at night. Pecking was the dominant foraging technique during the daytime, whereas probing was the preferred technique at night. Dropping analysis revealed quantitative differences between the birds' diurnal and nocturnal diets. It is proposed that nocturnal foraging may be important for restoring fat deposits in migrating birds.

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Nocturnal foraging in shorebirds has frequently been reported (Goss-Custard 1984, Burger 1984, Manseau and Ferron 1991, see McNeil et al. in press for details). However, because of the obvious difficulties in obtaining detailed observations during darkness, little is known about the relative importance of night-feeding or the particular techniques involved. Night-feeding has been reported for wintering shorebirds in English estuaries and, recently, from tropical environments (Robert and McNeil 1989, Robert et al. 1989, McNeil et al. in press). In these areas, night-feeding is mainly thought to compensate for insufficient energy intake during daylight, either because of low temperatures and short day-lengths in temperate latitudes in winter (Goss-Custard 1969, Heppleston 1971, Goss-Custard et al. 1977, Pienkowski 1981, 1982, Puttick 1984), or low prey availability because of desiccation of the substrate in the tropics (Engelmore et al. 1984, McNeil et al. in press). Increased prey availability at night is also considered to promote a preference for night-feeding (Dugan 1981, Pienkowski 1983a, Evans 1987, McNeil and Robert 1988). During migration periods, night-feeding may be connected with deposition of body fat (Batty 1988, Zwarts et al. 1990, Morrier and McNeil 1991).

Occasionally, shorebirds utilize different foraging sites

by day and night, this being explained by changed prey availability or vulnerability to predators (Townshend et al. 1984, Roberts et al. 1989). Feeding techniques may also differ between day and night. A switch from visual searching by day to more tactile prey detection at night is the usual pattern (Goss-Custard 1970, Hulscher 1976, Robert and McNeil 1989). Such differential use of habitats and feeding mode might be expected to affect the birds' diurnal and nocturnal diets, but this aspect is presently poorly known (see Robert and McNeil 1989).

During migration, Dunlins *Calidris alpina* are the most abundant shorebird species in the Danish Wadden Sea (Laursen and Frikke 1984). To achieve a more complete picture of the birds' impact on this ecosystem their nocturnal behaviour has to be known. The present paper reports on the Dunlins' diurnal and nocturnal preference for habitat, foraging technique and prey.

Materials and methods

Study area

The study was carried out at Højer tidal flat in the southern part of the Danish Wadden Sea (54°56'N, 8°39'E) in

September and October 1989. Two transects, each 100 m wide and 400 m apart, were established perpendicular to the coastline on a homogeneous mudflat (1500 m intertidal zone) and across a well-developed *Corophium*-bed (Reise 1978), respectively. The *Corophium*-bed was situated in the upper intertidal zone expanding from MHWL (mean high water level) to 800 m seaward, and which at low water comprised alternating emerged areas and pools. Four sites on the mudflat (400, 600, 800 and 1000 m from MHWL), and two sites on the *Corophium*-bed (400 and 600 m from MHWL), each 1 ha, were chosen as sampling and census sites.

Bird counts

The density of foraging Dunlins was recorded on all sites at maximum low water (± 1 h) during nine diurnal and nine nocturnal low tides. During daytime, the birds were observed using a telescope ($\times 25$), whereas at night a Zeiss Orion image-intensifier (intensifying capacity $> 40,000\times$) or a lamp to highlight the birds (on dark nights) was used. Brief illumination did not affect the birds in any notable manner. To ascertain whether Dunlins were feeding at night also outside the main study site, three other sites scattered along the 5 km shoreline were regularly visited during nocturnal low tides to determine the presence or absence of feeding Dunlins.

The overall population of Dunlins feeding at Højer tidal flat was estimated by counts along the 5 km shoreline about 1 h before maximum low water. On two occasions (around full moon and new moon), the tide receded at sunset. This made it possible to estimate the population of feeding Dunlins at the tide edge prior to a nocturnal low tide period and compare these figures with daytime records obtained a few days later.

Foraging technique

The Dunlins' diurnal and nocturnal foraging techniques were investigated on the *Corophium*-bed at maximum low water (± 1.5 h) on two days, two moonlit nights (full moon), and one dark night (half moon, clouded). Total sampling time was 327 minutes. The foraging behaviour of individual birds was observed over periods of usually 1 min using the telescope by day and the image-intensifier at night, and the observations were tape-recorded. The observed birds were observed *ad libitum* as they entered the field of vision. Feeding attempts and paces were recorded separately since the birds' fast-moving behaviour made simultaneous observations difficult. Foraging attempts were assigned to one of four categories: pecks (the bill inserted 0–1 cm into the sediment), intermediate probes (bill half inserted; 1–2 cm), deep probes (entire bill inserted; 2–3 cm), and drilling (probing several times at the same site), the latter being analyzed as a single feeding event. Because the proportion of deep probes

may increase as the intertidal flat dries up (see Boates and Smith 1989), observations were evenly scattered throughout the observation period to avoid biased data. No attempt was made to measure the Dunlins' foraging success directly.

Dropping analysis

Pellets regurgitated by Dunlins were never found in the study area. Faecal droppings were therefore collected to examine the Dunlins' choice of prey. Droppings were sampled in pools of 20, and subsequently stored in 80% ethanol. Diurnal and nocturnal collection was conducted on both transects around the time of full moon and half moon (clouded). On the bed, identification of droppings was straightforward since the Dunlins were the only sandpipers present prior to collection. The presence of some Ringed Plovers *Charadrius hiaticula* on the mudflat, particular at night, made it necessary to follow the Dunlins closely to ensure that the correct droppings were collected. As this procedure proved to be difficult on dark nights, night faeces were sampled only on moonlit nights on the mudflat.

The samples were analyzed in the laboratory using a stereomicroscope. Prey species were identified by means of mandibles, acicules, chetae, and tubes (Polychaeta); shell fragments (Molluscs); exoskeletons and setae (Crustaceans); scales (Pisces). The fragments were quantified in the case of molluscs (no. of shell fragments), crustaceans (no. of exoskeleton fragments) and *Nereis diversicolor* (no. of mandibles and acicules). To identify smaller chetae and setae, a subsample was withdrawn from each bulk sample and analyzed under a light microscope.

According to Worrall (1984), dropping analysis is not recommendable if the relative importance of various prey items has to be evaluated. Obviously, droppings contain only indigestible material, and soft-bodied prey items without conspicuous hard parts (e.g., oligochaets and amphipods) may be seriously underestimated. Furthermore, most indigestible fragments are voided orally, and only the smaller fragments pass into the droppings, so causing the quantification of hard parts to be biased (Worrall 1984). It is, however, reasonable to expect a positive relationship between the number of a specific prey species ingested and the amount of indigestible hard parts passing into the droppings. So, as long as hard parts are quantified to determine the relative importance of a certain prey between different areas or at different times the approach should be valid.

Invertebrate sampling

To determine the density of infaunal prey, 5–10 sediment cores (50 cm², 25 cm deep) were collected randomly at each study site. Samples were sieved in the field through

Fig. 1. Density of foraging Dunlins during daytime and night-time at the study site. Mean numbers per ha ($\pm$ SE) at low water are given. (A) The mudflat ($n = 9$), (B) the *Corophium*-bed ($n = 8$). Light and dark bars denote densities at diurnal and nocturnal low tides, respectively. MHWL = mean high water level.

a 500 μ m mesh and retained organisms were fixed in 10% formalin.

The diurnal and nocturnal surface activity of invertebrates was recorded on the *Corophium*-bed (600 m, emerged areas) and on the mudflat (800 m) at maximum low water. The number of individuals present at the surface within either a 0.01 m², 0.04 m² or 0.16 m² frame (depending on the density of the species involved) were counted in ten plots at each site. In addition, the sediment (at 1 cm depth) and air temperatures were measured. Specimens of *Corophium volutator* crawling on the sediment surface were collected on the *Corophium*-bed (600 m, emerged areas) at maximum low water during three diurnal and three nocturnal low tides. The animals were stored in 10% formalin and their length (rostrum to telson) measured in the laboratory. Since almost equal numbers were collected at each low tide, the diurnal and nocturnal size distributions of surface active *Corophium* specimens obtained are based on pooled data.

In order to determine the diurnal and nocturnal availability of *Corophium* to the Dunlins, a "sample-sledge" was used to plane off the upper sediment strata. The sledge was pushed over the substrate (speed about 1 m s⁻¹), at a distance of c. 1.5 m from the user, thereby giving tube-dwelling animals minimal time to react to the disturbance. At the end of each track, the sledge contained the last 100 cm² of the sediment that was planed off. On two consecutive low tides, one diurnal and one nocturnal, five 1.5 cm deep and five 3.0 cm deep sledge samples were collected at maximum low water on the *Corophium*-bed (600 m, emerged areas) and treated as the other sediment samples collected.

Sediment analysis

Since the softness of the substrate is known to affect the distribution and foraging behaviour of shorebirds (Tjallingii 1972, Myers et al. 1980, Grant 1984, Kelsey and Hassall 1989, Mouritsen and Jensen 1992), the penetrability of the sediment was recorded on both transects (600 m on the *Corophium*-bed (emerged areas and pools); 400–1000 m on the mudflat) by using a penetrometer of own design. A conical steel rod (12.0 cm long, 0.2–1.0 cm diameter, 61.3 g) with scale markings was dropped from a standard height (180 cm) through a tube mounted on a stand. Penetrability was measured as the distance (cm) the rod penetrated the sediment.

Results

Distribution of foraging Dunlins

During all diurnal and nocturnal low tide periods in which the intertidal zone was visited, Dunlins were present in the main study area as well as on the other sites inspected. Records of birds feeding at Højer tidal flat at dusk prior to nocturnal low tides were roughly similar to those records obtained during diurnal low tides. At full moon c. 34,800 Dunlins were feeding at dusk compared with c. 41,350 in the daytime. At new moon, the figures were c. 23,650 and c. 26,450, respectively. Because birds feeding at dusk continued to do so after dark on all sites inspected, these observations suggest that the foraging activity by day and by night is of the same order of magnitude.

The diurnal and nocturnal densities of foraging Dunlins were different on the two transects (Fig. 1). Two-way

Table 1. The foraging behaviour of Dunlins during daytime, moonlit nights (full moon), and a dark night (half moon, clouded). Values are means ($\pm$ SE) [no. of birds observed]. Intervals of cm indicate the depth to which the bill was inserted. P: Normal approximated Wilcoxon two-sample test. ns = non-significant ($P > 0.1$), ** $P < 0.01$, *** $P < 0.001$. The difference between daylight and the dark night is significant at least on the 5% level if not otherwise indicated.

Behaviour	Day	P	Night (Moonlight)	P	Night (Dark)
Peck/probe s ⁻¹	1.1 (0.1) [40]	***	1.5 (0.1) [28]	**	1.7 (0.1) [62]
% Peck (0–1 cm)	66.4 (2.8)	**	55.2 (1.5)	***	40.0 (2.3)
Probe (1–2 cm)	20.5 (1.4)	ns	17.9 (1.3)	ns	16.7 (0.8)
			ns		
Probe (2–3 cm)	12.6 (2.0)	***	26.3 (1.0)	***	41.6 (2.2)
Drilling	0.6 (0.3)	ns	0.8 (0.2)	ns	1.8 (0.5)
Pace s ⁻¹	2.4 (0.1) [34]	***	3.0 (0.1) [33]	**	2.4 (0.1) [62]
			ns		

ANOVA performed on ln-transformed data (to obtain homogeneity of variance) showed that bird densities on the mudflat were significantly higher by day than at night ($F_{1,70} = 22.68$, $P < 0.001$, Fig. 1A). In contrast, densities on the *Corophium*-bed were significantly higher at night than in daytime ($F_{1,30} = 5.79$, $P = 0.023$, Fig. 1B). Comparison of all sites using one-way ANOVA followed by a SNK-test revealed that the *Corophium*-bed at night supported considerably more birds than any site on the mudflat ($F_{5,46} = 43.76$, $P < 0.001$; SNK-test, $P < 0.05$). During daytime, however, the pattern was less clear. The density at 600 m on the *Corophium*-bed was significantly higher than at all other sites ($F_{5,46} = 4.82$, $P = 0.001$; SNK-test, P

< 0.05), whereas no difference could be demonstrated among the sites on the mudflat and at 400 m on the *Corophium*-bed (SNK-test, $P > 0.05$). Estimation of bird-minutes on the two transects during a few diurnal and nocturnal low tide periods were in general agreement with the above distribution pattern (see Mouritsen 1991).

Foraging technique

The Dunlins' foraging rate (pecks or probes per second) was significantly higher on the dark night than in daytime (Table 1). Pecking was the predominant feeding tech-

Table 2. The Dunlins' diurnal and nocturnal diets. Values are mean number of prey fragments found in bulk samples of faecal droppings ($n = 20$). + denotes that the species is identified but not quantified. P: ns = non-significant ($P > 0.1$), * $P < 0.05$, ** $P < 0.01$ by Mann-Whitney test.

Species	<i>Corophium</i> -bed			Mudflat			P ¹	P ²
	Day	Night	P	Day	Night	P		
Polychaeta								
<i>Nereis diversicolor</i>	4.3	7.4	**	15.6	17.6	ns	**	**
<i>Nephtys</i> spp.	0	0	—	+	0	—	—	—
Phyllodoceids	0	0	—	+	+	—	—	—
Spionids	0	+	—	+	0	—	—	—
<i>Arenicola marina</i>	0	0	—	+	0	—	—	—
Gastropoda								
<i>Hydrobia ulvae</i>	37.5	11.9	**	43.8	10.4	**	ns	ns
<i>Retusa obtusa</i>	+	+	—	0	0	—	—	—
Bivalvia								
<i>Macoma balthica</i> / <i>Mya arenaria</i>	14.1	14.9	ns	31.5	25.9	ns	**	*
<i>Cerastoderma edule</i>	5.7	4.1	ns	24.3	31.4	ns	**	**
Crustaceans								
<i>Carcinus maenas</i>	0	0	—	2.4	0	*	*	—
<i>Corophium</i> spp.	1.6	4.0	**	0.9	1.1	ns	ns	**
Pisces	+	0	—	+	0	—	—	—
No. of bulk samples analyzed	16	18		20	7			

^{1,2} Comparison between the mudflat and the *Corophium*-bed by day¹ and at night².

Table 3. The densities of the most relevant invertebrate prey species on the *Corophium*-bed (600 m) and on the mudflat. Values are mean number per 50 cm² ($\pm$ SE). Densities were compared using one-way ANOVA (ns = non-significant, $P > 0.05$, * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$), followed by an SNK-test. Underlined values are not significantly different ($P > 0.05$). Data analysis was performed on $\ln(x+1)$ transformed data to ensure homogeneity of variance ($P > 0.05$).

Species	<i>Corophium</i> -bed		Mudflat				P
	Emerged area (n = 10)	Pools (n = 6)	400 m (n = 10)	600 m (n = 5)	800 m (n = 10)	1000 m (n = 5)	
Polychaeta							
<i>Phylodoce maculata</i>	0.1(0.1)	0	0	0.2(0.2)	0.4(0.2)	1.2(0.6)	**
<i>Nereis diversicolor</i>	1.2(0.4)	0.6(0.2)	0.3(0.2)	0.6(0.3)	0.1(0.1)	0.6(0.3)	*
<i>Pygospio elegans</i>	2.4(1.3)	0.8(0.4)	13.6(2.5)	4.2(0.7)	5.8(1.1)	5.8(1.5)	***
Mollusca							
<i>Hydrobia ulvae</i>	35.9(3.6)	124.0(15.7)	57.2(3.1)	131.8(11.8)	88.1(5.2)	150.8(28.5)	***
<i>Cerastoderma edule</i>	0.4(0.2)	0.3(0.2)	0	0.8(0.4)	1.7(0.4)	3.4(0.9)	***
<i>Macoma balthica</i>	0.9(0.4)	2.5(0.5)	2.7(0.4)	3.0(0.5)	2.5(0.4)	2.0(0.6)	**
<i>Mya arenaria</i>	1.1(0.5)	1.5(0.9)	0.1(0.1)	0.2(0.2)	1.8(0.7)	1.0(0.5)	ns
Amphipoda							
<i>Corophium volutator</i>	589.4(9.0)	46.7(12.3)	0.1(0.1)	0	0	0	***

nique in daylight, whereas deep probing was considerably more important in darkness, especially on the dark night. For all types of behaviour, except pace rate and proportion of intermediate probes, the Dunlins' foraging behaviour on moonlit nights occupied an intermediate position between daytime and the dark night.

At night, two rather distinct types of foraging behaviour occurred: a fast-moving pecking type, and a slow-moving probing type. An individual bird could perform these behaviours consecutively. Another notable feature of the Dunlins' nocturnal foraging behaviour was the occurrence of "double-pecks" made almost exclusively by the fast-moving birds. Such double-pecks were extremely rare in day-feeding birds regardless of a high peck rate.

Choice of prey

The Dunlins' diurnal and nocturnal diet is summarized in Table 2. Data from full and half moon periods are pooled, as no significant difference was found among quantified prey species (Mann-Whitney test, $P > 0.05$). *H. ulvae* and *Carcinus maenas* were more important prey by day than by night at the mudflat, whereas the other quantified species seemed equally important by day and night. On the *Corophium*-bed, *H. ulvae* was again more important during the daytime, while both *N. diversicolor* and *Corophium* were more important at night. The comparison between the two transects shows that bivalves and *N. diversicolor* comprised a larger part of the diet on the mudflat than on the *Corophium*-bed both by day and by night. In contrast, *Corophium* was more important on the *Corophium*-bed than on the mudflat, but only at night. In the daytime samples, no significant difference was found between the two areas. Analysis of droppings (light mi-

croscopy) revealed that all diurnal as well as nocturnal bulk samples from the *Corophium*-bed contained immense amounts of *Corophium* setae compared with those from the mudflat. Although these setae were not quantified, this obvious difference suggests that *C. volutator* is an important prey item when the Dunlins feed at the *Corophium*-bed, regardless of illumination level. Inclusion of more droppings in each bulk sample is required if soft-bodied amphipods are to be quantified reliably by fragments of exoskeletons.

Prey density and availability

The main difference between the *Corophium*-bed and mudflat was the dominance of the amphipod *Corophium volutator* on the former (about 118,000 m⁻² on emerged areas), whereas polychaete worms (except *Nereis diversicolor*) and molluscs tended to be most abundant on the mudflat (Table 3). The population of *C. volutator* found on the *Corophium*-bed comprised mainly younger individuals (median length: 2.8 mm; range: 1.3–8.6 mm; $n = 1150$). A comparison between the population density obtained by ordinary core samples and by the sledge samples (divided by two to obtain the sampling area of the corers) showed that 89.3% of the *Corophium* population were within the Dunlins' reach (the top 3 cm of the sediment) during the daytime, and 92.4% at night. No significant difference between day and night could be demonstrated (two-tailed z-test, $z_c = 1.85$, $P > 0.05$). However, the proportion of the population present in the upper 1.5 cm of the substrate was greater at night (69.8%) than by day (48.6%) ($z_c = 7.34$, $P < 0.001$), and comprised significantly larger individuals at night (median 2.8 mm; range: 1.3–7.8 mm; $n = 121$) than by day (median 2.2 mm; range: 1.3–8.2 mm; $n = 139$) (Kolmo-

Table 4. The diurnal and nocturnal surface activity of *Phylodoce maculata*, *Corophium volutator* and *Hydrobia ulvae* encountered on the sediment surface of the *Corophium*-bed (emerged area, 600 m) and the mudflat (800 m) at low water. Values are mean number per sample area (n = 10). Values in () are 95% CI, whereas values in [] show asymmetric 95% CL for log(x+1) transformed data. The proportion of the population (Table 1) which constitutes the surface active individuals is also given. N and F denote the dates of new and full moon, respectively. Temperature measurements were carried out only on the bed when both areas were censused.

	Date	<i>Corophium</i> -bed		Mudflat		Temperature (°C)	
		<i>Corophium</i>	<i>Hydrobia</i>	<i>Phylodoce</i>	<i>Hydrobia</i>	air	sediment
Day	13 Sep	0.6[0–1.0]	22.3(3.7)	0	45.3(2.3)	15.5	15.3
	23 Sep	1.0(0.5)	13.2(1.4)	0.1[0–0.2]	37.0(4.3)	19.0	18.9
	24 Sep	0	7.9(1.9)	0	41.1(3.8)	16.2	20.0
	25 Sep N	0.4[0–0.7]	4.3(2.2)			13.2	13.7
% of population		< 0.1	6–31	0–3	21–26		
Night	15 Sep F	3.1(1.6)	12.0(1.1)	0.6[0.1–1.0]	24.8(5.7)	12.9	13.0
	19 Sep	1.0(0.7)	32.0(5.3)	0.9(0.7)	21.8(2.8)	16.9	15.1
	23 Sep	3.2(0.9)	20.1(2.1)	0.4[0–0.7]	26.8(4.1)	14.3	13.6
	25 Sep	1.3(0.9)	15.2(2.4)			12.0	11.8
% of population		< 0.2	17–45	13–28	12–15		
Sample area (m ²)		0.16	0.01	0.04	0.01		

gorov-Smirnov test, $D = 0.30$, $P < 0.001$). *C. volutator* individuals crawling at the sediment surface during low water were larger at night than by day (Kolmogorov-Smirnov test, $D = 0.32$, $P < 0.001$), the median lengths being 5.0 mm (range: 2.1–8.3; $n = 130$) by day and 6.2 mm (range: 1.6–8.5 mm; $n = 122$) at night.

Of surface active species, only the polychaete *Phylodoce maculata*, the mudsnail *Hydrobia ulvae* and *Corophium volutator* occurred in numbers suitable for enumeration. On the *Corophium*-bed, no difference was found between the diurnal and nocturnal surface activity of *H. ulvae*, whereas there was a weak tendency for higher surface activity of *C. volutator* at night (Table 4). No daytime activities of *C. volutator* exceeded those at night, and on two nights the nocturnal activity was significantly higher than any activities found during daytime. On the mudflat, the surface activity of *H. ulvae* was significantly higher by day than by night, whereas the opposite tendency occurred for *P. maculata*. Inspection of the data in Table 4 does not suggest any relationship between the surface activity of invertebrates and air temperature, sediment temperature, or lunar cycle.

Sediment penetrability

On the *Corophium*-bed the mean sediment penetrability was 8.3 cm and 5.3 cm on the emerged areas and in the pools, respectively, whereas on the mudflat the mean values were between 4.5 and 4.9 cm ($SE = 0.1$ and $n = 30$ for all values). The ln-transformed data were compared using one-way ANOVA followed by a SNK-test. The sediment penetrability differed among sites ($F_{5,174} = 265.7$, $P < 0.001$), and was significantly higher on the *Corophium*-bed than at all sites on the mudflat ($P < 0.05$). Although the penetration scores exceeded the maximum probing depth of Dunlins (about 3 cm corresponding to

bill length), it is believed that the data show features also experienced by the birds.

Discussion

Present results suggest that during autumn migration Dunlins feed regularly at night, following the tidal cycle. However, they tend to utilize different habitats during daytime and night-time. At night, the birds congregated on the *Corophium*-bed, while day-feeding birds were more evenly distributed between the two transects. The available evidence regarding diurnal and nocturnal habitat use (see McNeil et al. in press) suggests increased prey availability at night as the decisive factor (Townsend et al. 1984, Roberts and McNeil 1989). In addition, reduced predation risk at night has been proposed to explain the finding that tropical shorebirds use foraging sites at night that are avoided during daytime (Roberts et al. 1989). This latter explanation can, however, be ruled out in the present study due to the proximity of the habitats. Dunlins are predominantly tactile feeders at night, this mode of feeding appearing to be less effective than visual prey detection (Evans 1986). To offset this disadvantage of tactile feeding, Dunlins should select nocturnal foraging sites that are characterized by high densities of infaunal prey in the upper sediment strata to maximize prey encounter during probing. Also, high sediment penetrability may be an important factor by reducing foraging costs when probing or by increasing the probing depth and, in turn, prey accessibility (Tjallingii 1972, Myers et al. 1980, Grant 1984, Kelsey and Hassall 1989, Mouritsen and Jensen 1992). Such conditions are achieved on the *Corophium*-bed where both the density and the average length of *Corophium* individuals occurring at or close to the sediment surface are greater at night

than during the daytime. In addition, the sediment on the *Corophium*-bed is extremely soft compared with the surrounding flat. Consequently, profitable *Corophium* individuals are easier (or cheaper) to catch at night.

Pecking predominated in day-feeding Dunlins, whereas probing prevailed at night. Traditionally, pecking and probing have been interpreted as visual and tactile foraging, respectively. Accordingly, the Dunlins are mainly visual hunters during the daytime and tactile hunters at night, as reported for several other shorebirds, e. g. *Tringa* spp. (Goss-Custard 1970, Robert and McNeil 1989). However, to claim a direct relationship between the proportion of pecks and the degree of visual prey detection may be too simplistic. Sandpipers have high densities of both mechano- and chemoreceptors in the tip of their bill (Gerritsen and Sevenster 1985, Martin 1990), and therefore surface pecks may be attempts at both tactile prey detection and visual prey captures. The peculiar double-pecks performed only by night-feeding Dunlins could be interpreted as a tactile "search-peck" followed by prey capture. However, despite their apparent reliance on tactile searching at night, the higher pecking rate on moonlit nights compared with the dark night suggests that Dunlins take advantage of the moonlight and feed at least to some extent by sight.

Apart from fish (probably *Pomatoschistus minutus*), the Dunlins' diet included well known prey species (see Ehlert 1964, Bengtson and Svensson 1968, Worrall 1984, Durrell and Kelly 1990). The difference in prey items selected by Dunlins during day and night supports the idea that mode of feeding was different. The greater importance of *H. ulvae* by day than by night, and the greater importance of *C. volutator* and *N. diversicolor* on the *Corophium*-bed at night than during the daytime, most probably reflect the birds' use of mainly visual and tactile searching by day and night, respectively. Because *H. ulvae* individuals are active at the sediment surface by day, they must be an easy prey to birds feeding by sight. Difference in prey choice between the habitats probably reflected variation in abundance of prey. However, the greater importance of *N. diversicolor* on the mudflat compared with the *Corophium*-bed, regardless of higher densities on the latter, might suggest that Dunlins have a "search-image" for *Corophium* when feeding on the *Corophium*-bed (*sensu* Goss-Custard 1977).

There are two main hypotheses explaining nocturnal foraging in shorebirds: the "supplementary hypothesis", i.e. shorebirds feed at night only when their daytime feeding has been inadequate to meet daily energy requirements, and the "preference hypothesis", i.e. shorebirds prefer to feed at night because it is more profitable (e.g. high prey availability) or safer (e.g. avoidance of diurnal predators) (see McNeil et al. in press for details and references). Since Dunlins apparently feed throughout both diurnal and nocturnal low tide periods, their foraging pattern supports the supplementary hypothesis, though it does not contradict the preference hypothesis. It seems probable that the Dunlins' nocturnal foraging be-

haviour was aimed at fat depositing, in accordance with previous studies showing higher incidence of nocturnal feeding during pre-migration or migration periods (Batty 1988, Zwarts et al. 1990, Morrier and McNeil 1991). The Danish Wadden Sea is the first major stop-over area during the birds' southward migration (Smit and Wolff 1981), and refuelling of fat deposits may be necessary.

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