Diurnal and nocturnal prey detection by Dunlins *Calidris alpina*

K. N. MOURITSEN *Institute of Biological Sciences, Department of Ecology and Genetics, Aarhus University, Ny Munkegade, Building 540, DK-8000 Aarhus C, Denmark*

Field experiments suggest that Dunlins rely on visual prey detection by day and tactile prey detection by night to a larger extent than observations of their foraging technique would initially indicate.

During daytime, many shorebirds are able to locate prey both by visual and tactile means.^{1–3} However, nocturnal foraging is common among several species of shorebirds and appears to be essential for the successful completion of their annual cycle.^{3–8} It may therefore be asked to what extent darkness hampers visual searching, forcing the birds to rely more on tactile prey detection. In some species, the nocturnal feeding technique itself reveals the sensory mechanism involved. For example, stitching used by Oystercatchers *Haematopus ostralegus* feeding on Cockles *Cerastoderma edule*,¹ and the scythe-like sweeps applied by some stilts, avocets and yellow-legs,⁹ almost certainly indicate tactile prey detection. Conversely, the characteristic stop-run-peck behaviour of plovers represents visual foraging.¹⁰ However, in many sandpipers, e.g. Dunlins *Calidris alpina*, the diurnal and nocturnal foraging methods are similar and provide few clues as to the senses involved.¹¹ Hence, it is difficult to ascertain the relative importance of visual and tactile prey detection during day and night. The present study was carried out in an attempt to clarify this question.

FIELD OBSERVATIONS

In September 1989, large numbers of Dunlins were observed to feed both by day and by night on a *Corophium*-bed situated in the

southern-most part of the Danish Wadden Sea (54°56'N, 8°39'E).¹¹ At low water, the *Corophium*-bed was composed of alternating emerged areas and pools, extending from mean high water level to 800 m down the shore. The non-submerged areas were inhabited by the amphipod, *Corophium volutator*, in densities exceeding 100 000 m², which corresponded to more than 90% of the entire population of infaunal macroinvertebrates.¹¹

On the upper shore, the interfaces between the emerged areas and pools were often steep, exposing 4–6 cm of almost vertical sediment edges. On these edges, numerous horizontally directed Dunlin probe marks were often observed especially at nocturnal low tides, whereas comparatively few were found on the top of the non-submerged areas. To explain this apparent preference for horizontal probing into the edges of the plateaux, it was hypothesized that the probability of a Dunlin encountering a *Corophium* specimen would be higher during horizontal probing than during vertical probing from above. Theoretical considerations support this hypothesis.

MODEL

Corophium volutator is a tube-dwelling species that makes 4–5 cm deep U-shaped burrows in the substrate, into which it retracts during low water.¹² For simplicity, consider a uniformly distributed population of *Corophium volutator*

inhabiting 4.0 cm deep burrows. Then imagine sediment cube (4 cm × 4 cm × 4 cm) which is dug out of the substrate and where a Dunlin is allowed to probe (Fig. 1). As the Dunlin's bill is about 3 cm in length,¹³ the probing bird is only able to penetrate (and reach prey within) 3/4 of the sediment cube from any direction (Fig. 1). Based on these assumptions, the Dunlin's probability of encountering a *Corophium* specimen by a single and randomly placed probe (3 cm deep), can be calculated for both a vertically and a horizontally probing bird:

$$P_v(\text{prey detection} \mid \text{vertical probing}) = 2Npa_b/A \quad (1)$$

$$P_h(\text{prey detection} \mid \text{horizontal probing}) = Nqa_c/A \quad (2)$$

where N = the number of *Corophium* specimens present in the sediment cube; p = the probability of encountering a *Corophium* specimen in the probed burrow section; a_b = the area of burrow entrances (mm^2); A = the total area (1600 mm^2); q = the probability that a *Corophium* specimen is within reach (assumed to be 0.75 in this model); and a_c = the touch area (mm^2) of the *Corophium* specimens present (length [rostrum to telson] × head width).

The values of P_v and P_h will depend on the density, size frequency distribution and depth distribution of the *Corophium* population as well as the area of tube entrances. Estimates of these parameters were obtained by analysis of core and sledge samples collected in the area (K. N. Mouritsen, unpublished data). Concentrating on the larger individuals (3–8 mm in

length), on average about 44 000 occurred per m^2 on the emerged areas. Thus $N=70$ in the considered sediment cube. A range of *Corophium* lengths were used for computing corresponding body width and tube diameter values from a body width-body length regression ($BW(\text{mm})=0.17 \text{ BL}(\text{mm})+0.19$; $r=0.92$; $df=65$; $P<0.001$) and a tube diameter-body length regression ($TD(\text{mm})=0.19 \text{ BL}(\text{mm})+0.25$; $r=0.84$; $df=23$; $P<0.001$), respectively. Estimates of a_c and a_b were then calculated using the length frequency distribution of the *Corophium* population. Analysis of sledge samples collecting the upper 3.0 cm of the sediment, showed that about 90% of the *Corophium* population were within the reach of vertically probing Dunlins both by day (89.2%) and at night (92.3%). Because there are two entrances to each tube p equals 0.45. Using these empirical estimates in Equations (1) and (2), $P_v=0.03$ and $P_h=0.10$. So, the probability of a Dunlin detecting a *Corophium* specimen by horizontal probing is three times greater than by probing from above. This also holds true if the entire *Corophium* population were accessible to the birds ($P=0.5$). Using $P=0.5$ as a conservative estimate, the ratio of P_h to P_v will be independent of *Corophium* densities, and the only critical parameter is the size frequency distribution of the amphipods affecting a_b and a_c . For *Corophium* individuals between 1 mm (juveniles) and 8 mm (large adults) in length, the ratio P_h/P_v varies between 1.8 and 3.8.

The model demonstrates that the probability of detecting a *Corophium* specimen by touch is considerably higher when birds are probing horizontally rather than vertically. It might be expected therefore that tactile-searching birds will be attracted to any exposed vertical sediment surfaces within the *Corophium*-bed.

EXPERIMENTS

Experiments were conducted in order to test the above prediction. During each of two diurnal low tides and two nocturnal low tides (one dark night and one moonlit night), about 20 footprints, 4–6 cm deep, were made on the emerged areas about 1 hr after exposure from the receding water. The resulting almost vertical sediment surfaces were without visual cues to indicate prey position (Fig. 2a). Just before high water, the number of probe/peck

Figure 1. Schematic outline of the sediment cubes (dimensions shown in cm) on which the described model is based (see text). Probing surface (P) and direction (large arrows) are indicated for vertical (a) and horizontal (b) probing birds. Shaded regions are beyond the reach of probing Dunlins.

Figure 2. Experimental footprints as they were found after diurnal (a) and nocturnal (b) low tide periods. Probe marks (1) and peck marks (2) as well as *Corophium* burrows (3) are indicated.

marks made by Dunlins was recorded within a 5 cm × 20 cm frame in footprints (vertical surface) and within a 10 cm × 10 cm frame on randomly selected plots on the emerged areas. Only footprints in which water did not collect were censused. To ensure that birds were feeding and actually encountered the footprints, the experimental area was observed using a telescope by day and a Zeiss Orion image-intensifier at night.

RESULTS

At night, the Dunlins showed a strong preference for the vertical sediment edges as probing sites (Fig. 2b). On both the dark and the moonlit night, the depressions became quickly occupied by probing birds, which vigorously defended their positions against intruding conspecifics. After nocturnal low tide periods, the median density of probe/peck marks was 74.0/100 cm² ($n=10$) within footprints, which was significantly higher than that found on the sediment surface outside footprints (3.8/100 cm², ($n=10$), Mann-Whitney U -test, $t=55$, $P<0.01$). During diurnal low tides, feeding Dunlins paid only occasional attention to such sediment topographic features (Fig. 2a). A median density of only 0.0 probe/peck marks per 100 cm² (range: 0–2,

$n=10$) were found in the footprints after diurnal low tide periods, which is considerably less than after nocturnal low tides (Mann-Whitney U -test, $T=55$, $P<0.01$). The medians are based on pooled data from the two nocturnal (dark and moonlit night) and the two diurnal low tide periods, as no difference could be demonstrated (Mann-Whitney U -tests, $T>25.5$, $P>0.05$; $n_1=n_2=5$ for all comparisons). It is unlikely that probe/peck marks became obscured or collapsed at different rates during night and day. The substrate inhabited by high densities of *Corophium* is made stable by the secretion of binding material by the amphipods.¹⁴ This causes probe and peck marks to be preserved unchanged in the sediment throughout diurnal as well as nocturnal low tides. In substrate not exposed to tides, peck marks have been seen to persist for more than 48 hr.

DISCUSSION

The marked preference for footprints as probing sites at night suggests that tactile foraging is of major importance at night, and that birds are able to select probing sites that should, in theory, increase the probability of encountering prey. The lack of attention given to footprints during daylight suggests that tactile prey detection is of relatively little importance at this time. Visually searching Dunlins should reject the footprints due to the absence of visual cues. As visual searching in Dunlins seems to be more successful with respect to prey encounter than tactile detection,² the former should be applied whenever possible. Observations of intensive probing in footprints during moonlit nights suggests that the vision of Dunlins is not improved sufficiently by the increased illumination level to enforce a decisive trade-off between tactile and visual prey detection.

More detailed observations of the Dunlin's foraging technique (probe/peck frequencies) in the same area, showed that the birds made deep probes more frequently at night (60%) than by day (33%).¹¹ Traditionally, probes and pecks by shorebirds are interpreted as tactile and visual foraging, respectively, and so the higher frequency of probes at night suggests increased tactile foraging compared with daytime. Although this interpretation is in general agreement with the present findings, the

change in probe/peck ratio fails to show the abrupt trade-off between day and night feeding techniques demonstrated here. This discrepancy may be explained partly by the occurrence of mechano- and chemoreceptors in the tip of a sandpiper's bill.^{15,16} Hence, surface pecks could represent tactile searching as well as attempts to intercept visually detected prey; the presence of peck marks in the footprints (Fig. 2b) found after nocturnal low tide periods supports this view. Likewise, probes may be taken as evidence of tactile searching as well as attempts to intercept visually detected prey.¹⁷ Although analysis of the probe/peck ratio in shorebirds can be useful in comparative studies of foraging behaviour, it may not be a reliable indicator of the relative importance of tactile and visual prey detection. Caution is therefore advised when such data are interpreted.

The evidence presented here for a trade-off between visual and tactile prey detection from daytime to night-time, suggests that the vision of Dunlins is seriously hampered at night, causing tactile foraging to be necessary regardless of nocturnal illumination.

ACKNOWLEDGEMENTS

I thank K. T. Jensen and referees for constructive comments on an earlier draft and the National Research Institute, Division of Wildlife Ecology for necessary equipment. The study was supported by a grant from the Carlsberg Foundation, Denmark.

REFERENCES

- Hulscher, J.B. (1976) Localisation of Cockles (*Cardium edule* L.) by the Oystercatcher (*Haematopus ostralegus* L.) in darkness and daylight. *Ardea*, **64**, 292–310.
- Evans, A. (1986) Experimental evidence for the use of visual cues by foraging Dunlins. *Wader Study Group Bulletin*, **48**, 14–15.
- Robert, M. & McNeil, R. (1989) Comparative day and night feeding strategies of shorebirds species in a tropical environment. *Ibis*, **131**, 69–79.
- Burger, J. (1984) Abiotic factors affecting migrant shorebirds. In *Behavior of marine animals* vol. 6 (eds J. Burger & B. Olla), pp. 1–72. Plenum Press, New York.
- Goss-Custard, J.D. (1984) Intake rates and food supply in migrating and wintering shorebirds. In *Behavior of marine animals* vol. 6 (eds J. Burger & B. Olla), pp. 233–270. Plenum Press, New York.
- Pienkowski, M.W., Ferns, P.N., Davidson, N.C. & Worrall, D.H. (1984) Balancing the budget: measuring the energy intake and requirements of shorebirds in the field. In *Coastal waders and wildfowl in winter* (eds P.R. Evans, J.D. Goss-Custard & W.G. Hale), pp. 29–56. Cambridge University Press, Cambridge.
- Robert, M., McNeil, R. & Leduc, A. (1989) Conditions and significance of night feeding in shorebirds and other water birds in a tropical lagoon. *Auk*, **106**, 94–101.
- McNeil, R. (1991) Nocturnality in shorebirds. *Proc. 20th Intern. Ornithol. Congr.* 1098–1104.
- McNeil, R. & Robert, M. (1988) Nocturnal feeding strategies of some shorebird species in a tropical environment. *Proc. 19th Intern. Ornithol. Congr.* 2328–2336.
- Pienkowski, M.W. (1983) Changes in the foraging pattern of plovers in relation to environmental factors. *Anim. Behav.* **31**, 244–264.
- Mouritsen, K.N. (1991) Diurnal and nocturnal foraging behaviour in Dunlins *Calidris alpina*. Thesis, Department of Ecology and Genetics, Aarhus University, Denmark.
- Jensen, K.T. & Kristensen, L.D. (1990) A field experiment on competition between *Corophium volutator* (Pallas) and *C. arenarium* Crawford (Crustacea: Amphipoda): effects on survival, reproduction and recruitment. *J. Exp. Mar. Biol. Ecol.* **137**, 1–24.
- Prater, A.J., Marchant, J.H. & Vuorinen, J. (1977) *Guide to identification and ageing of holarctic waders*. British Trust for Ornithology, Herts.
- Meadows, P.S., Tait, J. & Hussain, S.A. (1990) Effects of estuarine infauna on sediment stability and particle sedimentation. *Hydrobiol.* **190**, 263–266.
- Gerritsen, A.F.C. & Sevenster, J.G. (1985) Foraging behaviour and bill anatomy in sandpipers. *Fortsch. Zool.* **30**, 237–239.
- Martin, G. (1990) *Birds by night*. Poyser, London.
- Evans, P.R. (1979) Adaptations shown by foraging shorebirds to cyclical variations in the activity and availability of their intertidal invertebrate prey. In *Cyclic phenomena in marine plants and animals* (eds E. Naylor & R.G. Hartnoll), pp. 357–366. Pergamon, Oxford.

(MS received 3 March 1992; revised MS accepted 20 September 1992)