

Relative availability of the prey of wading birds by day and by night

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ABSTRACT: The surface activity of 4 intertidal invertebrates that are preyed on by wading birds was assessed in the field during the day and at night. Nocturnal activity was greater than diurnal on each of 5 pairs of consecutive low-tide periods. The possibility of increased nocturnal activity as a predator-avoidance strategy is discussed.

INTRODUCTION

Nocturnal foraging is an aspect of wader behaviour that is often referred to in the literature, but is little understood. Many waders can and do feed nocturnally (Goss-Custard 1984), but due mainly to the problems of obtaining detailed direct observations at night, not much is known about the relative importance of this behaviour. Feeding at night is considered potentially important to provide diet supplement in severe conditions (Goss-Custard 1969); however it may actually be advantageous for a wader to forage in darkness – even in normal conditions – for instance if prey availability is greater than, or risk of predation (e.g. by diurnal raptors [Whitfield 1985]) less than, during the daytime.

The term 'availability' embraces 2 concepts (P. R. Evans 1979). If a prey item is lying buried in the substrate within one bill length of the surface it is *accessible* to a shorebird predator; if, however, it betrays its position by movement, for instance by extending a siphon or forming a burrow it becomes *detectable*, and therefore available to a visually-hunting wader. In this paper 'available' refers to prey that are visually detectable.

Certainly one prerequisite of nocturnal feeding is sufficient availability of prey at night to make foraging worthwhile. The limited data available suggest that the capture rates of both grey plovers *Pluvialis squatarola* and ringed plovers *Charadrius hiaticula* fall during darkness (Pienkowski 1981). This could be a result of a lowering of surface activity of prey items nocturnally, or of less efficient detection of prey at night. Dugan (1981) suggests that there is an increase in surface

activity of *Nereis* spp. at night, and Pienkowski (1983) found little diurnal variation in the number of outflows of water from worm holes. Plovers (Charadriidae) forage almost entirely by visual means and will therefore almost certainly be handicapped when foraging at low light intensities. Milsom (1984) showed by indirect means that lapwings *Vanellus vanellus* feed to a greater extent at night when the moon is full. Hulscher (1982) discovered that oystercatchers *Haematopus ostralegus* are less successful at locating prey in the dark as a result of being unable to utilise visual cues. Dunlin *Calidris alpina* also use visual cues to locate the position of buried prey, and thus lower their search times by up to 40% (A. D. Evans 1986). Presumably this means that they are also handicapped when foraging at low light intensities, although they can forage by tactile means alone. Other sandpipers (Scolopacidae) also switch from visual to tactile foraging techniques in darkness (Evans 1979).

Rhythmic cycles of activity have been documented for many species of intertidal invertebrates (Newell 1970), and have been related to environmental and physiological constraints (notably exposure by the tide, temperature, salinity and the need to feed). Predation pressure has rarely been mentioned as a possible constraint on activity (Evans 1979). It is possible that such animals experience a 'conflict' between the need to feed and the need to avoid predation. If the risk of predation to an individual invertebrate is indeed less at low light intensities, nocturnal activity may well have evolved as an anti-predator strategy (cf. Gliwicz 1986).

In the winter of 1982–3 I studied the diurnal and nocturnal activity of 4 intertidal invertebrates that are preyed on by wading birds.

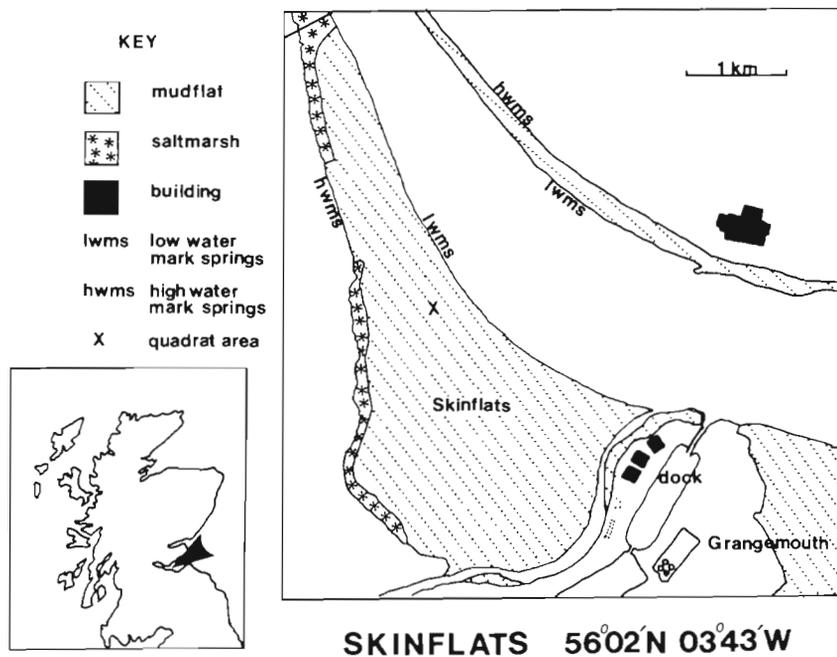


Fig. 1. Study site at Skinflats, Scotland, with inset showing location

STUDY SITE AND METHODS

Observations were made on the south shore of the inner part of the Firth of Forth at Skinflats, just to the west of Grangemouth, Scotland (Fig. 1). The intertidal zone consists of a small area of saltmarsh (10 m wide), and a large expanse of mudflat (about 1300 m wide). Even at low tide the sediment supports a surface film of water (> 1 mm deep).

There are 4 common invertebrate prey species at Skinflats: the gastropod *Hydrobia ulvae*, the bivalve *Macoma balthica*, the polychaete *Nereis diversicolor*, and the amphipod *Corophium volutator*. The first 3 of these are preyed upon by grey plover, and all 4 are taken by both dunlin and ringed plover (Cramp & Simmons 1983). The oligochaete *Pelocolex benedini* was also common, but is not considered as a prey species (it may be too small). All 4 prey species rely to some extent upon detritus feeding (Newell 1970), and are therefore periodically exposed on the surface where they are vulnerable to visual predators. Most intertidal invertebrates are sensitive to vibration and many burrow rapidly on disturbance, so that taking core samples is an unsuitable technique for assessing their depth distribution, despite the refinements made to the technique by Pienkowski (1983). Use of a device similar to the sledge sampler used by Clark (1983) is preferable, but at my study site the mud proved too soft for its efficient operation. I therefore made direct observations of invertebrate surface activity within a quadrat (cf. Dugan 1981, Pienkowski 1983). Quadrat size was 25 cm × 25 cm; chosen after reference to

McClusky (1979) and a preliminary trial, the determining factor being the number of animals likely to be seen within the area. To increase the accuracy of censusing the quadrat was subdivided by string divisions into 25 squares of 5 cm × 5 cm. A randomly chosen area of mudflat about halfway down the intertidal zone was marked with canes in order to allow observation from precisely the same 25 × 25 cm square throughout the study.

Hydrobia ulvae were commonly seen moving across the surface or 'erupting' from beneath it. Occasionally *Macoma balthica* siphons were observed, as were *Nereis diversicolor*, either protruding from their burrows or swimming free in the surface film at night. Only 6 *Corophium volutator* were seen in over 24 h of observation. Although invertebrates themselves were sighted comparatively rarely, they left an abundance of visual cues on the surface which betrayed their position. These were mainly burrow holes, but also included tracks and defaecatory heaps. It was assumed that the presence of a burrow indicated that the inhabitant was close to the surface and therefore accessible to many foraging waders. This assumption was based on the fact that burrows very quickly collapsed and were filled by silt in the surface film; 20 artificial burrows created with a syringe needle all vanished within 30 s. Furthermore, the results showed that only 14% of burrows remained throughout a 2 h observation period; these were normally either the large, shallow 'craters' formed by *H. ulvae* eruption or siphon holes of the sedentary *M. balthica*. The presence of the surface film meant that I was unable to use

outflows of water from worm holes as a reliable indication that the occupant was close to the surface (Pienkowski 1983).

Observations were taken by lying prone on an inflated air-bed to reduce the effects of vibration caused by movement of the observer. When taking observations at night, a torch masked with a red celluloid filter was used to illuminate the study plot; *Nereis diversicolor* is known to be extremely sensitive to white light (Clark 1960, S. M. Evans 1971).

After a 15 min 'settling' period observations commenced. This period seemed sufficient as there was no trend towards increase in activity with time during the observation period. Walking around the quadrat area at the end of an observation period appeared to depress surface activity, although no data were taken on this. Each subdivision of the quadrat was considered in strict rotation and the positions of every animal or burrow (except those of *Pelosclex benedini*) were plotted on a pre-drawn representation of the grid. In this way a complete, accurate map of the quadrat area was drawn up. Each map took about 20 min to prepare. A second map was drawn after a 10 min interval; on average 5 maps were completed in an observation period. In total, 61 maps were drawn in 12 observation periods between 3 March and 4 April 1983. Six daytime and 6 night-time observations were made, 5 pairs of which were taken on successive tides to reduce the effects of environmental variables. Before drawing each map I recorded the temperature of the surface film and the time since the area had been exposed by the tide. After 4 of the successive-tide observation periods a core sample (10.5 cm in diameter \times 10 cm deep) was taken from as close to the quadrat area as possible (within 20 cm). Cores were later suspended in cold water and sieved through a 0.7 mm mesh. All invertebrates were stored in 5% formalin before counting.

RESULTS

Fig. 2 suggests that total surface activity (in terms of number of burrows visible at the surface) is slightly greater (between 10 and 20%) during the night than in the day. The 3 observations when activity was very low are probably associated with low temperatures at the start of the study period. Surface activity did not decrease dramatically with time after exposure of the area by the tide, presumably due to the surface film of water retained. A test gave a figure of 24% by weight of water in the top 10 cm of mud, and 30% in the top 4 cm.

As expected (Pienkowski 1981, Clark 1983) surface activity was positively correlated with temperature (Fig. 3). For any given temperature up to 12 °C noctur-

nal activity was greater than diurnal; however, temperatures were lower at night. Surface activity appears to be affected less by temperature changes in the darkness than in the day, although the clumped nature of the data make detailed analysis inappropriate.

By tracing each map onto a transparency and overlaying it on the previous map I could work out the

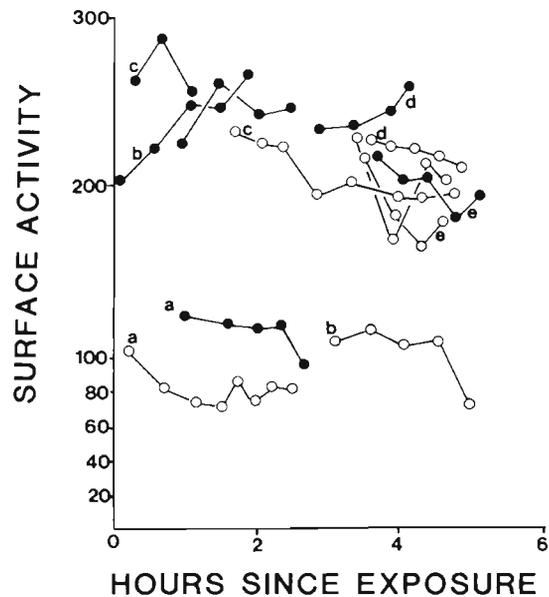


Fig. 2. Total surface activity (number of burrows or animals visible) in (○) daylight and (●) darkness against time since exposure by the tide. Letters indicate successive tides

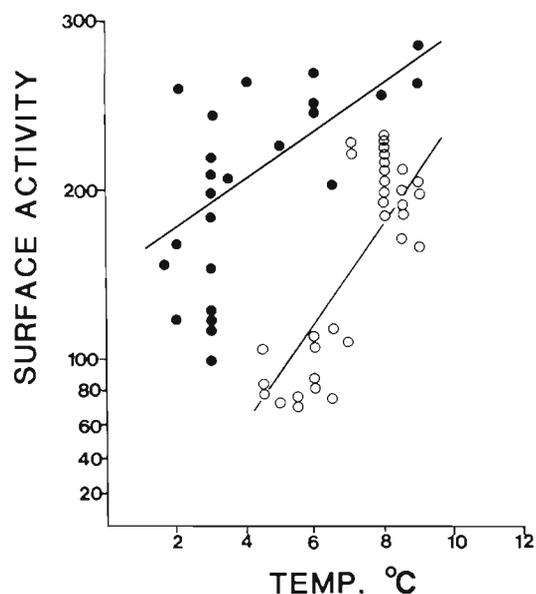


Fig. 3. Total surface activity in (○) daylight and (●) darkness plotted against temperature of the surface film. Linear regressions are given by: Daylight, $Y = 35.48X - 97.48$; Darkness, $Y = 16.02X + 131.52$. The 2 slopes are significantly different, $F = 55.26, p < 0.01$

Table 1. Numbers of individual invertebrates in core samples taken on successive tides. d: daytime; n: night-time

Date (1983)	<i>Hydrobia ulvae</i>	<i>Macoma balthica</i>	<i>Nereis diversicolor</i>	<i>Corophium volutator</i>	Oligochaetes
8 Mar: d	16	1	3	2	45
8 Mar: n	15	2	2	2	60
1 Apr: d	14	2	4	1	57
2 Apr: n	11	1	6	0	49
Mean \pm SE (n=4)	14.0 \pm 1.1	1.5 \pm 0.3	3.8 \pm 0.9	1.3 \pm 0.5	52.8 \pm 3.5

percentage change in the number of visible burrows. In consecutive maps (about a 30 min interval) between 25 and 50 % of holes were lost and a similar number of new burrows formed. This means that the surface population of invertebrates is highly mobile; either animals are moving laterally beneath the surface, or there is a high degree of turnover, with new animals continually replacing old at the surface.

Table 1 shows the mean number of invertebrates found in the core samples. There is little variation in core content; cores were taken within 5 cm of one another. By multiplying the number of invertebrates per core by a factor of 7.2 (the ratio of areas of core and quadrat) I arrived at an estimate of the number of each species present in the area beneath the quadrat. Table 2 shows that on average a very low percentage of these populations are active on the surface at any one time.

Table 2. Estimated populations of invertebrate species within quadrat (see text for method) and maximum and minimum levels of surface activity observed during study

Species	Mean no per core	Estimated quadrat pop.	% of quadrat pop. seen in any 1 map to nearest 5 %	
<i>Hydrobia ulvae</i>	14.0	101	45	0
<i>Macoma balthica</i>	1.5	10.8	75	0
<i>Nereis diversicolor</i>	3.8	27.0	10	0
<i>Corophium volutator</i>	1.3	9.4	10	0
Oligochaetes	52.8	380	–	–

DISCUSSION

As expected, temperature has an important effect upon the activity of the species studied. This is in accordance with findings for *Littorina obtusata* (= *littoralis*), *Gammarus oceanicus* (Newell 1970), *Corophium volutator* (Goss-Custard 1969), and *Nereis diversicolor* (Clark 1983). At a given temperature

below 12 °C nocturnal activity was greater than diurnal. It is likely, therefore, that more prey is available to visually foraging waders at night, providing that light intensities are sufficiently high to permit detection of surface activity. There is evidence to suggest that oystercatchers and lapwing feed to a greater extent on bright nights than less bright ones (Heppleston 1971, Milsom 1984). Dugan (1981) has suggested that the drop in capture rate experienced by grey plover nocturnally is offset by an increase in the proportion of large individual prey available at night. I often observed *N. diversicolor* on the surface at night, presumably on foraging excursions. They can also filter-feed from within their burrows (Newell 1970). Perhaps they adopt this technique in daylight when the risk of predation by a visually hunting shorebird is probably higher than at night. It would be interesting to know the relative profitability of the 2 feeding techniques, and the risk of predation when using each.

Dunlin preferentially use visual cues to locate prey (A. D. Evans 1986) but can forage purely by tactile means. They may also use chemoreception (van Heezik et al. 1983). The extent to which they are handicapped by darkness obscuring visual cues is currently under investigation here at Edinburgh. The accessibility of 'dormant' prey items is not known due to the difficulties of adequately assessing depth distribution. Absence of signs of surface activity does not necessarily mean prey were inaccessible. For instance although *Hydrobia ulvae* are less active at night, they probably remain in the top 3 cm of substrate (Goss-Custard 1969); *Macoma balthica* also seldom burrow deeply (Reading & McGroarty 1978).

Low temperatures at night will tend to depress surface activity. For instance *Littorina obtusata* exhibits positive rather than negative geotaxis below 3 °C (Newell 1970). During the study period the mean difference between day and night temperatures was only 3 °C, considerably less than the 30 yr monthly mean of 7 °C. The mean nightly minimum was 4.2 °C, compared with the long-term mean of 1.7 °C. These conditions will have tended to emphasise any increase in nocturnal activity. It is worth noting that when

conditions are favourable for detection of prey by visually hunting shorebirds (bright, clear nights) the temperature drop nocturnally, and thus depression of surface activity, will tend to be greatest. It is possible that the nocturnal increase in surface activity of invertebrates has evolved as an anti-predator strategy. Although speculative this is not an unreasonable proposition; the rapid evolution of diurnal vertical migration as a predator-avoidance strategy has been documented in the copepod *Cyclops abyssorum* (Gliwicz 1986). Predation pressure upon intertidal invertebrates can be extremely high, accounting for up to 90% of *Hydrobia ulvae* in the 1+ age class, and 93% of *Nereis diversicolor* in the 1+ age class in a single winter (Evans 1979).

The apparent high mobility and/or large turnover of prey items at the surface may have important implications when considering the depletion of areas by foraging waders. If a shorebird predator takes all visually available prey before moving on, it will have removed a maximum of only 10% of the *Nereis diversicolor* and *Corophium volutator* population, but up to 40% of *Hydrobia ulvae* and 75% of *Macoma balthica*. It may well be that the numbers of visually available *N. diversicolor* and *C. volutator* will very quickly recover.

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LITERATURE CITED

- Clark, N. A. (1983). The ecology of the dunlin *Calidris alpina* wintering on the Severn Estuary. Ph. D. thesis, Univ. of Edinburgh
- Clark, R. B. (1960). Habituation of the polychaete *Neries* to sudden stimuli (1). *Anim. Behav.* 8: 82–91
- Cramp, S., Simmons, K. E. C. (ed.) (1983). The handbook of the birds of the Western Palearctic, Vol. III. Oxford Univ. Press, Oxford
- Dugan, P. J. (1981). The importance of nocturnal foraging in shorebirds: a consequence of increased invertebrate prey activity. In: Jones, N. V., Wolff, W. J. (ed.) Feeding and survival strategies of estuarine organisms. Plenum Press, London, p. 251–261
- Evans, A. D. (1986). Experimental evidence for use of visual cues by dunlin. *Water Study Group Bull.* 48: 14–15
- Evans, P. R. (1979). Adaptations shown by foraging shorebirds to cyclic variations in the activity and availability of their intertidal invertebrate prey. In: Naylor, E., Hartnoll, R. G. (ed.) Cyclic phenomena in marine plants and animals. Pergamon Press, Oxford, p. 357–366
- Evans, S. M. (1971). Behaviour in polychaetes. *Q. Rev. Biol.* 46: 379–405
- Gliwicz, M. J. (1986). Predation and the evolution of vertical migration in zooplankton. *Nature, Lond.* 320: 746–748
- Goss-Custard, J. D. (1969). The winter feeding ecology of the redshank *Tringa totanus* L. *Ibis* 111: 338–356
- Goss-Custard, J. D. (1984). Intake rates and food supply in migrating and wintering shorebirds. In: Burger, J., Olla, B. L. (ed.) Shorebirds: migration and foraging behavior. Plenum Press, New York, p. 233–270
- Heppleston, P. B. (1971). The feeding ecology of oystercatchers (*Haematopus ostralegus* L.) in winter in northern Scotland. *J. Anim. Ecol.* 40: 651–672
- Hulscher, J. B. (1982). The oystercatcher as a predator of *Macoma* Ardea 70: 89–152
- McClusky, D. S. (1979). Invertebrate fauna of the Forth Estuary mudflats. (January). Report to Nature Conservancy Council, Edinburgh
- Milsom, T. P. (1984). Diurnal behaviour of lapwings in relation to moon phase during winter. *Bird Study* 31: 117–120
- Newell, R. C. (1970). Biology of intertidal animals. Logos, London
- Pienkowski, M. W. (1981). How foraging plovers cope with environmental effects on invertebrate behaviour and availability. In: Jones, N. V., Wolff, W. J. (ed.) Feeding and survival strategies of estuarine organisms. Plenum Press, London, p. 179–192
- Pienkowski, M. W. (1983). Surface activity of some intertidal invertebrates in relation to temperature and the foraging behaviour of their shorebird predators. *Mar. Ecol. Prog. Ser.* 11: 141–150
- Reading, C. J., McGrorty, S. (1978). Seasonal variations in the burrowing depth of *Macoma balthica*, and its accessibility to wading birds. *Estuar. coast. mar. Sci.* 6: 135–144
- van Heezik, Y. M., Gerritsen, A. F. C., Swennen, C. (1983). The influence of chemoreception on the foraging behaviour of two species of sandpiper, *Calidris alba* and *Calidris alpina*. *Neth. J. Sea Res.* 17 (1): 47–56
- Whitfield, D. P. (1985). Raptor predation on wintering waders in south-east Scotland. *Ibis* 127: 544–558

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