Because of the tidal restrictions on their foraging, disturbance of waders and waterfowl by human activities during their feeding periods might have potentially serious effects on their ability to acquire sufficient food for their needs. This is particularly important at times of the year when energy demands are high, for example in midwinter, on migration and during moult. Disturbance can cause a reduction in food intake in several ways: the presence of people leads to increased vigilance by foraging waders and to a decrease in the proportion of time devoted to feeding; the birds may stop foraging altogether and they may leave the foraging site, perhaps changing to a less profitable site at which they have a lower food intake rate. In addition to this reduction in food intake, energy expenditure can be increased by avoidance behaviour, particularly if the birds fly away. The combination of these effects may produce serious deficits in the daily energy budget of the disturbed birds, or necessitate extra compensatory foraging, for example, at night.

The summer seasonal peak of human recreational use of beaches coincides with one of the times of peak energy demands for waterbirds, during the postbreeding migration and subsequent moult. In this study, the types and extent of human recreational disturbances on a beach and their effects on the foraging behaviour of three species of wader (Oystercatcher, Curlew and Redshank) were studied during June–August 1996, with the aim of assessing the relative impacts of differing types and locations of human activity in the vicinity of the beach on the waders' foraging rates.
METHODS

Study site

The beach and adjacent land at the Loughshore Park, Jordanstown, Co. Antrim (54°41' N 5°55' W) on the north shore of Belfast Lough, form the following contiguous site zones:

1. Grass. A mown area, with paths and seats, terminating at its seaward edge at the storm strand line.
2. Sand. A 10-m wide zone of coarse sand, extending from the storm strand line to just below extreme high water neap tides.
3. Upper shore. Substrate dominated by low boulders mostly 15–30 cm high, sparsely colonized by the seaweed Ascophyllum nodosum. Some pools and sand between the boulders. Zone 50 m wide.
4. Mid-shore. Substrate similarly dominated by low boulders 15–30 cm high, but with larger rockpools and the seaweed Chondrus crispus occurring mainly in the pools. Some sandy mud around boulders in drier areas. 50 m wide.
5. Low shore. A mussel Mytilus edulis bed, density 1200 mussels per m², with otherwise muddy sand substrate and only occasional boulders. About 50 m wide at neap tides, extending to 100 m at spring tides.

Winkles Littorina littorea, barnacles Balanus spp. and shore crabs Carcinus maenas were found throughout the upper, mid- and low shore zones. Observations of a 1-km stretch of beach were made from the grass zone at the mid-point.

Disturbance factors

The location and number of people and of dogs in each of the above site zones were recorded at every behavioural observation (see below).

The activity levels of the people and any accompanying dogs were categorized as: sitting – people/dogs stationary; walking – slow movement; fast activities – running, jogging, running children's play, bicycles. The activities were recorded separately but combined for analysis. Other disturbance factors (e.g. aircraft) were also recorded, but were too infrequent for analysis.

Behavioural observations

Two observers made a total of 185 hours of observation between 18 June and 8 August. Each observer studied different aspects of behaviour in order to avoid problems of inter-observer differences. Binoculars of 8 × 50 and 7 × 50 magnification were used.

Oystercatcher, Curlew and Redshank were present at the site from 18 June, 24 June and 19 July, respectively, and the following aspects of their behaviour were recorded.

Use of the beach

Arrival from and departure to high-tide roosts

The times (relative to the time of low water) of arrival at the beach from the roost, and of departure from the beach to the roost, were noted for each species with the concurrent disturbance factors on the beach. The effects of disturbance were analysed by comparing disturbed and undisturbed arrival times and departure times using Mann–Whitney U tests.

Occupation of beach zones

Using half-hourly scan sampling, the number of waders of each species in the upper, mid- and low shore zones was recorded. The disturbance factors were recorded immediately after each scan. The data were collated with times (relative to low water) categorized into half-hour intervals.

Undisturbed behaviour

Half-hourly scan sampling was used to record the number of Oystercatcher and Curlew: (a) actively searching for food and feeding; (b) sitting or standing inactive; (c) preening. In order to reduce any effects from disturbance, scans were performed only when people were absent from the upper, mid- and low shore zones. Because of the boulders in upper and mid-shore, Redshank could not be censused quickly and accurately enough for this analysis. The data were collated with times (relative to low water) categorized into half-hour intervals.

Behaviour of foraging birds

Vigilance

Focal bird sampling for from 0.5 to 1 minute was used. An actively foraging wader was selected and the number of times it looked up was recorded (i.e. when it raised its beak clear of the substrate and to within 10° of horizontal
Disturbance factors were recorded immediately after each observation. As far as possible, different focal birds were selected for subsequent observations, but as the birds were unmarked and moved around the beach, the same individuals could have been recorded at various times during the day. Each record was, however, treated as independent in analyses.

Bird scan rates (scans per minute) were calculated, the data checked for normality and log-transformed before analysis. Two-way ANOVAs were used to analyse the scan rates of each species by beach zone of the bird and:
(a) site zone of closest human; (b) greatest level of human activity; (c) site zone of closest dog.

Probing for food
Focal bird sampling for 0.5 to 1 minute periods was similarly used to record the number of times an actively foraging wader pecked the substrate. The duration of the observation (seconds) and the disturbance factors were also recorded. As with scan records, it is possible that some birds were recorded more than once during the day, but the records were treated as independent in analyses. Peck rates (probes per minute) were calculated, checked for normality and transformed as follows for analysis: Curlew, no transformation necessary; Oystercatcher and Redshank, log transformation. Two-way ANOVAs were used to analyse the peck rates of each species by beach zone of the bird and:
(a) site zone of closest human; (b) greatest level of human activity; (c) site zone of closest dog.

Capture rate
For Oystercatcher and Curlew, the rate of prey capture was recorded by focal bird samples of 2–3 minutes duration. For actively foraging waders, the following were recorded: the number of items captured and eaten; items captured but lost; identity of prey; duration of observation in seconds; disturbance factors. Capture rates (items eaten per minute) were calculated and the data checked for normality. Oystercatcher capture rates were log (x + 1) transformed and Curlew capture rates were square-root transformed for analysis. Two-way ANOVAs were used to analyse the capture rates of each species by beach zone of the bird and:
(a) site zone of the closest human; (b) greatest level of human activity; (c) site zone of closest dog.

Overall loss rates of captured prey were calculated as a percentage of total captures and categorized according to the apparent reason for loss. As the majority of Redshank prey items were small, the captures made during probing were not always visible and capture rates were not recorded.

Responses to disturbance
The reactions of birds to disturbance were recorded when they occurred, in as much detail as possible. The distances between the bird and the cause of the disturbance, and the distance moved by the bird, were estimated directly in some cases. In others they were subsequently estimated from the site zones recorded for the disturbance factor and the description of the event (a 50-m distance was used for a disturbance occurring at the closest approach of a person on the upper, mid- or low shore zone to a bird in the adjacent shore zone, and a 100-m distance for a disturbance occurring at the closest approach of a person on the upper shore zone to a bird in the low shore zone). For analysis, reactions were categorized as: (a) stopped feeding but did not move away; (b) walked or ran away; (c) flew to another part of the beach; (d) flew away from the beach. The frequencies of each type of reaction were compared between the three species and the total responses of each species by zone of bird and zone of disturbance were analysed using χ² tests.

RESULTS

Use of beach
The birds arrived between 3 and 4 hours before low water (Fig. 1a). The arrival times of Oystercatcher and Curlew were significantly later (relative to low water) when there were people on the beach (Oystercatcher, U = 4, N = 3,13, P = 0.05; Curlew, U = 0, N = 3,9, P = 0.01). When people were active, Redshank did not arrive until considerably later, after we had begun recording the other observations and could not consistently note their arrival.

Departure occurred between 3 and 4 hours after low water (Fig 1b). The departures of Redshank and Oystercatcher were significantly
Figure 1. Effects of human disturbance on times of arrival (a) and departure (b), relative to low tide. Error bars show se. ■, Disturbed; □, undisturbed.

Figure 2. Frequency of occurrence of Oystercatcher (a), Curlew (b) and Redshank (c) in shore zones relative to time of low tide. Error bars show se.
earlier when disturbed (Redshank, \( U = 1, N = 4.5, P = 0.05 \); Oystercatcher, \( U = 19, N = 9, P < 0.05 \)). The departures of Curlew did not differ with disturbance (\( U = 17, N = 5, P > 0.05 \)).

**Undisturbed behaviour**

On arrival, the upper shore zone was the only part of the beach available to the birds; they moved into the mid-shore as it became uncovered (Fig. 2) and then moved from the mid-shore into the low shore as it, in turn, became available. All Oystercatcher and most Curlew were in the low shore shortly before low water (Fig. 2a, b), but Redshank utilized all shore zones during the period of low water, moving back into the upper shore from the mid-shore (Fig. 2c). All three species, but particularly Redshank and Curlew, foraged in the mid-shore increasingly after low water, even though the low shore was still available. Foraging continued in the mid-shore once the low shore was covered, but only Redshank foraged in the upper shore on the rising tide.

Immediately after arrival, most Oystercatcher preened (Fig. 3a); only a few actively foraged. The proportion foraging increased as the tide ebbed; for about 6 hours of the low tide period, typically 80–90% of the Oystercatchers were foraging at any given moment. About 3 hours after low water, a higher proportion rested and preened, followed by a further intensive period of foraging. As the Oystercatchers prepared to leave for the high-tide roost, more birds preened, bathed and rested, although some still foraged.

Most Curlew started foraging immediately on arrival (Fig 3b); preening seemed to occur...
periodically through the low tide period after 1–2 h of more intensive foraging. Before going to roost, the Curlew stopped feeding and rested without preening. Through the 6.5 hours when Curlew were actively foraging, 50–100% were foraging at any given time.

Behaviour of foraging birds

Vigilance

Focal observations for calculating scan rates totalled 253 for Oystercatcher, 202 for Curlew and 267 for Redshank. The set of two-way ANOVAs (Table 1) showed that, in all three species, the most important factors influencing scan rates were the zone of the bird and the type of human activity. For all species, the scan rate was greatest in the upper shore and least in the low shore, and increased with faster human activities (Fig. 4). The site zone in which people were active was relatively unimportant, giving a marginally significant result for Redshank only (Table 1) and was not significant for any species when type of human activity was included. The presence and zone of activity of dogs had no effect on the scan rate.

Probing for food

Focal observations for calculating peck rates totalled 281 for Oystercatcher, 232 for Curlew and 234 for Redshank. The rate at which all species probed for food was hardly affected

Table 1. Results of two-way ANOVAs of scan rate. Significant effects are underlined. No interaction terms were significant and are therefore omitted.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Oystercatcher</th>
<th>Curlew</th>
<th>Redshank</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
<td>P</td>
</tr>
<tr>
<td>Zone</td>
<td>2.241</td>
<td>0.702</td>
<td>0.4965</td>
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<tr>
<td>Place</td>
<td>4.241</td>
<td>0.539</td>
<td>0.7073</td>
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<tr>
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<td>2.244</td>
<td>10.301</td>
<td>0.0001</td>
</tr>
<tr>
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<td>8.045</td>
<td>0.0044</td>
</tr>
<tr>
<td>Zone</td>
<td>2.244</td>
<td>14.357</td>
<td>0.0001</td>
</tr>
<tr>
<td>Dog</td>
<td>2.244</td>
<td>0.793</td>
<td>0.4537</td>
</tr>
<tr>
<td>Place</td>
<td>4.243</td>
<td>0.842</td>
<td>0.4995</td>
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<tr>
<td>Activity</td>
<td>2.243</td>
<td>8.13</td>
<td>0.0004</td>
</tr>
</tbody>
</table>

Zone, zone occupied by bird; Place, zone of human activity; Activity, type of human activity; Dog, zone of dog activity.

Figure 4. Scan rates (untransformed) of Oystercatcher (a), Curlew (b) and Redshank (c) according to zone of beach occupied by the bird and the type of human activity (sit, walk or fast).
Disturbance of foraging waders

by either the zone of the bird or any of the disturbance factors (Table 2). The only highly significant effects were due to bird zone for Oystercatcher and place of humans for Redshank (Fig. 5). The type of human activity had marginally significant effects in comparison with place of humans for Curlew and Redshank (Table 2); dogs had no significant effect.

Capture rate
The majority of prey identified for both Oystercatcher and Curlew was shore crabs; in addition, Oystercatcher foraging in the low shore ate mussels and a mid-shore Curlew was observed to capture a rockpool fish. Focal observations used for calculating capture rates totalled 260 for Oystercatcher and 254 for Curlew.

The capture rate of Oystercatcher was significantly affected by both zone of bird and place of human activity. It was also weakly but significantly affected by type of human activity (Table 3). The place of human activity, however,

Table 2. Results of two-way ANOVAs of peck rate. Significant effects are underlined. No interaction terms were significant and are therefore omitted.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Oystercatcher</th>
<th></th>
<th>Curlew</th>
<th></th>
<th>Redshank</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
<td>P</td>
<td>df</td>
<td>F</td>
<td>P</td>
</tr>
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<td>2,220</td>
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<td>0.9171</td>
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<td>0.7033</td>
</tr>
<tr>
<td>Activity</td>
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<td>4,223</td>
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<td>2,222</td>
<td>1.297</td>
<td>0.2755</td>
</tr>
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<td>0.0003</td>
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<td>0.3458</td>
</tr>
<tr>
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<td>2.971</td>
<td>0.0529</td>
<td>2221</td>
<td>1.251</td>
<td>0.0278</td>
</tr>
</tbody>
</table>

Zone, zone occupied by bird; Place, zone of human activity; Activity, type of human activity; Dog, zone of dog activity.

Table 3. Results of two-way ANOVAs of capture rate. Significant effects are underlined. No interaction terms were significant and are therefore omitted.

<table>
<thead>
<tr>
<th>Factor</th>
<th>Oystercatcher</th>
<th></th>
<th>Curlew</th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>df</td>
<td>F</td>
<td>P</td>
<td>df</td>
</tr>
<tr>
<td>Zone</td>
<td>2,247</td>
<td>14.463</td>
<td>0.0001</td>
<td>2,241</td>
</tr>
<tr>
<td>Place</td>
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<td>5.506</td>
<td>0.0003</td>
<td>4,241</td>
</tr>
<tr>
<td>Zone</td>
<td>2,251</td>
<td>0.931</td>
<td>0.3955</td>
<td>2,246</td>
</tr>
<tr>
<td>Activity</td>
<td>2,251</td>
<td>3.116</td>
<td>0.0461</td>
<td>2,246</td>
</tr>
<tr>
<td>Zone</td>
<td>2,250</td>
<td>0.147</td>
<td>0.8634</td>
<td>2,243</td>
</tr>
<tr>
<td>Dog</td>
<td>3,250</td>
<td>1.097</td>
<td>0.351</td>
<td>4,243</td>
</tr>
<tr>
<td>Place</td>
<td>4,250</td>
<td>0.001</td>
<td>1.0</td>
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</tr>
<tr>
<td>Activity</td>
<td>2,250</td>
<td>2.731</td>
<td>0.0671</td>
<td>4,244</td>
</tr>
</tbody>
</table>

Zone, zone occupied by bird; Place, zone of human activity; Activity, type of human activity; Dog, zone of dog activity.
had an unexpected effect: the capture rate of Oystercatcher increased when humans were in the same or an adjacent beach zone (Fig. 6a). Capture rates were generally higher in the mid-shore zone.

For Curlew, the capture rate varied only weakly but significantly with zone of bird in the comparison including dog presence (Table 3). The place of human activity had a significant influence when analysed with respect to zone of bird (Fig. 6b). This effect was similarly unexpected, with capture rate higher in the upper and mid-shore zones when humans were also in the same or adjacent zones. This effect remained significant when the type of human activity (of marginal significance) was included (Table 3). The presence of dogs did not have any significant effect on the capture rate for either species.

**Loss of captured prey**

Oystercatcher were observed to capture 517 prey, of which they lost four. In two cases, the prey was apparently discarded by its captor, in the other two cases the loss was apparently due to disturbance. The loss of prey by Oystercatcher due to disturbance was therefore 0.4%.

Captures of 341 prey by Curlew were observed; nine items were lost; in three cases...
due to kleptoparasitism (by conspecifics and Herring Gull *Larus argentatus*) and in six cases apparently due to human disturbance – the Curlew looked up abruptly during the early stages of prey handling and the prey (crabs) escaped. The prey loss by Curlews due to human disturbance was therefore 1.8%.

The low losses due to kleptoparasitism, in spite of numerous attempts by conspecifics and by gulls (*Larus* spp.), appeared to be due to the captor running and/or flying away with the prey. Both species were observed flying with prey from low or mid-shore to the upper shore when avoiding kleptoparasitism.

**Disturbance**

The Loughshore Park is a popular recreational area; from mid-morning to late afternoon the mean number of people present was usually over 5 (Fig. 7a). However, most people remained on the grass or the sand at the top of the beach (Fig. 7b). Most people were walking, with faster activities more common in the middle of the day (Fig. 7c). The morning and late afternoon peaks of sitting shown in Fig. 7c are due to the presence of the observers (sitting) at times when other people (e.g. walkers) were infrequent.

We recorded 319 disturbances of the birds. This is an underestimate of the frequency of disturbance, as brief disturbances on one part of the beach may have been undetected during focal bird observation procedures if the focal bird was on another part of the beach. An average of three to four disturbances per hour is a realistic estimate for this beach.

**Responses to disturbance**

All species responded to disturbance in all four ways categorized, but there were significant differences between the species in the frequencies of these responses ($\chi^2 = 30.532$, df = 6, $P = 0.0001$, $N = 319$). Oystercatcher walked away more frequently, but stopped feeding and flew away from the site less frequently than expected (Fig. 8). Curlew stopped feeding more frequently and walked or flew to another part of the beach less frequently than expected.

---

**Figure 6.** Prey capture rates (untransformed) of Oystercatcher (a) and Curlew (b) according to zone of beach occupied by the bird and place of human activity.
Redshank also walked away less frequently than expected. Note that the null expectation of no difference in frequency of behaviours between the species assumes that the observed disturbance factors are equivalent across all species.

Combining all types of response, each species was most often observed reacting to disturbance occurring in the same beach zone or in an adjacent zone (Fig. 9). These distributions of responses are significantly non-random (Oystercatchers $\chi^2 = 105.963$, Curlew $\chi^2 = 49.888$, Redshank $\chi^2 = 39.09$; $P < 0.0001$, 8 df in all cases). More disturbances occurred to birds in the upper and mid-shore zones than to birds in low shore zones (Table 4).

Estimates of flight distances are given in Table 4.

**Table 4.** Percentage of disturbances occurring in relation to zone of bird.

<table>
<thead>
<tr>
<th>Bird zone</th>
<th>Oystercatcher</th>
<th>Curlew</th>
<th>Redshank</th>
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<tbody>
<tr>
<td>Upper</td>
<td>38.6</td>
<td>31.6</td>
<td>28.2</td>
</tr>
<tr>
<td>Mid</td>
<td>35.3</td>
<td>38.9</td>
<td>52.1</td>
</tr>
<tr>
<td>Low</td>
<td>26.1</td>
<td>29.5</td>
<td>19.7</td>
</tr>
</tbody>
</table>
In comparison with published values, the flight distances are relatively low. Most disturbed birds which remained on the beach resumed feeding within 1–2 minutes. However, on days when many people were on the low shore zone, continuous disturbances of 20–25 minutes were recorded.

DISCUSSION

The effects of human disturbance on the foraging behaviour of the waders on Jordans-town beach were, in general, surprisingly small and apparently had subtle effects on the waders’ foraging rate during the single summer period of this study. Most obviously, disturbance reduced potential feeding time by influencing arrival and departure times of the waders. The delayed start of feeding caused by later arrival might have had little effect on the food intake of the Oystercatchers as they mainly loafed and preened after arrival and

Table 5. Flight distances.

<table>
<thead>
<tr>
<th></th>
<th>Oystercatcher</th>
<th>Curlew</th>
<th>Redshank</th>
</tr>
</thead>
<tbody>
<tr>
<td>Present study</td>
<td>29 ± 2 (53)</td>
<td>38 ± 4 (41)</td>
<td>37 ± 4 (29)</td>
</tr>
<tr>
<td>Smit &amp; Visser*</td>
<td>79</td>
<td>140</td>
<td>200</td>
</tr>
<tr>
<td></td>
<td>113</td>
<td>196</td>
<td></td>
</tr>
<tr>
<td></td>
<td>77</td>
<td>102</td>
<td></td>
</tr>
<tr>
<td></td>
<td>85</td>
<td>211</td>
<td></td>
</tr>
<tr>
<td></td>
<td>136</td>
<td>339</td>
<td></td>
</tr>
<tr>
<td>Urfi et al.15</td>
<td>48 ± 2 (27)</td>
<td>41 ± 2 (33)</td>
<td>26 ± 1 (23)</td>
</tr>
<tr>
<td>Scott (1989) cited in ref. 24</td>
<td>10</td>
<td>10–15</td>
<td></td>
</tr>
</tbody>
</table>

Mean ± se (N); se calculated from published data when available.15

Figure 8. Occurrence of each type of behavioural response by waders to disturbance. Asterisks show expected values if all species reacted in the same way.
only gradually started feeding. Similarly, early departure probably replaced resting and/or preening by Oystercatchers on the site. Oystercatchers, in addition, foraged on neighbouring grassland areas during the high tide period, as has been recorded elsewhere.12 The other two species, however, appeared to experience a reduction in foraging time due to disturbance.

An estimated average of three to four disturbances per hour, serious enough to cause nearby birds to stop feeding and/or move away, further reduced the feeding time of the affected individuals while they were on the beach. A reduction of feeding time by only 3 minutes per hour would represent 5% of the total low-tide time available on this beach. However, as 10–30% of the Curlew and Oystercatcher were

Figure 9. Position of disturbed bird on beach in relation to position of human disturbance. a, Oystercatcher; b, Curlew; c, Redshank.

normally resting and preening rather than feeding during the behavioural sampling of undisturbed birds, it is possible that short-term effects of disturbance could usually be compensated for by reducing these resting periods. If the resting/preening periods represent time needed for digestion due to slow processing of food, the resting time requirement of a disturbed, non-feeding bird could well be reduced as digestion presumably continues during the disturbance.

From the capture rate data, the most profitable foraging sites were apparently in the mid-shore zone on this beach. The movement by all species back into the mid-shore while the low shore was still available suggests some preference for this zone. However, it was subject to greater disturbance than the low shore, and a further effect of disturbance could be to reduce the time spent by the birds in this most profitable zone. Although foraging, birds forced to use less profitable sites can experience some reduction in daily food intake due to disturbance of the better sites.

Although increased foraging rates by Oystercatchers have been observed when feeding time was reduced in captivity, increases immediately after disturbance have not been observed in the field. Oystercatchers, however, sometimes increased their intake rate towards the end of the low-tide foraging period. The present study showed an increase in capture rate in birds with a disturbance factor present in the same or a neighbouring beach zone. This finding suggests an anticipatory response: the bird, observing an approaching disturbance, increased its capture rate before the other responses to disturbance were evoked. However, an alternative explanation is possible: birds in a poor foraging patch might stop foraging and/or depart when the disturbance factor is at a greater distance than elicits departure from birds foraging in a highly productive patch, in which they achieve a better-than-average capture rate. As the sample included only birds remaining to forage, this bias might produce an artefactual increase in mean capture rate with disturbance. The short, and not particularly variable, flight distances observed in this study lessen the likelihood of this, however. Further studies of disturbed and undisturbed foraging waders are needed to clarify these changes in capture rate with disturbance.

Scan rates can vary with both bird density and reduced visibility. During this study, bird density on the Jordanstown beach was high; greater than the 0–5 birds within a 10-m radius found to lead to increased scan rates and/or scan durations. Reduced visibility was unlikely to affect the larger waders, as the low height of the boulders allowed Oystercatchers and Curlew to scan over the top. The higher scan rates of these species in the boulder-strewn upper and mid-shore zones may thus be attributed to their greater proximity to people on the grass and sand, but an influence of topography cannot be ruled out, especially for the smaller Redshank.

The greater vigilance shown by all species with increasingly vigorous human activities, and the continued foraging of these birds in the presence of seated humans at distances less than the flight distance from walking people, confirm the greater disturbance effects caused by more rapid movements. The lack of a significant increase in vigilance in response to dogs is surprising, as dogs exercising on the beach sometimes chased the waders, and dogs have been shown to be major disturbance factors in other studies.

In this study, the expected trade-off between vigilance (scan rate) and foraging (probing rate) was not found. Whereas scan rate increased with disturbance (particularly with fast human activities), implying a greater proportion of time spent in vigilance, probing rate remained essentially unaltered—the birds appeared able to search for food at the same rate while increasing vigilance. Frequent quick scans, of short duration, may be fairly easily incorporated into food-searching techniques in which the bird walks forward, probing occasionally as it moves, without causing a significant reduction in probing rate. The apparently increased capture rates found with approaching disturbance factors were also achieved with these increased scan rates. A full description of vigilance behaviour would require observations of scan duration in addition to the scan rates recorded, as these can be independently varied; an increased scan duration might be less compatible with maintaining probing rate. One possible explanation for this unexpected lack of a trade-off between vigilance and feeding is that these
waders were not, when undisturbed, foraging at their maximum possible rate, as has been indicated in other studies.\textsuperscript{6,13,15} They could therefore increase their vigilance without reducing their foraging rate. Thus, at highly profitable foraging sites where food intake is limited by a digestive bottleneck rather than by food capture rates, a small loss of feeding time due to disturbance may not be detrimental to the birds’ energy budgets, because it can be compensated for within the same tidal cycle.

The waders using the beach at Jordanstown appeared well habituated to the presence of people. Their flight distances, although not the smallest recorded for Oystercatcher and Redshank (Table 5), were considerably less than those found in Holland.\textsuperscript{6} The Curlew were remarkably tame in comparison. During the study, however, a few Curlew were obviously more wary, with a flight distance approximately the entire width of the beach (two values of 120 m are included in the mean given). These wary Curlew were precluded from using the site most of the time by their reaction to disturbance.

The differences between species in frequency of the various responses to disturbance – stopping feeding, walking or flying away – may reflect differing trade-offs between energy expenditure and predation risk. The higher frequency, in Curlew and Redshank, of stopping feeding while remaining still in the same place might be associated with their cryptic plumage; they were extremely difficult to distinguish when motionless on this beach. As this camouflage is destroyed by walking, a two-tier response to disturbance – freeze then fly if necessary – may be effective. By immediately walking away from disturbance, the highly visible Oystercatchers, unlikely to remain undetected when still, increased their distance from the potential danger with less energy expenditure than by using flight.

On popular recreational beaches such as Jordanstown, with people continuously present and potentially disturbing the birds throughout the whole low tide period, additional feeding could be achieved only by the waders foraging in the upper shore on the rising tide, delaying the departure to roost. However, the upper shore was more subject to disturbance, and the usual response of the birds to disturbance later in the tidal cycle was an earlier departure to roost. Any disturbance-induced reduction in food intake is therefore unlikely to be compensated for by increasing further the total foraging time on the beach, as was possible for Oystercatchers in the Exe estuary.\textsuperscript{15} The waders at Jordanstown appeared to cope with disturbance by habituation to continued but benign human presence, continuing to feed in the presence of humans while adjusting their vigilance according to the level of disturbance. This may be an important means of bringing the disturbance-induced reduction in their food intake down to a level which could be compensated for by normal foraging behaviour within their usual feeding period on this apparently highly profitable beach. However, this study was conducted in the summer; differing feeding conditions in winter would possibly alter the ability of these waders to compensate for the effects of disturbance. Their responses to disturbance in winter might therefore also differ.

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**REFERENCES**


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