THE WINTER FEEDING ECOLOGY OF THE BLACK-TAILED GODWIT - A PRELIMINARY STUDY

S. Ward & D.J. Bullock

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The feeding ecology and energy budget of an overwintering flock of Black-tailed Godwits was studied on the Eden Estuary, Fife. The godwits kept in a compact flock and showed the same movements each day. They fed exclusively in glutinous black mud, and the main feeding period was between 8 and 11 hours after high tide. The godwits fed by "stitching" (the more fequently used method) and "probing". Stitch rate was positively correlated with feeding rate and feeding rate was positively correlated with temperature. Daylight energy intake per bird was estimated to be between 0.1% and 23.8% of theoretical requirements. Even allowing for errors in estimation the large discrepancy between intake and requirements suggested that the godwits fed extensively at night.

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INTRODUCTION

In Britain over half the wintering population of the Black-tailed Godwit *Limosa limosa* is concentrated in five estuaries. The population has increased since the 1930s to around 4 800 birds, most of which are of the Islandic race *islandica* (Cramp and Simmons 1983, Moser 1987). Despite their increasing numbers and their restriction to a few estuaries, little is known of their winter feeding ecology. Moser (1987) reported that Black-tailed Godwits are the only entirely estuarine species of wader overwintering on British coasts and as such they may suffer relatively more from development of this environment than other wader species.

Black-tailed Godwits are highly gregarious (Goss-Custard 1970, Greenhalgh 1975). They feed in fine mud by both touch and sight, making small exploratory probes as they walk, and they sometimes probe deeply and vigorously to extract prey. In autumn on the Ribble Estuary the main foods were the lugworm *Arenicola marina*, the bivalve *Macoma balthica* and the ragworm *Nereis diversicolor*. These prey were taken from a relatively small area of glutinous black mud. These Black-tailed Godwits apparently failed to achieve energy balance by daylight feeding, and it was suggested that the birds fed at night to make up the deficit (Greenhalgh 1975). This paper describes observations on the feeding behaviour and movements of the Black-tailed Godwit on the Eden Estuary, Fife (56°22'N 2°52'W; Figure 1), the site of the northernmost wintering flock in Britain. Feeding was examined in relation to environmental factors, and a first estimate of energy budget was calculated for the average bird.

Between 90 and 130 Black-tailed Godwits were present on the Eden Estuary during January and February 1986. The estuary has areas of sand, mud, mussel beds and glutinous black mud. The last substrate predominates in the western part of the estuary where the godwits are found (Figure 1). Preliminary mud sampling in this area revealed that the main potential prey species were the amphipod *Corophium volutator*, the gastropod *Hydrobia ulvae*, *Macoma* and *Nereis*.

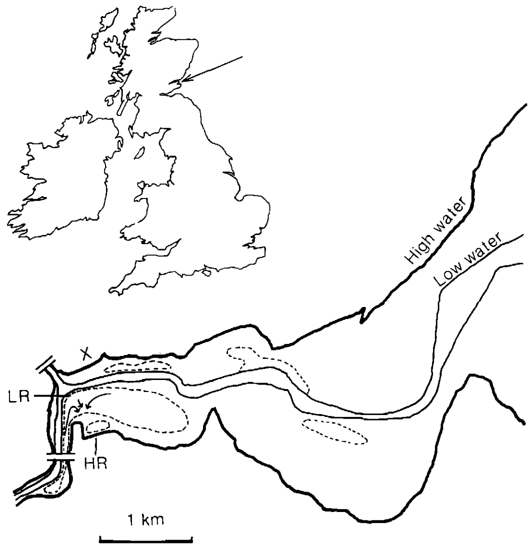

Figure 1. The Eden estuary showing observation point (x), the extent of glutinous black mud (dotted line, after Johnstone *et al.* 1979), the direction of movements of the godwit flock on the incoming tide (indicated by arrows), low tide roost (LR) and high tide roost (HR).

METHODS

Most observations were made from the north shore of the estuary. Feeding rate (number of items ingested/minute) was recorded by watching birds for two minutes of foraging (time spent in surveillance, interactions and preening was not included in this period). An observation period of two minutes was chosen after examination of a running mean of feeding rates. The number of prey taken was estimated by recording the frequency with which the head was lifted and jerked back in a swallowing action, as distinct from being withdrawn from the mud to move to a new feeding site. Prey items were often too small to be seen in the bill, but an attempt was made to identify larger items. Prey items were recorded as "bivalve" (assumed to be *Macoma*), "large" or "small worm" (probably *Nereis*), or "very small" item (probably *Corophium, Hydrobia* or small *Macoma*). At the end of each observation period a record was made of the time of day, proximity of the bird to the water's edge, and details of any aggressive behaviour which had involved the focal bird. Every 15 minutes the estuary was scanned from the observation point, and the position and activity of all Black-tailed Godwits was recorded. Flock scans of the percentage of birds feeding were only used in the analysis when more than seventy birds (approximately two-thirds of the population) were in sight. Several times on each day of observation air and mud (at 2 cm depth) temperature and windspeed measurements were made as close to the birds as possible; interpolations were made for intervening periods. Windspeed and temperature recordings were also obtained from Leuchars RAF airbase which is situated along the northern edge of the estuary. The daylight energy intake of the average Black-tailed Godwit was estimated using the following equation:

$$\text{Energy intake} = T \sum_{1}^{i} n_i c_i$$

Where T = mean time (min) spent feeding per daylight period, calculated from an eight-hour period of the area under the histogram of percentage of birds feeding against tidal state (Figure 2); n = mean number of ith species eaten per minute; c = energy content of ith prey species (calories/item). Theoretical daily energy requirement was calculated as a multiple of basal metabolic rate (BMR), using Lasiewski and Dawson's equation for non-passerine birds:

$$\ln BMR = \ln 78.3 + \ln W$$

Where W = mass of bird (kg) (Fisher 1972).

Daily energy requirements were taken as between 1.35 and 6.8 x BMR (Smith 1975, Puttick 1980).

RESULTS

General behaviour and movements

The Black-tailed Godwit usually fed and roosted in monospecific flocks. They were seen feeding only on glutinous black mud, and their movements were similar each day. At low tide the birds formed a single compact roost in the north-west corner of the Edenside flat (Figure 1). On the incoming tide they gradually dispersed to the south and east to feed along the edge of the river channel. Feeding stopped around high tide when the waters became too deep, and the godwits flew to salt marsh on the south shore to roost with other wader species (Figure 1). The pattern of movements on the falling tide was less predictable; the godwits usually fed in smaller groups, before concentrating at the low tide roost when the water level fell below the edge of the area of glutinous black mud.

Two feeding methods were observed, both of which were used by individual godwits during a two minute observation period. "Stitching" was the more frequently used method, in which prey was apparently searched for by touch as the tip of the bill was moved rapidly up and down in the substrate. This was distinct from the slower "probing" where the bill was thrust deeply into the substrate, presumably in response to a visual cue. The majority of feeding godwits (70%, n = 385) were in or adjacent to the water's edge; when on exposed mudflats, they usually fed in wet patches.

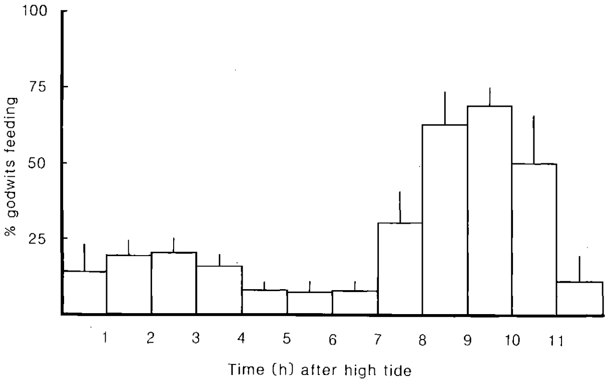

Figure 2. Variation in the percentage (x+ 95% C.L.) of godwits feeding during the tidal cycle. Arcsin transformation of percentages did not alter percentage values to any great extent and untransformed values were used.

Tidal effects upon feeding ecology

Feeding appeared to be possible for Black-tailed Godwits on all exposed mud or in shallow water. However, they roosted during a large part of the tidal cycle. The main feeding period, when over 60% of the birds were feeding, was between 8 and 11 hours after high tide (Figure 2). The overall feeding rate was 1.84 items/minute (N = 380), with *Macoma, Nereis* and "very small" items taken at rates of 0.24, 0.09 and 1.53 per minute respectively. There was no significant difference between mean feeding rate during the main feeding period, and during the rest of the tidal cycle ($t = 0.63$, $df = 356$, $p>0.5$). However, significantly more *Macoma* were taken during the main feeding period than at other times ($t = 4.4$, $df = 282$, $p<0.001$). Fewer "very small" items were taken during the main feeding period but the difference was not significant ($t = 1.75$, $df = 356$, $p>0.05$).

Stitching was observed at all states of the tide while most probing occurred around low tide. No probing was observed during the two hours before or after high tide. Feeding rates were significantly higher when the birds were stitching than when probing ($t = 4.18$, $df = 116$, $p<0.001$).

Stitching rate was significantly correlated with feeding rate ($r = 0.168$, $p<0.05$) but there was no significant relationship between probe rate and feeding rate ($r = 0.14$, $p>0.05$).

Influence of weather upon feeding

Air temperature and windspeed records from Leuchars RAF Base were highly correlated with our own records, so the latter were used where possible as they were more relevant. Air temperature on the estuary was significantly correlated with mud temperature at 2 cm depth ($r = 0.838$, $p<0.001$). Feeding rate was significantly correlated with temperature ($r = 0.166$, $p<0.05$ for mud temperature, Figure 3). This was due to the correlation between feeding rate on "very small items" and mud temperature ($r = 0.206$, $p<0.01$). Similar relationships between the feeding rate on *Macoma* or *Nereis* and mud temperature were not significant ($r = 0.139$, $p>0.05$; and $r = 0.042$, $p>0.05$). Feeding

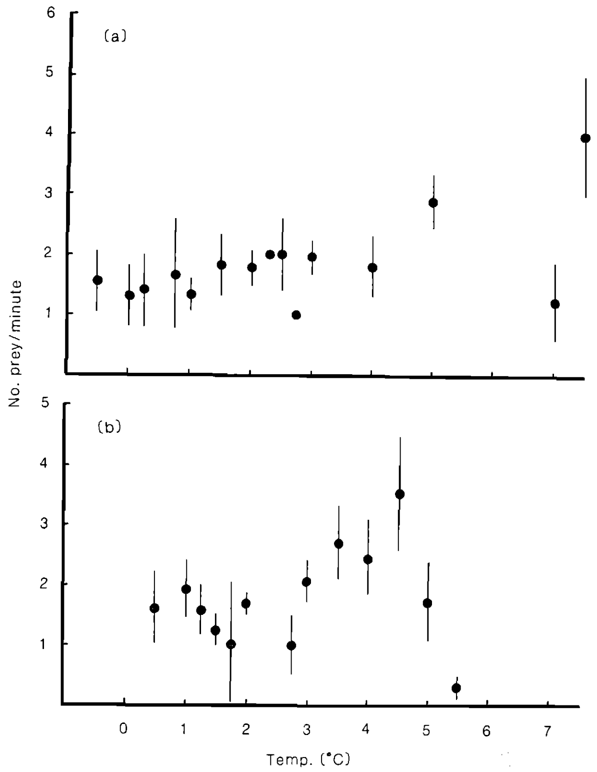

Figure 3. Relationships between feeding rate (no. prey/minute) and a). air temperature (°C). $Y = 1.39 + 0.16x$, $F_{1,378} = 23.92$, <p 0.001 and b). mud temperature $Y = 1.37 + 0.18\ x$ $F_{1,378} = 10.74$, <p 0.001. x + 95% C.L. shown. Regressions were calculated using raw data. Points without confidence limits show solitary data.

rate did not correlate with windspeed (r = 0.080, p>0.05).

Aggressive behaviour

Intraspecific aggressive behaviour involved disputes over food or feeding sites in 83% of cases. In the remaining cases, the reason for aggressive behaviour was unknown. An attacking godwit would run towards another with bill horizontal, uttering sharp calls. In 95% of cases the aggressor supplanted the recipient bird (n = 56). No significant relationship was found between mud temperature and the number of aggressive interactions (r = 0.003, p>0.05). Interspecific aggression was observed between Black-tailed Godwits and Bar-tailed Godwit *L. lapponica*, Common Gull *Larus canus*, Mallard *Anas platyrhynchos* and Oystercatcher *Haematopus ostralegus*. In all these interactions, Black-tailed Godwits were displaced. Black-headed Gulls *L. ridibundus* and Bar-tailed Godwits were also supplanted by Black-tailed Godwits.

Energy balance

Daylight energy intake of the average godwit was calculated from data on time spent feeding, feeding rate and the size of items taken. These parameters varied daily with tidal state and weather. Warm weather with low tide around noon, as opposed to cold conditions with high tide near noon were the most the least favourable feeding conditions. Corresponding high and low estimations of the calorific value of each prey category, feeding time and feeding rate were used to calculate maximum and minimum energy intakes during an eight hour day. Energy values of prey were taken for *Macoma* as 9.53 cal/item, large and small *Nereis* as 235 and 47 cal/item, and "very small" items a maximum of 2.5 cal/item and a minimum of 0.12 cal/item (Chambers & Milne 1975, Evans *et al.* 1979, Pienkowski 1982). Further details of how these energy values were selected are given in the Appendix.

Maximum and minimum BMR were calculated using Black-tailed Godwit weights of 250g and 160g (Cramp & Simmons 1983) in Lasiewski and Dawson's equation (Fisher 1972). Widely differing multiples of BMR have been used to estimate the daily energy requirements of waders. These range from 1.35 for roosting Curlew Sandpiper *Calidris ferruginea*, (Puttick 1980) to 6.8 for Oystercatcher (Smith 1975). Using these values the theoretical daily energy requirement of a Black-tailed Godwit was estimated to be between 28 to 195 Kcal. Comparison of estimated maximum and minimum energy intakes with requirements showed that an average Black-tailed Godwit was obtaining between 0.10% and 23.8% of its requirement during daylight.

DISCUSSION

On average, a Black-tailed Godwit on the Eden Estuary fed for 188 minutes during daylight, i.e. about 25% of the tidal cycle. However, the time spent feeding each day would vary due to the interaction between daylight and tidal state. Time spent feeding was considerably less than that observed for Black-tailed Godwits on the Ribble Estuary in autumn. Similarly, other wader species appear to feed for more of the tidal cycle in daylight than do Black-tailed Godwits overwintering on the Eden Estuary. For example, Hale (1980) found that Curlew *Numenius arquata* fed for 47% of the tidal cycle, whilst Knot *C. canutus*, Dunlin *C. alpina* and Redshank *Tringa totanus* fed for 95% of available daylight in winter (Goss-Custard *et al.* 1977). In common with Black-tailed Godwits on the Ribble Estuary, those on the Eden formed a secondary roost ("intermediate roost", Greenhalgh 1975), and concentrated their feeding and movements in a relatively small area compared with other wader species.

Feeding rate was around 1.5 items/minute at mud temperatures of 0.5°C, rising to 2.4 items/minute at 5.5°C. This is similar to the 1.8-3.5 items/minute observed by Greenhalgh (1975). Stitching and probing rates were higher than those previously recorded for Black-tailed Godwits: stitching rates reached 100 pecks/minute on the Eden compared with 36 pecks/minute on the Ribble (Greenhalgh 1975).

The number of Black-tailed Godwits feeding and their feeding rates appeared to be influenced by both tidal state and weather. Tidal state, temperature and condition of the substrate can all alter the depth of burial or activity of invertebrates. *Macoma* moves deeper in cold weather whilst *Nereis* remains below the water table, so that the depth of burial at low tide depends upon drainage (Prater 1972, Pienkowski 1983). These observations suggest that environmental factors determined the availability of prey, and hence the feeding rate of godwits.

There were two major potential sources of error in the estimation of energy intake. Firstly, during observations made between one and four hours after high water when the godwits were widely scattered, it is likely that the percentage of birds feeding was underestimated.

However, even allowing for a doubling in the time spent feeding per day, the average godwit would not have achieved energy balance. The second potential error was in the calculation of energy intake per minute of feeding. This might arise from errors in estimation of the calorific value of prey items; these were thought to be greatest for *Macoma* which varies greatly in energy content over a relatively small size range (Chambers & Milne 1975) (see Appendix). There was also the possibility that items might be ingested without a perceptible pause and swallowing action during stitching.

The calculation of energy requirements relied upon data from the literature for winter weight of Black-tailed Godwits, on estimation of how these weights were related to BMR, and estimation of the amount of energy above BMR expended by a free-living godwit. Smith (1975) found that the daily requirement of captive Bar-tailed Godwits was about 3 x BMR. Greenhalgh (1975) estimated that a wild Black-tailed Godwit ingested the equivalent of 1.5 - 2 x BMR per day in autumn (which he considered to be well below requirement). These data suggest that the deficit in energy intake indicated by our analysis was not simply a result of errors in assumptions.

The most likely explanation for the discrepancy between calculated energy intake and theoretical energy requirement is that the godwits fed at night. Nocturnal feeding occurs in several species of wader, but is thought to be avoided where possible because it is relatively less profitable in terms of energy intake than feeding in daylight (Heppleston 1971, Prater 1972, Evans 1979, Pienkowski 1983). However, Dugan (1981) suggested that for Grey Plover *Pluvialis squatarola*, a visual feeder, the disadvantage of reduced vision at night could be offset by increased prey avilability. Even if prey availability does not increase at night, a predominantly tactile feeder like the Black-tailed Godwit would presumably experience less difficulty in feeding at night than a visual feeder. Fat reserves of over-wintering waders are only sufficient to sustain the bird for a few days of severe storms (Pienkowski *et al.* 1984). Thus despite potential errors in estimating energy budget we suggest that nocturnal feeding accounted for much of the discrepancy between calculated daily energy intake and requirement.

ACKNOWLEDGEMENTS

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APPENDIX

In this short-term study, estimation of energy content of prey items from the study site was not possible. Consequently, all the prey energy content value used have been extracted from the literature and as such may differ substantially from those from the Eden estuary. However, the majority of values used were from estuarine studies on the east coast of Britain in winter. Given the preliminary nature of the present study use of such extracted data was considered appropriate. Details of how prey values were selected are as follows:

Macoma. Energy content estimated for the median age class (shell height 4.62 mm) in January on Ythan Estuary as 9.53 cal (Chambers and Milne 1975, Tables 1 and 2). In calculating the median, *Macoma* in the smallest class (shell height 2 mm) were omitted since these would have been recorded as "very small items".

Nereis. Values for the 0-1 and 1+ year classes of 47 and 235 cal/item were used (Evans *et al.* 1979, Table 9).

Very small items. Extreme values of 0.12 cal and 2.5 cal were used; the former is for 0-1 year *Hydrobia ulvae* (Evans *et al.* 1979, Table 9) and the latter is as determined by Pienkowski (1982) for this prey type.

WADERS WORLDWIDE

Members of the British Trust for Ornithology (BTO) will know that towards the end of 1986, the Estuaries Programme of the BTO initiated a regular double-page feature entitled "Shorelines" in *BTO News*, in order to keep BTO members informed of developments in the wader world. Some articles in "Shorelines" relate to studies involving BTO staff and membership participation, whereas others are aimed at providing the global perspective necessary for an appreciation of wader biology. Among the latter is a continuing series providing overviews of wader studies taking place in different parts of the world. We felt that these articles are of considerable interest to wader enthusiasts worldwide. With the agreement of the BTO, we will be reprinting some of these articles in the *Wader Study Group Bulletin*. The first of the series, on southern Africa, appears below.

The Editors

WADERS IN SOUTHERN AFRICA

Les Underhill

Reprinted from BTO News No. 152: 14-15 (Sept-Oct 1987)

The BTO ethos strongly permeates wader studies in southern Africa. Most ringers here are either first or second generation BTO-trained. First Clive Elliott and later Ron Summers provided professional leadership and input to the Western Cape Wader Study Group (WCWSG) since its inception in 1971, making it the first wader group in the southern hemisphere. Like the various wader groups in Britain, the WCWSG links and coordinates the activities of mainly amateur ringers.

Based on his pioneering work in eastern Scotland, Ron Summers coaxed the WCWSG into counting waders along the southern Africa coastline in 1975, long before he helped in motivating the Winter Shorebird Count in Britain. Due to the small teams of counters we could muster, the southern Africa coast was covered in a series of surveys over several years. The results of each survey have been published: an up-to-date list of these reports and papers may be found in *Wader Study Group Bulletin* 49: *Suppl.*: 15-34. A few sections of coast remain to be done. The coast of the Transkei is scheduled for December 1987, leaving only the diamond prospecting areas of southern Namibia and parts of the northern Cape unsurveyed for waders.

LANGEBAAN LAGOON

Important wader projects of the WCWSG completed in the past ten years have resulted in publications on the Curlew Sandpiper, Knot, Terek Sandpiper and Sanderling. The WCWSG has organised midwinter and midsummer counts at Langebaan Lagoon, on the Atlantic coast 100 km north of Cape Town and the most important wetland for waders in South Africa. A summary paper is in press (Underhill, *Ostrich* 1987). Our efforts played at least a small part in the proclamation of Langebaan Lagoon as a National Park in 1985. The January wader population at Langebaan Lagoon averages 34 500 birds, placing it among the major wetlands for waders along the East Atlantic Flyway. Table 1 gives a comparison of the species composition and abundance of waders in January at Langebaan with that at Lindisfarne, an estuary on the northeast coast of England holding a similar number of waders. Some striking points emerge. These distant sites both hold seven of the top twelve waders. Much the most abundant waders at Langebaan and Lindisfarne respectively are the ecologically similar Curlew Sandpiper and Dunlin. Only one resident African wader, the White-fronted Sandplover, closely related to the Kentish Plover, appears among the top twelve at Langebaan.

The Percy Fitzpatrick Institute of African Ornithology at the University of Cape Town is the local equivalent of the Edward Grey Institute at Oxford. There, Phil Hockey and Alison Bosman are doing fascinating work on predator-prey relationships between African Black Oystercatchers and limpets. They have found that limpets grow bigger and faster on offshore islands where the run-off after rain is enriched by the guano of the seabird colonies. Oystercatcher densities are about five times higher on these islands than the adjacent mainland. They remove mostly medium-sized limpets - the largest ones are left to breed and the smallest to grow.

In Port Elizabeth, on the Cape south coast, Paul Martin is completing a PhD on the ecology of waders on the Swartkops estuary. He also holds the rare distinction of being the first person in Africa to observe a Hudsonian Godwit - this bird appeared on the estuary early in