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Studies of shorebirds at Lindisfarne, Northumberland. 1. Feeding ecology and behaviour of the Bar-tailed Godwit

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Introduction

The Lindisfarne National Nature Reserve in north Northumberland (Figure 1) covers about 3,000 ha (12 sq. miles), chiefly tidal mud- and sand-flats, saltmarsh and dunes. It is famous chiefly for its wildfowl and shorebirds, as described in the vivid writings of Abel Chapman (1907). Lindisfarne is an important wintering area for Wigeon *Anas penelope*, Pale-bellied Brent Geese *Branta bernicla hrota* and Whooper Swans *Cygnus cygnus* among the wildfowl; maximum counts of these species in the winter of 1970–71 were 27,000, 1,000 and 430 respectively (Prater, 1971). In that same winter the total sum of the maximum counts of all shorebird species was 33,320, which placed the area eleventh in importance amongst British estuaries. The nearest estuaries which hold appreciable numbers of waders are the Forth (80 km north) and Teesmouth (130 km south), both of which are threatened by reclamation and further industrialization, and by oil pollution. Their loss would displace at least 60,000 shorebirds and several thousand Shelduck *Tadorna tadorna*. In these circumstances, it seemed imperative to investigate the potential 'carrying capacity' of the Lindisfarne Reserve for different species of waders and wildfowl. Studies were begun in January 1970, with the full co-operation of the Nature Conservancy and under the general

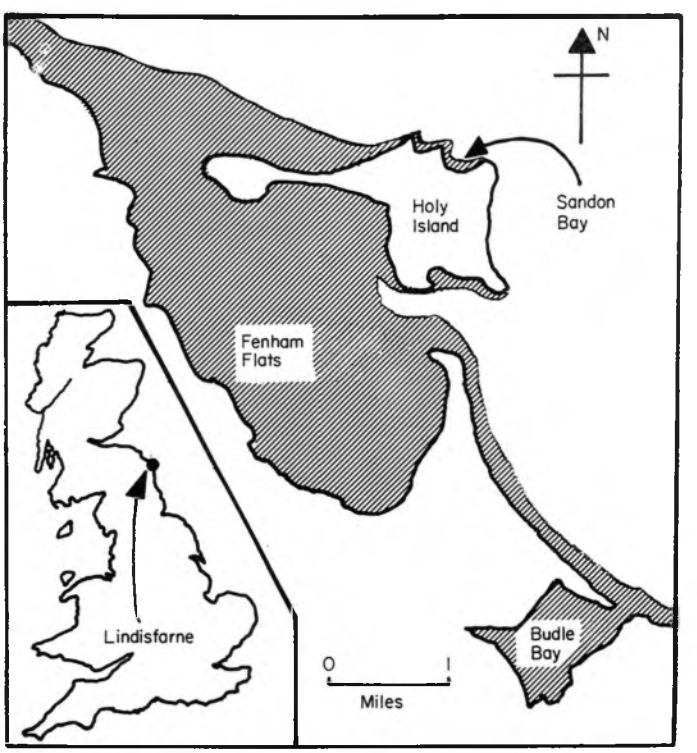

Figure 1. Lindisfarne, Northumberland. The intertidal sand and mud-flats lying within the National Nature Reserve are shown cross-hatched.

direction of P.R.E. This paper summarizes part of the findings of 3 years' research by P.C.S., particularly on the relationship of sexual dimorphism to feeding ecology and behaviour of Bar-tailed Godwits *Limosa lapponica*. While data were collected on this species, which both feeds and roosts on the Reserve, observations were also made on the use of the mudflats by several other wader species, notably Curlew *Numenius arquata*. These observations will be reported later.

The British Isles hold an important fraction of the populations of Bar-tailed Godwits which winter in western Europe. A total of just over 37,000 were recorded on British estuaries in January 1971 (Prater, 1971). Lindisfarne holds about 10% of that number in most winters. The majority of the birds arrive in late August and September, young preceding adults, and peak numbers are usually reached in December and January. In the recent mild winters, numbers have dropped below 1,000 as early as mid-February, but some wintering birds normally stay until April. Migrants pass through later, in May.

Remarkably little has been published on the feeding ecology of Bar-tailed Godwits, probably because the large flocks are found only on extensive sand- and mud-flats during the non-roosting period. Thus, while feeding, they remain beyond convenient observational range from the shore, except where small flocks and individuals occur, scattered in sandy bays along the coast. As will be mentioned later, the feeding behaviour of these solitary birds is not typical of the behaviour shown by birds in flocks.

Godwits feed chiefly at the tide edge or in water up to about 15 cm (6 in) deep. They return from high tide roosts as their feeding areas are uncovered by the ebbing tide, usually 2–3 hours after high water. They then follow the tide in its ebb and flow, feeding for 4–6 hours (depending on daylength and weather). Some birds also feed by night during periods of full moon and on dark nights in mid-winter, but as yet we have insufficient data to indicate how important such feeding is to satisfy the birds' daily energy requirements.

In terms of biomass, the most important food of the Bar-tailed Godwit at Lindisfarne is the lugworm *Arenicola marina*. (Intensive bait-digging by fishermen in the major wintering areas may thus seriously affect the future of this wading bird.) Other important prey are the ragworm *Nereis diversicolor* and a variety of small oligochaetes, polychaetes and molluscs, which often dominate the diet in numbers taken but are less important in terms of weight. Female Godwits take slightly larger size-classes of prey than do males. The importance of the different worm species in the diet was assessed mainly by direct observation of prey taken. The gut and gizzard contents of birds shot while feeding gave information chiefly on size-classes and on 'hard-shelled' items of diet.

The species shows sexual dimorphism, females larger than males, as in all British wader species except Ruff *Philomachus pugnax*. This dimorphism is greatest in bill-length; that of females averaging about 30% more than that of males (Table 1). It is probable that adults of each sex have slightly longer bills than the corresponding juveniles. Females are also slightly longer in the leg, and can thus wade in deeper water than males.

With a little practice the two sexes can be separated quite reliably in the field by comparing the length of the bill against that of the head (which varies very little between the sexes).

Table 1. Bill and tarsus lengths of Bar-tailed Godwits at Lindisfarne, Northumberland

	Bill	Tarsus
Males	77·0±3·1 mm	48·5±1·0 mm
Females	97·7±3·5	54·3±1·1

Figures quoted are mean ± standard error for sample sizes of twenty of each sex. Bill length was measured from feathers to the tip of the upper mandible, tarsus from the proximal end of the tibio-tarsus to the hallux.

Methods

Observations were made by telescope from the dunes at Sandon Bay, Holy Island and from simple hides, constructed from straw bales, set near low water mark out on the mudflats. Data were recorded on tape and transcribed later. When birds were feeding in flocks, observational periods of 60–100 minutes were used, divided into alternate periods of 10 minutes in which the locations of feeding birds were noted every 30 seconds, and 10 minutes in which probing and success rates of individual birds were measured. When birds were feeding solitarily, probing and success rates were measured for periods of 4–10 minutes immediately before or after observations on a nearby flock. The data were collected chiefly in the winters of 1970–71 and 1971–72.

Results

The data analysed below were collected from fifteen flocks at Sandon Bay, each containing between seven and sixteen birds. (It was difficult to make comprehensive observations on birds in flocks of greater numbers.) The fifteen flocks comprised five each of males only and females only, and five containing approximately equal numbers of the two sexes. All observations were made at the same stage of the tidal cycle (about an hour after low water) and under similar weather conditions. Data on feeding behaviour of single birds were collected from fifteen individuals of each sex.

This information has been analysed with respect to feeding situation, probing rate and success rate, and is summarized in Tables 2 and 3. Two feeding situations are recognized: 'at the tide-line' and 'beyond the tide-line'. Birds wading in water up to 'knee'-depth were in the former category, over 'knee'-level in the latter.

In both single- and mixed-sex flocks, males fed chiefly at the tide-line, but females beyond the tide-line. These preferences were more marked in mixed flocks: significantly fewer females fed at the tide-line in mixed-sex than in all-female flocks (*t*-test, $P < 0.001$), while significantly fewer males fed in deeper water in mixed-sex than in all-male flocks (*t*-test, $P < 0.01$) (Table 2).

Table 2. Feeding situations of male and female Bar-tailed Godwits feeding in flocks of different sex ratio

	Single-sex flock		Mixed-sex flock	
Males				
At tide-line	72%	(360)	81%	(380)
Beyond tide-line	28%		19%	
Females				
At tide-line	45%	(420)	26%	(380)
Beyond tide-line	55%		74%	

Figures in parentheses are the numbers of observations made (for details, see text).

The feeding situation markedly affected the feeding performance of males, but not of females (Table 3). When males fed beyond the tide-line they probed significantly less often and were less successful than when they fed at the tide-line (*t*-test, $P < 0.001$, < 0.05 respectively), no matter whether they were feeding in flocks with other males or with females. Females also probed slightly less often when feeding in deep water (though the differences are of doubtful statistical significance), but were equally successful in obtaining prey in both locations. Data obtained on the main mudflats support the above conclusions. The feeding performance of solitary birds showed high variability in both probing and success rates. To reduce the standard errors, data for all fifteen males and fifteen females have been pooled. Their average feeding rate was 50.3 ± 11.5 probes per minute and success rate 0.7 ± 0.3 items swallowed per minute. These observations refer to single birds feeding in the vicinity of, but not within, the flocks whose behaviour was detailed in Tables 2 and 3. Their feeding performance can therefore be compared directly with the means of the pooled data for all birds feeding in flocks, viz. 76.4 ± 3.1 probes per minute and 1.9 ± 0.2 items swallowed per minute. Thus solitary birds are clearly less successful than birds feeding in flocks, and often spend more time standing in an upright alert posture.

Discussion

In view of the poor feeding performances of solitary godwits, it is perhaps surprising that birds are so regularly seen feeding

Table 3. Feeding rates (F.R.) and success rates (S.R.) of male and female Bar-tailed Godwits in single-sex and mixed-sex flocks in two feeding situations

	Single-sex flock		Mixed-sex flock	
	F.R.	S.R.	F.R.	S.R.
Males				
At tide-line	78·5±1·4	2·1±0·4	83·6±1·5	2·3±0·2
Beyond tide-line	55·2±1·1	1·3±0·2	54·1±2·7	1·4±0·2
Females				
At tide-line	80·3±1·8	2·3±0·4	83·1±2·0	2·4±0·3
Beyond tide-line	72·2±1·3	2·2±0·4	76·3±1·7	2·4±0·4

Feeding and success rates are the number of probes and items swallowed per minute. Values given are means ± standard errors.

alone at Lindisfarne. Although they might merely be satiated, there is no evidence of an increase in the number of solitary feeders towards the end of the low tide period. Possibly they may be physically unfit. Whatever the reason for their behaviour, solitary individuals form a very small proportion of the total godwit population. Hence, for calculations of the impact of godwits on their prey during a winter, the feeding success rates of flocking birds must be used, even though these are more difficult to obtain. From observations of other species, we believe that greater feeding success in groups of birds is widespread in those shorebirds which flock regularly. We therefore urge caution in using measurements of feeding performance of solitary birds to estimate food consumption of whole wintering populations.

A feeding flock of godwits maintains an approximately oval shape, elongated parallel to the tide edge. Since flocking birds feed more successfully than solitary individuals, which spend more time on the alert, there may well be a selective advantage in flocking. (This can be confirmed only when the reasons for solitary behaviour are identified conclusively.) If a flock contains only males, some will be forced into deep water where their feeding performance drops (Table 3). Hence, it is of advantage to males to feed in mixed flocks, in which the females can utilize feeding situations beyond the tide-line without a reduction in their success rate. As expected, most flocks (about 90%) at Lindisfarne contain both sexes.

The division of feeding situations between males and females, the latter in deeper water, may help to reduce competition between the sexes when numbers are high in relation to the areas available for feeding. Sexual dimorphism in bill- and body-size has often been suggested as a means of reducing intraspecific competition for food, by for example, Selander (1966), Newton (1967) and Reynolds (1972). The long-billed female godwits may be at an advantage in some hard weather conditions. Although no prolonged cold spells have occurred in the last two winters at Lindisfarne, during brief cold periods two important prey species, *Arenicola marina* and *Nereis diversicolor*, were found deeper in the mud and sand than usual. At such times, female godwits took more of these prey than did the short-billed males. They by contrast took more of the small oligochaetes and polychaetes, which do not burrow so deeply. Males may therefore have found it more difficult to satisfy their daily energy requirements than females, in the short term. In prolonged or severe cold spells, however, females are at a potential disadvantage in that they require about 11% more food per day than males (This figure is derived from comparison of metabolic rates, calculated from Lasiewski & Dawson's (1967) equation, of birds of mean weight 340 g (females) and 300 g (males)).

In no other wader species occurring in Britain is the dimorphism in bill-size so great as in the Bar-tailed Godwit. It is not known whether selection for size occurs on the breeding or wintering grounds or both, though Salomonsen (1955) has argued that selection in the Ringed Plover *Charadius hiaticula* acts primarily in winter. At this time of year, different races are distributed in accordance with Bergmann's Rule, with the larger birds furthest north. In summer, the reverse is true; the largest birds breed furthest south, in contravention of Bergmann's Rule. Hence, Salomonsen argued, selection acts in winter. However, in arctic breeding species such as the Bar-tailed Godwit, selection might also occur on the breeding grounds, where long-billed females might be at an advantage over short-billed females in being able to feed in a greater diversity of sites upon first arrival, when food for egg-formation is needed. This does not wholly explain why males have much shorter bills. Sexual selection, as described for two North American sandpipers (Jehl, 1970), may also be involved. Jehl found that pairs formed between the smallest males and the largest females were among the earliest to breed in each season. The explanation proposed for the origin of sexual dimorphism in raptors by Cade (1960)—that the female must dominate the male to keep him in his role as food provider during incubation and care of the young—cannot apply in waders as the young are precocial. The problem will remain unresolved at least until we are able to study the godwits at Lindisfarne through a severe winter.

Acknowledgments

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Summary

An outline is given of the status and feeding ecology of the Bar-tailed Godwit *Limosa lapponica* at Lindisfarne, Northumberland. Sexual dimorphism in bill-length is pronounced, those of females averaging 30% longer than those of males. Birds feed close to the tide edge, but females tend to feed in deeper water than males. Males feeding in deep water are less successful in capturing prey than males feeding at the tide line, but females are equally successful in both locations. Godwits feed more successfully in flocks than solitarily. Selective advantages of long- and short-billed birds are discussed speculatively.

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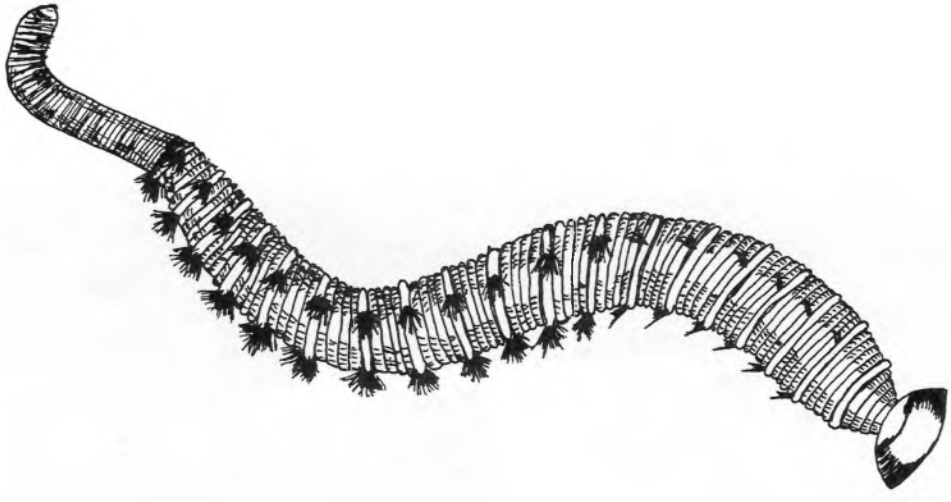

Lugworm *Arenicola marina*

Philippa Scott

Plate VI. Above: this unusually marked wild male Shoveler *Anas clypeata* has been coming to Slimbridge for four winters. Below: something of an identification problem. It is actually a Falkland Island Flightless Steamer Duck *Tachyeres brachypterus*.

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