Feeding behaviour of wintering Shelduck on the Clyde Estuary

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Introduction

Wintering Shelduck *Tadorna tadorna* are gregarious on sandy and muddy coasts and estuaries. There they feed on available invertebrates by sieving the upper layers of intertidal sediments. Campbell (1947), Goethe (1961) and Olney (1965a) found a predominance of the small gastropod *Hydrobia ulvae*, while others have reported a wider range of food items, with small worms possibly being important (Swennen & Van der Baan 1959; Jenkins *et al* 1975; Smyth *et al* 1977; Evans *et al* 1979). Bryant and Leng (1975) and Buxton (1975) studied the winter feeding behaviour of Shelduck on the Forth and on the Ythan Estuary respectively. They concluded that there was an association between feeding intensity and the density and biomass of *Hydrobia*.

Aspects of gregariousness in birds have been reviewed by Caraco (1980) and explained as a behavioural response to variable distribution of food supplies (i.e. patchiness), defence against predation, and enhancement of foraging efficiency. The tendencies for waders to flock whilst feeding on tidal flats have been discussed extensively (Goss-Custard 1970a, 1976; Evans 1976; Zwarts 1978; Bryant 1979). Unlike their smaller neighbours, Shelduck sieve sediment and so need water. Different feeding methods and patterns are therefore adjusted to water depth. In addition they may be related to density, as in Teal *Anas crecca*, (Zwarts 1976), or to the varying availability of invertebrates caused by tidal rhythms of behaviour. Bryant & Leng (1975) observed that the tidally-imposed behaviour of *Hydrobia* strongly influenced the spatial distribution of feeding flocks and feeding methods used. Though interactions between foraging waders and the seasonal and tidal rhythms of their preferred estuarine invertebrate prey have been reviewed (Evans 1979), they have not been fully considered in the less selective Shelduck.

Study area and methods

The tidal flats of the Clyde Estuary (Figure 1) extend over a total of 19·3 Km^2. Numbers and feeding distribution of Shelduck and other wildfowl are reported by Smyth *et al* (1977). The mid-winter feeding distribution of Shelduck is shown in Figure 1.

Two study areas offering somewhat different food resources were selected on the south bank (Figure 1). Woodhall on the lower estuary was a flat of muddy sand with gravel and shell fragments. Longhaugh Bay, higher up the estuary, was relatively sheltered with a finer substrate of muddy sand. Supplementary observations were made on Pillar Bank, and 'mudbank'. Principal Shelduck flocks on the two study areas were observed from hides for 4–5 hour daylight observation periods on six to eight days during each month from late November to mid-March. Two aspects of feeding activity were investigated, using check sheet sampling (Altman 1975), and are described below.

(a) Flock movement. During each quarter-hour 'scan' the following were recorded: (i) spatial position (numbers on sediment, sediment-water edge, and in water); (ii) spatial conformation, and (iii) linear density.

(b) Feeding activity of flock. The proportional use of different feeding techniques within the flock was recorded each quarter hour. Feeding methods were categorized after earlier workers as 'surface digging' on exposed sediment, 'scything' on sediment with a moist surface, 'dabbling' in shallow water (1–10 cm deep) on the tidal fringe or in pools, 'head-dipping' in deeper water (10–25 cm) from a swimming position and 'upending' in yet deeper water (20–40 cm). Focal animal studies were conducted on the third bird from the left edge of the flock (to avoid sampling bias) for five minutes each quarter hour. During this period the contact time with sediment, or below water, was recorded for each feeding method.

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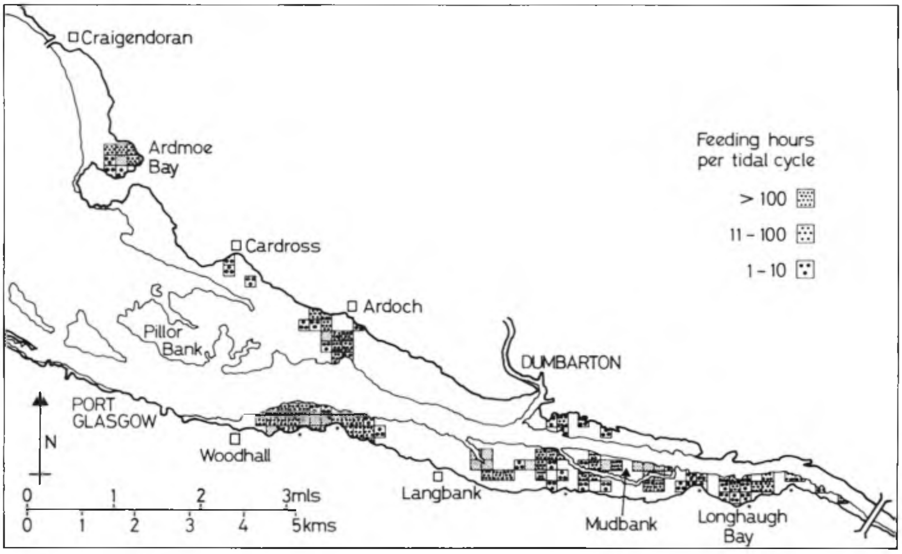

Figure 1. The Clyde Estuary showing the location of the two study areas. The observation points are indicated by stars. The distribution of Shelduck feeding during the winter of 1976–77 (December–February) is quantified as No. of Shelduck × feeding hours in each 0·04 Km^2 of tidal flat.

Computer analysis was applied to detect extent of clumping in feeding and non-feeding birds at Longhaugh, by plotting position of birds in a 1 cm: 50 m field map. All observations are presented in relation to tidal state (hours 1–12).

Results

Shelduck population wintering on the Clyde

Each year from October onwards there is a steady influx of birds from their moulting grounds, with a high proportion residing in the lower estuary, feeding in discrete concentrations. Maximum numbers up to 1200 have occurred during late January and early February, making the Clyde nationally and internationally important for wintering Shelduck (Prater 1976). March heralds a wider dispersal and shift up the estuary, where some 20 pairs take up territories.

The winter numbers in 1978/79 were much lower than in previous years with maxima of 352 at Woodhall in early February and 204 in mid-March at Longhaugh. A mid-February count of the whole estuary population gave 750, almost 500 fewer than in 1976/77. Counting feeding Shelduck on the Clyde is complicated by intra-estuary movements related to alternately exposed feeding areas e.g. during low tide many birds would move off-shore onto the lower lying Pillar Bank in the west and 'mudbank' in the east (Figure 1). This aspect of distribution is comprehensively covered by Halliday & Smyth (1978). Bryant (1978) mentions that up to 59% of a population moved to feed during ebb tide, returning during flow tide.

The wintering population has been declining during the last 6 years (1973–1979) with numbers during 1978–79 lowest. Dobinson and Richards (1964) reported that the 1962–63 hard winter caused a high mortality of Shelduck. However despite the very cold winter experienced during this study no dead birds were found. Invertebrate sampling indicated densities similar to previous years. Other factors could be responsible, such as poor breeding in areas from which Clyde birds are recruited.

Food availability

The highest density and biomass of the main macro-invertebrates is found in the mid-shore region (Curtis 1978). These invertebrates were most abundant in early winter, declining to low levels in March, mainly due to predation by the wintering population of birds including internationally important Redshank *Tringa totanus* and Dunlin *Calidris alpina* flocks. Up to 3000 *Hydrobia* have been found in a single alimentary tract of a Shelduck (Olney 1965), illustrating mass removal of invertebrates by birds.

Previous literature suggests Shelduck are capable of ingesting larger food particles in the upper 2·0 cm of sediment. At Woodhall *Hydrobia ulvae* and small worms including *Tubifex costatus* and *Manayunkia aestuarina* were abundant, along with less abundant *Corophium volutator*, *Nereis diversicolor* and sparse *Macoma balthica*. At Longhaugh the food supply was somewhat different with abundant *Nereis* and *Corophium*, and small worms as above. On the Pillar Bank there was a preponderance of *Hydrobia*, and in the 'mudbank' *Nereis* was very dense. It is worthy of note that *Nereis* and *Corophium* are particularly dense on the Clyde compared with other estuaries (Smyth *et al* 1977) and that *Corophium*, *Hydrobia* and most small worm species tend to be patchily distributed (Curtis 1978).

Several workers have investigated the behavioural rhythms of these invertebrates associated with tidal movements, affecting their surface availability. In summary, Vader (1964) reports that *Nereis* and *Corophium* become active on the mud surface immediately on being immersed; *Nereis* goes relatively deep during low tide whilst *Corophium* moves just below the surface. On the Ythan *Corophium* only surfaced if the air temperature was above 6°C (Goss-Custard 1969). Bryant & Leng (1975) correlated a decline in number of *Hydrobia* on the mud surface with temperature decline. On the Clyde highest densities of *Hydrobia* were visible on the exposed mud surfaces when air temperature was above 10°C. Winter daytime studies by Vader (1964) showed that the proportion of *Hydrobia* on the mud surface declined during low tide to almost 40%. On immersion they began to surface again (some having done so just prior to immersion), and as water deepened the population in the submerged mud surface increased to around 90% of the total population at a water depth of 5–10 cm. Throughout the ebb tide a proportion once again burrowed to a depth of 1–1·5 cm. *Macoma* always resides at least 2 cm deep and the majority of small worms are always in the upper 2 cm.

These observations suggest maximal availability of invertebrates on the sediment surface during flow tide i.e. just prior to and during tidal flat immersion.

Flock movements

Movement of Shelduck onto and away from feeding areas was determined mainly by tidal state and type (spring and neap). Proximity of human disturbance influenced movement during early winter, though later on Shelduck apparently habituated to this, noticeably during freeze conditions. Constraints imposed by spring tides included prolonged low tide exposure and high tide submergence, along with rapid water movement over the mid-shore. Neap tides had the opposite effect, permitting feeding throughout the entire tidal cycle in some areas e.g. Ardmore Bay, as observed on the Ythan (Buxton 1975) and the Forth (Bryant & Leng 1975). Data were collected for spring, 'intermediate' and neap tides; observations are presented for 'intermediate' tides, with spring and neap tide variations mentioned where appropriate.

Feeding commenced shortly after high tide, with the majority of Shelduck at Woodhall floating inshore from the channel area where they roosted, whereas the majority at Longhaugh flew down from adjacent saltmarsh (Figure 2). Ebb tide pattern was as follows: having arrived offshore as a dispersed floating flock, the birds swam inshore, moving closer together as they commenced feeding towards and at the tidal fringe. As the water level continued to drop the concentrated formation stretched laterally to form an ellipse and eventually a straight line along the tidal fringe over the mid-shore. During tidal hours 5 and 6 some birds remained to feed (and wander) on exposed sediment whilst others continued to follow the tide line. Thus the flock dispersed. During the low tide many roosted on the tidal flats in small pockets, usually in shallow pools, and much 'wandering' was observed with pairs covering as much as 200 metres in half an hour.

This ebb tide pattern of flock movement was observed on both study areas with Longhaugh birds having to spend longer periods on exposed tidal flat. There were anomalies, for example at Woodhall birds sometimes broke out from the resting flock during hours 2 and 3 before water became shallow enough for feeding (0·45 m) at the resting site. On such occasions they quickly

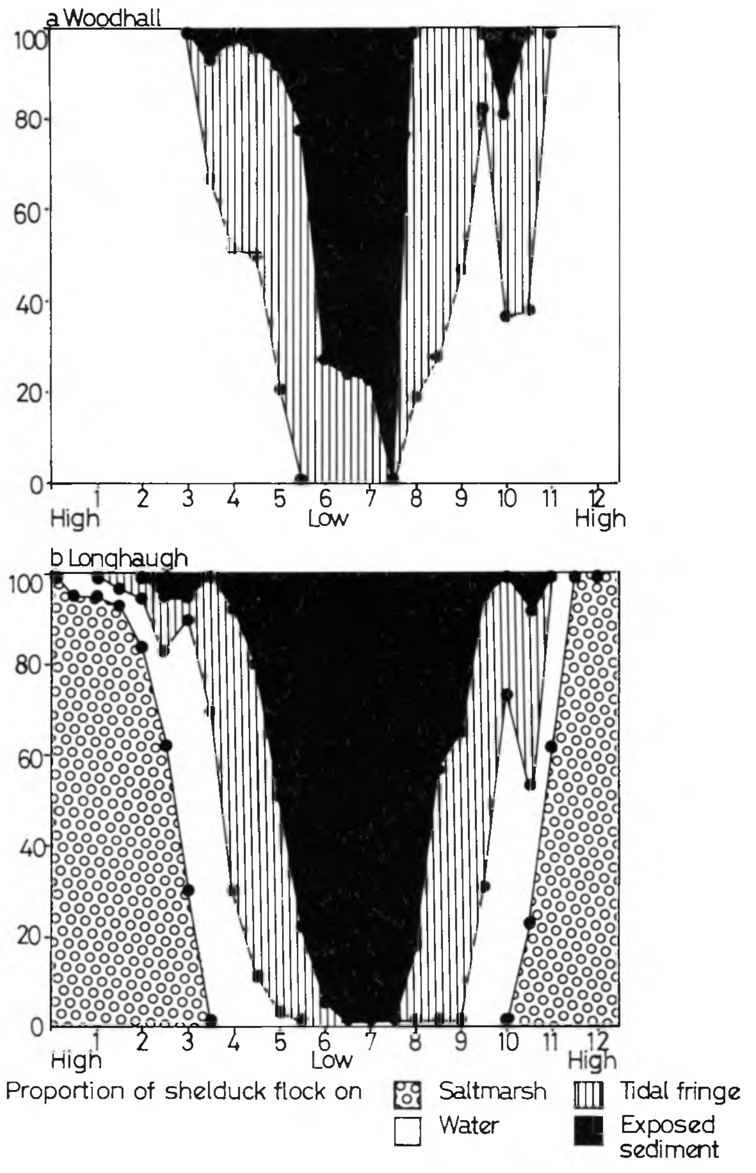

Figure 2. Movements of the flocks in relation to tidal cycle.

swam 'in file' towards the shore, where they dispersed along the tide line, feeding all the time.

The flowing tide overtook Shelduck on the lower mid shore during hour $8\frac{1}{2}$ at Woodhall and hour 9 at Longhaugh. Instead of moving up, feeding along the tide line, they fed in 'clumps' on the mid-shore initially by dabbling and later head-dipping and upending. For as long as 30 minutes they fed over the same area, resulting in floating ellipse formations 200 m offshore at Woodhall and 400 m offshore at Longhaugh. Later when water was too deep for feeding they moved inshore to feed along the rising tidal fringe. Feeding ceased as rising water took birds onto the upper flats containing little food. This is unlike the situation on the Forth where food is available in the mid and upper shore (Bryant & Leng 1975) enabling profitable feeding throughout high neap tides.

Feeding in highest densities occurred during ebb-tide (Figures 3 and 4) coincid-

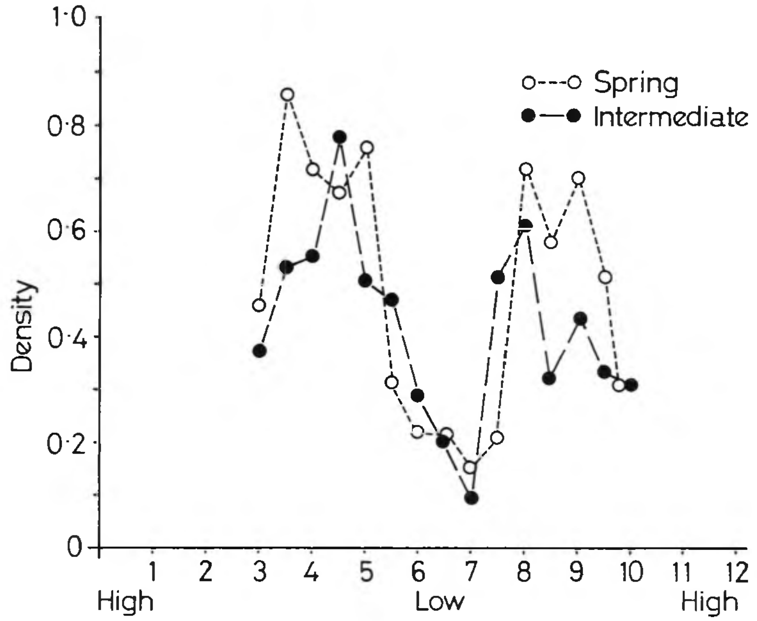

Figure 3. Density of flock whilst feeding in relation to tidal cycle. Observations at Woodhall where density was calculated as No. of birds/waterline length of flock (metres). Flock size varied between 15 and 150 and 14 and 86 during intermediate and spring tides respectively.

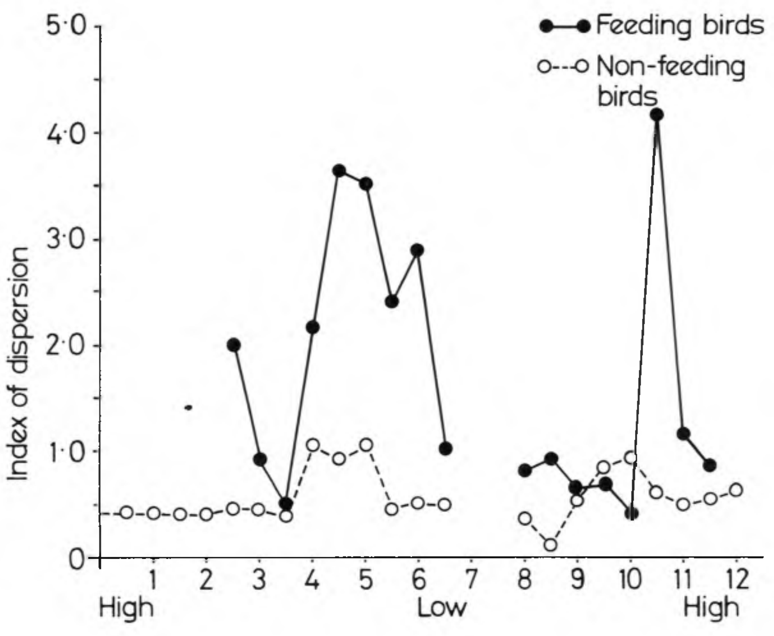

Figure 4. Indices of dispersion of Shelduck flock in Longhaugh Bay in relation to spring tidal cycle. When index of dispersion (variance: mean ratio) exceeds 1 the distribution is clumped.

ing with birds feeding in a straight line. Non-feeding and feeding patterns were similar (Figure 4) because feeders and non-feeders were intermingled. Although Shelduck congregated over 'patches' prior to and during early flow tide, their density was lower than during ebb tide because individual 'patches' were fragmented. True clumping during flow was not statistically detected until the birds moved inshore to concentrate their feeding on the limited upper shore still shallow enough for feeding.

Feeding methods

Shelduck exhibited a diphasic tidal rhythm of feeding, the two peaks occurring on the ebb and flow tide over the mid-shore (Figure 5). Apparently the feeding pattern did not change noticeably throughout the winter period or with temperature change, though if consistently low temperatures were experienced one would expect the proportion of time spent feeding to increase.

Rather more Shelduck fed through the ebb than flow tide, agreeing with a previous study at Woodhall (Halliday & Smyth 1978). However at Longhaugh they observed Shelduck feeding during ebb tide only. There is great variation in tidal rhythm of feeding between consecutive tides and days, probably accounting for this discrepancy. Tide type did not have a pronounced effect on feeding patterns though during spring tides there was apparently a greater proportion of feeding activity at peak tidal feeding hours to complement loss of feeding towards high tide. There was little feeding during low tide, partly because large numbers had departed to the Pillar Bank and mudbank (maxima of 204 and 236 counted respectively). Such movement was probably a result of exposed sediments being too dry for effective sieving, and the alternative lower lying areas having an adequate coverage of water for sieving.

Interaction between feeding method, tidal hours and tide type was significant ($X^2 = 60{\cdot}6$, $p < 0{\cdot}05$, df = 44). Furthermore interaction between feeding methods (already described) and tidal hours was highly significant ($X^2 = 450$, $p < 0{\cdot}001$, df = 88). At no time, except occasionally during low tide at Longhaugh, did the flock use only one feeding method. Head-dipping predominated during early ebb and flow (hours $3\frac{1}{2}$–4 and $9\frac{1}{2}$–$10\frac{1}{2}$ at Woodhall and hours $3\frac{1}{2}$–$4\frac{1}{2}$ and 10 at Longhaugh). Upending was used more commonly on the flow tide, suggesting it was most suitable for picking off already located available food on the submerged

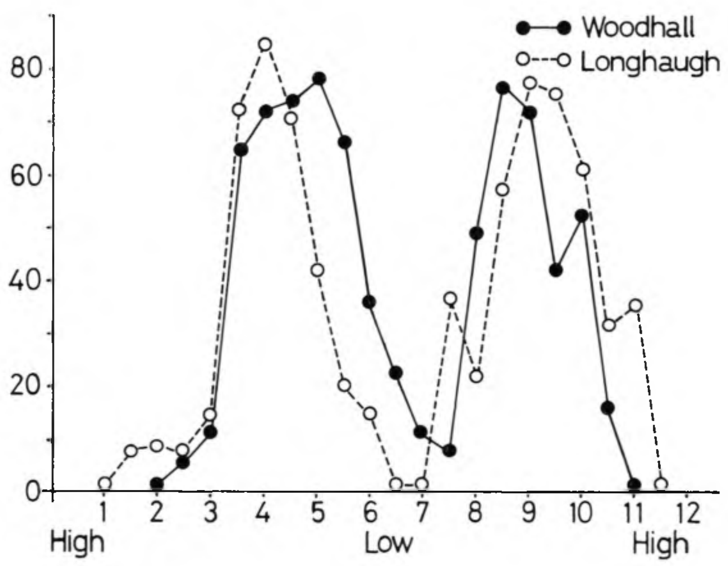

Figure 5. Proportion of Shelduck flock feeding at different tide levels. Flock size varied between 15 and 150 at Woodhall and between 15 and 235 at Longhaugh.

sediment surface. See Figure 6.

During mid-ebb Shelduck dabbled on the tidal fringe, changing to 'scything' (and sometimes 'surface digging' at Longhaugh) on exposed sediment. The commoner usage of head dipping during flow and especially upending during spring flow tides possibly resulted from greater duration and

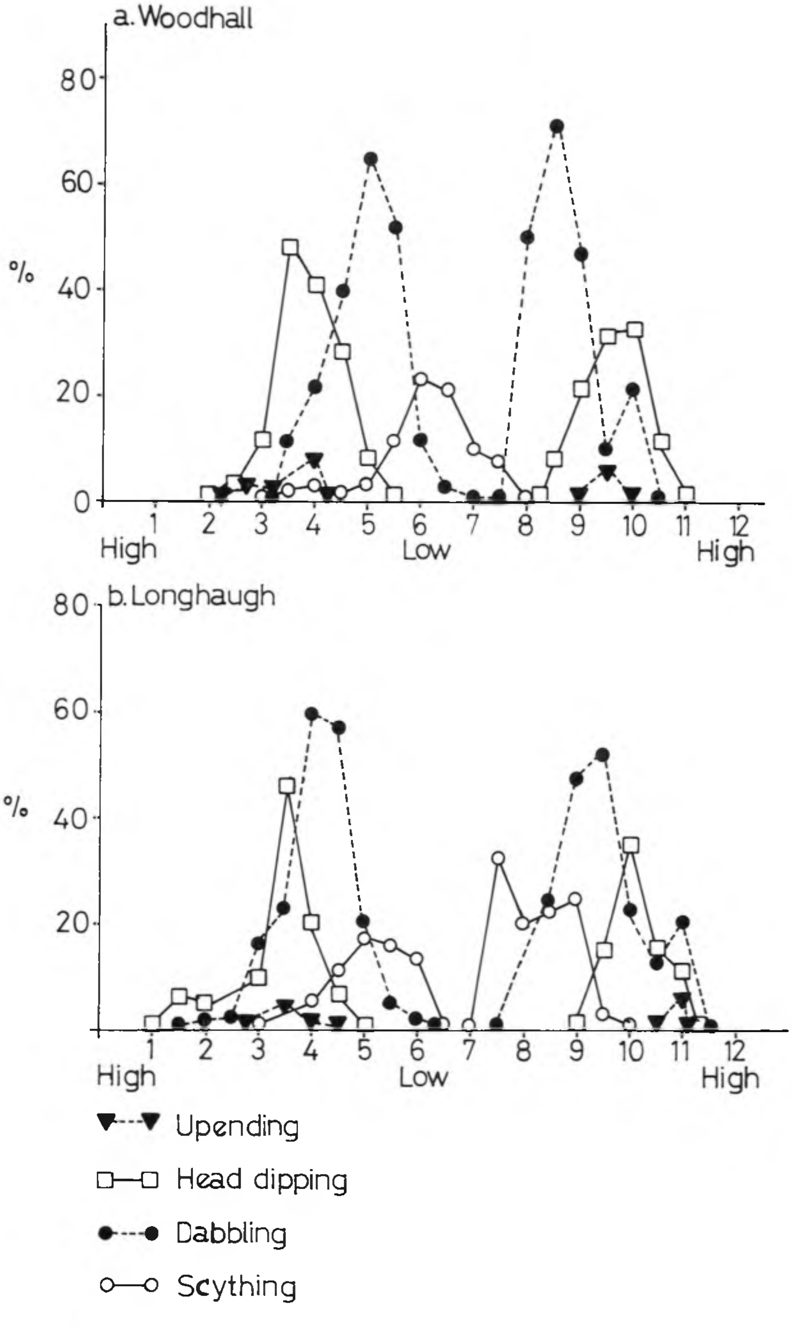

Figure 6. Usage of different feeding methods at different tide levels. Flock sizes as in Figure 5 (feeding methods described in text).

depth of coverage of good feeding areas, as observed for upending on the Forth (Bryant & Leng 1975).

Sometimes Shelduck searched prior to head-dipping (Thompson 1980). They dabbled in deeper water at Longhaugh than at Woodhall, possibly to exploit *Nereis* which only remains in the upper sediment in deep water (Vader 1965). In that case dabbling would penetrate to a greater depth than head dipping to capture *Nereis* in shallow water (10–15 cm). Durations of feeding methods, defined as the time the bill was in contact with the mud ('scything' or 'digging') or below water ('upending', 'head dipping' or 'dabbling') are given in Table 1. If feeding performance is broadly considered in terms of net energy yield per unit feeding time then assuming similar substrate conditions, food supply and intervals between contacts, the lengthier feeding action per unit time will be more rewarding. Contrary to the findings of Buxton (1975) contact times of different feeding methods did vary in relation to tidal state. Head-dipping did not last significantly longer than upending ($p > 0{\cdot}05$) within and between the two study areas, but the difference was significant ($d = 6{\cdot}76$, $p < 0{\cdot}01$, $df = 17, 7$) during flow tide at Longhaugh. There pool-dabbling lasted longer than tidal fringe dabbling ($t = 2{\cdot}02$, $p < 0{\cdot}05$, $df = 40$). Also scything was more prolonged than dabbling ($d = 5{\cdot}05$, $p < 0{\cdot}001$ $df = 30, 7$). Ebb and flow tide durations of all feeding methods did not differ significantly ($p > 0{\cdot}05$).

Having contrasted adoption and duration of different feeding methods one can describe their impact on the sediment. The 'mini-crater' created by dabbling Shelduck on the tidal fringe is illustrated in Figure 7. This has not been described elsewhere. Craters were of similar dimensions (5–6 cm diameter by 1–3 cm deep), often reaching a depth of 4 cm suggesting that Shelduck fed deeper than previously stated. In deeper water 'head-dipping' and 'upending' were used; their impressions were approximately 0·5–1·0 cm deep by 2 cm wide by 1·5–2·0 m long, hence suited for picking organisms off the sediment. The 'fern leaves' trail (described by Olney 1965a, and Swennen & van der Baan 1959) left by 'scything' Shelduck was rarely observed.

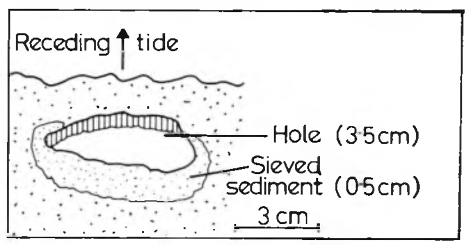

Figure 7. The 'mini-crater' formed by Shelduck 'dabbling' on the tidal fringe in water 1–10 cm deep when facing receding water.

Table 1. Durations of feeding methods (± Standard Error) at different tide levels.

Tidal hour	Scything	Dabbling	Dabbling (tidal fringe)	Head dipping	Upending
Woodhall					
3					2·50 ± 0·20
4			12·40 ± 1·90	3·61 ± 0·18	
5		19·00 ± 1·58		5·40 ± 0·38	
6		14·60 ± 0·80	8·80 ± 1·01		
7	17·20 ± 0·84				
8					3·42 ± 0·37
9			15·60 ± 0·22	3·20 ± 0·22	
10			14·70 ± 1·70		
Longhaugh					
3			15·10 ± 3·19		3·36 ± 0·25
4			16·40 ± 5·70	4·00 ± 0·53	
5	39·0 ± 2·53		13·20 ± 4·10	4·66 ± 0·25	
6	17·3 ± 4·40		5·70 ± 0·72	4·70 ± 1·29	
7	71·2 ± 14·40	17·2 ± 7·30	8·10 ± 1·89		
8		13·8 ± 2·23	5·25 ± 0·22		
9	18·0 ± 1·6		21·50 ± 2·45	4·15 ± 0·18	2·60 ± 0·23
10			24·00 ± 2·30	4·80 ± 0·30	

Discussion

Discrete concentrations of wintering Shelduck fed along the tidal flats of the Clyde Estuary (Figure 1). Their wide distribution indicated a varied diet composed of macroinvertebrates and small worms, available in the upper sediment. Their availability to surface feeding Shelduck depended on duration and extent of tidal coverage, weather conditions and human disturbance. (Compare with factors influencing waders described by Evans 1976.)

Past studies on behaviour and availability of tidal flat invertebrates suggest maximal availability just prior to and during flow tide (immersion), Bryant & Leng (1975) proposed this as the reason for the majority of Shelduck feeding on the flow tide in the Forth in areas where *Hydrobia* was abundant. This statement has caused controversy, partly because *Hydrobia* constituted only 28% of the invertebrate biomass (max) in the upper 2 cm of sediment there and because on some estuaries the main food organisms are likely to include small worms. On the Thames Shelduck fed predominantly on the ebb tide (Olney 1965) and on the Ythan and Clyde they fed on both ebb and flow tides (Buxton 1975; Halliday & Smyth 1978). Clearly in addition to food supply, the rate of drainage and coverage of sediment is one important factor influencing the feeding pattern.

Two peaks of feeding intensity (Figure 5) represented Shelduck feeding in ideal water depths (for sieving) over the midshore, where they could exploit the greatest abundance of food. This diphasic feeding rhythm, which continued through the night, is in contrast to that of diving ducks which are less restricted by varying water depth, and so exhibit fluctuating diurnal and tidal feeding patterns (Nilsson 1970, 1971; Player 1971; Campbell & Milne 1977).

The noticeable decline in feeding during low tide followed drainage of tidal flats, which reduced the effectiveness of sieving and of surface availability of invertebrates. Alternatively the birds may have been satiated, or required time to digest their food. Unsatisfied birds probably formed the bulk of those which moved to the Pillar Bank and 'mudbank' to feed during low tide. Alternatively aggressive interactions during peak feeding times could have led to exclusion of 'subordinates' from rich mud by low tide. Jenkins *et al.* (1975) reported this from February onwards at Aberlady on the Forth. Aggressive interactions (also detailed by Patterson 1977 on the Ythan) were not observed till early March on the Clyde, though there were frequent 'chases' between individuals during low tide throughout winter. Possibly absence of aggression resulted from low numbers falling short of the holding capacity of the Clyde.

During ebb tide feeding activity was maximal when Shelduck dabbled close together along the receding tidal fringe, thus avoiding depletion of food resources. Such mutual clumping was probably mainly due to a temporarily optimal water depth for sieving. Additionally clumping may have reduced time spent being vigilant and induced a faster feeding rate than might be maintained by more solitary feeders—which were not observed. Such dense feeding could reduce feeding by sight, by reduction of the 'search path' (Goss-Custard 1970, 1976), and impose tactile feeding. The latter was considered as the main mode of detection (Bryant & Leng 1975).

With commencement of flow tide the majority of Shelduck congregated in 'clumps' rather than in the previous straight line formation. Instead of moving up with the rising tidal fringe, they apparently fed over specific areas. They first fed by dabbling, then by head-dipping and upending over the same area, presumably to offset increasing water depth. Such a pattern was especially evident during spring tides, and always at Longhaugh. This indicated feeding responses to a readily available supply of patchy food, and *Hydrobia*, *Corophium* and most small worm species are patchily distributed on the Clyde (Curtis 1978). Presumably Shelduck moved off these patches when either too great a water depth prevented feeding, or when the energy cost of searching nearly equalled the energy derived from feeding there. As the food is abundant temporarily it is unlikely that individuals would compete for food. The tidal pattern of dispersion was somewhat different to that reported for Teal by Zwarts (1977). During receding and low tide they fed on exposed but very wet tidal flats, at a lower density than when they foraged below the tide line in the narrow zone of shallow water during flow tide.

No correlation was found between temperature and feeding intensity though this has been noted ($r = -0{\cdot}76$) by Zwarts

(1976), with high correlation between feeding density and temperature ($r = +0{\cdot}61$). In warmer conditions *Corophium* and *Hydrobia* are more available in the upper sediment (Goss-Custard 1970; Bryant & Leng 1975). It is also of interest to note that Buxton (1975) did not detect correlation between number of 'bird feeding hours' and prey abundance.

Clearly the large goose-like Shelduck sustains itself on a variety of tiny invertebrates abundant in the upper sediment. To achieve this it adopts a variety of feeding methods to enable maximal exploitation over the tidal cycle. Bryant and Leng (1975) found 'head dipping' commonest on the Forth, they explained this as being the best means to exploit surface available *Hydrobia* which had moved up in response to submergence of the sediment by the flowing tide. On the Ythan and Thames, where Shelduck fed on the ebb tide, 'dabbling' was considered commonest (Olney 1965 a, Buxton 1975). On the Clyde 'dabbling' was considered as the most effective sieving method being undertaken on the tidal fringe (usually) from a relatively stationary position. Its usage by the flock enabled high density feeding; with individuals thoroughly sieving a unit volume of sediment yielding organisms as deep as 4 cm. 'Head-dipping' used by relatively mobile birds feeding at lower densities (Figure 3) apparently exploited less mud per unit area. It is suggested this was still a profitable technique because the Shelduck fed on abundantly available (and conspicuous) invertebrates, all reacting to tidal immersion; and because the birds could cover a greater surface area than dabbling enabled. The other feeding techniques were adaptations to varying degrees of tidal exposure. As such they were likely to be less rewarding of effort, except on very rich areas, since they were more selective. This pattern was very different from that of the accompanying more numerous and smaller waders which fed selectively by pecking at individual organisms. Emphasis on non-selective feeding may thus relate to the large size of the bird in comparison with the small size of its prey.

Variations in dispersion over the tidal cycle and during winter, are difficult to explain because vigilance and enhanced foraging were not measured. In addition the availability of food supply is determined temporarily in various ways by tidal state. Smith & Evans (1973) and Evans (1979) have considered how tidal rhythm of invertebrate availability can enhance shorebirds' foraging activities. The possibility of such interactions between Shelduck and prey need further investigation.

Proposed industrial developments may reduce or eliminate valuable tidal flats on the Clyde. The value to conservation of this study, in conjunction with the earlier one described by Halliday & Smyth (1978) has been (i) to describe where and when an internationally important flock of Shelduck feeds and (ii) to assess which factors determined their dispersion. By appreciating these it should be possible to predict how Shelduck will adapt to newly imposed feeding conditions, and whether or not they will remain on the Clyde.

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Summary

The feeding distribution and routine of Shelduck *Tadorna tadorna* on the intertidal flats of the Clyde Estuary were studied during the winter of 1978–79. Flocks on two areas offering somewhat different food resources were selected for intensive observations. Invertebrates were exploited by 'dabbling', 'head-dipping' and less frequently by 'scything' and 'upending'. 'Mini-craters', the impressions formed as a result of 'dabbling' are described. A diphasic tidal rhythm of feeding was observed, with peak intensities occurring over the mid shore. Shelduck fed in a tight straight line on the fringe of the ebbing tide, predominantly by 'dabbling', ingesting available organisms in the upper 3 cm of sediment. They dispersed during low tide to roost and occasionally feed, whilst others departed to lower lying feeding grounds. During flow tide several hours after the tide had turned, Shelduck tended to converge on patches on the mid-shore. Possibly such clumping was a response to surface availability of *Hydrobia ulvae*, *Corophium volutator* and less patchy *Nereis diversicolor*.

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