The importance of food in the determination of the winter flock sites of the Shelduck

N. E. BUXTON

Introduction

The Shelduck *Tadorna tadorna* arrives back from its summer moult migration to the Ythan Estuary, Aberdeenshire, in mid-December. From then until May, the population continues to increase as first the older birds return, followed later by the immatures. The birds associate in flocks which frequent favoured sites scattered throughout the estuary, tending to be highly faithful to their particular flock site (Williams 1973). All feeding takes place on these sites until the birds go to roost over high tide (Buxton 1975). However, certain sites are more popular, both from the regularity with which they are attended, and from the numbers of birds that use them.

An initial study of the general ecology and population structure of the Shelduck in the Ythan (Young 1964) was followed by an investigation into the dispersion of the birds throughout the year especially in relation to the breeding cycle (Williams loc. cit.). A further study is still in progress investigating social behaviour and social organization in relation to the limitation of the population. Thus, with the existing extensive background information, it was considered important to examine the role of food in the dispersion of the birds.

Study area

The Ythan Estuary (Figure 1) is situated 21 km north of Aberdeen. It is 8 km long and averages 300 m wide throughout its length. Many research workers have adequately described the physical structure and hydrology of the estuary in the past (Walton 1966; Leach 1969; Milne & Dunnet 1972) so further reference here is unnecessary.

Three flock areas were chosen for study. Cowstane Hirst (Figure 1) was the largest flock area in the lower regions of the river situated about 1 km from the estuary mouth on the west bank. It was a mixture of fine mud, sand and mussel beds. The Sleek of Tarty (Figure 1) was a large mudflat about 2·5 km from the estuary mouth. It was bounded to the south by the Tarty Burn and to the north and west by saltmarsh. The area used by the flock was a fairly uniform substratum of sand and very fine mud. The Forvie Bank, on the east side of the estuary was the most uniform of all the three areas. The sandy shore sloped slightly from the high-tide mark where there was an area of boulders and small pebbles to a few weed covered boulders only exposed at the lowest tides.

Methods

Transects along the length of the estuary were used to determine the feeding behaviour of the birds. These covered the whole width of the estuary from Cowstane Hirst past the Sleek of Tarty to the Forvie Bank. Observations were made from a car and one transect could be completed in $\frac{1}{2}$-hour.

The transects were continued for a tidal cycle, completed in one day if daylight allowed. In January and February this was not possible and the tidal cycles were 'compounded' from two days as close together as possible, whilst allowing the full twelve hours of tidal flow to be covered during daylight. During 1972 only one complete tidal cycle was obtained for each month. However, in 1973, data were collected for both a complete neap and a spring tide in all months except January.

At each location the birds present and the number feeding were counted. By summing the total numbers of birds present and the numbers of birds feeding during a tidal cycle in any area, the total proportion of time spent feeding was calculated.

Once the number of feeding birds on any flock site was known during a thirty minute transect, the number of bird feeding hours could be calculated in that period and hence during the tidal cycle.

The numbers of prey in the flock sites were estimated in early spring by means of sampling transects down the beach between the tidal extremes.

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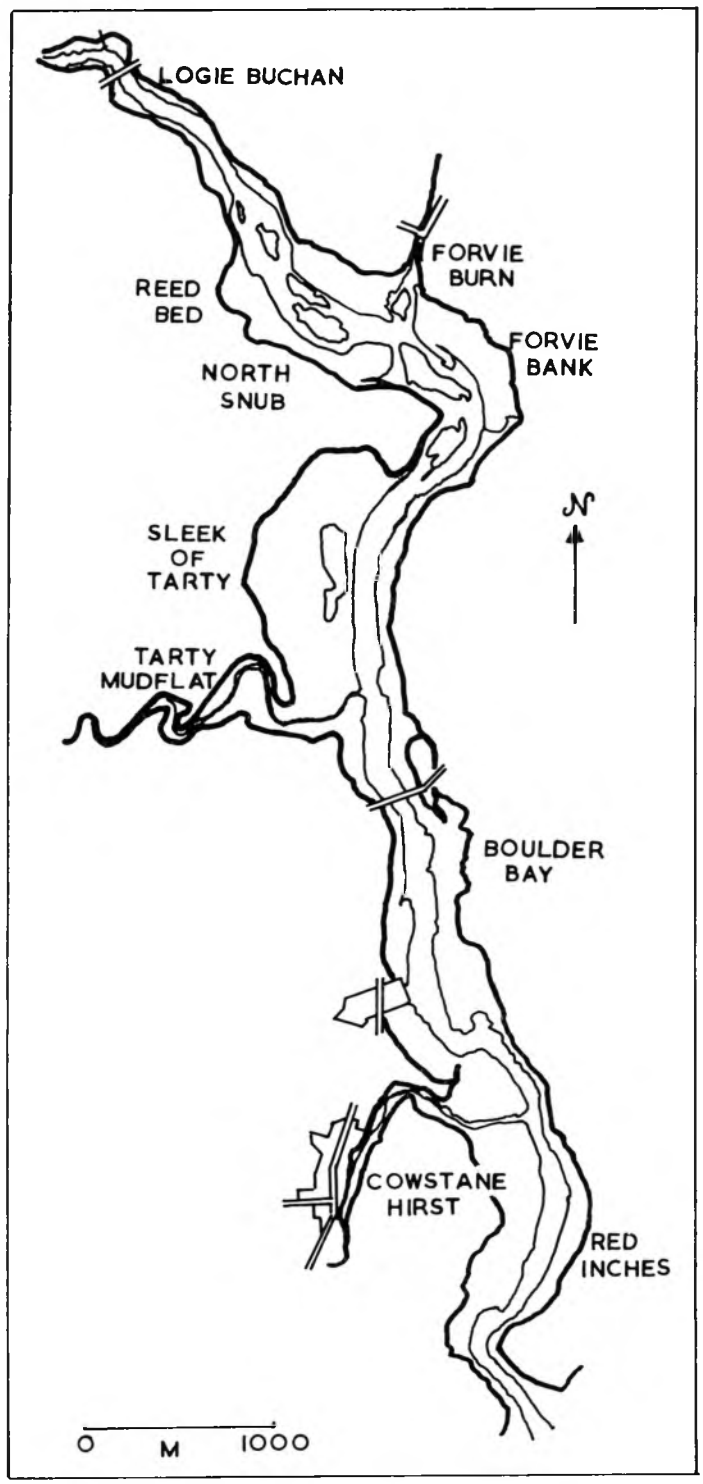

Figure 1. The Ythan Estuary, showing feeding areas.

a) *Hydrobia* and *Corophium*

The method used was devised by A. Anderson to overcome the problems caused by non-random distributions. The transect was divided into three zones, each of which ran for 10 metres on either side of the centre line, giving six half zones. Four samples taken from stations within each half zone by means of a 5 × 5 cm corer were paired to give two compound samples per half zone, and 12 compound samples from the transect.

Although most *Hydrobia* are found in the upper 1·5 cm of mud (Vader 1964), between 25–37% of the *Corophium* occurred below 2 cm (M. R. Chambers, pers. com.), and these were mostly large animals important to the Shelduck. The samples were therefore taken to a depth of 7 cm. In the laboratory each compound sample was stirred to randomize the contents, then sub-sampled, an essential procedure due to the high numbers of invertebrates in some areas.

Half a compound sample was washed through a 500 μ sieve to retain the *Corophium*. One quarter was washed through a 250 μ sieve to retain small *Hydrobia*.

b) *Nereis*

At each sampling site a cylindrical corer of 69 mm diameter was inserted to a depth of 30 cm to collect *Nereis*. The *Nereis* samples were washed through a 500 μ sieve. All invertebrates were stored in 10% formalin, counting and measuring being undertaken later.

Results

The distribution of ducks and their prey

Shelduck were generally restricted to areas in which *Hydrobia* were present (Figure 2). Most sightings were on the three study sites and these coincided with the greatest densities of *Hydrobia* (>1000/m^2). The South Sleek was the most extensively used site and was exceptional in the large areas densely populated with *Hydrobia* (>10,000/m^2). These densities are from Young (1970) and are probably underestimates due to his different counting methods. Substantial invertebrate populations were also present on Cowstane Hirst and the Forvie Bank. Few ducks were observed during the winter at either Logie Buchan in the upper regions of the estuary or at the estuary mouth.

Feeding effort at the flock sites

The proportion of time spent feeding over a tidal cycle varied between flock sites (Table 1). During both 1972 and 1973, the lowest proportion of time spent feeding in any month was by birds feeding on Sleek (max. 38·9%—min. 15·9%). In contrast, on Forvie and Cowstane, birds occasionally fed for over 50% of their time.

The only exceptions to this were during the neap tides of January and March 1973. In January 1973 the proportion of time spent feeding on Sleek was higher than expected, that on Cowstane lower. The numbers of the birds on Sleek and Cowstane over this tide fluctuated in parallel (Figure 3) and hence in this instance the

Table 1. The proportion of time spent feeding (%) in the flock areas over a tidal cycle.

		Spring tide				Neap tide		
	Locality	Jan.	Feb.	March		Jan.	Feb.	March
1972	Cowstane	–	48·6	–	–	–	–	46·4
	Sleek	–	23·9	–	–	–	–	33·8
	Forvie	–	73·6	–	–	–	–	55·5
1973	Cowstane	–	57·2	57·6	41·5	35·5	52·9	39·2
	Sleek	–	15·9	22·7	21·9	38·0	30·1	38·9
	Forvie	–	35·2	32·3	37·4	37·9	41·3	15·9

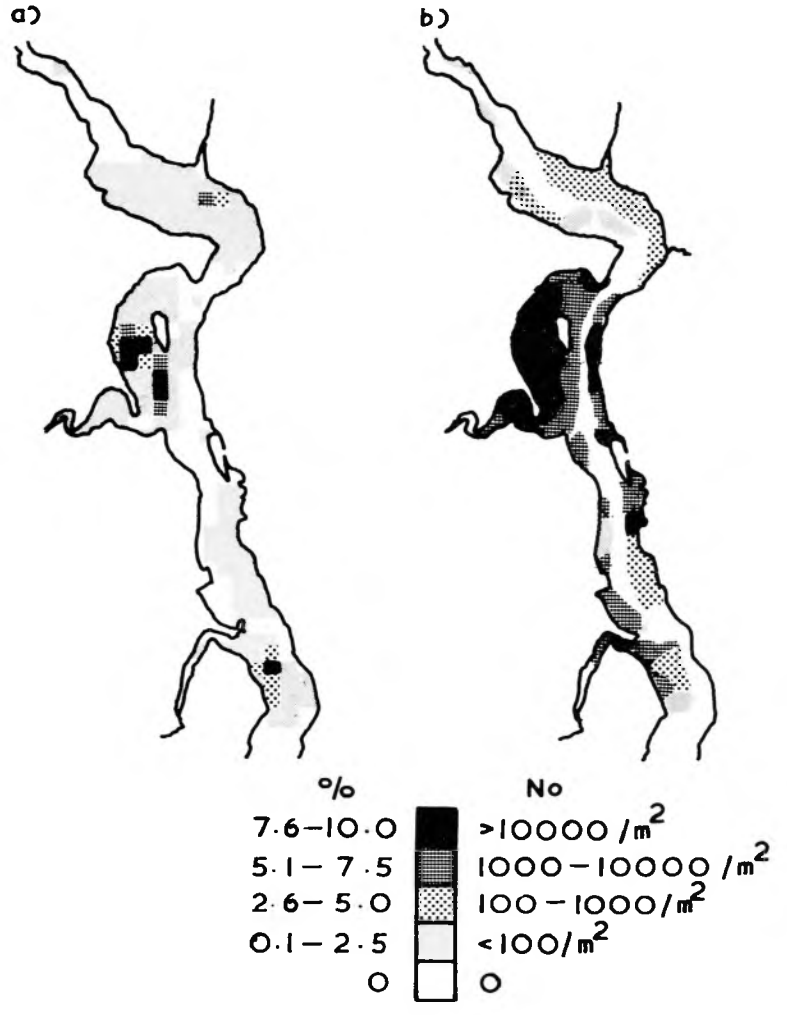

Figure 2. (a) Distribution of Shelduck sightings (%). (b) Densities of *Hydrobia ulvae* (adapted from Young 1970).

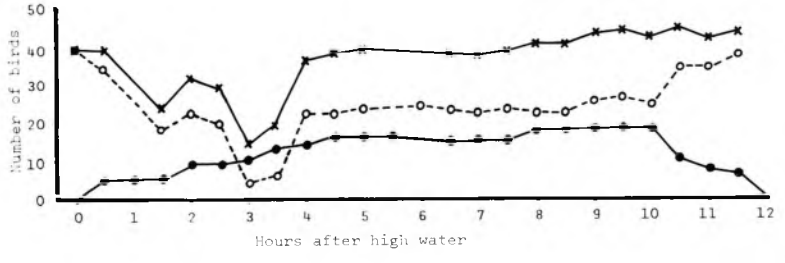

Figure 3. The number of birds on the Sleek and Cowstane Hirst on a neap tide in January, 1973.
●—● Cowstane Hirst ○---○ Sleek, ×—× Total.

two flocks were not truly separate entities. The high proportion of time spent feeding on the Sleek may have been due to birds newly arrived from Cowstane feeding on Sleek in the three hours prior to high water. Feeding behaviour in March was probably modified by a proportion of the food being obtained outside the estuary. From 492 observations on feeding birds, 82 (17%) were feeding on grain in fields.

During February 1972, a maximum of 63 out of 85 birds (74%) on the estuary were on Forvie, during March 60(51%) out of 118 birds. Sleek supported the majority of the rest. In 1973 the largest flock on Forvie was 29 birds. Although this accounted for 45% of the birds in the estuary, a number of birds were known to be feeding in the fields.

Thus certain flock areas were extremely attractive even though the proportion of time spent feeding was very high, i.e. 55·5% and 73·6% on Forvie. The importance of Forvie in 1972 was emphasized by the large number of feeding hours spent on it (Table 2), reflecting the large numbers of birds using the area. Sleek in March also increased in importance.

In contrast, in 1973 the distribution of feeding time was more equal between sites. Only on neap tides did Sleek support extensive feeding. The low number of feeding hours on Forvie in January reflected the extremely small number of birds using that area.

The decrease in the number of feeding hours on Sleek and Cowstane on the neap tide of March 1973 suggested that the birds were beginning to use alternative food sources outside the estuary, since the population was still increasing and the overall decrease in feeding hours was not compensated by the increase on Forvie.

Hence the use of flock sites varied widely between years and also between months. If available food alone were to explain this, it must be subject to large scale fluctuations in either quantity or availability.

The prey populations

Hydrobia total densities on Sleek in both 1972 and 1973 were significantly higher than those on Cowstane and Forvie (Table 3). Those on Cowstane were higher than those on Forvie ($P < 0{\cdot}001$) in 1972 but not in 1973. Large-scale changes in population size were evident on all the feeding grounds. The large increase in numbers on Forvie in 1973 was due to many very small (0·5–1·0 mm) molluscs. Cowstane also supported a large proportion of very small molluscs during 1973, but it did not support the number of medium-sized (1·5–2·5 mm) individuals of the previous year, thus giving an overall decrease in density.

Only a proportion of the total *Hydrobia* (those between 3·0–4·5 mm) were actively sought by the ducks (Buxton & Young 1981). The sizes selected were only a large proportion of the total population on Forvie in 1972 (74%), but in both years were in greater densities on Sleek than on either

Table 2. The bird feeding hours spent on flock areas over a tidal cycle.

		Spring tide			Neap tide		
	Locality	Jan.	Feb.	March	Jan.	Feb.	March
1972	Cowstane	–	61·5	– –	–	–	85·0
	Sleek	–	39·0	– –	–	–	175·5
	Forvie	–	368·5	– –	–	–	291·0
1973	Cowstane	–	43·5	56·5 27·0	49·0	81·0	34·5
	Sleek	–	50·0	71·0 66·0	104·0	114·0	47·5
	Forvie	–	55·5	62·0 64·0	12·5	28·5	33·0

Table 3. Densities (No./m^2) of *Hydrobia*.

Locality	All sizes ± S.E.		Selected sizes ± S.E.	
	1972	1973	1972	1973
Cowstane	33,870 ± 10,900	14,930 ± 4,310	6,330 ± 1,380	4,670 ± 1,080
Sleek	94,400 ± 14,990	80,400 ± 6,020	35,400 ± 5,710	47,670 ± 5,760
Forvie	4,670 ± 860	15,000 ± 2,750	3,470 ± 700	4,200 ± 650

of the other areas ($P < 0{\cdot}001$). The biomass of both the total prey and the selected sizes were also greatest on Sleek.

Corophium (Table 4) in both years had total densities on Forvie significantly greater than on the other two areas ($P < 0{\cdot}001$). The sparse but clumped distribution of the animals accounted for the high standard error.

The differences were significant when considering densities of the selected sizes (those longer than 4·0 mm). Except for Cowstane in 1973, these larger individuals accounted for over 60% of the total in all areas. As with *Hydrobia* the differences in density were reflected in the biomass.

Nereis populations occur at their maximum density in the mid-regions of an estuary and hence in the Ythan the greatest numbers were present on Forvie in both years (Table 5). The distributions on Cowstane and Sleek were highly clumped due to the varied sediment types. This gave rise to a wider variation between samples and hence a high standard error. The differences in the total densities of *Nereis* were significant between all areas in both years, ($P < 0{\cdot}01$). In general, the total densities were lower in 1973 than 1972 on all sites, but the decrease was only significant on the Sleek ($P < 0{\cdot}002$).

Similarly, the densities of the selected sizes (longer than 60 mm) were significantly different between all areas in both years ($P < 0{\cdot}01$), and these larger animals accounted for over 50% of the total nereids.

Since the density of the selected sizes of *Hydrobia* on Sleek was so great, the combined prey density was also much greater on that area than the other two (Table 6). The high densities of *Corophium* and *Nereis* on Forvie meant that this site was in second place.

The effect of available food upon feeding behaviour

Feeding behaviour on spring tides in February and neap tides in March of both years was related to the amounts of prey present on each of the flock areas. During February birds on low combined prey den-

Table 4. Densities (No./m²) of *Corophium*.

	All sizes ± S.E.		Selected sizes + S.E.	
	1972	1973	1972	1973
Cowstane	500 ± 250	870 ± 410	500 ± 250	370 ± 160
Sleek	530 ± 250	30 ± 30	500 ± 240	30 ± 30
Forvie	4,500 ± 610	6,170 ± 980	3,130 ± 470	3,870 ± 930

Table 5. Densities (No./m²) of *Nereis*.

	All sizes ± S.E.		Selected sizes ± S.E.	
	1972	1973	1972	1973
Cowstane	190 ± 50	100 ± 40	120 ± 40	90 ± 40
Sleek	860 ± 110	360 ± 80	460 ± 80	310 ± 70
Forvie	1,890 ± 180	920 ± 130	1,270 ± 120	770 ± 120

Table 6. The combined prey densities (No./m²) of the selected sizes.

Year	Locality	Selected sizes
1972	Cowstane	6,950
	Sleek	36,360
	Forvie	7,870
1973	Cowstane	5,130
	Sleek	48,010
	Forvie	8,840

sity areas, i.e. Forvie, fed for the greatest proportion of their time ($r = -0{\cdot}03$, $p < 0{\cdot}05$). However, *Hydrobia* accounted for so much of the combined prey density of selected sizes that the proportion of time spent feeding was negatively correlated with the density of *Hydrobia* ($r = -0{\cdot}83$, $0{\cdot}02 < P < 0{\cdot}05$. Figure 4).

However, differences in proportion of time spent feeding were apparent between areas which had similar *Hydrobia* densities. In 1972 on Forvie, birds spent 74% of their time feeding on a prey density of 3470/m^2 but in the same area in 1973 when the density was 4200/m^2 the birds only spent 35% of their time feeding. In contrast, there was a slight increase in *Hydrobia* density on Sleek from 1972 to 1973, with a corresponding decrease in the proportion of time spent feeding. At the same time the *Hydrobia* density on Cowstane decreased but there was an increase in the proportion of time spent feeding. Thus a complex relationship with other influences is suggested.

There was no significant correlation in March between the proportion of time spent feeding and the density of the combined selected sizes of prey or of individual species. Probably supplementary food collected in the fields reduced estuarine feeding and masked the relationship.

The density and biomass of *Hydrobia* were highly correlated ($r = 0{\cdot}94$ $P < 0{\cdot}01$) and hence there was a negative correlation between the biomass of *Hydrobia* and the proportion of time spent feeding ($r = 0{\cdot}82$, $0{\cdot}02 < P < 0{\cdot}05$). However, *Nereis* comprised a relatively large proportion of the combined biomass (60% on Forvie in 1972) and thus the combined prey biomass was not so correlated.

Overall, there was no correlation between either the combined prey density or *Hydrobia* density and bird feeding hours. The combined densities of prey on Cowstane decreased from 1972 to 1973 with a corresponding decrease in bird feeding hours spent on that area. In contrast, there was a slightly greater density of prey in 1973 than 1972 on Sleek and Forvie, but the number of bird feeding hours decreased considerably in both February and March 1973 on Forvie and in March 1973 on Sleek.

Discussion

Shelduck fed on most areas which supported *Hydrobia* but those areas where flocks occurred regularly had the highest prey densities. Yet Sleek with a very high prey density alternated with the low prey density Forvie as the most important flock site.

The amount of food present upon each flock area affected the proportion of time spent feeding. However, this is by no means universal among ducks since Tamisier (1975) found that the proportion of

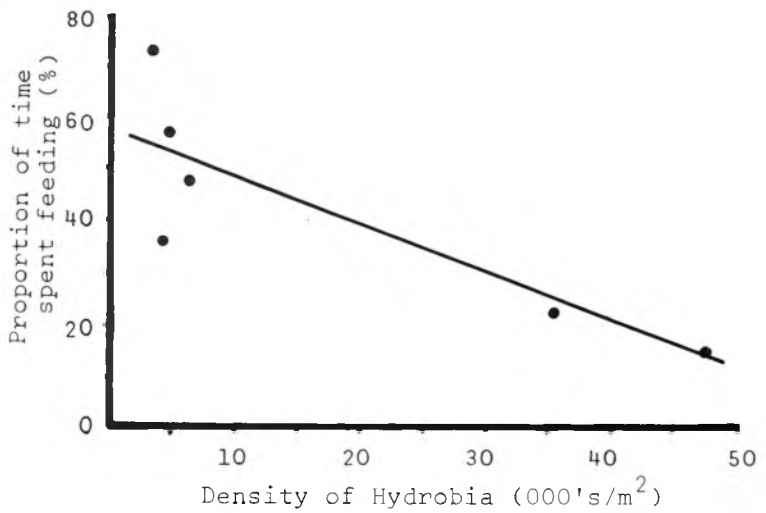

Figure 4. The proportion of time spent feeding by Shelduck in relation to *Hydrobia* density ($y = 57{\cdot}93–0{\cdot}0009x$).

time spent feeding by Teal *Anas crecca* was independent of the amount of available food. It may be that all the Teal sites were optimum feeding habitats and that the proportion of time spent feeding was dependent upon factors other than available food.

If the proportion of time spent feeding is an important feature then the feeding areas varied in their suitability as flock sites. Under the observed environmental conditions there appeared to be no severe selection pressure against feeding on any site. Thus the advantage of a site with a high density of prey may be in extreme conditions. High winds can hold water back within the estuary, and freezing conditions may make the mud-flat unavailable for feeding except along the tide-line. Both of these instances would effectively reduce feeding time, making it advantageous to collect the food requirements quickly.

Where birds spend a large proportion of time feeding they lack time to participate in other activities. Schoener (1971) suggests that where population density is low, a decrease in mating success may be directly proportional to the time spent feeding. The existence of flocks makes this unlikely in Shelduck but it may be more important later in the year when time spent feeding could affect attendance in the nesting area. Shoener dismisses as less important other competing activities such as grooming.

Many ducks are either diurnal or nocturnal feeders (Nilsson 1970) in contrast to Shelduck which feed during both the day and night. This might suggest that the day's food requirements cannot be obtained during one tidal cycle. However if this were the case and it were best for birds to gather their food quickly, then birds would feed for all available time, especially in the low abundance areas. This did not occur; the maximum proportion of time spent feeding being 74% and the minimum 16% of a tidal cycle.

If, in low abundance areas, 26% of the time was adequate for other activities, then why did birds on other sites with over 50% of their time not required for feeding, not take advantage of the situation and complete the day's requirements on a single tide?

It is probable that birds ingesting a high proportion of indigestible calcareous material, and *Hydrobia* are 82–84% by weight of shell (T. Wood, pers. com.), have to fill the gut several times during 24 hours in order to obtain their food requirements. Together with the necessary digestive processes this might require two tidal cycles. Thus the proportion of time spent feeding merely reflects the ease which the gut is filled.

There is, generally, little disadvantage in being on the low abundance areas, with the result that large numbers of bird feeding hours are spent on them. When birds left an extremely high density prey area, such as Sleek, for a much inferior one, the amount of prey was clearly not the ultimate factor determining site importance.

Wildfowling occurs widely on Sleek, a site where flock size varies. Any wildfowling that occurs on Forvie is generally to the north, not directly in the flock area. Cowstane is susceptible to disturbance on the upper shore from a golf course. However it is difficult to understand why disturbance from wildfowling or golfers alone should vary so much between years as to cause the shift of a large proportion of the population.

Even though the varying usage of the flock sites remains unexplained, the importance of food, i.e. *Hydrobia* in defining the areas extensively used, is apparent. The amount of prey present upon a site determines the amount of time required for feeding and hence may be critical to the population in unfavourable conditions.

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Summary

The distribution of the Shelduck *Tadorna tadorna* in the estuary was related to the overall distribution of the main prey *Hydrobia*. The areas with the most dense prey were the favoured sites. The proportion of time spent feeding by birds varied between flock sites and between years. The bird feeding hours also

varied considerably. Prey was not distributed equally between the flock sites. The maximum density of selected sizes of *Hydrobia* was 47,670/m^2 and the minimum 3470/m^2. *Hydrobia* accounted for over 90% of the combined prey except where there were relatively high numbers of *Corophium* and *Nereis*.

The proportion of time spent feeding was related to the combined prey density but the correlation was, in reality, due to the density of *Hydrobia*. Prey density does not define the relative importance of sites. The role of disturbance is discussed. The disadvantage of spending a large proportion of time feeding is probably not important except in occasional severe conditions.

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Dr N. E. Buxton, Culterty Field Station, Newsburgh, Ellon, Aberdeen, AB4 0AA.

Present address: Nature Conservancy Council, 42 Aird Tong, Isle of Lewis, Western Isles, Scotland.