The abundance and distribution of intertidal invertebrates, and an estimation of their selection by Shelduck

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Introduction

The interpretation of diet selection by birds has relied on observable comparisons between prey items taken and those available (e.g. Barnard & Stephens 1981). In dabbling ducks this form of study has been impossible because they usually sieve variable quantities of sediment containing food organisms too small to see. Studies of diet have therefore been made by sampling sediments where ducks fed and by examination of gut and faecal contents. All three forms of diet assessment have been used for Shelduck *Tadorna tadorna* (see review in Cramp & Simmons 1977) with differing success, largely because gut and faecal samples were biased towards more robust invertebrates and because exact origin of food was uncertain.

During 1978/79 I investigated the feeding behaviour of Shelduck wintering on the Clyde Estuary, West Scotland (Thompson 1981), and illustrated the impression ('mini-crater') they formed whilst 'dabbling' on the receding tidal fringe from a relatively stationary position in water 1–10 cm deep (Bryant & Leng 1975). The crater consisted of a shallow depression in the sediment partly surrounded by a pile of sediment which had passed through the shelduck's bill. I suggested this resulted from a thorough mode of sieving which extracted the majority of invertebrates (including very small worms) from the upper sediment layers, rather than concentrating on macro-invertebrates such as *Hydrobia ulvae* as has been suggested by several workers (Olney 1965; Bryant & Leng 1975; Buxton & Young 1981). In this article I concentrate on prey selection. Specifically I examine whether there is any relationship between the distribution of food and the adoption of a particular feeding technique, namely, 'dabbling'.

Methods

The study was carried out on the Clyde Estuary during January and February 1980. Having recorded the distribution of Shelduck flocks (mean flock size = 28·5 ± 3·58, range 14–55) I observed randomly-picked individuals which were 'dabbling' on the ebbing tidal fringe. Having recorded time allocated to dabbling and pacing (using a cassette recorder and stop watch) I located the area of feeding and sampled deposited 'mini-craters' (mean diameter 8·3 ± 0·29 cm; depth 1·6 ±0·17 cm). This was done by collecting all sieved sediment (pile) of approximate height 0·5 cm and two adjacent core samples (82 cm^2) containing a representative sample of unsieved and presumably available invertebrates, to a depth of 4 cm (equal to maximum depth of a Shelduck's probe). Samples were weighed, then sieved, through a 0·5 mm sieve; the retained invertebrates were counted, measured and weighed individually. Two general areas, Woodhall and Longhaugh 8 km apart, were sampled because they offered different compositions of food supplies (Table 1).

Estimation of food selection and intake was made by subtracting the individual sizes and quantity of invertebrates within the sieved pile from a comparable sample in unsieved sediment, adjusting the pile sample by weight to make it directly comparable with the invariably larger volume of unsieved (= undisturbed) sediment. I calculated the forage ratio (after Buxton & Young 1981) by dividing the percentage frequency of each size category or species assumed removed by Shelduck, by the corresponding class frequency available in the sediment. A forage ratio of greater than unity suggests active selection for a given class, the opposite if less than unity, and if equal to unity there is no selection.

Core samples (82 cm^2) were taken from the search path of dabbling Shelduck (between craters) and from adjacent control cells to quantify any relationship between the location of foraging and abundance of invertebrates, samples were treated as above. Sieved and unsieved sediments were also collected for particle size analysis. Briefly this involved oven-drying collected sediments at 80–90°C for 24 hours, followed by thorough mixing. A weighed sample was removed and mixed thoroughly

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Table 1. Mean density and biomass ($\bar{x}$ gm ± sd) and degree of aggregation (index of dispersion) m^{-2} in sediments sampled at Woodhall and Longhaugh (upper 4 cm).

Species	Woodhall	Idx	Longhaugh	Idx	d statistic(n)
Nereis diversicolor					
density	403 ± 43	4·58☐	1,336 ± 64	3.10☐	24·4**(40)
Corophium volutator					
density	972 ± 93	8·89☐	775 ± 80	8·30☐	1·6 (40)
Nereis and *Corophium*					
biomass	0·85 ± 0·12	0·02	0·73 ± 0·11	0·02	1·3 (40)
Hydrobia ulvae					
density	7,428 ± 320	13·70☐	—	—	—
biomass	6·46 ± 0·27	0·01	—	—	—
Tubifex costatus					
density	20,588 ± 1,624	128·00☐	25,262 ± 1,979	149·10☐	2·2* (80)
Other small worms					
density	13,575 ± 1,144	96·40☐	8,323 ± 533	34·10☐	4·5**(80)
All small worms					
biomass	9·63 ± 1·20	0·14	12·64 ± 1·80	0·25	1·4 (80)

* = $p<0\cdot05$, ** = $p<0\cdot01$. Probability values refer to d statistics because of significantly different variances in all cases. See text for calculation Idx, ☐ indicates significant aggregation ($p<0\cdot001$): expected range for random distribution of $S^2\ (n-1)/\bar{x}$ is $\chi^2_{39;\ 0\cdot95-0\cdot05} = 29\cdot1 = 43\cdot8$ and $\chi^2_{79;\ 0\cdot95-0\cdot05} = 64\cdot3 - 101\cdot9$.

with aqueous sodium hexametaphosphate ($6\cdot2$ g. l^{-1}) and left for 24 hours. Subsequently the solution was poured off and the remaining sediment oven-dried (80°C) for 24 hours. The dried sample was then passed through a soil shaker containing sieves of mesh diameter 2, 1, 0·5, 0·25, 0·125 and 0·063 mm. Samples from each sieve were then weighed and their relative contributions to the particle size spectrum calculated.

Results

Selection and removal of invertebrates

During ebb and early flow tide the majority of Shelduck 'dabbled' over the mid-shore. When feeding like this they pass variable quantities of sediment and water through their bill, and extract invertebrates by straining this mixture through coarse lamellae on the inner mandibles, using the tongue as a kind of suction pump (D. M. Bryant & I. J. Patterson, pers. com; pers. obs.). When sampling craters formed by this action I defined 'sieved' sediment as that which had passed through the bill. The deficit of invertebrates absent from the sieved pile compared with adjacent untouched sediment was assumed to have been removed by Shelduck.

The distribution of available invertebrates was patchy. This was quantified by computation of the index of dispersion (Idx = Variance (S^2)/Mean ($\bar{x}$), see Southwood 1966). Results are given in Table 1, where significant patchiness i.e. non-randomness, is indicated by a ratio of $S^2/\bar{x}$ significantly greater than unity. Small worms especially *Tubifex costatus* were the patchiest invertebrates, with some areas containing as many as 125,000 m^{-2}. *H. ulvae* and *Corophium volutator* were the patchiest macro-invertebrates.

The assessment of invertebrates selected compared with available are given in Table 2. The size classes used for categorizing macro-invertebrates were chosen for comparability with previous studies of diet (Buxton & Young 1981; Warnes *et al* 1980). Forage ratios were calculated for comparison of different size classes of macro-invertebrates on a species basis, and for all small worms combined. There was selection for smaller *C. volutator* and larger *H. ulvae* at Woodhall, for larger *Nereis diversicolor* at Longhaugh, and clearly for *T. costatus* at both sites. The greatest biomass contribution to intake was from small worms and to a lesser extent from *Hydrobia* of which 85–87% consists of shell (pers. obs.). Differences between invertebrate quantities removed and available were low particularly for *N. diversicolor* and *C. volutator* suggesting that 'dabbling' was a technique which extracted the majority of food available.

A simple calculation was used to test the reliability of these assessments. The mean duration of 'dabbling' (time bill was in contact with sediment) was 11·34 ± 1·51 seconds, range 1–31 s, n = 91. The mean duration of pacing between 'dabbles' was 3·88 ± 0·83 s, range 1–18 s, n = 72. Shel-

Table 2. Assay of invertebrates (x ± sd. area of crater^{-1}) selected and removed (= 'ingested') compared with available (= unsieved).

Invertebrates' size, categories (mm) and biomass (mg)		Woodhall 'Ingested'	Woodhall Unsieved	Woodhall Forage ratio	Longhaugh 'Ingested'	Longhaugh Unsieved	Longhaugh Forage ratio
Nereis	⩾10	0·30 ± 0·28	0·30 ± 0·28	1·0	1·34 ± 0·68	1·35 ± 0·69	1·35
	<10	0·15 ± 0·22	0·15 ± 0·20	1·0	0·73 ± 0·51	0·80 ± 0·49	0·94
	mg	0·80 ± 0·37	0·70 ± 0·32		2·10 ± 1·0	2·20 ± 0·90	
Corophium	⩾4	0·05 ± 0·32	0·65 ± 0·37	0·95	0·60 ± 0·46	0·60 ± 0·46	1·02
	<4	0·11 ± 0·15	0·10 ± 0·04	1·28	0·18 ± 0·17	0·20 ± 0·18	0·92
	mg	1·10 ± 0·75	1·20 ± 0·75		0·64 ± 0·59	0·72 ± 0·55	
Hydrobia	⩾2	9·28 ± 2·34	13·60 ± 3·17	1·15	—	—	
	<2	1·79 ± 1·22	5·15 ± 1·29	0·59	—	—	
	mg	40·00 ± 15·0	69·00 ± 19·0		—	—	
Tubifex	⩾2	10·12 ± 4·5	11·35 ± 4·30	1·71	18·0 ± 3·65	18·20 ± 3·60	1·57
	mg	46·00 ± 32·0	83·00 ± 38·0		5·0 ± 1·70	5·60 ± 1·40	
Tubes	⩾2	7·12 ± 3·87	16·30 ± 5·10	0·83	—	—	
Other small worms, predominantly *Manayunkia aestuarina*	⩾2	10·70 ± 7·72	26·30 ± 7·20	0·79	14·5 ± 7·30	33·2 ± 8·14	0·69
	mg	15·00 ± 18·0	34·00 ± 19·0		5·70 ± 3·30	9·30 ± 3·50	

Calculated 'ingested' quantity = [quantity available in undisturbed sediment − quantity remaining in sieved pile], see text.

Data for 30 'mini-craters', sampled at Woodhall (n = 20) and Longhaugh (n = 10). Sample area = 82 cm^2 to a depth of 4 cm.

duck spent approximately 28% of their time feeding by dabbling during the ebb tide, for approximately 4,000 seconds (after Thompson 1982, Figure 5). Using the mean length of a bout of 'dabbling' (11·3 + 3·9 = 15·2 s) as a denominator to give intensity of dabbling, Shelduck made approximately 265 dabble contacts. That is they formed at least 265 craters. An intake rate of 9·3 *H. ulvae* (⩾ 2·0 mm) per dabble contact (Table 2) gives a rounded off total intake of 2,500 *H. ulvae* during the ebb tide. If Shelduck had not taken other invertebrate species then this figure would be much higher, and of course adoption of other techniques would supplement the overall quantity of intake. The obtained figure does however compare favourably with others for *H. ulvae* found in the stomach of Shelduck; such as 3,000 in Shelduck which fed almost entirely by 'dabbling' on the ebb tide on the Thames (Olney 1965); and 11,597 in the gut of an incubating Shelduck which had been feeding for approximately 1 hour (Buxton & Young 1981).

The association between distribution of craters (therefore location of feeding effort) and prey supply was tested at Woodhall. Table 3 shows *N. diversicolor* and other small worms were denser along the forage path than in control areas, and that *H. ulvae* was the only prey species significantly less dense along the forage path.

Influence of particle size

Knowing that separation of sediment from

Table 3. Mean number (X̄ ± SE) of invertebrates in feeding and control cells (82 cm^2) at Woodhall.

Species	Feeding	Control	Z statistic
Nereis	1·17 ± 0·57	0·45 ± 0·26	2·0*
Corophium	1·16 ± 0·64	0·86 ± 0·44	0·4
Hydrobia	19·78 ± 4·34	25·86 ± 3·45	2·6**
Tubifex	12·83 ± 5·80	10·77 ± 4·12	0·9
Tubes	6·33 ± 3·15	7·77 ± 2·08	0·05
Other small worms	25·67 ± 9·11	22·86 ± 10·67	1·1

** = $p<0·01$, * = $p<0·05$, Mann-Whitney U test probabilities refer to comparisons between feeding (n = 18) and control (n = 22) samples.

invertebrates was integral to feeding I tested whether foraging Shelduck might concentrate on areas of sediment with a specific particle size distribution. This might have corresponded with the favoured size range of invertegrates, around 2·0 mm, to facilitate their extraction. The particle size ranges of unsieved and sieved sediments were different ($X^2_{(5)}$ = 18·36 and 18·79, P<0·01 in both areas). Figure 1 compares size ranges in sieved and unsieved sediments. At Woodhall, where sediments were coarser, the difference was significant ($X^2_{(5)}$ = 16·39, p<0·01), with the sieved pile containing proportionately fewer larger particles (>2·0 mm) than available ($X^2_{(2)}$ = 5·54, p<0·06), suggesting these were removed whilst foraging. Particle size ranges for sediment taken from the forage path and from adjacent control cells were similar ($X^2_{(5)}$ = 1·18, p>0·90). Thus there was no preference for areas predominated by certain particle sizes, though substrate patches do exist in the Clyde Estuary (Smyth *et al* 1977).

Evidence for patch utilization

It was not obvious how food patches were exploited. Although patch utilization has been described (e.g. Smith & Sweatman 1974; Cowie & Krebs 1979; Zach & Falls 1979), few workers have considered a relationship between patchy forage effort and food supply (see Zach & Falls 1979). One possibility is that because invertebrate

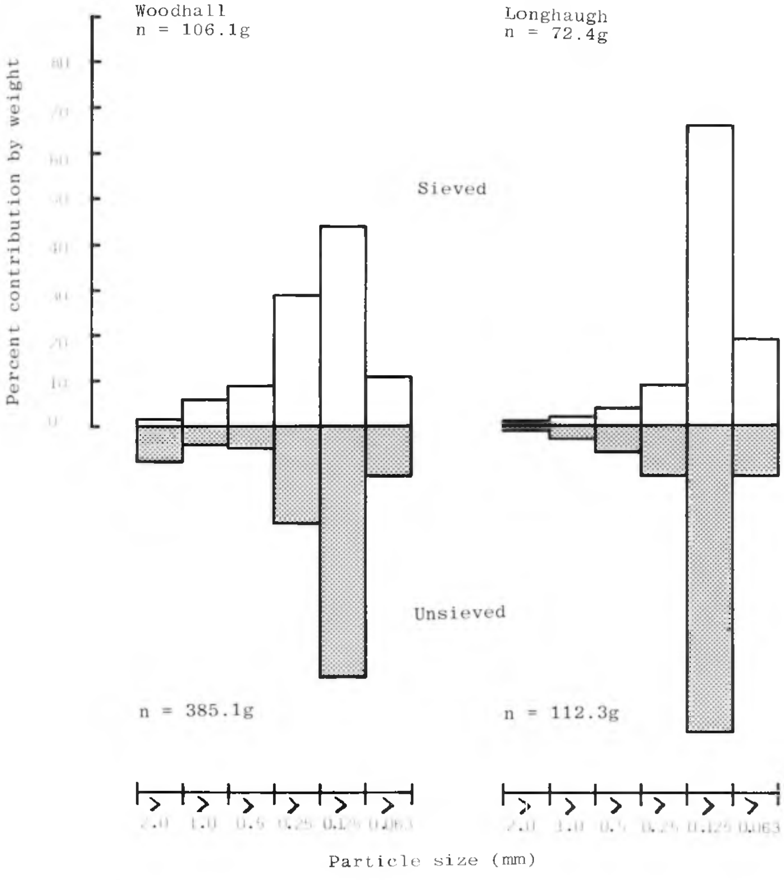

Figure 1. Comparisons between particle size ranges within sieved (constituting pile of mini-crater) and unsieved sediments. At Woodhall differences between two summed distributions (n = 10) were significant ($X^2_{(5)}$ = 16·39, p<0·01); at Longhaugh (n = 6) differences were not significant ($X^2_{(5)}$ = 4·30, 0·9> p>0·5).

patches are ill-defined and highly variable in size and distribution, some birds should be able to discriminate between rich and poor areas whilst foraging (Smith & Sweatman 1974; Zach & Falls 1976), and concentrate on rich areas (Goss-Custard 1970b; O'Connor & Brown 1977). Although the broad association between feeding dispersion of Shelduck flocks and patchy resources has been described (Thompson 1981), I wished to test for any sign of patchy foraging effort.

There were positive relationships between duration of pacing in sequence and dabbling in sequence (Spearman rank correlation coefficient, rs = 0·644, p<0·001, and rs = 0·735, p<0·001 respectively). This indicated a non-random order of these behaviours in sequence (Figure 2). Then I tested for a relationship between the durations of pacing and dabbling in sequence. My null hypothesis was that there was no relationship between these durations, and that a correlation between the two would yield a random scatter. This was rejected (Figure 3), instead there was a negative relationship between the duration of pacing and the subsequent duration of 'dabbling' (r = −0·254, p<0·03). This may have indicated continual exploitation of a patchy resource, with long profitable 'dabbles' being accompanied by reduced travel times (Barnard & Stephens 1981), keeping foragers within the confines of rich located patches. There was certainly considerable variation in the forage effort, and this was probably partly due to variations in food distribution. Unfortunately a lack of cases prevented a correlation analysis between these two aspects, though this certainly merits further investigation.

Discussion

'Dabbling' was one of four feeding methods used by flock members. The adoption of any of these was largely influenced by tidal movements (Thompson 1981). The majority of invertebrates removed by 'dabbling' were just greater than 2·0 mm long, and were predominantly

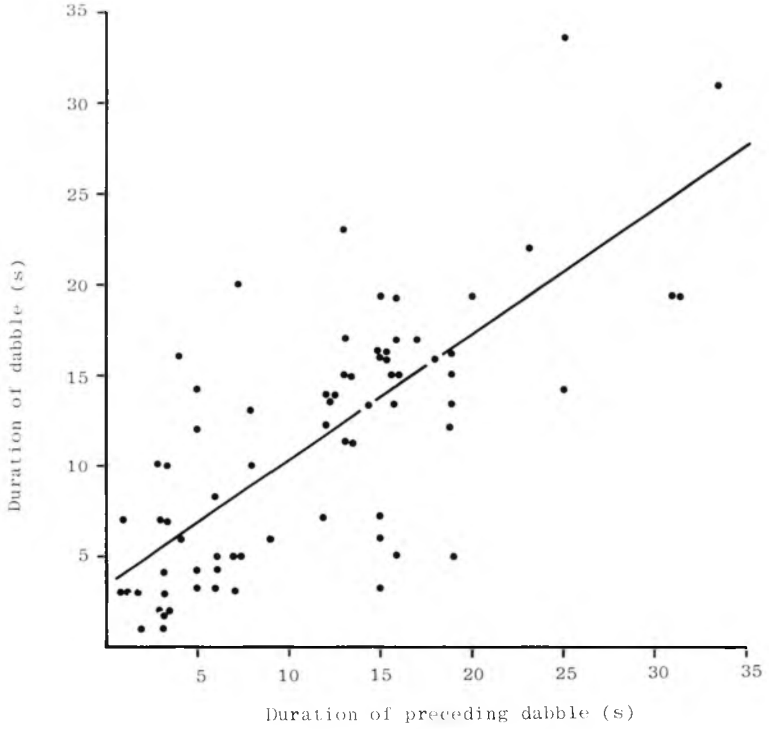

Figure 2. Relationship between durations of preceding and following dabbles. The graph shows a significant positive relationship (Spearman correlation coefficient =+·735, p<0·001, degrees of freedom = 69).

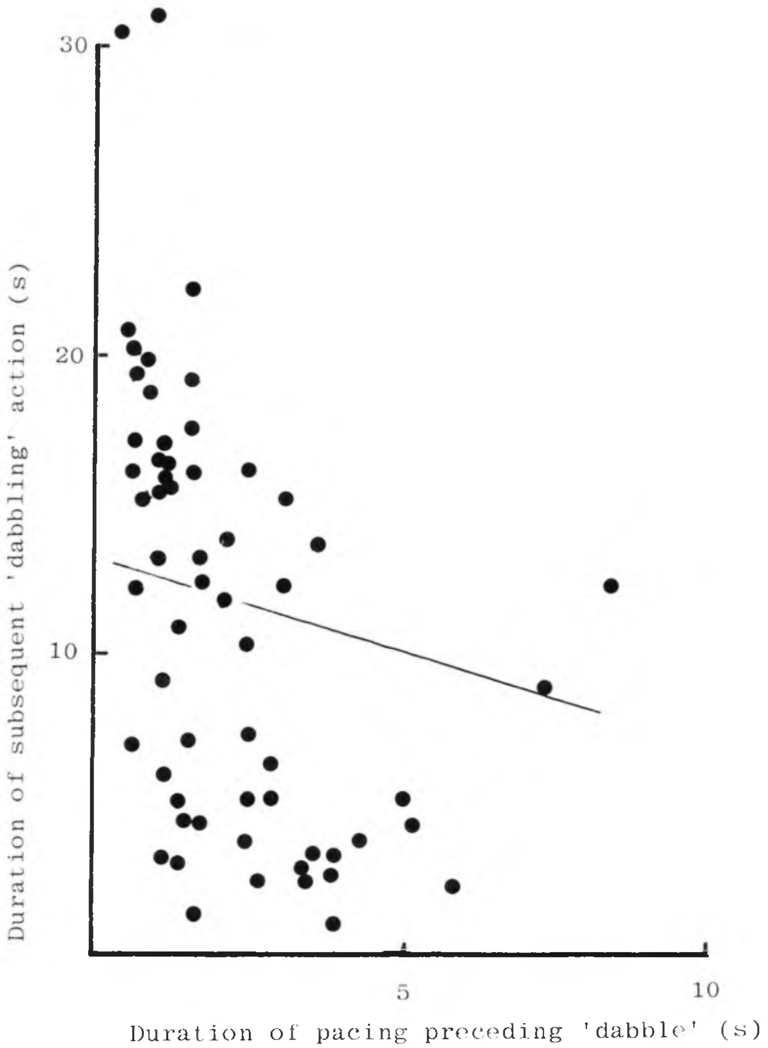

Figure 3. Regression of duration of dabbling with duration of preceding pacing ($Y = -0{\cdot}53x + 13{\cdot}9$, $r = -0{\cdot}257$, $p = 0{\cdot}026$, df = 58), **indicating short travel times were followed by long bouts of 'dabbling'.**

small worms. It has been shown that tubificid worms have a comparatively high caloric value, and Hale (1980) quotes their energetic value as almost treble that of *H. ulvae* (5·1 of 1·9 k.cals.g dry weight^{-1}) and higher than that of *N. diversicolor* and *C. volutator*. An energetic preference for *T. costatus* and other small worms possibly explains the wide geographical distribution of Shelduck on the Clyde Estuary, as their distribution does not correlate with any single macro-invertebrate species (cf. Bryant & Leng 1975). Another reason for a preference for small worms might be due to some macro-invertebrate species, especially *C. volutator* and *H. ulvae*, exhibiting tremendous population fluctuations in the Clyde, with their populations sometimes experiencing sudden crashes.

The sampling of craters was biased towards the small sedentary worms. Macro-invertebrates vary in their availability at the surface, partly in response to tidal movements (see Vader 1964; Evans 1979), responding positively to submergence and becoming less available in freshly exposed sediments. Additionally macro-invertebrates may have responded negatively to surface pressure of Shelduck, as Goss-Custard (1970) showed for *C. volutator* reacting to Redshank *Tringa totanus*. Any invertebrates remaining in the deposited pile of the crater might have departed, this could particularly referer to mobile *N. diversicolor* and *C. volutator*. Although I could not control these factors I minimized errors by sampling very fresh craters (within 5 min since formation). I had no way of accounting for any loss of invertebrates to tidal turbulence.

Warnes *et al* (1980) suggested a form of size selection operated in Shelduck whilst 'scything' on exposed moist sediments of the Forth Estuary. Thus small worms (less than 2·00 mm) were ingested (and selected for) along with *H. ulvae* of less than 2·00 mm in height; selection for larger *H. ulvae* (up to 4·5 mm) would have excluded small worms (predominantly *Manayunkia aestuarina*) and possibly provided an energetically less profitable diet. Buxton & Young (1981) however found selection for larger classes of *H. ulvae* (3–4·5 mm) and *C. volutator* ($\geqslant$4·0 mm). Buxton (pers. com.) also found correlation between proportion of time spent feeding ('dabbling') and the density and biomass of *H. ulvae* available. On the Clyde such a 'one or the other' occurrence of *H. ulvae* or small worms such as *T. costatus* in the diet apparently did not occur. Instead *T. costatus* (between 2–4 mm long) were apparently selected, and *H. ulvae* less than 2 mm high were avoided (Forage ratio = 0·59, Table 2). There was no preferred particle size range, although as Bryant & Leng (1975) found, the very coarse sediments in the vicinity of dense mussel beds and shell deposits were avoided.

One aspect which is not at all clear is the importance of food patchiness. It is likely that the observed discrete concentrations of Shelduck which occur within the Clyde correlate with rich food patches, and that the maintenance of these patches is largely governed by substrate and tidal conditions. A complicating factor is shifting water level because this prevents any long term 'area-restricted' feeding (Smith 1971). This must largely account for weak correlations between feeding intensity and food abundance. Possibly Shelduck monitor their net rate of energy intake (see Krebs *et al* 1974) over a period of minutes, and facilitate this by concentrating on a single species such as *T. costatus*. Often only some individuals in a flock extend their feeding method from 'dabbling' in shallow water to 'upending' in much deeper water over the same area. This may be an adoption to prolong utilization of located patches.

It is difficult to compare the benefits of feeding on small compared with large food items, and during ebb and flow tides. This is partly because handicap constraints such as prey size dependent handling and search time costs are not visible so impossible to quantify. Hopefully future assays of deposited craters will contribute to a study comparable with that of prey size selection by neighbouring Charadriiformes (e.g. Goss-Custard 1977; O'Connor & Brown 1977).

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Summary

A study was made to estimate prey selection by wintering Shelduck *Tadorna tadorna* foraging on the intertidal flats of the Clyde Estuary. This involved sampling from craters which had been formed by the 'dabbling' feeding action of Shelduck. Assays of invertebrates from sediments which had passed through the bill and from undisturbed sediments showed there was general selection for invertebrates just greater than 2·0 mm long. Small worms, especially *Tubifex costatus*, constituted the patchiest and greatest biomass component available, and were assessed prevalent in the diet. Simple calculation showed broad agreement between an estimation for intake of *Hydrobia ulvae* and its known inclusion in stomach contents. There was no association between feeding intensity and abundance of any single prey species or with any particle size range. A negative relationship between durations of feeding and intervening movement was apparent, suggesting that continual exploitation of a patchy resource was accompanied by a reduction in travel times.

References

Barnard, C. J. & Stephens, H. 1981. Prey size selection by lapwings in lapwing-gull associations. *Behaviour* 77: 1–22.

Bryant, D. M. & Leng, J. M. 1975. Feeding distribution and behaviour of Shelduck in relation to food supply. *Wildfowl* 26: 20–30.

Buxton, N. E. & Young, C. M. 1981. The food of the Shelduck in North-East Scotland. *Bird Study* 28: 41–8.

Cowie, R. J. & Krebs, J. R. 1979. Optimal foraging in patchy environments. In *Population Dynamics*, ed. by R. M. Anderson, B. D. Turner and L. R. Taylor. London: Blackwell.

Cramp, S. & Simmons, K. E. L. (Eds.) 1977. *The Birds of the Western Palearctic*, Vol. 1 Oxford: University Press.

Evans, P. R. 1979. Adaptations shown by foraging shorebirds to cyclical variations in the activity and availability of their intertidal prey. In E. Naylor and R. G. Hartnell (Eds.) *Cyclical Phenomena in Marine Plants and Animals.* Oxford: Pergamon Press.

Goss-Custard, J. D. 1970a. Feeding dispersion in some overwintering wading birds. In J. H. Crook (ed.) *Social Behaviour in Birds and Mammals.* London: Academic Press.

Goss-Custard, J. D. 1970b. The responses of redshank (*Tringa totanus* L.) to spatial variations in the density of their prey. *J. Anim. Ecol.* 39: 91–113.

Goss-Custard, J. D. 1977. Optimal foraging and the size selection of worms by redshank *Tringa totanus*, in the field. *Anim. Behav.* 25: 10–29.

Hale, W. G. 1980. *Waders.* London: Collins.

Krebs, J. R., Ryan, J. C. & Charnov, E. L. 1974. Hunting by expectation or optimal foraging? A study of patch use by chickadees. *Anim. Behav.* 22: 953–64.

O'Connor, R. J. & Brown, R. A. 1977. Prey depletion and foraging strategy in the Oystercatcher (*Haematopus ostralegus*). *Oecologia* 27: 75–92.

Olney, P. J. S. 1965. The food and feeding habits of the shelduck *Tadorna tadora. Ibis* 107: 527–32.

Smith, J. N. 1971. The food searching behaviour of European thrushes. II: The adaptiveness of search patterns. *Behaviour* 49: 1–61.

Smith, J. N. & Sweatman, H. P. A. 1974. Food searching behaviour of titmice in patchy environments. *Ecology* 55: 1216–32.

Southwood, T. R. E. 1966. *Ecological Methods.* London: Methuen.

Smyth, J. C, Curtis, D. J., Halliday, J. B., Stobie, R. E. F. & Gray, H. 1977. Birds and Invertebrates of the Clyde Estuary tidal flats. *West Nat.* 6: 73–101.

Thompson, D. B. A. 1981. Feeding behaviour of wintering Shelduck in the Clyde Estuary. *Wildfowl* 32: 88–98.

Vader, W. J. M. 1964. A preliminary investigation into the reactions of the infauna of the tidal flats to tidal fluctuations in water level. *Neth. J. Sea. Res.* 2: 189–222.

Warnes, J., Bryant, D. M. & Waugh, D. R. 1980. Feeding habits and diets of shorebirds on the Forth Estuary. Report to the N.C.C. Held at Biology Department, University of Stirling.

Zach, R. & Falls, F. B. 1976. Foraging behaviour, learning, and exploration by capitve oven birds (Aves: Parulidae). *Can. J. Zool.* 54: 1880–93.

Zach, R. & Falls, F. B. 1979. Foraging and territoriality of male ovenbirds (Aves: Parulidae) in a heterogenous habitat. *J. Anim. Ecol.* 48: 33–52.

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